Transmission dynamics of the monogenean *Gyrodactylus salaris* under semi-natural conditions

Running title: Transmission dynamics of *G. salaris*

Ditte K. Hendrichsen*[1], Roar Kristoffersen[2], Karl Ø. Gjelland[3], Rune Knudsen[2], Stefan Kusterle[2], Audun Rikardsen[2,3], Eirik H. Henriksen[2], Aslak Smalås[2], Kjetil Olstad[4]

[1]Norwegian Institute for Nature Research, Høgskoleringen 9, NO-7034 Trondheim, Norway

[2]Department of Arctic and Marine Biology, University of Tromsø, N-9037 Tromsø, Norway

[3]Norwegian Institute for Nature Research, Fram Centre, NO-9296 Tromsø, Norway

[4]Norwegian Institute for Nature Research, Fakkelgården, NO-2624 Lillehammer, Norway

*Correspondence: Ditte K. Hendrichsen, Norwegian Institute for Nature Research, Høgskoleringen 9, NO-7034 Trondheim, Norway. E-mail: Ditte.Hendrichsen@nina.no Phone: +47 96857084

Abstract

Tracking individual variation in the dynamics of parasite infections in wild populations is often complicated by lack of knowledge of the epidemiological history of hosts. Whereas the dynamics and development of *Gyrodactylus salaris* Malmberg, 1957, on Atlantic salmon, *Salmo salar* L., is well known in laboratory studies, knowledge about infection development on individual wild fishes is currently sparse. In this study, the dynamics of an infection of *G. salaris* on individually marked Atlantic salmon parr was followed in a section of a natural stream. During the six-week experiment, the prevalence increased from 3.3% to 60.0%, with an average increase in intensity of 4.1% day^{-1}. Survival analyses showed an initially high probability (93.6%) of staying uninfected by *G. salaris*, decreasing significantly to 37% after six weeks. The results showed that even at subarctic water temperatures and with an initially low risk of infection, the parasite spread rapidly in the Atlantic salmon population, with the capacity to reach 100% prevalence within a short summer season. The study thus track individual infection trajectories of Atlantic salmon living under near-natural conditions, providing an integration of key population parameters from controlled experiments with the dynamics of the epizootic observed in free-living living populations.

Keywords: infection probability, host-parasite interactions, infection development, fish parasite, invasive species, parasite population dynamics.

Introduction

Parasites play a fundamental role in shaping life histories of a wide range of organisms (Begon, Harper & Townsend 1996). The impacts of parasites on fitness, survival and behaviour can be severe, with consequences for evolution, population dynamics and ecosystem functioning (Lima *et al.* 2012, Poisot, Thrall & Hochberg 2012). Pioneering theoretical work by Anderson and May (Anderson & May 1978, Anderson & May 1979, May & Anderson 1979, Dobson & May 1987) showed that host-parasite interactions can be pivotal for the long-term patterns in population dynamics. Such long-term patterns have also been observed in natural populations, like the cyclic nature of the red grouse, *Lagopus lagopus scoticus* (Latham, 1787) population in Scotland infected by the parasitic nematode, *Trichostrongylus tenuis* (Mehlin, 1846) (see Dobson & Hudson 1992, Hudson, Newborn & Dobson 1992), or the population collapse of red fox, *Vulpes vulpes* (L., 1758), populations following an infection with sarcoptic mange, *Sarcoptes scabiei* (L., 1758) (see Forchhammer & Asferg 2000).

Tracking the underlying mechanisms of the structural dynamics of an infection in wild populations is complicated by the fact that the epidemiological and environmental history of hosts collected in the field is often unknown. This is particularly the case in systems with limited possibility to follow individuals, such as in aquatic systems. Experimental laboratory studies allow deciphering of mechanistic relationships, but at the expense of environmental complexity (Grenfell & Dobson 1995). Interactions between hosts, parasites and environment, however, are often highly complex (Dobson & Hudson 1986, Hatcher, Dick & Dunn 2006, Tompkins *et al.* 2011, Dunn *et al.* 2012), and there is a need for studies integrating individual, longitudinal data with field data (Lefebvre *et al.* 2013).

Since the introduction of the monogenean *Gyrodactylus salaris* Malmberg, 1957, into Norway in the 1970s (Johnsen & Jensen 1991, Johnsen, Møkkelgjerd & Jensen 1999, Hansen,

Bachmann & Bakke 2003), the parasite has caused a considerable decline in the survival of wild Atlantic salmon *Salmo salar* L., 1758, in affected rivers (Johnsen & Jensen 1986, 1988, Mo 1992, Jansen & Bakke 1993a). The parasite is highly pathogenic to several of the east Atlantic populations of Atlantic salmon and is considered one of the most important threats to Atlantic salmon in Norway (Bakke, Cable & Harris 2007). Studies from infected rivers show that more than 80 % of a cohort of juvenile Atlantic salmon may be killed (Anon 2011). The dynamics of *G. salaris* under laboratory conditions is well known (e.g. Jansen & Bakke 1991, Harris, Jansen & Bakke 1994). Likewise, the occurrence of *G. salaris* in populations of wild Atlantic salmon has been recorded repeatedly in field surveys (Heggberget & Johnsen 1982, Johnsen & Jensen 1986, 1991, Johnsen *et al.* 1999, Jansen, Matthews & Toft 2007). While such surveys provide an instantaneous census of status, prevalence and intensity of the infection in a given river, they do not provide detailed information on how the parasite population develops over time. The early stages of infection and the initial transmission dynamics in free-living Atlantic salmon parr was studied by Soleng, Jansen & Bakke (1999), but the rate at which naïve fish living under natural conditions are infected and the development of the infection on individual fishes over time is poorly known. The present study aimed at following the development and dynamics of *G. salaris* on infra- and metapopulation level (*sensu* Bush *et al.* 1997) in a group of newly infected Atlantic salmon parr during the initial weeks of an infection, to document temporal changes in prevalence, intensity and population growth, and to test whether the risk of infection changed over time in relation to biotic (weight, length, behaviour) and abiotic (temperature) factors.

Materials and Methods

Study site

The experiment was carried out in a small tributary of the River Skibotnelva in northern Norway (69°22′N, 20°15′E). The River Skibotnelva runs for 74 km from the origin in Lake Gálggojávri near the Finnish border, to the outlet in Lyngenfjord (NVE 2012) (Fig. 1). The catchment area is approximately 784 km^2, primarily dominated by birch and pine forest. The fish community in the River Skibotnelva consists primarily of brown trout, *Salmo trutta* L., 1758, Atlantic salmon, Arctic char, *Salvelinus alpinus* (L., 1758) and burbot, *Lota lota* (L., 1758) (see Kristoffersen *et al.* 2005). Anadromous fish can migrate approximately 20 km upstream.

(Figure 1 around here)

The experiments were conducted in a section of a small spring-fed stream running into the lower part of the main stem of the River Skibotnelva (Fig. 1) between the 19th of July and 5th of September 2012. The stream was 1.5 m wide with a mean water depth of 7.5 cm (range: 5-30 cm, occasionally slightly higher at the upper and lower barrier), and a water velocity of 70 l/sec. Due to its natural spring origin, temperature in the experimental stream was relatively constant during the experimental period (mean daily temperature: 5.4 °C, range: 4.8 – 6.2 °C). The parasite *G. salaris* was first recorded in the River Skibotnelva in 1979 (Heggberget & Johnsen 1982). The river has since been treated twice, in 1988 and 1995, with CFT Legumin (rotenone) in an attempt to eradicate the parasite, but without success (Kristoffersen *et al.* 2005). The local population of Atlantic salmon is regarded as severely threatened due to the *G. salaris* infection (Thorstad *et al.* 2001).

Experimental setup

A 23 metre section of the stream was closed for upward and downward migration by migration barriers (Fig. 2) and sub-divided into four sub-sections. Fish could move freely between sub-sections. The setup was checked approximately every second day and any debris

that was present was removed from the barriers to prevent them from clogging up. Water temperature was recorded by a temperature logger every hour (Hobo® pendant temperature/Light Data Logger, Onset Computer Corporation).

(Figure 2 around here)

Sixty-seven naïve Atlantic salmon parr of the local River Skibotnelva strain were used in the experiment (mean weight 1.59 g, s.e.m 0.04 g). The fish were bred in the hatchery of the Norwegian Directorate for Nature Management gene bank at Haukvik, central Norway, and transported to Skibotn in early June. Prior to the experiment, the fish were kept in 20L perforated plastic containers in the stream with continuously running river water. All fish were weighed and measured, and individually tagged with 8 mm PIT-tags (Biomark HPT8) implanted into the abdominal cavity during anaesthesia (Finquel vet®; tricaine methane sulfonate, at a concentration of 142.9 mg metacain/l). Fish were released into the stream two days after PIT-tagging and left for an additional five days to establish before the experiment was initiated. At this point (Day 0 of the experiment), eight fish were found dead at the lower migration barrier, thus the initial population size was 59 fish (171 fish per 100 m^2).

At the start of the experiment, 24th of July 2012 (Day 0), three donor fish, each with ca. 150-200 *G. salaris*, were released into the experimental stream. They were of the same hatchery bred stock as the recipient fish, and infected with *G. salaris* from wild-caught Atlantic salmon from the River Skibotnelva (haplotype B according to Hansen *et al*. 2003) for a period of up to two weeks in a 20 L tank.

To follow the development of the *G. salaris* infection in the recipient fish population, 15-30 fish were collected weekly by electro fishing (Geomega FA4, Terik Technology AS), anaesthetized (Finquel vet®; tricaine methane sulfonate, same concentration as above), and examined for *G. salaris* infection. During examination, the fish was placed in a rectangular plastic tray with the outside painted black to provide a clearer contrast, and any *G. salaris*

specimens present on the skin and fins were counted under a stereomicroscope. Fish were released back into the stream after examination and recovery from anaesthesia. In order to avoid cross-infection, all fish were kept individually isolated throughout the process of catching, examination, and recovery.

After a six week experimental period (43 days), all the remaining fish in the experimental stretch of the stream were caught by electro fishing. The fishing was repeated until no fish were caught for three consecutive rounds. All the fish were killed by an overdose of anaesthetics, weighed and measured, and stored in 96% ethanol. The final count of *G. salaris* was performed in the laboratory.

Statistical analyses

The intrinsic rates of increase, *r*, of the *G. salaris* infra- and metapopulations were estimated by means of linear regression on the log-transformed total number of *G. salaris* on recipient and donor fish each census day. The daily infection increase (R) expressed as percentage per day was then calculated as $R = 1 - e^{-r}$. Linear regression was also used to estimate the average intensity of *G. salaris* in the fish population.

A Kaplan-Meier survival function was applied to model the probability of escaping infection at a given time during the experiment. Since the exact day of infection was not known, we used Turnbull's estimator for interval-censored data (Turnbull 1976), which is considered to be more accurate than using mid-points (Odell, Anderson & Dagostino 1992). Infected fish were scored as events, and fish that were still uninfected when the experiment was terminated were right censored (i.e. still available for infection at the end of the survey). Fish that disappeared during the experiment were included in the analysis until their disappearance.

Due to the presence of interval-censored data (Kleinbaum & Klein 2005), a parametric survival regression model was used to investigate whether fish growth (measured as absolute

and relative weight gain during the experimental period), behaviour (propensity to move between sections of the stream) and temperature (measured as mean and max temperature in the stream in the week prior to the census) affected the risk of infection. Several different distributions were tested; the Weibull model outperformed the exponential model with ΔAIC = 11.36 (Klein & Moeschberger 2003, Kleinbaum & Klein 2005). Model selection was based on AIC, models with ΔAIC < 2 were considered to have equal support (Burnham & Anderson 2002). A small number (0.0001) was added to all survival times to allow the survival regression model to handle observation intervals starting at time 0 (i.e. on the 24th of July).

All statistical analyses were run in the statistical programme R, version 2.15.1 (R Development Core Team 2008). The package 'survival' (Therneau 2012) was used for the survival analyses.

Results

During the six week experiment, a *G. salaris* infection was recorded on 30 of the 59 initially naïve fish. The first infection was recorded at the first census after one week. Infection spread rapidly and when the experiment was terminated six weeks later, prevalence had increased from 3.3 % to 60.0 % of the remaining fish (Fig. 3A,B). Prevalence was low (< 7 %) during the first weeks of the experiment, but increased sharply to 33.3 % during the third week (Fig. 3A,B).

(Figure 3 around here)

Simultaneously, the average intensity of *G. salaris* on recipient fish increased from one to 5.3 parasites per fish, corresponding to an increase in average intensity of 4.1 % per day (Fig. 3A,B). The average intensity increased throughout the experiment, except for a period of apparent stabilisation at two parasites per fish during week 2-4, coinciding with the increase in prevalence (Fig. 3A,B).

The *G. salaris* metapopulation on the naïve Atlantic salmon population grew approximately exponentially (Fig. 3C) with an intrinsic rate of increase of 0.14 (12.7 %) per day (t = 16.5, p < 0.0001, R^2 = 0.98), corresponding to a rate of 0.12 (10.9 %) per day (t = 6.5, p = 0.003, R^2 = 0.89) when corrected for the estimated number of fish in the population at a constant disappearance rate (see below).

The three donor fish were recaptured at all census days except one. The development of the infection was similar in all three fish, with an intensity of 150-200 *G. salaris* per donor fish at the onset of the experiment, increasing linearly to 800-900 at the end, corresponding to a linear increase of 18.1 parasites per fish per day (t = 14.9, p < 0.004, R^2 = 0.99, last census day excluded due to the death, and subsequent loss of parasites in one donor fish) (Fig. 3C). The intrinsic rates of increase of the *G. salaris* infra-populations were highly variable on newly infected fish, but displayed a stable trend decreasing with infra-population size in the donor fish (Fig. 3D).

The Kaplan-Meier survival function showed that the probability of escaping of infection was high (93.6%) during the first three weeks of the experiment, decreasing significantly (no overlap in 95% confidence intervals) after 18 days to 69% (Fig. 4). By the end of the experiment, the probability of not being infected had decreased to 37 %. The probability of escaping infection decreased with an average of 1.5 percentage points per day (Fig. 4). Neither weight gain (relative and absolute), nor behaviour (propensity to move within the stream) affected the risk of infection. The effect of temperature was inconclusive and strongly dependent on whether data from the last survey day were included, due to a slight increase in water temperature during the last week of the experiment.

(Figure 4 around here)

During the six weeks of the experiment, the number of fish in the stream decreased from 59 fish released (171 fish or 282 g fish per 100 m^2) to 45 fish at the final round up (130 fish or

249 g fish per 100 m^2). This corresponds to an average loss of 2.3 fish per week. The cause of loss / mortality remains unknown. Fish that disappeared during the experiment had significantly lower *G. salaris* infections (mean intensity = 0.09, max = 2) than fish that were still in the stream at the end of the experiment (mean intensity = 3.31, max = 18) (Welch Two Sample t-test, t = -4.90, $d.f.$ = 45.7, $p < 0.0001$). Despite the observation of *Saprolegnia* sp., Nees, 1823, on some fish during the period, this was not considered substantial enough to have caused an increase in mortality. Of the 20 fish that were infected with *Saprolegnia* during the experiment, all were recaptured alive on the last census day.

Discussion

The present study show that the probability that a fish of could stay uninfected by *G. salaris* decreased throughout the experimental period. The probability of staying uninfected was significantly higher during the first weeks of the experiment than during later stages, and decreased with the size of the *G. salaris* metapopulation. The change in the probability of infection around the third week of the experiment was mirrored in the dynamics of the *G. salaris* metapopulation on recipient fish, which displayed a sudden increase in prevalence and a corresponding stable level of intensity. Since the growth rate of the parasite metapopulation remained unchanged, this could suggest a phase of increased transmission from one host to another as a consequence of the age structure of the parasite infra-population in the early stage of an infection. *Gyrodactylus salaris* show increased activity after giving birth and the mother may shift to a new host if possible (Harris *et al.* 1994), presumably to avoid competition with her daughter. The observed pattern during the third week may therefore be caused by several equally aged parasites giving birth and moving to a new host at approximately the same time,

thereby increasing the prevalence, whilst keeping the intensity constant. Both experimental and modelling studies have shown the importance of the timing of births in the dynamics and growths of *G. salaris* populations. Cable, Harris & Bakke (2000) suggested that the timing of the first birth, in particular, was critical for the population dynamics. In accordance with this, Denholm *et al*. (2013) found that delaying the first birth by 24 hours subsequently caused a major drop in the number of parasites, and an increased risk of population extinction of *G. salaris*. The simultaneous change in infection probability, prevalence and intensity in the present study can thus indicate that this sensitivity to timing of births, through modifying the infrapopulation growth rate and the transmission between fish, may influence the underlying probability of naïve fish being infected.

In the present study, the population growth of the *G. salaris* metapopulation in the recipient fish was similar to or higher than that reported on Atlantic salmon under controlled conditions (Olstad *et al.* 2007). Jansen & Bakke (1991) found an intrinsic rate of increase of 0.06 parasites per day per parasite at a temperature of 6.6° C. The observed rate of increase in this study was closer to 0.12, which was a somewhat surprising given the lower water temperature (mean 5.4° C) during the experimental period. The high growth rate was presumably caused both by the reproduction of *G. salaris* on the recipient fish and, on top of that, a considerable and continuous transmission of parasites from the donor fish. Other factors may also have influenced the results, in particular the weekly electrofishing, anesthetising, and handling of fish. Studies across a wide range of taxa show that stress influences the immune response and that occurrence, intensity, and severity of infections increase when animals are in poor condition (Beldomenico & Begon 2010). For example, in a study on a range of salmonid species with different susceptibility to *G. salaris*, Harris, Soleng and Bakke (2000) showed that stress induced immunosuppression may facilitate the population growth of the parasite. Johnson *et al*. (2011) showed that the risk of infection in guppies (*Poecilia reticulata*) was

related to fish density. The density of fish in the present experiment was 2-3 times higher than observed in other water bodies in Fennoscandia, although there are considerable differences between sites and years (Johansen, Elliott & Klemetsen 2005, Jonsson *et al*. 2011). Atlantic salmon are territorial, and generally avoid direct contact (Aas *et al*. 2011), and it is possible that the high density together with the frequent electrofishing may have caused a higher degree of interaction between individual fish than would naturally occur, leading to a higher probability of infection.

The exponential growth in the metapopulation of *G. salaris* on the recipient fish, and a more moderate, linear growth in the metapopulation of the donor fish, corresponds with the tenet of density-dependent regulation of population growth in classical population theory (Hassell, Lawton & May 1976, Case 2005). Whereas negative density dependence has been reported in macroparasites (e.g. Tyre *et al.* 2003), host-parasite interactions in freshwater systems commonly display non-equilibrium dynamics (Kennedy 2009). Detection of such patterns requires long-term studies and is beyond the scope of this study. According to the same schedule, we find that the intrinsic rate of increase in the individual infra-populations of the recipient fish was, not surprisingly, highly variable. Small populations are highly sensitive to demographic stochasticity (Lande 1993), and in *G. salaris* where each individual give birth to a single daughter, even small variations in individual timing can give considerable differences in life-history trajectories and fitness, as described above (Cable *et al*. 2000, Ramirez, Harris & Bakke 2012, Denholm *et al*. 2013).

In the present experiment, there was no clear effect of temperature on the probability of being infected. Water temperature is known to play a pivotal role in the population dynamics and life history of gyrodactylids (Jansen & Bakke 1993a,b, Andersen & Buchmann 1998) through a strong impact on reproduction and survival (Scott & Nokes 1984, Jansen & Bakke 1991, Olstad *et al*. 2006). As a consequence of this, temperature influences the potential for spread

to previously unaffected populations (Denholm *et al*. 2013). Transmission rate of *G. salaris* increases with increasing water temperature (Bakke, Jansen & Hansen 1991, Soleng *et al*. 1999), and studies of free-living populations of Atlantic salmon have shown that the observed seasonality in parasite abundance is related to water temperature (Jansen & Bakke 1993a,b, Appleby & Mo 1997). The lack of a temperature effect in the present study was likely due to the natural spring origin of the water in the stream, causing little variation in water temperature during the course of the experiment.

Transmission can be rapid. For example, Soleng *et al*. (1999) found a prevalence of 44.4% in Atlantic salmon parr released into a *G. salaris* infected river for 24 hours, increasing to 57.9% after 48 hours. Several studies have shown rapid development of *G. salaris* on Atlantic salmon (Heggberget & Johnsen 1982, Johnsen & Jensen 1986, 1988, Mo 1992, Appleby & Mo 1997, Johnsen *et al.* 1999, Bakke *et al.* 2007, Ramirez *et al.* 2012), both in free-living populations and under controlled conditions, demonstrating considerable potential for population growth and transmission to new hosts. The present study extends this approach to show how an epidemic may develop during early stages of an infection under near-natural conditions. The results show, that if the spread of infection were to continue at a constant rate Fig. 4), 100% prevalence could theoretically be reached after 68 days, provided that all fish in the naïve population were susceptible/receptive to infection. This period is well within the duration of the short summer season with elevated water temperatures in the subarctic region (see e.g. Winger *et al.* 2008), facilitating rapid population growth in the parasite (Jansen & Bakke 1991). This corresponds with observations of seasonal dynamics of *G. salaris* epizootics where prevalence and intensity may change dramatically over a short period of time. For example, Appleby & Mo (1997) reported a consistent pattern of a shift in prevalence from 0-20% to 80-100% over the course of one month across four consecutive years. The arrival of a few highly infected fish to a free-living population of initially uninfected juvenile

Atlantic salmon mimics a situation where a new cohort of juvenile Atlantic salmon hatch and establishes in early spring among older, already highly infected parr that have survived the winter, or where an infected fish migrates to a previously uninfected site (Soleng, Bakke & Hansen 1998). This is particularly relevant in the light of the large scale eradication programmes of *G. salaris* in Norway, where entire river systems are treated with CFT Legumin (rotenone). Whereas this strategy has been successful in several rivers, it has failed in others (Anon 2011). It has been proposed that salmonid fish escaping the rotenone treatment, or migrating from nearby infected regions may reintroduce the parasite into treated populations (Hansen *et al*. 2003, Kristoffersen *et al.* 2005, Winger *et al.* 2008).

Ethical statement

The animal work presented was approved by the Norwegian Animal Research Authority (NARA; 2012/98665).

Author Contributions

KO, DKH, RKr, KØG, RKn and AR designed the experiments. SK, EHH, AS, RKn, RKr and KØG performed the field experiments. DKH and KO analysed the data and wrote the manuscript with contributions from RKr, KØG, RKn, AR, SK, EHH and AS.

References

Aas, Ø., Einum, S., Klemetsen, A. & Skurdal, J. (Eds.) (2011) *Atlantic Salmon Ecology*. Wiley-Blackwell, Oxford, 467 pp.

Andersen, P.S. & Buchmann, K. (1998) Temperature dependent population growth of *Gyrodactylus derjavini* on rainbow trout, *Oncorhynchus mykiss*. *Journal of Helminthology* **72**, 9-14.

Anderson, R.M. & May, R.M. (1978) Regulation and stability of host–parasite population interactions. I. Regulatory processes. *Journal of Animal Ecology*, **47,** 219-247.

Anderson, R.M. & May, R.M. (1979) Population biology of infectious diseases: Part I. *Nature*, **280,** 361-367.

Anon (2011) Status of Norwegian salmon populations in 2011. Norwegian scientific advisory committee for Atlantic salmon management 3, 285 pp (in Norwegian). Available at http://www.Nina.No/archive/nina/pppbasepdf/rapport%20fra%20vitenskapelig%20råd%20for%20lakseforvaltning/2013/thorstad%20status%20rapport%20fra%20vitenskapsrådet%20for%20lakseforvaltning%205%202013.pdf.

Appleby, C. & Mo, T.A. (1997) Population dynamics of *Gyrodactylus salaris* (Monogenea) infecting Atlantic salmon (*Salmo salar*) parr in the river Batnfjordselva, Norway. *Journal of Parasitology*, **83,** 23-30.

Bakke, T.A., Jansen, P.A. & Hansen, L.P. (1991). Experimental transmission of *Gyrodactylus salaris* Malmberg, 1957 (Platyhelminthes, Monogenea) between the Atlantic salmon (*Salmo salar*) and the European eel (*Anquilla anquilla*). *Canadian Journal of Zoology*, **69**, 733-737.

Bakke, T.A., Cable, J. & Harris, P.D. (2007) The biology of gyrodactylid monogeneans: The "Russian-doll killers". *Advances in parasitology*, **64,** 161-378.

Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology: Individuals, populations and ecology*, Blackwell Scientific, Oxford.

Beldomenico, P. and & Begon, M. (2010) Disease spread, susceptibility and infection intensity: vicious circles? *Trends in Ecology and Evolution* **25**, 21-27.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference*, Springer, New York.

Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology,* **83,** 575-583.

Cable, J., Harris, P.D. & Bakke, T.A. (2000) Population growth of *Gyrodactylus salaris* (Monogenea) on Norwegian and Baltic Atlantic salmon (*Salmo salar*) stocks. *Parasitology,* **121,** 621-629.

Case, T.J. (2005) *An illustrated guide to theoretical ecology*, Oxford University Press, Oxford.

Denholm, S.J., Norman, R.A., Hoyle, A.S., Shinn, A.P. & Taylor, N.G.H. (2013) Reproductive trade-offs may moderate the impact of gyrodactylus salaris in warmer climates. *PLoS ONE,* **8**(10): e78909. doi:10.1371/journal.pone.0078909

Dobson, A. & Hudson, P.J. (1986) Parasites, disease and the structure of ecological communities. *Trends in Ecology & Evolution,* **1,** 11-15.

Dobson, A.P. & Hudson, P.J. (1992) Regulation and stability of a free-living host-parasite system – *Trichostrongylus tenuis* in red grouse. 2. Population-models. *Journal of Animal Ecology,* **61,** 487-498.

Dobson, A.P. & May, R.M. (1987) The effects of parasites on fish populations - theoretical aspects. *International Journal for Parasitology,* **17,** 363-370.

Dunn, A.M., Torchin, M.E., Hatcher, M.J., Kotanen, P.M., Blumenthal, D.M., Byers, J.E., Coon, C.a.C., Frankel, V.M., Holt, R.D., Hufbauer, R.A., Kanarek, A.R., Schierenbeck, K.A., Wolfe, L.M. & Perkins, S.E. (2012) Indirect effects of parasites in invasions. *Functional Ecology,* **26,** 1262-1274.

Forchhammer, M.C. & Asferg, T. (2000) Invading parasites cause a structural shift in red fox dynamics. *Proceedings of the Royal Society of London, Series B,* **267,** 779-786.

Grenfell, B.T. & Dobson, A. (1995) *Ecology of infectious diseases in natural populations*. Cambridge University Press, Cambridge.

Hansen, H., Bachmann, L. & Bakke, T.A. (2003) Mitochondrial DNA variation of *Gyrodactylus* spp. (Monogenea, Gyrodactylidae) populations infecting Atlantic salmon, grayling, and rainbow trout in Norway and Sweden. *International Journal for Parasitology,* **33,** 1471-1478.

Harris, P.D., Jansen, P.A. & Bakke, T.A. (1994) The population age structure and reproductive biology of *Gyrodactylus salaris* Malmberg (Monogenea). *Parasitology,* **108,** 167-173.

Harris, P.D., Soleng, A. & Bakke, T.A. (2000) Increased susceptibility of salmonids to the monogenean *Gyrodactylus salaris* following administration of hydrocortisone acetate. *Parasitology,* 120, 57-64.

Hassell, M.P., Lawton, J.H. & May, R.M. (1976) Patterns of dynamical behavious in single-species populations. *Journal of Animal Ecology,* **45,** 471-486.

Hatcher, M.J., Dick, J.T.A. & Dunn, A.M. (2006) How parasites affect interactions between competitors and predators. *Ecology Letters,* **9,** 1253-1271.

Heggberget, T.O. & Johnsen, B.O. (1982) Infestation of *Gyrodactylus* sp. of Atlantic salmon, *Salmo salar* L., in Norwegian rivers. *Journal of Fish Biology,* **21,** 15-16.

Hudson, P.J., Newborn, D. & Dobson, A.P. (1992) Regulation and stability of a free-living host-parasite system – *Trichostrongylus tenuis* in red grouse. 1. Monitoring and parasite reduction experiments. *Journal of Animal Ecology,* **61,** 477-486.

Jansen, P.A. & Bakke, T.A. (1991) Temperature-dependent reproduction and survival of *Gyrodactylus salaris* malmberg, 1957 (Platylhelminthes: Monogenea) on Atlantic salmon (*Salmo salar* L.). *Parasitology,* **102,** 105-112.

Jansen, P.A. & Bakke, T.A. (1993a) Regulatory processes in the monogenean *Gyrodactylus salaris* Malmberg - Atlantic salmon (*Salmo salar* L.) association. I. Field studies in southeast Norway. *Fisheries Research,* **17,** 87-101.

Jansen, P.A. & Bakke, T.A. (1993b) Regulatory processes in the monogenean *Gyrodactylus salaris* Malmberg - Atlantic salmon (*Salmo salar* L.) association. II. Experimental studies. *Fisheries Research,* **17,** 103-114.

Jansen, P.A., Matthews, L. & Toft, N. (2007) Geographic risk factors for inter-river dispersal of *Gyrodactylus salaris* in fjord systems in Norway. *Diseases of Aquatic Organisms,* **74,** 139-149.

Johansen, M., Elliott, J.M. & Klemetsen, A. 2005. A comparative study of juvenile salmon density in 20 streams throughout a very large river system in northern Norway. *Ecology of Freshwater Fish*, **14**, 96-110.

Johnsen, B.O. & Jensen, A.J. (1986) Infestations of Atlantic salmon, *Salmo salar*, by *Gyrodactylus salaris* in Norwegian rivers. *Journal of Fish Biology,* **29,** 233-241.

Johnsen, B.O. & Jensen, A.J. (1988) Introduction and establishment of *Gyrodactylus salaris* Malmberg, 1957, on Atlantic salmon, *Salmo salar* L., fry and parr in the river Vefsna, northern Norway. *Journal of Fish Diseases,* **11,** 35-45.

Johnsen, B.O. & Jensen, A.J. (1991) The gyrodactylus story in Norway. *Aquaculture,* **98,** 289-302.

Johnsen, B.O., Møkkelgjerd, P.I. & Jensen, A.J. (1999) The parasite *Gyrodactylus salaris* on salmon parr in Norwegian rivers, status report at the beginning of year 2000 [in Norwegian, English summary]. *NINA Oppdragsmelding,* **617,** 1-129.

Johnson, M.B., Lafferty, K.D., van Oosterhout, C. & Cable, J. (2011) Parasite transmission in social interacting hosts: Monogenean epidemics in guppies. *PLoS ONE* **6**(8), e22634

Jonsson, B., Jonsson, N. & Ugedal, O. 2011. Production of juvenile salmonids in small Norwegian streams is affected by agricultural land use. *Freshwater Biology*, **56**, 2529-2542.

Kennedy, C.R. (2009) The ecology of parasites of freshwater fishes: The search for patterns. *Parasitology,* **136,** 1653-1662.

Klein, J.P. & Moeschberger, M.L. (2003) *Survival analysis: Techniques for censored and truncated data.* , Springer, New York, USA.

Kleinbaum, D.G. & Klein, M. (2005) *Survival analysis: A self-learning text,* Springer, New York, USA.

Kristoffersen, R., Rikardsen, A.H., Winger, A.C., Adolfsen, P. & Knudsen, R. (2005) Røye som langtidsvert og smittereservoar for *Gyrodactylus salaris* i Skibotnelva i Troms [in Norwegian, English summary]. *NINA Report,* **36**, 1-27.

Lande, R. (1993) Risk of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**, 911–927.

Lefebvre, F., Fazio, G., Mounaix, B. & Crivelli, A.J. (2013) Is the continental life of the european eel *Anguilla anguilla* affected by the parasitic invader *Anguillicoloides crassus*? *Proceedings of the Royal Society B-Biological Sciences,* **280,** 1754 20122916.

Lima, D.P., Giacomini, H.C., Takemoto, R.M., Agostinho, A.A. & Bini, L.M. (2012) Patterns of interactions of a large fish-parasite network in a tropical floodplain. *Journal of Animal Ecology,* **81,** 905-913.

May, R.M. & Anderson, R.M. (1979) Population biology of infectious diseases: Part II. *Nature,* **280,** 455-461.

Mo, T.A. (1992) Seasonal variations in the prevalence and infestation intensity of *Gyrodactylus salaris* Malmberg, 1957 (Monogenea: Gyrodactylidae) on Atlantic salmon parr, *Salmo salar* L., in the river Batnfjordselva, Norway. *Journal of Fish Biology,* **41,** 697-707.

Nve (2012) http://atlas.nve.no. Norwegian Water and Energy Directorate

Odell, P.M., Anderson, K.M. & Dagostino, R.B. (1992) Maximum-likelihood-estimation for interval-censored data using a Weibull based accelerated failure time model. *Biometrics,* **48,** 951-959.

Olstad, K., Cable, J., Robertsen, G. & Bakke, T.A. (2006) Unpredicted transmission strategy of *Gyrodactylus salaris* (Monogenea: Gyrodactylidae): survival and infectivity of parasites on dead hosts. *Parasitology*, **133**, 33–41.

Olstad, K., Robertsen, G., Bachmann, L. & Bakke, T.A. (2007) Variation in host preference within *Gyrodactylus salaris* (Monogenea): An experimental approach. *Parasitology,* **134,** 589-597.

Poisot, T., Thrall, P.H. & Hochberg, M.E. (2012) Trophic network structure emerges through antagonistic coevolution in temporally varying environments. *Proceedings of the Royal Society of London, Series B,* **279,** 299-308.

R Development Core Team (2008) R: A language and environment for statistical computing. R foundation for statistical computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Ramirez, R., Harris, P.D. & Bakke, T.A. (2012) An agent-based modelling approach to estimate error in gyrodactylid population growth. *International Journal for Parasitology,* **42,** 809-817.

Scott, M.E. & Nokes, D.J. 1984. Temperature-dependent reproduction and survival of *Gyrodactylus bullatarudis* (Monogenea) on guppies (*Poecilla reticulata*). *Parasitology* **89**, 221-228.

Soleng, A., Bakke, T.A. & Hansen, L.P. (1998) Potential for dispersal of Gyrodactylus salaris (Platyhelminthes, Monogenea) by sea-running stages of Atlantic salmon (Salmo salar): field and laboratory studies. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 507-514.

Soleng, A., Jansen, P.A. & Bakke, T.A. 1999. Transmission of the monogenean Gyrodactylus salaris. *Folia Parasitologica*, **46**, 179-184.

Therneau, T. (2012) A package for survival analysis in S. R package version 2.36-14, http://CRAN.R-project.org/package=survival.

Thorstad, E.B., Johnsen, B.O., Forseth, T., Alfredsen, K., Berg, O.K., Bremset, G., Fjellstad, H.-P., Grande, R., Lund, E., Myhre, K.O. & Ugedal, O. (2001) Fiskesperrer som supplement eller alternativ til kjemisk behandling av vassdrag infisert med *Gyrodactylus salaris* [In Norwegian]. Directorate of Nature Management, Report 9-2001, 66 pp.

Tompkins, D.M., Dunn, A.M., Smith, M.J. & Telfer, S. (2011) Wildlife diseases: From individuals to ecosystems. *Journal of Animal Ecology,* **80,** 19-38.

Turnbull, B.W. (1976) The empirical distribution function with arbitrarily grouped, censored, and truncated data. *Journal of the Royal Statistical Society, Ser. B,* **38,** 290–295.

Tyre, A.J., Bull, C.M., Tenhumberg, B. & Chilton, N. (2003) Indirect evidence of density-dependent population regulation in *Aponomma hydrosauri* (Acari: Ixodidae), an ectoparasite of reptiles. *Austral Ecology*, **28,** 196-203.

Winger, A.C., Kanck, M., Kristoffersen, R. & Knudsen, R. (2008) Seasonal dynamics and persistence of *Gyrodactylus salaris* in two riverine anadromous Arctic charr populations. *Environmental Biology of Fishes,* **83,** 117-123.

Figure legends

Figure 1: Map with the location of the experimental stream indicated by the star and arrow. The location in Norway is indicated by the square on the inset map.

Figure 2: Experimental setup. a) Picture of the experimental stream with a view from the lower barrier, b) Principal drawing of the stretch between the upper and lower barriers. Flow direction is indicated by arrows. The stream is divided into sub-sections by wooden pegs at every 5 metres (marked by squares).

Figure 3: Temporal development of *Gyrodactylus salaris* infection in juvenile Atlantic salmon, *Salmo salar*, in the experimental stream. A) Temporal change in prevalence and intensity (full and dashed lines, respectively). B) Relationship between prevalence and mean intensity in the experimental population (donor fish excluded). Numbers denote number of days passed since onset of the experiment. C) Total numbers of *G. salaris* in the recipient fish population as a function of time. Black dots represent the observed number of *G. salaris* in the fish captured at a given census day (donor fish excluded) and open dots the estimated number of *G. salaris* in the total population of recipient fish. The full and dashed lines are the corresponding predicted growth estimated from linear regressions on log-transformed counts. Triangles represent the observed number of *G. salaris* on the donor fish, and the dotted line the corresponding predicted growth estimated from linear regression on non-transformed counts. D) Intrinsic rate of increase for *G. salaris* infrapopulations as a function of infrapopulation size. Open dots denote recipient fish, black dots the donor fish.

Figure 4: Baseline probability of not being infected as a function of the time passed since the start of the experiment, modelled as a Kaplan-Meier survival function. The bold line indicates

the observed ‘‘survival’’ function. The dashed lines indicate 95% confidence intervals around the estimated survival. The dotted line shows the predicted survival function given a constant (time independent) hazard rate. Vertical bars denote right censored data, where fish disappeared from the experiment before any infection was recorded.

Acknowledgments

We thank Svein Eriksen for assistance in the field, and two anonymous reviewers for valuable comments to an earlier version of the manuscript. The project was supported by Norwegian Institute for Nature Research internal strategic funds, the Research Council of Norway (project nr. 196332/S30), the Department of Marine and Arctic Biology at University of Tromsø and the Directorate for Nature Management. None of the authors have any commercial or other relationship which would represent a conflict of interest in this study.