Лососевидные рыбы Восточной Фенноскандии.
Петрозаводск, 2005. С. 47-55.

POTENTIALLY DANGEROUS *GYRODACTYLUS SALARIS* IN RUSSIAN KARELIA: HARMLESS AND HARMFUL COMBINATIONS OF HOST SPECIES AND PARASITE STRAINS

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Gyrodactylus parasites in grayling (*Thymallus thymallus*) and salmon (*Salmo salar*) were studied by molecular analysis of mitochondrial DNA in Russian Karelia. It was confirmed that grayling parasites do not infect salmon, even if it is difficult to consider them as a different species. Grayling parasites are divided to White Sea basin and Baltic basin lineages, indicating separate glacial refugia for the host. Salmon stock in the river Keret is infected by *Gyrodactylus salaris* originating from the lake Onega, where the parasite is rare and causing no harm. In Keret, the salmon population has no intrinsic or induced resistance, thus allowing the parasite to reproduce without restriction. The Pistojoki salmon population, spawning in Kuitozero, is infected by *Gyrodactylus salaris* of rainbow trout type, most probably originating from Finnish fish farms upstream. First observations in 2001 indicated that the salmon stock of Pistojoki is parasite tolerant; further follow-up is needed to confirm this. The tolerance of certain salmon populations is correlated with the origin in freshwater glacial refugia, and long coexistence with *Gyrodactylus*.

ЮССИ КУУСЕЛА[a], РИИККА ХОЛОПАЙНЕН[a], МАРИЯ МЕЙНИЛЯ[a], АЛЕКСЕЙ ВЕСЕЛОВ[b], ИГОРЬ ЩУРОВ[b], ЕВГЕНИЙ ИЕШКО[b], ЯККО ЛУММЕ[a]. ПОТЕНЦИАЛЬНО ОПАСНЫЙ ПАРАЗИТ *GYRODACTYLUS SALARIS* В РЕСПУБЛИКЕ КАРЕЛИЯ: БЕЗВРЕДНЫЕ И ОПАСНЫЕ КОМБИНАЦИИ РАС ВИДА-ХОЗЯИНА И ПАРАЗИТА

Паразиты *Gyrodactylus* у хариуса (*Thymallus thymallus*) и лосося (*Salmo salar*) на территории Республики Карелия исследовались при помощи анализа митохондриальной ДНК. Исследования подтвердили, что паразиты хариуса не заражают семгу, несмотря на то, что их вряд ли можно рассматривать как различные виды. Паразиты хариуса разделены на линии бассейна Белого моря и бассейна Балтийского моря, указывая на наличие изолированных ледниковых рефугиумов вида-хозяина. Лосось в реке Кереть заражен *Gyrodactylus salaris* из Онежского озера, где данный паразит встречается редко и не наносит вреда. У популяции лосося р. Кереть нет ни врожденной, ни приобретенной устойчивости к паразиту, что позволяет ему беспрепятственно размножаться. Лосось в популяции реки Писта, заходящий на нерест в оз. Куйто, заражен *Gyrodactylus salaris*, относящимся к типу, заражающему радужную форель, и вероятно занесен с финских рыбозаводов, находящихся выше по течению. Первые наблюдения, проведенные в 2001

г., показали, что популяция лосося р. Писта устойчива к паразиту, но чтобы убедиться в этом, необходимы дальнейшие исследования. Устойчивость отдельных популяций лосося связана с их происхождением из пресноводных ледниковых рефугиумов и продолжительным сосуществованием с *Gyrodactylus*.

Introduction

Gyrodactylus salaris is a small Monogenean flatworm, which is infamous since causing the destruction of natural salmons stocks in 45 Norwegian rivers. The genus *Gyrodactylus* is suggested to contain 25 000 species (Bakke et al., 2002), and due to a reduced body, small size and uniform ecological habitat on the fish surfaces or gills, the species identification and naming is extremely difficult.

It is generally assumed that *Gyrodactylus salaris* infecting the Norwegian rivers originated from the Baltic Sea Basin, where it is found as a rare and more or less harmless. Indeed, before the Norwegian catastrophe, only few scattered observations existed: the species attracted no interest at all. Now it is known that *Gyrodactylus salaris* is not rare at all among the Tornio river system, where the overall prevalence was observed to be 23%, still without any pathogenic symptoms (Anttila et al., in preparation).

One of the taxonomic problems concerning *Gyrodactylus salaris* was that a *Gyrodactylus* hosted by grayling, *Thymallus thymallus*, is morphologically extremely similar. In Slovakia, a species *Gyrodactylus thymalli* was formally described by Zitnan (1960), and most researchers have accepted this name for the parasites found on grayling. However, in some cases it remained obscure whether the parasite could move from one host to the other (Ieshko et al., in preperation).

The confusion was even more difficult when the molecular marker, internal transcribed spacer (ITS) of nuclear ribosomal gene cassette was utilized. This marker readily separates very large number of sibling species (e.g., Ziętara and Lumme, 2002, 2003), but several samples of *Gyrodactylus* from grayling, salmon and also rainbow trout were identical.

To solve this problem, a more sensitive DNA marker was needed, and primers for amplifying the CO1 gene region of mitochondrial DNA were developed (Meinilä et al., 2002). By using this marker, the problem of *Gyrodactylus thymalli* and *Gyrodactylus salaris* can be solved, and the marker also offered means to identify parasite strains in fine geographical details.

In Russian Karelia, the *Gyrodactylus* infection in the river Keret was a reason to concentrate on this parasite. The salmon juvenile production dropped to 2% of the normal, thus destructing a significant economy along this river. In this paper, we present observations on this epidemic, and compare the parasites with other *Gyrodactylus* strains in Russian Karelia. It will be shown that the Keret infection was introduced from lake Onega, where the parasite is native and harmless. Also, we demonstrate that the *Gyrodactylus salaris* infection in the lacustrine salmon stock in Pistojoki, Kuitozero, is of rainbow trout type of parasite, thus most probably originating from the Finnish fish farms in Kuusamo, upstream of Pistojoki.

Material and Methods

Description of the rivers and sampling sites

The Keret River, in Russian Karelia (66°15' N, 33°34' E, Fig. 1) is 110 km long, and includes four large lakes over a 34 km section. The mean annual water discharge is 23.3 m^3/s. The river has 18 separate rapids. The salmon growing area is 675,500 m^2, of which 135,800 m^2 is suitable for spawning. The average duration of the river period of the parr ranges from 2.2 to 2.4 years, the dominant age group of smolt being 2+ years (60-78 %). The river drains into the western coast of the White Sea, near the town of Chupa (Fig. 1).

The juvenile salmon from the Keret River were collected during July 21-22, 2001. The Lake Onega rivers screened for this study were The Shuja River (July 3, 2004, N=11, clean), Kumsha River (July 5, 2004, N=50, one infected fish), Lizhma River (August 8, 2002, N=15, one infected; July 4, 2004, N=24, one infected), Pjalma River (August 4, 2001, N=48, clean; July 6, 2004, N=50, clean), Tuba River (August 4, 2001, N = 44, clean: July 7, 2004, N=35, clean) and Vama River (July 8, 2004, N=16, clean). Annual spawning stock of the Kumsha is estimated to be ~ 250 and of Lizhma ~ 150 adults salmon.

The Pisto River was sampled on July 20, 2001. The parasite haplotyping has been published earlier (Meinilä et al., 2004). Also, *Gyrodactylus salaris* observations on grayling (*Thymallus thymallus*) depicted on the map in Fig. 1 are from Meinilä et al. (2004).

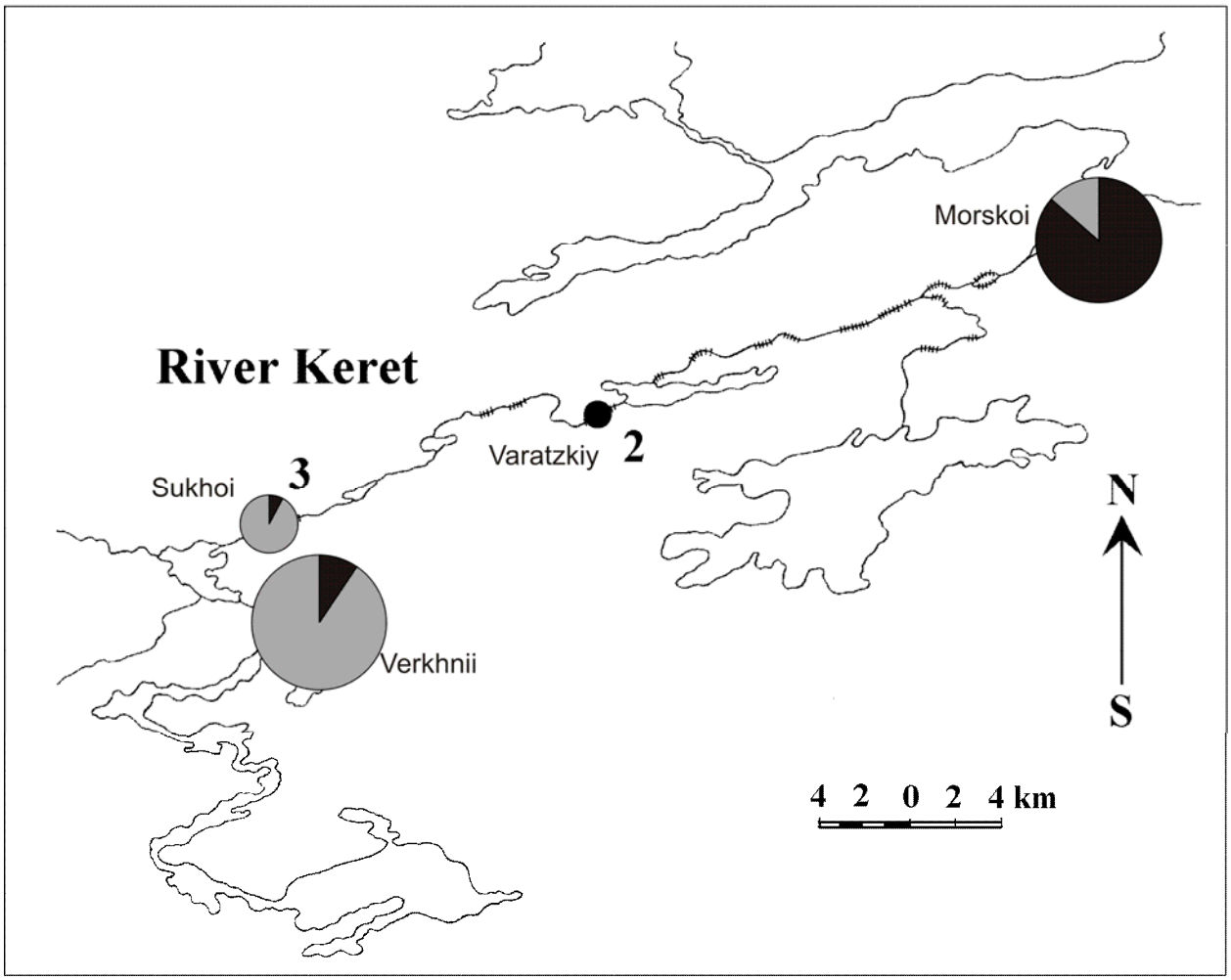

Fig. 1 Distribution of *Gyrodactylus salaris* haplotypes *KA* (black sector, also found in Kumsha) and *KB* (gray sector, type found in Lizhma) along the river Keret. The uppermost rapid Verhnyi is located 53 km from the rivermouth. Other rapids are Sukhoi, Varatskiy (three fish, no parasites) and Morskoi

DNA extraction and sequencing

Primers for amplification a partial mitochondrial cytochrome *c* oxidase subunit I (COI) gene of *Gyrodactylus salaris* were developed by Meinilä et al. (2002). The sequences from the Keret River are deposited in GenBank (**AF540891**, **AF540892**). The phylogenetic position of the haplotypes has been determined (Meinilä et al., 2004). The new sequences from Lake Onega rivers have been deposited by accession numbers **AY840222** (Lizhma) and **AY840223** (Kumsha).

Long sequences (> 813 bp) were used to delineate a segment separating the two Keret haplotypes from each other and from all known haplotypes infecting grayling or rainbow trout. For routine identification of large numbers of the two observed haplotypes, two new primers were utilized: forward 5'-GTTTTCGCTTCACCTGTCTGG and reverse 5'-TACACCCACCACACGATTGG. These amplified a segment of 371 bp, out of which 281 bp could be reliably read. The short segment identifies 20 out of the 31 known haplotypes (Meinilä et al., 2004) and contains diagnostic nucleotide substitutions separating all six major clades.

The proteinase K digestion of the parasites, the PCR conditions, and the sequencing protocol were conducted as described in Meinilä et al. (2002). Sequencing was based on Big Dye Terminator Cycle Sequencing kit protocol and ABI 377 DNA sequencer (PE Applied Biosystems).

Molecular cloning of PCR products for separating mitochondrial genes from putative nuclear copies in the Keret River parasite strains was conducted by Invitrogen's TA-cloning kit, following the instructions of the manufacturer. The GenBank accession of Keret Numt is AY225307.

Data analysis

The sequences were aligned and inspected by Sequencher 4.0.5 (Gene Codes). Only two haplotypes were found in the Keret River on the basis of full length (813 bp) sequences. Nine diagnostic nucleotide changes separated haplotypes *KA* and *KB*. In the data analysis, haplotype diversity was calculated as $H = (n/(n-1))(1 - \sum p^2)$. Conventional F_{ST} statistics based on haplotype frequencies were used to estimate the level of population differentiation $F_{ST} = (H_{total} - H_{mean})/H_{total}$

For testing the interference between the parasite clones, a simulation program was written to estimate the expected numbers of doubly infected fish and the probability of obtaining the observed number or less by chance.

Results

Infection in the river Keret

A schematic map of the river Keret and sampling sites is given in Fig. 1. We have molecularly analyzed 150 parasites collected in 2001 from the rapids Verhnyi, Sukhoi and Morskoi. Two clearly different haplotypes were observed (Fig. 2). The haplotypes *KA* and *KB* were not in drift-migration equilibrium: In Morskoi, type *KB* comprised 84% of parasites, while type KA was dominant in Verhnyi and Sukhoi (90%).

The two parasite haplotypes from Keret were characterized and their unique position in the phylogenetic tree of all *G. salaris* was solved already in Meinilä et al. (2004). They both belong to the Baltic Sea salmon specific evolutionary lineage, and one of them is very basal in the tree.

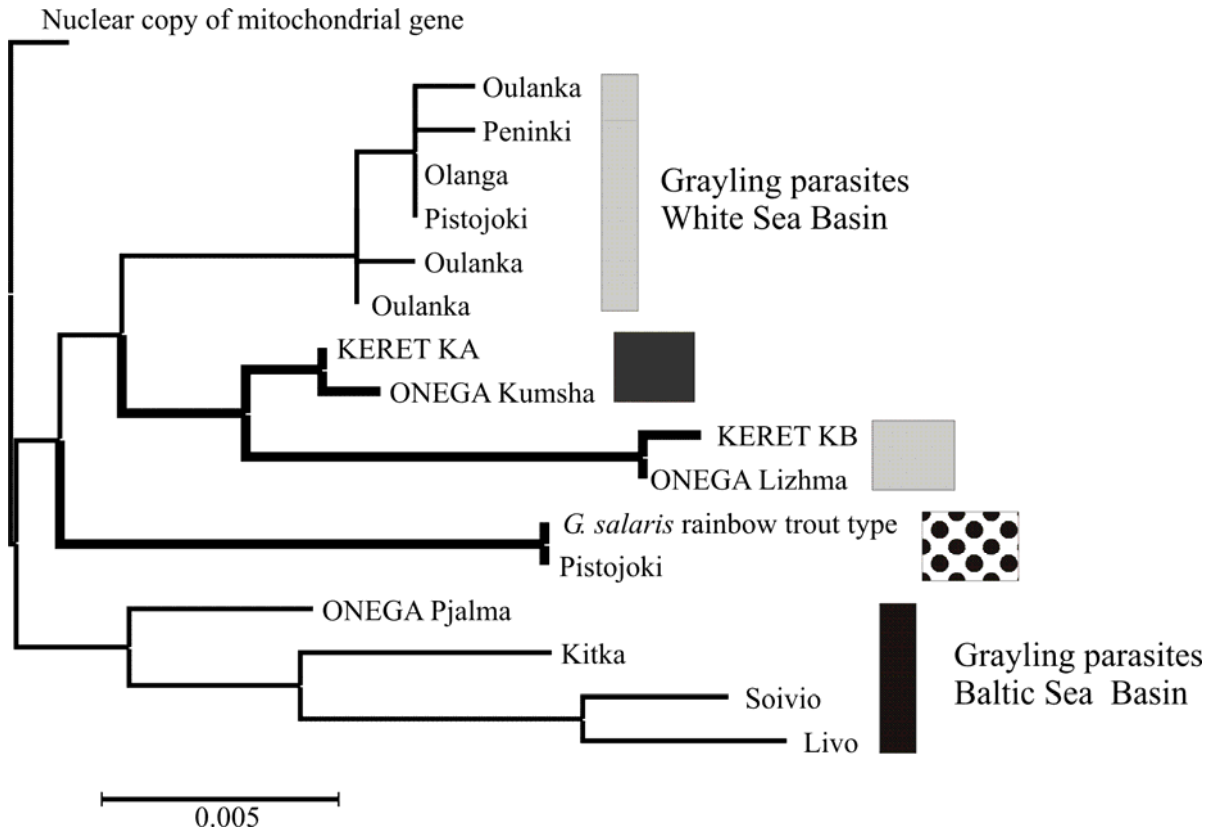

Fig. 2. Phylogenetic tree of mitochondrial COI sequences of the *Gyrodactylus salaris* sensu lato types found in salmon (thick line) and grayling in the study area in Karelian Republic, Russia. The tree is rooted by a nuclear copy of the sequence cloned from samples from the river Keret. The sampling sites of each type are marked in the map in Fig. 3

Origin of the Keret infection is found in Lake Onega

The mitochondrial haplotypes in the Lake Onega rivers Lizhma and Kumsha

Only three out of the 293 salmon juveniles sampled in 2001, 2002 and 2004 expeditions to Lake Onega carried *G. salaris* infection. The single parasite found in 2002 in the Lizhma River was lost during molecular analysis. However, in 2004, several worms were successfully sequenced from both Lizhma and Kumsha river fish. In Lizhma River, the COI haplotype was almost identical with *KB*, differing from it by a single T>C transition at site 79 (numbering according to the rainbow trout type of *G. salaris* standard **AF479750**). The KB sequence has been deposited in GenBank (accession **AF540892**). The haplotype in Kumsha River similarly differed by one nucleotide (A>G at 793) from *KA* (accession number **AF540891**). The *KA* and *KB* differ from each other by nine nucleotides (K2P distance ~1.1%), and they are unique among the sequences of *Gyrodactylus salaris* observed in *Salmo salar* (Meinilä et al., 2004).

The mtDNA haplotypes from the Keret River and Lake Onega are positioned in a phylogenetic tree in Fig. 3 depicting all *G. salaris* haplotypes found in the area mapped in Fig. 1. Parasites in both grayling and in salmon from the Pisto River (rainbow trout type) are included in Figs. 1 and 3.

Total number of salmon parr inspected in lake Onega rivers is so far 293, and three of them have been infected by *Gyrodactylus* (1 %). Out of those infected, one had only one parasite, and the others few, less than 15 worms. The prevalence and intensity of the infection thus is extremely low in lake Onega area.

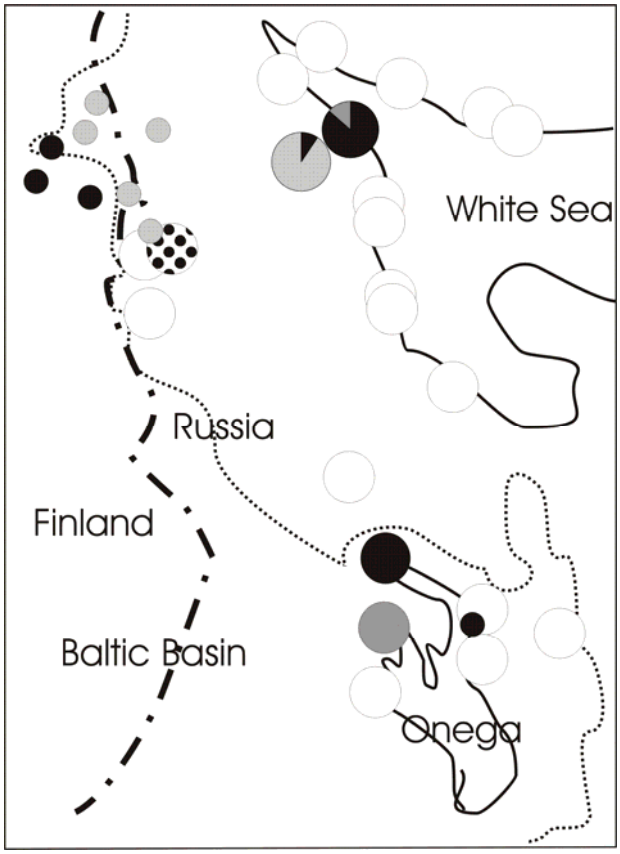

Fig. 3. A map of Russian Karelia showing the location of the rivers where salmon (large circles) or grayling (small circles) *Gyrodactylus* parasites were sampled. The color code is the same than in the phylogenetic tree in Fig. 2. The watershed separating the Baltic Sea and White Sea basins is marked by a dotted line. Large white circles indicate salmon populations observed, but clean of *Gyrodactylus*

Apparent heteroplasmy caused by a nuclear copy of mtDNA in the parasites from the Keret River

Among the parasite specimens sequenced from the Keret River, apparent heteroplasmy was observed in almost all individuals, in both haplotypes *KA* and *KB*. By molecular cloning, a third sequence (**AY225307**) was revealed to be identical to the consensus sequence of the mitochondrial COI gene for all *Gyrodactylus salaris* haplotypes, *i.e.*, it represented a hypothetical central haplotype in the starlike phylogeny (Meinilä et al., 2004). From this phylogenetic position, we concluded that this sequence was a nuclear copy of the actual mitochondrial COI gene. Because the signal in the sequencing gel was invariably lower than that of the actual mitochondrial sequence and the variable sites were always the same, the NUMT did not distract the identification of the mtDNA haplotypes once it was cloned.

This phenomenon of apparent heteroplasmy was not observed in the samples from Lake Onega rivers.

***Gyrodactylus salaris* in Pistojoki is of rainbow trout specific type**

The *Gyrodactylus salaris* observed in the lacustrine salmon population in Pistojoki (Kuitoezero), is of the type found frequently in rainbow trout farms (Meinilä et al., 2004). In the map of Koski and Malmberg (1995), one of the infected rainbow trout farms is along the headwaters of Pistojoki in Kuusamo. It is important to note that the infection

of the salmon in Pistojoki is not from the local grayling.

Gyrodactylus in Karelian graylings (*Thymallus thymallus*) is not infecting salmon

In Fig. 2 we have included the grayling specific *Gyrodactylus* samples from Karelia. They are divided into two geographically separate clades, reflecting the postglacial recolonization history of the area. One clade is found in graylings of Pistojoki and Kovda river system (Oulankajoki, Olanga). The other clade contains parasites of the Baltic basin, extending from Pjalma (Lake Onega), to lake Kitka, which since 8400 BP belongs to the Kovda river system, but obtained the fish fauna earlier, from the Anclylus lake phase of the Baltic Sea.

Discussion

We have been observing *Gyrodactylus* in Karelia and Kola Peninsula since the beginning of the Baltic- White Sea- Barents salmonid project (BWB). All the salmon fins in ethanol were inspected by binocular microscope after our expedition 1999, without seeing any parasites (Landlocked Karelian populations Kamennaya, Kurzhma, and Pistojoki, anadromous White Sea populations Nilma, Pulanga, Kuzema, Pongoma, Suma). Marek Ziętara inspected hundreds of salmons in a field laboratory during our expedition in 2000, but all were clean (Landlocked Karelian Luzhma (Segozero), Barents Sea rivers Titovka, Zapadnaja Lica, and Ura, and White Sea rivers Kica, Olenica, and Kolvica). No *Gyrodactylus* was found.

Until present, the river Keret infection is the only pathogenic case of gyrodactylosis in Russia. The international community of *Gyrodactylus* researchers was ready to assign the Keret infection to a Finnish source, possibly to a rainbow trout farm, as suggested by Malmberg (1993), repeated by Johnsen et al. (1999) and by Bakke et al. (2004). The claim was immature; the actual origin of infection can be ascertained now. The *Gyrodactylus salaris* strains can only be identified by mtDNA analysis, developed by Meinilä et al. (2002) and successfully used by Hansen et al. (2003) and Meinilä et al. (2004).

It is possible that *Gyrodactylus salaris* was introduced to the Keret River during 1986-1989 (Ieshko et al., in preparation). During this period, hatchery raised native salmon juveniles were transferred in a canvas bag carried by helicopter from the Vyg (White Sea) hatchery to the Keret River. It is possible that the same container had been used shortly before for salmon transport in Lake Onega, where *Gyrodactylus salaris* is known as a rare and harmless parasite of endemic lake salmon. The parasite was observed for the first time in 1992 in the Varatskij rapid of the Keret River (25 km upstream of Morskoi or Sea Rapid). The uppermost rapid, Verhnyi, was observed to be clean as late as in 1995, (Ieshko et al., in preparation).

As a contrast to both Keret, the *Gyrodactylus* salaris in the lake Onega salmon shows clear symptoms of strong host defence, leading to fugitive life cycle of the parasite. Only one per cent of the fish were infected. Two strains were found, but they don't occur together. The salmon populations in different spawning rivers probably are well isolated, so that the reinfection after a recovery is a rare event, and the parasite clones are rare and don't mix between the spawning rivers. In Tornio, the host's population structure is continuous, and the reinfection rate is high, so the parasite load is rather permanent. However, there were no indications of pathological density, and seven out of 23 rapids were parasite free.

It is important to study the Keret once more, to compare the pattern observed in 2001 with later development of the infection. The distribution of two parasite clones can be explained either by two introductions, or by clonal competition and random drift, after one introduction. This could be solved by a new sample. The first hypothesis will be supported if the clones are more mixed by the second visit, and the latter one if the repulsion is still maintained.

Tolerant salmon in Karelian lakes, and susceptible in the White Sea: a legacy of the Ice Ages

All cases of pathological gyrodactylosis are reported from salmon rivers connected to, and influenced by, gene flow from the Atlantic Ocean. The observations here complement this picture.

The anadromous salmon stocks in the White Sea basin originate in part from ice dammed freshwater Lake Komi, as evident from the distribution of mitochondrial haplotypes (Asplund et al., 2004). However, since the opening of the White Sea Ice Lake to the Barents Sea, immigration of especially male salmon is supposed to have introduced new alleles, which have changed the composition of the anadromous stocks (Tonteri et al., 2005). The White Sea and Lake Onega salmon are not closely related, and most probably originate from different glacial refugia. This is indicated by the divergent

composition of mitochondrial and nuclear genes. In particular, the genetic influence of the Atlantic salmon populations is excluded in Lake Onega salmon populations, which belong to the Baltic group (Nilsson et al., 2002; Tonteri et al., 2005). The Kuitozero lacustrine salmon probably was isolated before much of Atlantic influence as well (Nilsson et al., 2002; Tonteri et al., 2005), which may explain the apparent tolerance to *Gyrodactylus salaris* in Pistojoki.

Tolerant salmon in Lake Onega, and susceptible in the White Sea: a legacy of the Ice Ages

The anadromous salmon stocks in the White Sea basin originate in part from preglacial freshwater Lake Komi, as evident from the distribution of mitochondrial haplotypes. (Asplund et al., 2004). However, since the opening of the White Sea to the Barents Sea, immigration of male salmon is supposed to have introduced new alleles, which have changed the composition of the anadromous stocks (Tonteri et al., 2005). The White Sea and Lake Onega salmon are not closely related, and most probably originate from different glacial refugia. This is indicated by the divergent composition of mitochondrial and nuclear genes. In particular, the genetic influence of the Atlantic salmon populations is excluded in Lake Onega salmon populations, which belong to the Baltic group (Nilsson et al., 2002; Tonteri et al., 2005).

All the cases of pathological gyrodactylosis are reported from salmon rivers connected to, and influenced by, gene flow from the Atlantic Ocean. The observations here complement this picture.

Rainbow trout: accused vector, but not guilty of infecting the KeretRiver

Without molecular identification, it has been difficult to exclude the role of rainbow trout as a vector of the *Gyrodactylus salaris* infection in the Keret River. This was suggested by Malmberg (1993), and repeated by Johnsen et al. (1999), and still by Bakke et al. (2004). The rainbow trout type of parasite has caused a serious gyrodactylosis in three Norwegian rivers (Laerdalselven, Drammen and Lierelva, Hansen et al., 2003), and it has also infected landlocked salmon in the Pisto River (Kuitozero, Karelia, see the Map in Fig. 1). The Pisto River is geographically the closest (<100 km) known area of infection to the Keret River (Meinilä et al., 2004), but is not located in the same watercourse. The rainbow trout specific clade of *G. salaris* was not found in the Keret River, or in Lake Onega. As it now stands, the assertion made by the international community, assigning as the source of the Keret infection to Finnish rainbow trout farms, can now be robustly refuted.

However, in Russian Karelia, rainbow trout farming is expected to expand in the future. This is likely to seriously threaten the natural salmon rivers of the White Sea Basin.

Closely related grayling parasites do not infect salmon

The *Gyrodactylus* parasites in grayling (*Thymallus thymallus*) are divided into several geographical races (Baltic, Karelian, Oslo fjord, Lake Vännern), which differ from each other as much as they differ from the two races found in salmon (Hansen et al., 2003; Meinilä et al., 2004). In the study area described in this paper, two of these grayling-specific races have been recorded. The mtDNA sequences of these types and the sampling sites are illustrated in the phylogeny in Fig. 3, and on the map in Fig. 1. On the basis of the phylogeny it is clear that the grayling-specific types are not responsible for the salmon infections.

This happens to be the first study where a gyrodactylosis case has been explored by examining a relatively large number of parasite specimens. During the epidemic in central Norway, not only the separate rivers are considered homogeneous, *i.e.*, occupied by one clone, but the whole area was infected by one clone. No evidence of other sources of infection was found (Hansen et al., 2003). The interplay of two simultaneous clones offers a possibility to explore the demography of the parasite in more detail. It is important to follow the development of the infection pattern in the Keret River over the next few years to better understand the dynamics of the epidemics. From a single temporal observation, we cannot separate two opposite scenarios. First possibility is that the *G. salaris* population is approaching equilibrium after an original introduction of two haplotypes in different parts of the river. The alternative is that the two clones were introduced in one shipment in one locality and are now spreading and excluding each other competitively, amplifying the drift-based disequilibrium. The time scale seems appropriate for distinguishing between these alternatives by future sampling, provided that the salmon population survives.

The possibility of eradicating the parasite by methods commonly applied in Norway,must be seriously considered to protect the other White Sea salmon populations from *G. salaris*. However, the

Rotenon poisoning and the building of migration barriers is ecologically costly.

Demography of Gyrodactylus salaris *depends on the host defense system*

The observations in this study concern two fundamentally different host-parasite combinations. In the Keret River, the salmon population is susceptible and most probably not able to develop a defence reaction which could restrict the growth of parasite clones. The pathogenic situation resembles that of the Norwegian epidemic (reviewed in Bakke et al., 2002). The density of parasites is high and the salmon population is dying in spite of supportive stocking. The co-occurrence of both clones on the same fish was observed in 8/21 fish in the Keret River. This was not significantly less than expected by chance when the frequency of the parasites in each locality is taken into account (P(random ≤ observed) = 0.0541).

In Lake Onega, the two parasite clones did not occur simultaneously on the same fish, as only three fish specimens out of 293 were infected, and the two analyzed clones were caught in separate rivers. The freshwater feeding phase of adult fish is expected to facilitate the dispersal of parasites between separate spawning rivers, yet the distribution of the parasite is extremely sporadic. Because the parasite is most probably native to Lake Onega salmon, the sporadic distribution may reflect the strong inducible defence reaction of the host, leading to a fugitive demography of *G. salaris*.

The clonal structure of *G. salaris* has been studied in another supposedly coadapted combination (Kuusela et al., in preparation). In the Baltic Tornio River, located between Finland and Sweden, a native *G. salaris* population was found among salmon in 16 out of 23 rapids studied. In comparison to Lake Onega, the prevalence of the parasite was much higher; 23.4% of all fish were carrying *G. salaris* (Anttila et al., in preparation). The co-occurrence of two *G. salaris* clones on the same fish was highly significantly less common than by chance, the probability reaching zero in one million simulation repeats. We suggest that the negative interference between the parasite clones, observed on the co-adapted Baltic salmon, is transmitted by the host defence reaction, which is missing in the Keret River. A population which has been infected by *G. salaris* but has recovered, is a restrictive environment with respect to the next infection. The extreme form of this demographic model was seen in Lake Onega.

An explanation for the difference in parasite occurrence between the Tornio River and Lake Onega may be that the host population structure is fundamentally different. In the river, the salmon spawning and growing range extends linearly over 560 kilometres and the subpopulations in separate rapids are connected by regular migrations of juvenile and adult salmon. In Lake Onega, the salmon spawning rivers are quite small, and the host fish populations are possibly isolated by strict homing behaviour. The direct distance between the Lizhma and Kumsha river mouths is only 50 km, but it is about 230 km along the lake. In the metapopulation structure of Lake Onega, the recolonization (reinfection) of the separate subpopulations by a parasite must be much less common than in large, continuous and linear population in the Tornio River.

Acknowledgements

Kalevi Kuusela participated in the expedition to the Pisto and Keret Rivers in 2001. Igor Bakhmet, Dmitry Stepanov, Heikki Ryynänen, Anni Tonteri and Paula Lehtonen helped during Lake Onega expeditions. This study was supported by the Academy of Finland (№ 44124), by Naturpolis Kuusamo (for J.K. and R.H.), by the Emil Aaltonen Foundation and the Finnish Cultural Foundation (for M.M.) and by the Ministry of Agriculture and Forestry of Finland.

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