

Monogenean assemblages and the apparent transmission capability of monogeneans between related fish species: an experimental study

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Abstract Gyrodactylid monogeneans are considered to be the most invasive fish parasites. They are omnipresent on teleost fishes and host change might play a crucial role in their biology. In the present study, related fish species were kept in single- or mixed-species groups to test the ability of *Gyrodactylus* species to change their host fish under experimental conditions. The first group included two percid fish species, perch *Perca fluviatilis* L. and ruffe *Gymnocephalus cernuus* (L.), and the second group two cyprinid species, roach *Rutilus rutilus* (L.) and minnow *Phoxinus phoxinus* (L.). A total of 4,182 specimens of 19 monogenean species belonging to five genera were observed, and eight species of *Gyrodactylus* were identified. There were three species of *Gyrodactylus* found on roach and six species on minnow. *Gyrodactylus vimbi* parasitized both cyprinid fish species and was the only species that increased in intensity during the experiments and also assumed to transmit from minnow to roach, while the other recorded host change case, *Gyrodactylus macronychus*, was represented by a single individual that transmitted from minnow to roach. *Gyrodactylus rutilensis* and *Gyrodactylus pannonicus* remained on their original hosts (roach and minnow, respectively). *Gyrodactylus cernuae* was the only species observed on both ruffe and perch, but ruffe appeared more susceptible to this parasite. Most of the

gyrodactylids observed on roach and minnow were situated on the fins, while gyrodactylids of perch and ruffe parasitized mainly the gill chamber and head.

Introduction

The host specificity of parasites varies considerably within and between groups. Monogeneans are suggested to be among the most host-specific parasites (Poulin 1992). Gyrodactylid monogeneans, however, are suggested to be less specific and there are extremely catholic species in this group (Whittington et al. 2000). Host response mechanisms as well as the initial parasite population growth on a fish determine observed specificity (Buchmann and Lindenstrøm 2002).

Due to their direct life cycle and the absence of specialized transmission stages, gyrodactylids have constant opportunities to move on a host or between host individuals, a strategy which may favor host switching (Kearn 1994). Host switching is considered common for gyrodactylids (Bakke et al. 2002). Harris (1993) also hypothesized that host switching may occur between fish species sharing the same habitat. Gyrodactylids kept under experimental conditions may transmit to atypical host even more frequently (King and Cable 2007). Transmission of gyrodactylids is temperature dependent; parasites transmit more often and are less selective at higher temperatures (Bakke et al. 1991). Another important factor in the transmission and dissemination of gyrodactylids is stress-induced immunosuppression during fish handling or transport (Harris et al. 2000). The ability of gyrodactylids to emigrate from the host at any time during their life cycle should favor colonization of new host individuals or a new host species (Boeger et al. 2005). The availability of new

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colonizable hosts is necessary for host change to occur. Especially, host species related phylogenetically or ecologically to a parasite's original host may provide the conditions necessary for parasite transmission and survival and thus successful colonization (Kennedy 1975).

In the present study, we studied the possible gyrodactylid movements between related fish species. Higher population growth and an increased level of parasite transmission was expected between two related host species kept together in increased water temperature (see Scott and Nokes 1984; Gelnar 1990; Jansen and Bakke 1991; Andersen and Buchmann 1998). Further, because wild fish were caught and kept in tanks, they were exposed to stress and induced immunosuppression. This situation was expected to favor the growth of parasite populations and thus increased host change (Harris et al. 2000).

Materials and methods

Ruffe (*Gymnocephalus cernuus*), perch (*Perca fluviatilis*), and roach (*Rutilus rutilus*) were caught by seine net in Lake Kuuhankavesi (62.339° N, 26.402° E) and minnow (*Phoxinus phoxinus*) were caught by electrofishing in the Köyhänoja stream (62.228° N, 25.729° E) flowing to Lake Jyväsjärvi in Jyväskylä city, Finland at the end of September 2000. Fish were kept in aerated lake or stream water and gradually acclimated over 5 days from 9°C or 6.5°C to the experimental conditions of 16°C (range 15.8°C to 16.2°C). Altogether, 100 specimens of each fish species were used in the experiments (ruffe, mean standard length \pm SD 43.8 \pm 2.4 mm, mean weight \pm SD 1.3 \pm 0.2 g; perch, 52.2 \pm 3.9 mm, 2.1 \pm 0.6 g; roach, 49.5 \pm 8.1 mm, 1.7 \pm 0.8 g and minnow, 61.5 \pm 7.6 mm, 3.5 \pm 2.1 g). Ten randomly chosen fish of each species were dissected for the presence of monogeneans prior to the experiments. Two separate experiments were performed. In the first experiment, three tanks with 20 ruffe in each, three tanks with 20 perch, and three mixed-species tanks of ten ruffe and ten perch in each were set up. Fish were placed randomly into the tanks. A similar experimental set up was used with the two cyprinid hosts; three tanks of 20 minnow in each, three tanks of 20 roach, and three mixed-species tanks of ten minnow and ten roach. The experiments were performed in 50-l white plastic tanks under constant dim illumination. The experiment with percid hosts was terminated after 14 to 16 days and the experiment with cyprinid hosts after 19 to 21 days. Ten randomly chosen fish from each single-species tank and all the fish from the mixed-species tanks were examined for parasites. Several fish jumped out of tanks or died during the experiment (altogether 18 fish), and they were excluded from the calculations. All fish were measured to the nearest 0.1 mm, weighed to the nearest

0.1 g, and for minnow, sex was determined. Perch, ruffe, and roach were juveniles. Fish were examined by stereomicroscope and all of 4,182 monogenean parasites found were preserved in glycerin ammonium picrate (Malmberg 1970) to record also occasional cases of host change. Species were later determined according to Gussev (1985) using an Olympus BX 50 microscope with phase contrast. The microhabitat of each parasite was recorded. Microhabitats were defined as fins (pectoral, ventral, dorsal, anal, and caudal), gill chamber (cartilage and filaments), and skin (head, proximal, and distal part of body surface).

Ecological parameters such as abundance, prevalence, and intensity of infection follow the recommendations of Bush et al. (1997). The statistical analyses were carried out in Statistica for Windows 7.1 (StatSoft Inc. 2006). Chi-square tests were used to determine the difference in prevalence of monogeneans among single- and mixed-species treatments and between host species. Log-transformed intensity data were used in all tests. Nested analysis of variance (ANOVA) was used to test for differences in the intensity of monogeneans among treatments. Student *t* tests were used to evaluate the difference in the intensity of monogeneans between host species and the difference in the intensity between male and female minnow. Wilcoxon test on log-transformed data was used to assess microhabitat selection between treatments. The relationship between the number of parasites and fish length and weight was measured by Spearman correlations.

Results

Percid host experiment

Eight of ten prescreened perch were infected with *Gyrodactylus cernuae* and five harbored *Ancyrocephalus percae*. All prescreened ruffe were infected with *G. cernuae* and *Dactylogyrus amphibothrium*, while four had *Dactylogyrus hemiamphibothrium* (Table 1). *G. cernuae* was the only species occurring in both percid species, but it was much more common on ruffe (Student *t* test, $t = -4.251$, $df = 18$, $P < 0.001$).

No gyrodactylids were found on perch taken from the single-fish-species tanks after the experiment. On the other hand, 39% of perch from the mixed-fish-species tanks were infected by *G. cernuae*. *A. percae* was found in low intensities and prevalences on perch from both single- and mixed-fish-species tanks. Neither *G. cernuae* nor dactylogyrids differed in intensity or prevalence on ruffe between single- and mixed-fish-species tanks (nested ANOVA for intensity, see Table 3, χ^2 test for prevalence, $P > 0.129$ for both *G. cernuae* and dactylogyrids). The intensity and prevalence of *G. cernuae* was significantly higher on ruffe as compared to

Table 1 Monogenean infection parameters from percid hosts (*P. fluviatilis*, *G. cernuus*)

Fish species	Parasite species	Prescreened fish		Single-species tanks		Mixed-species tanks	
		Prevalence %	Mean intensity (SD) max	Prevalence %	Mean intensity (SD) max	Prevalence %	Mean intensity (SD) max
<i>P. fluviatilis</i> ^a	<i>G. cernuae</i>	80	1.9 (2.1) 7	0	0	39	0.5 (0.8) 3
	<i>A. percae</i>	50	0.6 (0.7) 2	7	0.1 (0.3) 1	21	0.4 (0.9) 4
<i>G. cernuus</i> ^b	<i>G. cernuae</i>	100	17.1 (17.5) 47	93	8.7 (11.0) 55	80	11.2 (17.7) 77
	<i>D. amphibothrium</i>	100	13.4 (5.9) 26	100	5.1 (3.5) 15	100	5.9 (3.1) 12
	<i>D. hemiamphibothrium</i>	40	1.0 (1.3) 3	23	0.3 (0.6) 2	20	0.2 (0.5) 2

The number of prescreened fish and fish assigned to each treatment (single-species tanks, mixed-species tanks) are given as well as the monogeneans infecting them (*Ancyrocephalus*, *Gyrodactylus*, and *Dactylogyrus*). Prevalence, mean, and maximum intensity of infection are given after each parasite species

^aNumber of fish: prescreened fish=10, single-species tank=30, mixed-species tank=28

^bNumber of fish: prescreened fish=10, single-species tank=30, mixed-species tank=30

perch in the mixed-species tanks (Student *t* test for intensity, $t = -10.514$, $df = 116$, $P < 0.001$, χ^2 test for prevalence, $P < 0.002$). Species of *Dactylogyrus* or *Ancyrocephalus* did not seem to transmit from their original host species in the mixed-species tanks.

G. cernuae on perch were found mainly (88%) in the gill chamber and 54% of these were found on cartilages of the gill arches. The remaining individuals were attached to the skin (2%) and fins (10%). In the case of ruffe, 38% of *G. cernuae* specimens were found on the skin (31% of these were on the mouth), 19% were on the fins (8% on the dorsal fins), and 43% were in the gill chamber (37% on gill cartilages; see Fig. 1).

There was no relationship between the number of parasites on either perch or ruffe and host length or weight (Spearman correlation, $P > 0.05$, for all four cases).

Cyprinid host experiment

Altogether, six *Gyrodactylus* species were found infecting prescreened minnow (*Gyrodactylus macronychus*, *Gyrodactylus limneus*, *Gyrodactylus pannonicus*, *Gyrodactylus vimbi*, *Gyrodactylus laevis*, and *Gyrodactylus magnificus*). The most prevalent and abundant species were *G. macronychus* and *G. limneus* (Table 2). Other monogeneans parasitizing prescreened minnow were *Dactylogyrus borealis*, *Paradiplozoon homoion*,

Fig. 1 The microhabitat selection of *Gyrodactylus* species on ruffe (*G. cernuus*—GC), perch (*P. fluviatilis*—PF), roach (*R. rutilus*—RR), and minnow (*P. phoxinus*—PP) from prescreened fish and both treatments together. The number of individual parasites of each species (*N*) is indicated above the bars

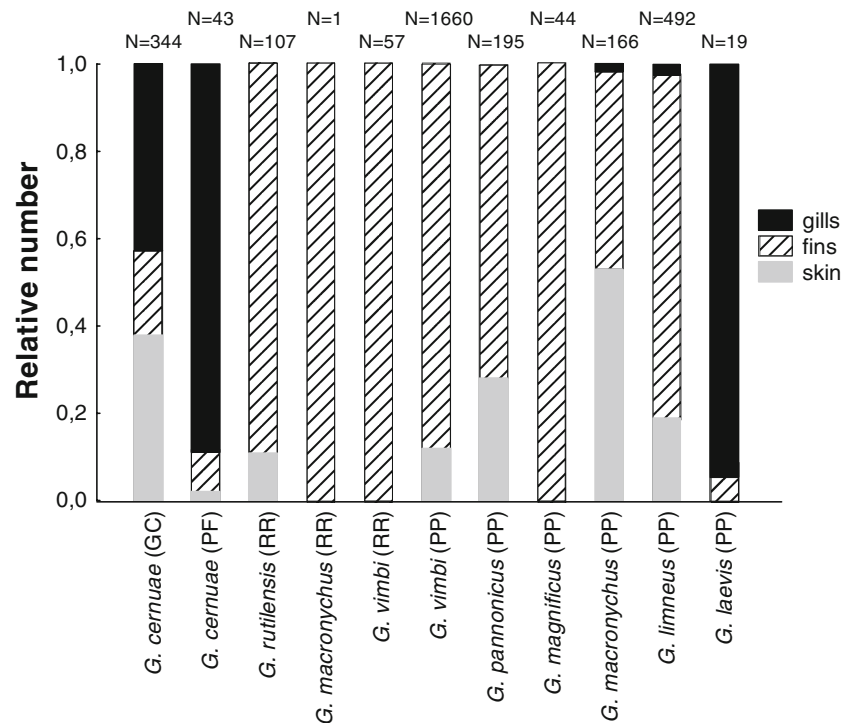


Table 2 Monogenean infection parameters from cyprinid hosts (*P. phoxinus*, *R. rutilus*)

Fish species	Parasite species	Prescreened fish		Single-species tanks		Mixed-species tanks	
		Prevalence %	Mean Intensity (SD) max	Prevalence %	Mean Intensity (SD) max	Prevalence %	Mean Intensity (SD) max
<i>P. phoxinus</i> ^a	<i>G. limneus</i>	90	12.5 (14.9) 50	63	4 (6.5) 25	0	0
	<i>G. laevis</i>	30	0.5 (0.9) 3	0	0	0	0
	<i>G. macronychus</i>	100	8.6 (4.5) 17	43	1.5 (2.9) 14	10	0.2 (0.7) 3
	<i>G. magnificus</i>	10	0.1 (0.3) 1	23	0.6 (1.9) 10	0	0
	<i>G. pannonicus</i>	60	4.5 (6.4) 17	60	2.9 (4.7) 21	29	1.2 (2.3) 7
	<i>G. vimbi</i>	60	2.4 (2.9) 9	100	37.5 (55.9) 268	86	19.0 (29.3) 127
	<i>D. borealis</i>	50	0.6 (0.7) 2	0	0	0	0
	<i>P. homoion</i>	20	0.2 (0.4) 1	0	0	0	0
	<i>P. merus</i>	10	0.1 (0.3) 1	0	0	0	0
<i>R. rutilus</i> ^b	<i>G. rutilensis</i>	0	0	20	0.6 (1.7) 8	23	4.0 (8.2) 29
	<i>G. vimbi</i>	0	0	10	0.2 (0.5) 2	64	2.0 (2.2) 7
	<i>G. macronychus</i>	0	0	0	0	5	0.1 (0.2) 1
	<i>D. crucifer</i>	0	0	33	0.4 (0.7) 2	18	0.2 (0.4) 1
	<i>D. nanus</i>	90	2.1 (1.7) 6	43	0.9 (1.4) 4	82	2.1 (2.2) 9
	<i>D. micracanthus</i>	30	0.3 (0.5) 1	33	0.4 (0.7) 3	36	0.5 (0.8) 2
	<i>D. suecicus</i>	0	0	0	0	9	0.1 (0.3) 1
	<i>D. sphyrna</i>	0	0	3	0.0 (0.2) 1	0	0
	<i>D. juv. spp.</i>	40	0.5 (0.7) 2	10	0.2 (0.7) 3	5	0.1 (0.2) 1
	<i>P. homoion</i>	10	0.1 (0.3) 1	0	0	9	0.1 (0.3) 1

The number of prescreened fish and fish assigned to each treatment (single-species tanks, mixed-species tanks) are given as well as the monogeneans infecting them (*Gyrodactylus*, *Dactylogyrus*, *Paradiplozoon*, and *Pellucidhaptor*). Prevalence, mean, and maximum intensity of infection are given after each parasite species

^a Number of fish: prescreened fish=10, single-species tank=30, mixed-species tank=21

^b Number of fish: prescreened fish=10, single-species tank=30, mixed-species tank=22

and *Pellucidhaptor merus*. No gyrodactylids were observed on prescreened roach, but two species of *Dactylogyrus* (*Dactylogyrus nanus* and *Dactylogyrus micracanthus*) as well as *P. homoion* were found (Table 2). The only monogenean species common to both cyprinid species found on the prescreened fish was *P. homoion*.

Neither *D. borealis*, *P. homoion*, *P. merus*, nor *G. laevis* was observed on the minnows from either the single- or the mixed-species tanks. Additionally, two *Gyrodactylus* species found on prescreened fish were not seen on fish from the two-species tanks (*G. limneus* and *G. magnificus*). In all these cases, with the exception *G. limneus*, the abundance in prescreened fish was very low (<0.6; Table 2). *G. vimbi*, *G. pannonicus*, and *G. macronychus* were observed in both treatments, but their prevalence and intensity was lower in mixed-species tanks (nested ANOVA for intensity, see Table 3, χ^2 test for prevalence, all $P < 0.05$). The prosperity of *G. vimbi* under these experimental conditions was notable. The intensity of this species was higher in both treatments compared to prescreened fish (Student *t* test, $t < -3.677$, $df_1 = 38$, $df_2 = 29$, $P < 0.001$ for both treatments). Prevalence however was significantly higher than prescreened fish only in single-species tanks (χ^2 test, $P < 0.01$). The intensity of *G. vimbi* was exceptionally high

in tanks with only minnow (mean intensity 37.5; maximum 268).

Only two *Dactylogyrus* species (*D. nanus* and *D. micracanthus*) and *P. homoion* were found in prescreened roach. However, several additional species (*Gyrodactylus rutilensis*, *G. vimbi*, *Dactylogyrus crucifer*, and *Dactylogyrus sphyrna*) were found on fish from the single-species tanks. They also occurred at low abundance in mixed-fish-species tanks (Table 2). *G. macronychus* may have changed hosts, i.e., from minnow to roach. This host change case was represented by just one specimen of *G. macronychus*. Another species which may have transmitted from minnow to roach was *G. vimbi*. Its prevalence (64%) and mean intensity (2) on roach was higher in mixed-species tanks than in single-species tanks (nested ANOVA for intensity, see Table 3, χ^2 test for prevalence $P < 0.001$). Prevalence of *G. vimbi* did not differ between roach and minnow in the mixed-species tanks (χ^2 test, $P = 0.097$), but its intensity was higher on minnow (Student *t* test, $t = -3.818$, $df = 41$, $P < 0.001$). Neither *G. pannonicus* on minnow nor *G. rutilensis* nor the dactylogyrids on roach were found to change host species in mixed-species tanks.

On roach, *G. vimbi* was primarily on the dorsal (34%) and pectoral (32%) fins. *G. rutilensis* was also attached

Table 3 The effect of treatment (single fish species or mixed species) and tank on the intensity of monogenean parasites on *G. cernuus*, *P. phoxinus*, and *R. rutilus*

Parasite (host)	Factor	MS	F	df	p
<i>G. cernuae</i> (<i>G. cernuus</i>)	Treatment	0.146	0.675	1	0.415
	Tank (treatment)	0.496	2.288	4	0.072
	Error	0.217		52	
Dactylogyrids (<i>G. cernuus</i>)	Treatment	0.046	0.790	1	0.378
	Tank (treatment)	0.070	1.216	4	0.315
	Error	0.057		52	
<i>G. vimbi</i> (<i>P. phoxinus</i>)	Treatment	1.234	8.827	1	0.005
	Tank (treatment)	1.638	11.714	4	<0.001
	Error	0.139		45	
<i>G. pannonicus</i> (<i>P. phoxinus</i>)	Treatment	0.386	3.776	1	0.058
	Tank (treatment)	0.532	5.206	4	0.002
	Error	0.102		45	
<i>G. macronychus</i> (<i>P. phoxinus</i>)	Treatment	0.433	9.245	1	0.004
	Tank (treatment)	0.356	7.614	4	<0.001
	Error	0.047		45	
<i>G. vimbi</i> (<i>R. rutilus</i>)	Treatment	1.216	38.000	1	<0.001
	Tank (treatment)	0.329	10.288	4	<0.001
	Error	0.032		46	

Tank was nested factor within treatment in an ANOVA on log-transformed data

mainly to the dorsal (39%) and pectoral (36%) fins. The single specimen of *G. macronychus* found on roach was attached to a pectoral fin. The microhabitat preference of *Gyrodactylus* species on minnow did not differ significantly among treatments and prescreened fish (Wilcoxon test, all $z < 1.5$, $P > 0.1$, Fig. 1). About 95% of *G. laevis* individuals on minnow were observed on the gills. *G. macronychus* was recorded mainly on the fish skin with 21% of all specimens on the distal part of their host. *G. limneus*, *G. pannonicus*, and *G. vimbi* were attached mainly to pectoral fins (31%, 28%, and 33%, respectively), but *G. magnificus* was most common (41%) on dorsal fin.

No relationship between the number of parasites and host length and weight was observed in roach or minnow (Spearman correlation, $P > 0.05$ for all four cases). There was no difference in the number of parasites between male and female minnow (Student *t* test, $t = -0.731$, $df = 62$, $P = 0.467$).

Discussion

In this study, a total of 4,182 specimens of monogenean parasites infecting experimental fish were found. Altogether, seven *Dactylogyrus* and eight *Gyrodactylus* species among 19 monogenean species were identified. Shape and size of haptor sclerites together with copulatory organ of oviparous monogeneans allowed easy species determination in accordance to Gussev (1985). On the other hand, identification of *Gyrodactylus* species based on morphological

characteristics might be problematic. Especially in the case of cryptic species molecular identification techniques such as analysis of nuclear ribosomal DNA (rDNA) internal transcribed spacers (ITS-1, ITS-2) and 5.8S and 18S rDNA might be helpful (Cunningham et al. 1995; Matějusová et al. 2001; Ziętara et al. 2002; Ziętara and Lumme 2003). Unfortunately, in ecological studies, where thousands of worms are handled, molecular identification of each parasite individual is in practice impossible. Gyrodactylids in this study were distinguished by shape and size of central and marginal hooks into the species according to Gussev (1985).

In the present study, there were only two monogenean species common to both related fish species in the prescreened fish (*G. cernuae* to percids and *P. homoion* to cyprinids). No gyrodactylids were observed on prescreened roach. However, Koskivaara et al. (1991a) found four *Gyrodactylus* species (including *G. vimbi* but not *G. rutilensis*) in adult roach from the same watershed in which present roach were caught. The two gyrodactylid species found on roach from the single-species tanks of this study were found most likely just because more fish were examined (see Poulin 1997). This means that these monogeneans were already present on the fish prior to the experiment. There were only two apparent cases of host change and only one of these (*G. vimbi*) might have changed hosts more frequently while the other case (*G. macronychus*) was represented by a single individual that seemed to transmit from minnow to roach. Other gyrodactylids, all dactylogyrids, or *P. homoion* did not tend to transmit from their original hosts when given the opportunity.

Host change could be considered as a part of gyrodactylid dissemination (Kearn 1994). A high abundance and population growth may favor host change. Mo (1997) observed one *Gyrodactylus aphyae* and two specimens of *G. macronychus* parasitizing trout (*Salmo trutta*) in an area with high gyrodactylid abundance on minnow. Bakke et al. (1990, 1992), Bakke and Sharp (1990), and Soleng and Bakke (1998) found a significant proportion of gyrodactylids kept under experimental conditions to change host species. In their studies, *Gyrodactylus salaris* taken from *Salmo salar* transmit to several other fish species, but the parasites were eliminated within 2–8 days. In contrast, the experiments of King and Cable (2007) and Olstad et al. (2007) showed that *Gyrodactylus turnbulli* and *G. salaris* remain on related but atypical hosts as long as on its original hosts *Poecilia reticulata* and *S. salar*, respectively. Our experiment lasted 2–3 weeks, so it is also possible that parasite individuals changed hosts but were then eliminated from the novel host species before the end of the experiment.

An increased level of parasite transmission and on-host population growth was expected at the increased water temperatures in the laboratory (see Scott and Nokes 1984; Gelnar 1990; Jansen and Bakke 1991; Andersen and Buchmann 1998). Only *G. vimbi* benefited from the laboratory conditions and had high infrapopulation growth. The infrapopulations of species *G. vimbi* were larger on roach in the mixed-species tanks compared to roach kept alone, which suggests numerous transfers from minnow to roach bolstering *G. vimbi* populations on roach. *G. cernuae* was commonly found in prescreened ruffe but its infrapopulation size was lower in both the ruffe-only and mixed-species tanks, suggesting decreases in parasite abundance over time. Similarly, this parasite probably infected the experimental perch initially but then decreased in abundance over time, even disappeared in the perch-only tanks. Most monogeneans, with the exception of *G. vimbi*, were found at similar or lower abundances in the experimental fish as compared to the prescreened fish, which suggests that some species likely disappeared over the course of the experiment. Because water temperature was increased from 6°C or 9°C to 16°C for the experiment, monogenean numbers may have dropped due to increased parasite mortality and/or a more effective host response. A host response in roach to parasites is enhanced by spending a few weeks at 15°C (Aaltonen et al. 1994). During the summer, when the water temperature in Finland is the highest, the abundance of gyrodactylids and dactylogyrids decreases compared to the spring (Koskivaara et al. 1991a, b). Indeed, in various experimental studies, gyrodactylid infrapopulation increase was followed by decrease and in some cases also by elimination of parasite (Harris 1988; Richards and Chubb 1998; Olstad et al. 2007).

Gläser (1974) noted the importance of multispecies shoals of fishes for parasite transmission between different species of host. Juvenile perch and ruffe form relatively large shoals under natural conditions. These ecologically and phylogenetically related species provide appropriate conditions for *G. cernuae* to change hosts in nature, as indicated by the high prevalence in prescreened fish of both species. The cyprinids used in this experiment differed in habitat of origin and the exchange of gyrodactylids between these two species before experiment was thus unlikely. Naturally, roach is common in lakes, while minnow inhabits small streams or the stony littoral areas of lakes, where at least occasionally, both species do occur in sympatry (Mills and Eloranta 1985). In comparison, King and Cable (2007) observed that *G. turnbulli* changed readily related host species under experimental conditions whereas no host change of gyrodactylids between the same hosts was recorded under natural conditions, where these hosts form multispecies shoals (Cable et al. 2005).

Specificity is determined as the host range width, i.e., the number of host species infected by a population of a single parasite species (Lymbery 1989). Poulin (1992) noted that the number of known hosts is not an ideal measure of a parasite's host specificity because reported hosts may not actually be suitable for parasite reproduction. Moreover, King and Cable (2007) stated that host specificity can never be presumed unless experimentally tested. Present study supports the notion that the host specificity of gyrodactylids is strict in many cases. Consequently, we must consider the host specificity of most of the monogenean species in this study with great caution. Under conditions more suitable for infrapopulation growth, perhaps these species exhibit more generalized host preferences. We do not know if monogenean infrapopulation growth was reduced by increased unsuitable water temperature, enhanced immunity, or some other reason. The infrapopulation growth and infection duration of gyrodactylids commonly differs between related host species (Mo 1997; Boeger et al. 2005; Moen and Stockwell 2006; Olstad et al. 2007) and the chemical structure of the epidermis and mucus of related fish can differ substantially (Buchmann and Uldal 1997). This may explain different abundances of *G. cernuae* on percids and *G. vimbi* on cyprinids in the present study. Sympatric fish hosts unsuitable for parasite reproduction could be on the other hand used as transient hosts (Bakke et al. 2002). Nonetheless, we found it likely that *G. vimbi* is able to reproduce in both minnow and roach, that *G. cernuae* can at least occur in both ruffe and perch, and that *P. homoion* can infect both roach and minnow. Indeed, in addition to perch and ruffe, *G. cernuae* has also been found on the percid *Stizostedion lucioperca* (L.) and *G. vimbi* on several other cyprinid fish species (see Harris et al. 2004).

The gyrodactylids' selection of microhabitat on the hosts differs between species and change over time on the same host species (Buchmann and Uldal 1997). Present study confirms the difference in microhabitat preference of *Gyrodactylus* species. In addition, *G. cernuae* choose different sites on ruffe as compared to perch and *G. vimbi* on minnow as compared to roach (see Fig. 1).

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