

## REVIEW

# Host specificity and dispersal strategy in gyrodactylid monogeneans, with particular reference to *Gyrodactylus salaris* (Platyhelminthes, Monogenea)

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**ABSTRACT:** *Gyrodactylus salaris* Malmberg, 1957 is an important pathogen in Norwegian populations of Atlantic salmon *Salmo salar*. It can infect a wide range of salmonid host species, but on most the infections are probably ultimately limited by a host response. Generally, on Norwegian salmon stocks, infections grow unchecked until the host dies. On a Baltic salmon stock, originally from the Neva River, a host reaction is mounted, limiting parasite population growth on those fishes initially susceptible. Among rainbow trouts *Oncorhynchus mykiss* from the same stock and among full sib anadromous arctic char *Salvelinus alpinus*, both naturally resistant and susceptible individuals later mounting a host response can be observed. This is in contrast to an anadromous stock of brown trout *Salmo trutta* where only innately resistant individuals were found. A general feature of salmonid infections is the considerable variation of susceptibility between individual fish of the same stock, which appears genetic in origin. The parasite seems to be generally unable to reproduce on non-salmonids, and on cyprinids, individual behavioural mechanisms of the parasite may prevent infection. Transmission occurs directly through host contact, and by detached gyrodactylids and also from dead fishes. Relative importance of these routes and of different host species in the epidemiology of the disease is discussed with reference to laboratory experiments and existing knowledge concerning the host-parasite ecology.

## INTRODUCTION

Monogeneans of the genus *Gyrodactylus* are common parasites of freshwater and marine fishes. Although well known as pathogens of farmed fishes (Malmberg 1957, 1989a, b, Bauer 1958, 1988, Cone et al. 1983, Musselius 1988, Solomatova & Luzin 1988), they are believed to do little direct harm in natural infections. The present epidemic of *G. salaris* Malmberg, 1957 on wild Atlantic salmon *Salmo salar* L. along the Atlantic seaboard of Norway is therefore quite exceptional (Anonymous 1990). Over the past 15 yr severe mortality of young salmon due to *G. salaris* has been reported from many rivers (Johnsen & Jensen 1985,

1986, 1988) and this has been held responsible for declines of up to 520 t [20 % of the total catch; see Dolmen (1987) and Mo (1989)] per year in catches of adult salmon returning to the rivers to spawn. The ecological impact of the parasite, and of measures aimed at its control, is considerable (Johnsen & Jensen 1991); at present salmon from a number of Norwegian rivers are being eradicated using rotenone prior to restocking with disease-free stock (Johnsen et al. 1989).

Little is known of the epidemiology of *Gyrodactylus salaris* in Norway (see Johnsen & Jensen 1991). Gyrodactylids are unusual in being viviparous (Harris 1988a) and can transfer freely between hosts as adults. The population dynamics of gyrodactylids are therefore

more characteristic of bacterial and protozoan micro-parasites than of metazoan pathogens (Anderson & May 1978, Scott & Anderson 1984). High fish mortality and high parasite abundance is seen in salmon parr before they migrate to the sea, but other stages in the life cycle (smolts, precocious males, returning adults) and other fish species can support the parasite and may play a part in its transmission. Fish vary, both between and within species, in their susceptibility and response to *Gyrodactylus* infection. An understanding of the processes involved in such variability will contribute to our knowledge of the factors underlying disease epidemics. Furthermore, knowledge of the transmission and dispersal of *Gyrodactylus* species in space and time within the host community is essential for a proper understanding of the etiology of gyrodactylosis and ultimately for the best management practices for the Atlantic salmon against *G. salaris*. Much relevant literature on the host specificity and transmission of gyrodactylids is found in unpublished theses, research reports and foreign journals of restricted accessibility. Nevertheless, here we attempt to review and identify processes which may be important in the transmission of *G. salaris* between components of the natural ecosystem.

#### HOST SPECIFICITY OF GYRODACTYLIDS

Most parasites infect a range of host species which form a continuum from those which are infected but cannot support the parasite, through those on which some reproduction is possible, to hosts on which reproductive output is maximised (Holmes 1979). For gyrodactylids, even hosts which cannot support the parasite may transport it, facilitating transfer to more suitable hosts (Bakke et al. 1991b). Unfortunately, accounts of gyrodactylid specificity often fail to consider this spectrum and deal only with host range. Furthermore, many descriptions implicitly or explicitly utilise host identity as a character for specific diagnosis (Ergens 1965, Prudhoe & Bray 1982), which may overestimate the diversity and underestimate the host range of gyrodactylids. These problems, and the taxonomic complexity of the genus, make it difficult to analyse patterns of specificity. For example, Cone & Dechtiar (1986) showed that *Gyrodactylus katharineri* Malmberg, 1964, a parasite of *Cyprinus carpio* L., and *G. mizellei* Kritskyet Leiby, 1971, a Eurasian parasite of percid fishes in North America, are morphologically indistinguishable, despite the divergence in host and geographical distribution. Detailed laboratory study is needed for each species to determine the pattern of host utilisation. However, crowding of hosts in aquaria can break down barriers to cross-infections, allowing gyrodactylids to infect atypical hosts (Hargis 1953, Putz & Hoffman 1963, Malmberg

Table 1. *Gyrodactylus* spp. Number of hosts infected by *Gyrodactylus* species, derived from survey data. (A) Based upon total data set of 319 species descriptions, excluding obvious synonyms and misidentifications; (B) based upon 76 species which have featured in more than 1 faunistic survey or have been used in experimental work

No. of species descriptions	No. of hosts infected				
	1	2	3	4	>4
(A) 319	235	48	19	4	13
(B) 76	23	27	13	4	9

1970, 1972, 1973, Malmberg & Malmberg 1970, Ergens 1983a). To date such detailed analysis has only been applied to *G. salaris*.

Although Bychowsky (1957) considered gyrodactylids the least specific of monogeneans, subsequent authors (e.g. Malmberg 1970) have regarded them as narrowly host-specific. This is superficially confirmed by published host records; after eliminating obvious synonymies and misidentifications, 74 % of the 319 valid *Gyrodactylus* spp. are recorded from a single host species (Table 1A). However, by restricting analysis to those gyrodactylids which have featured in 2 or more field studies, or have been used experimentally, the proportion declines to 30 % of 76 species (Table 1B). This suggests that gyrodactylids are less host-specific than commonly thought, and that narrow specificity is an artifact based on numerous species descriptions of gyrodactylids collected from only a single host. The prominent difference in susceptibility/resistance between stocks of the same fish species (see Fig. 1) (Bakke et al. 1990b) and between individuals of the same stock (see Fig. 2) (Bakke et al. 1991a) examined experimentally further stresses the uncertainty in estimating host utilisation of gyrodactylids based on few observations.

Many gyrodactylids have been recorded on single occasions from hosts other than those normally infected; these transient infections are probably a result of inter-specific contact between fishes. An example is *Gyrodactylus errabundus* Malmberg, 1970 which could invade many other species from the true host *Zoarces viviparus* (L.) but could not live or feed on them (Malmberg 1970). Some gyrodactylids, however, exploit a range of fish species, reproducing on each. For example *G. macrochiri* Hoffman & Putz, 1964 is reported from 8 species and 3 genera of centrarchid fishes (Hoffman & Putz 1964, Hanek & Fernando 1971, Rawson & Rogers 1973, Barnhardt et al. 1976, Nicola & Cone 1987). It infects different hosts in different localities and it is not clear which is the principal host. The species *G. macrochiri* reported by Hanek & Fernando (1971) is an additional difficulty, suspected by Nicola & Cone (1987) to be misidentified.

Four salmonid gyrodactylids, *Gyrodactylus salaris*, *G. salmonis* Yin et Sproston, 1948, *G. colemanensis* Mizelle et Kritsky, 1967 and *G. derjavini* Mikailov, 1975, are reported from more than 4 hosts. *G. salaris* has a particularly broad range, as shown in Tables 2 & 3. This broad specificity for attachment and reproduction does not appear to be present amongst the gyrodactylids of other fish groups; for example, the majority of *Gyrodactylus* species infect cyprinids and yet only 1 infects more than 4 hosts. The pattern of specificity of *G. salaris* cannot be related to the evolutionary relationships of the hosts, as *Salmo trutta* L. is less susceptible than e.g. *Salvelinus fontinalis* (Mitchell), *S. alpinus* (L.), *Thymallus thymallus* (L.) or *Oncorhynchus mykiss* (Walbaum) in laboratory experiments (see Fig. 3) (Tanum 1983, Malmberg 1988, Bakke & Jansen 1991a, b, Bakke et al. 1991a). The host range of *G. salaris* outside the Salmonidae needs further investigation but the parasite does not appear to infect cyprinids [*Phoxinus phoxinus* (L.) and *Rutilus rutilus* (L.)], percids (*Perca fluviatilis* L.) or the lamprey *Lampetra planeri* (Bloch) (see Bakke & Sharp 1990, Bakke et al. 1990a), and it can infect and survive for up to 8 d but not feed upon the eel *Anguilla anguilla* (Bakke et al. 1991c). Malmberg (1987b) thought that *G. salaris* was most closely related to *G. thymalli* Zitnan, 1960, which infects another riverine salmonid, the grayling *T. thymallus*. Our preliminary experiments indicate that *G. salaris* can reproduce on *T. thymallus* (see Bakke & Jansen 1991b), and further work will examine the host range of *G. thymalli* (see Lux 1990, Malmberg & Malmberg 1991).

#### ETHOLOGICAL AND PHYSIOLOGICAL MECHANISMS OF HOST SPECIFICITY

We have found by a scrutiny of earlier observations that certain *Gyrodactylus* species vary from narrowly specific species which can utilise only a single host to those which can successfully attach for dispersal or establish and reproduce on several host genera. This includes *G. pungitii* Malmberg, 1964 (several host species during the colder periods of the year when fishes shoal), *G. pharyngicus* Malmberg, 1964 (2 host species), *G. arcuatus* (a number of temporary hosts) and *G. errabundus* Malmberg, 1970 (a pronounced ability to spread from its normal host to other fish species) (all according to Malmberg 1970); *G. unicopula* Gluchowa, 1955 (4 host species, according to MacKenzie 1970); *G. gasterostei* Gläser, 1974 (6 possible hosts, especially during the fish breeding season, according to Gläser 1974); *G. katharineri* (occurs on several fish genera, termed temporary substratum, especially at higher populations levels, according to Ergens 1983a); *G. colemanensis* (4 host species in the genera *Salmo* and

*Salvelinus*, according to Cone et al. 1983); *G. salmonis* (6 host species in the genera *Salmo*, *Salvelinus* and *Oncorhynchus*, according to Cone et al. 1983, Cone & Cusack 1988); *G. avalonia* Hanek & Threlfall, 1960 and

Table 2. *Gyrodactylus salaris* Malmberg, 1957. Review of records on freshwater fish in the Western Palaearctic. N: in nature; H: present in hatcheries or used in experiments

Host records	Sources
<i>Salmo salar</i> <sup>a</sup>	N: Ergens 1983b, Mo 1983, 1987, 1988, Tanum 1983, Johnsen & Jensen 1985, 1986, 1988, Malmberg 1988, Eken & Garnås 1989, Malmberg & Malmberg 1991 H: Malmberg 1957, 1973, 1987a, b, Malmberg & Malmberg 1970, 1991, Tanum 1983, Mo 1987, 1988, Bakke et al. 1990b
<i>Oncorhynchus mykiss</i> <sup>a</sup>	N: Lucky 1963 <sup>c</sup> , Zitnan & Cankovic 1970 <sup>c</sup> , Mo 1988 H: Zitnan & Cankovic 1970 <sup>c</sup> , Rehulka 1973 <sup>c</sup> , Tanum 1983, Malmberg 1987b, 1988, Mo 1988, Lux 1990, Bakke et al. 1991a, Malmberg & Malmberg 1991
<i>Salmo trutta</i> <sup>a</sup>	N: Ergens 1961 <sup>c</sup> , Zitnan & Cankovic 1970 <sup>c</sup> , Tanum 1983, Malmberg 1988, Malmberg & Malmberg 1991 H: Rehulka 1973 <sup>c</sup> , Tanum 1983, Mo 1987, 1988, Malmberg 1988, Lux 1990, Bakke & Jansen unpubl., present results
<i>Salvelinus alpinus</i> <sup>a</sup>	N: Mo 1988 H: Tanum 1983, Mo 1988, Eken & Garnås 1989, Bakke & Jansen 1991a
<i>Salvelinus fontinalis</i> <sup>a</sup>	H: Rehulka 1973 <sup>c</sup> , Mo 1987, Eken & Garnås 1989, Bakke et al. 1992a
<i>Salvelinus namaycush</i> <sup>a</sup>	H: Bakke et al. 1992b
<i>Thymallus thymallus</i> <sup>a</sup>	H: Bakke & Jansen 1991b
<i>Salmothymus obtusirostris</i>	N: Zitnan & Cankovic 1970
<i>Platichthys flesus</i> <sup>b</sup>	N: Mo 1987
<i>Anguilla anguilla</i> <sup>b</sup>	H: Bakke et al. 1991b
<i>Platichthys phoxinus</i> <sup>b</sup>	H: Sharp & Bakke 1990
<i>Lampetra planeri</i> <sup>b</sup>	H: Bakke et al. 1990a
<i>Rutilus rutilus</i> <sup>b</sup>	H: Bakke et al. 1990a
<i>Perca fluviatilis</i> <sup>b</sup>	H: Bakke et al. 1990a

<sup>a</sup>See text; <sup>b</sup>unsuitable host; <sup>c</sup>misidentification, according to Tanum (1983) and Ergens (1983b)

Table 3. *Gyrodactylus* spp. Review of gyrodactylid species (**bold**) associated with salmonids in the Western Palearctic. N: in nature; H: present in hatcheries or used in experiments

Host records	Sources
<b><i>Gyrodactylus truttae</i> Gläser, 1974, Fig. 6a<sup>c</sup></b>	
<i>Salmo trutta</i>	N: Ergens 1961, 1981, Gläser 1974, Mo 1983 <sup>d</sup> , Lux 1990 <sup>e</sup>
<i>Salmo salar</i>	N: Mo 1983 <sup>d</sup> H: Mo 1987 <sup>d</sup>
<i>Oncorhynchus mykiss</i>	N: Ergens 1983b, Mo 1988 <sup>d</sup> , Eken & Garnås 1989 <sup>h</sup> H: Lux 1990 <sup>i</sup>
<i>Salvelinus fontinalis</i>	N: Ergens 1983b, Eken & Garnås 1989 <sup>d</sup>
<b><i>Gyrodactylus derjavini</i> Mikailov, 1975</b>	
<i>Salmo trutta</i>	N: Campbell 1974 <sup>g</sup> , Gläser 1974, Mikailov 1975, Ergens 1983b, Malmberg 1987a, b, 1989b, Malmberg & Malmberg 1991 H: Malmberg 1989b
<i>Salmo salar</i>	N: Malmberg 1989b, Malmberg & Malmberg 1991 H: Malmberg & Malmberg 1991
<i>Salvelinus alpinus</i>	H: Malmberg & Malmberg 1991
<i>Salvelinus fontinalis</i>	H: Malmberg & Malmberg 1991
<i>Oncorhynchus mykiss</i>	N: Gläser 1974, Malmberg 1989b H: Malmberg 1987b, 1989b, Malmberg & Malmberg 1991
<i>Chondrostoma cyri</i> <sup>a</sup>	N: Ergens 1983b
<i>Cyprinus carpio</i> <sup>a</sup>	N: Ergens 1983b
<b><i>Gyrodactylus birmani</i> Konovalov, 1967</b>	
<i>Salvelinus alpinus</i>	N: Konovalov 1967, Mo pers. comm.
<b><i>Gyrodactylus lavareti</i> Malmberg, 1957</b>	
<i>Coregonus lavaretus</i>	N: Malmberg 1957, Ergens 1983b, Malmberg & Malmberg 1991
<i>Coregonus nasus</i>	N: Ergens 1983b
<b><i>Gyrodactylus thymalli</i> Zitnan, 1960</b>	
<i>Thymallus thymallus</i>	N: Zitnan 1960, Ergens 1983b, Malmberg & Malmberg 1991
<i>Thymallus arcticus</i>	N: Ergens 1983b
<b><i>Gyrodactylus aphyae</i> Malmberg, 1957</b>	
<i>Salmo salar</i> <sup>b</sup>	N: Mo 1983
<b><i>Gyrodactylus phoxini</i> Malmberg, 1957</b>	
<i>Salmo salar</i> <sup>b</sup>	N: Mo 1988
<b><i>Gyrodactylus arcuatus</i> Bychowsky, 1933</b>	
<i>Salmo salar</i> <sup>b</sup>	N: Tanum 1983
<b><i>Gyrodactylus gobii</i> Schulmann, 1953</b>	
<i>Oncorhynchus mykiss</i> <sup>b</sup>	H: Lux 1990
<b><i>Gyrodactylus macronychus</i> Malmberg, 1957</b>	
<i>Salmo trutta</i> <sup>b</sup>	N: Mo 1983

<sup>a</sup>Occasional host according to Ergens (1983b); <sup>b</sup>unsuitable host; <sup>c</sup>according to Malmberg (1987b); <sup>d</sup>probably *G. derjavini*; <sup>e</sup>sensu Ergens (1983); <sup>f</sup>sensu Gläser (1974); <sup>g</sup>misidentification, according to Tanum (1983) and Ergens (1983b)

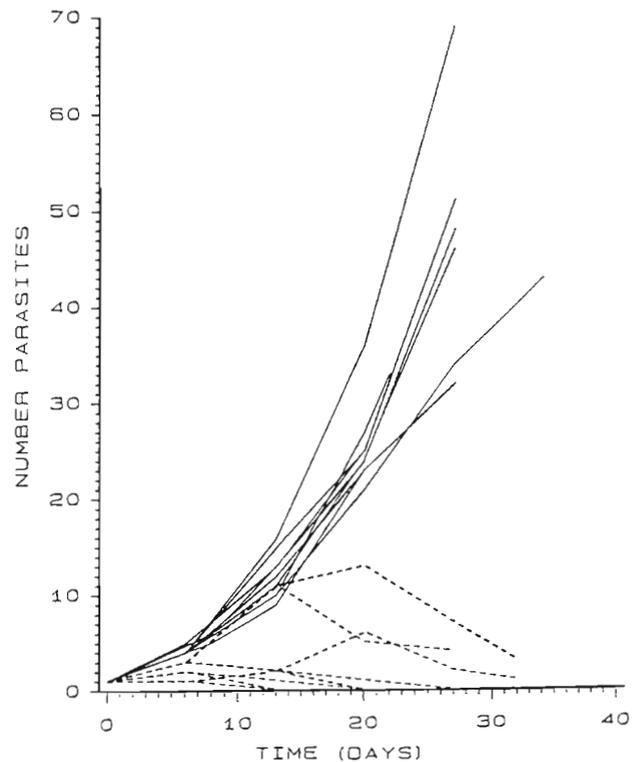


Fig. 1. *Gyrodactylus salaris*, *Salmo salar*. Influence of intraspecific stock differences in salmonids for intrapopulation growth of *G. salaris*. Hosts: individually isolated Atlantic salmon. Temperature: ca 12°C; infection started with 1 gravid parasite; dashed lines: Baltic Nøya stock (n = 10); continuous lines: Norwegian Lone stock (n = 10). (After Bakke et al. 1990b)

*G. canadensis* Hanek & Threlfall, 1969 (show only a weak specificity for salmonid fishes, according to Cone & Wiles 1985); *G. stellatus* Crane & Mizelle, 1967 (3 host species, of different genera, according to Kamiso & Olson 1986); *G. bullatarudis* Turnbull, 1956 (found on distinctly related hosts, according to Harris 1986); and *G. goerani* Hanek & Fernando, 1971 (4 host species, according to Nicola & Cone 1987). According to the results of Wood & Mizelle (1957), 22 % of a total of 28 *Gyrodactylus* spp. may occur on more than 1 host species and based on the data of 33 *Gyrodactylus* spp. listed by Margolis & Arthur (1979), 58 % could be characterized as being host specific, 39 % as narrow in host specificity and 3 % as having a broad host specificity. At least 3 mechanisms maintain these patterns.

Firstly, behavioural mechanisms may maintain the parasite on the normal host. For example *Gyrodactylus gasterostei* Gläser, 1974 transmits freely to uninfected *Gasterosteus aculeatus* (L.), up to 10 % per day transferring in laboratory experiments (Harris 1982, section 4.1). Under identical conditions, transmission

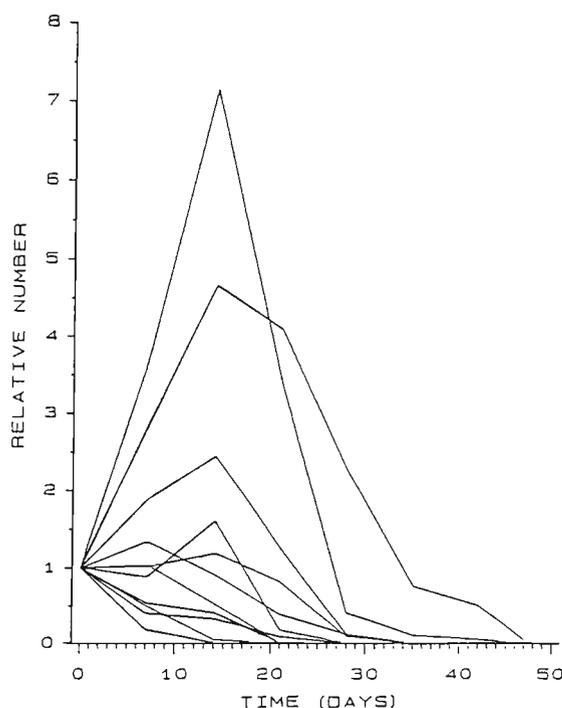


Fig. 2. *Gyrodactylus salaris*, *Oncorhynchus mykiss*. Influence of intraspecific differences within 1 salmonid host stock for in-frapopulation growth of *G. salaris*. Hosts: individually ( $n = 11$ ) isolated rainbow trout. Temperature: 12 to 13°C; relative number: no. of parasites in relation to start infection at time 0. (After Bakke et al. 1991a)

to *Pungitius pungitius* (L.) and *Phoxinus phoxinus* was, however, only 1%. *Gyrodactylus salaris* also shows a similar mechanism reducing the probability of attachment to *Phoxinus phoxinus*, *Rutilus rutilus* and *Perca fluviatilis* in relation to salmon (see Bakke & Sharp 1990, Bakke et al. 1990a), and also to bottom dwellers as the eel and lamprey. However, for such fish species with frequent bottom contact, the differences are less prominent (Bakke & Sharp 1990, Bakke et al. 1991b, authors' unpubl. data). *Gyrodactylus salaris*, detached or attached to a dead host, seems to change its behaviour. The characteristic 'searching activity' after a new host and transmission rate increases and the selective host-preference decreases. This seems to be a dispersal strategy as it increases the chance of incorporation of transport hosts (Harris 1980, Bakke et al. 1991b, authors' unpubl. data). Nevertheless, there seem to be mechanisms not linked to host behaviour, which generally prevent transfer to inappropriate hosts for reproduction and may allow narrowly specific gyrodactylids to coexist without competition (Harris 1985). The specific mechanisms and behavioural triggers involved in such transmission, both for attached and detached parasites of

different ontogenetical life cycle stages, are unknown for gyrodactylids.

A second physiological mechanism may limit *Gyrodactylus salaris* infections on eels. *G. salaris* infects this host more readily than it does *Phoxinus phoxinus*, *Rutilus rutilus*, *Perca fluviatilis* or *Lampetra planeri*, and persists for longer, but parasites cannot reproduce, and die after some days (Bakke & Sharp 1990, Bakke et al. 1990a, Bakke et al. 1991b). The short duration of infection (ca 8 d at 13 °C) compared to the normally longer lifespan of *G. salaris* at this temperature (see Jansen & Bakke 1991) suggests that the parasite is unable to feed on the eel. *G. salaris* attached to the skin of this host although Buchmann (1988) has pointed out that no monogenean successfully infects eel skin, while several species infect the gills. This suggests the presence of a non-specific mechanism, either mechanical barriers to feeding, such as the thickness of the mucus layer (Jakubowski 1960), or inhibitory or toxic component of eel skin or mucus, which could affect *G. salaris* in several ways, e.g. through inhibition of enzymes secreted from the pharyngeal glands and used for extracorporeal feeding.

The third mechanism maintaining specificity has only been noted in *Gyrodactylus salaris* infecting salmonids. The parasite appears to transmit to almost all salmonids tested (see Bakke 1991), although the species, stocks and individuals differ in their responses to the parasite. In experiments with Norwegian stocks of *Salmo salar* the parasite population generally increased without check until the hosts died. On a Baltic stock of this fish, however, and on e.g. *Oncorhynchus mykiss* (see Bakke et al. 1991a) and *Salvelinus fontinalis* (see Bakke et al. 1992a), parasite populations were limited on initially susceptible host individuals by a host response 8 to 20 d after infection (Fig. 1). Even amongst individual rainbow trout considerable heterogeneity of innate resistance and response is observed (Fig. 2), although all specimens eventually mobilised an effective immune response (Bakke et al. 1991a; while on *Salmo trutta*, *Coregonus lavaretus* (L.) and *Salvelinus namaycush* (Walbaum) the parasite population failed to grow significantly (Fig. 3) (Bakke et al. 1992b, authors' unpubl. data), although attachment occurred, but in these cases apparently at a reduced rate (see Bakke 1991). Variation is also seen, from highly susceptible to resistant, amongst the full sib progeny of arctic char *Salvelinus alpinus* (see Bakke & Jansen 1991a), which was found, however, not to influence the attachment rate (Bakke, Jansen & Sterud unpubl.). These differences in innate resistance and timing and efficacy of the host reaction are probably genetic, as has been shown in the case of the host response of guppies to *G. bullatarudis* (see Madhavi & Anderson 1985, Jansen et al. 1991).

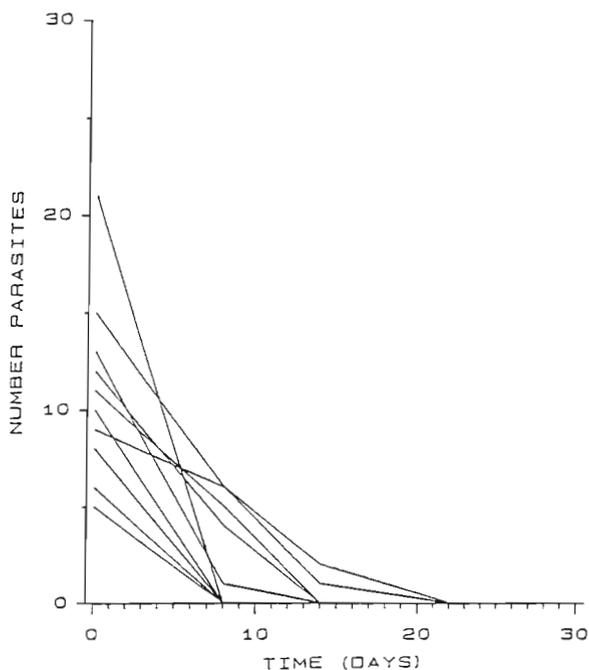


Fig. 3. *Gyrodactylus salaris*, *Salmo trutta*. Influence of a resistant salmonid host stock on the intrapopulation growth of *G. salaris*. Hosts: individually ( $n = 10$ ) isolated brown trout. Temperature: ca 12°C. (Original results)

## TRANSMISSION

Gyrodactylids cannot swim and are transmitted by 4 routes: (1) direct transfer during contacts between fishes; (2) contact between fishes and detached parasites on the substrate; (3) contact between fishes and detached parasites in the drift; (4) contact between living fishes and infected dead fishes.

### Direct transfer

Gyrodactylid transmission is reduced when infected and uninfected hosts are separated by a barrier through which the parasites can pass (Parker 1965, Malmberg 1970, Harris 1982), demonstrating the importance of host contact for transmission. Bychowsky (1957) felt this to be the most important route for transmission and Kamiso & Olson (1986) found that *Gyrodactylus stellatus* transferred most efficiently when there was unrestricted contact between fishes. Although host-host contact accounts for a large proportion of transmission, nevertheless a small proportion of parasites do succeed in transferring in the presence of a barrier, presumably by crawling through the mesh

and then being picked up by the fish from the substrate. Harris (1982) estimated that up to 10% of transmission could occur by this indirect route in *G. gasterostei*.

Host-host contact must be most important for gyrodactylids of pelagic hosts as dead hosts and detached parasites would rapidly be swept out of contact with living hosts. Llewellyn (1984) studied transmission of *Isancistrum subulatae*, a gyrodactylid infecting the pelagic squid *Alloteuthis subulata*, and demonstrated that transmission occurred when squid made contact with arms cut from infected squid. As the host never rests on the sea floor, and avoids contact with other squid, transmission probably occurs during agonistic behaviour or copulation, a hypothesis supported by the observation that prevalence increases in larger, sexually mature squid (Llewellyn 1984).

### Transmission by detached parasites

This route is probably most important for gyrodactylids of benthic hosts which have opportunities for contact with the substrate. Detached gyrodactylids readily attach to, and can move over, wet glass and plastic surfaces, making infections from landing nets which have previously contained infected hosts a possibility (Mo 1987).

*Gyrodactylus macrochiri* achieved higher infections when wire cages containing the hosts were placed in contact with the substrate rather than suspended in the water column (Hoffman & Putz 1964, see also Parker 1965), implying that transmission by detached parasites was occurring, although it is possible that host behaviour differed in the 2 experiments, affecting parasite transmission. Detached free-living *G. salaris* have been found in the outlet filters of infected salmon hatcheries in Norway and Mo (1987) found large numbers of *G. salaris* on the bottom of aquaria which had contained infected salmon for 20 h. Parker (1965), Harris (1982), Eken & Garnås (1989) and Bakke et al. (1991b, authors' unpubl. data) also report transmission of detached gyrodactylids.

Gyrodactylids may become detached from their hosts through accident, active migration or as a result of a host response (Lester 1972, Scott & Anderson 1984). Because detached parasites are not killed but are able to reinfect the same or a different host, the host response does not necessarily stabilize the parasite population behaviour (May & Anderson 1978), and at high host densities sufficient flukes may reattach to significantly reduce the impact of the host response on the parasite suprapopulation.

### Transmission by detached parasites in the drift

The ability of detached parasites within the planktonic drift to reinfect fishes may have been underestimated, at least under lotic conditions. Both Parker (1965) and Eken & Garnås (1989) reported transmission of detached, drifting gyrodactylids to fishes. We have observed a mean parasite intensity of 6.6 *Gyrodactylus salaris* per fish in 35 previously uninfected salmon parr (Age 1+) isolated in a cage in an infected river for 20 d, indicating that several *G. salaris* probably drifted into contact with the parr (Jansen & Bakke unpubl.).

### Transmission from dead fishes

When an infected fish dies the behaviour of its gyrodactylids changes. Although some species continue to feed (Kulemina 1979) others may abandon the host (Malmberg 1970) and their activity may increase (Harris 1980), increasing the chance of transmission to living fishes. Both transport and natural hosts were more heavily infected with *Gyrodactylus salaris* when exposed to dead salmon than when exposed to a living host (Bakke et al. 1991b), indicating the possible importance of dead fishes in gyrodactylid transmission. Scott & Anderson (1984) also found transmission from dead fishes as even more important than from living hosts in their studies of *G. bullatarudis* on guppies, possibly because dead fishes attract the attention of living guppies (Scott 1982). Although transmission from dead fishes is clearly efficient, the importance of this route in gyrodactylid epidemiology is limited by parasite survival after host death and by the speed at which parasites leave a dead fish. Up to 50 % of *G. gasterostei* left the dead host within 18 h at 15 °C (Harris 1980), and their subsequent chance of transmission, without the focus of the fish carcass to attract other potential hosts, is presumably the same as that for detached parasites. The importance of dead fishes is also limited by the number of infected hosts dying. In many gyrodactylid-host interactions this number is probably very small, but Scott & Anderson (1984) found parasite-induced host mortality to be important for parasite dispersion in *G. bullatarudis*. The same might be expected in Norwegian river systems for *G. salaris*, which generally is reported to grow exponentially until host death (Johnsen & Jensen 1986, 1991). In fact, the high abundance of *G. salaris* reported by Heggberget & Johnsen (1982) at low salmon densities due to parasite-induced fish mortality may be explained by such mechanisms, as the salmon parr also rest and have frequent contact with the bottom substrate.

### Transmission between host species

Gyrodactylids lack a specific transmission stage and as the mobility of detached parasites is limited, intra-specific transmission relies on host aggregation and contact during shoaling, agonistic or reproductive encounters. However, opportunities for interspecific transfer are more restricted. Gläser (1974) noted the importance of multispecies shoals of fishes for inter-specific transmission, and predator-prey and scavenger-dead fish interactions may also be important routes. Predator-prey interactions may have been important in the speciation of gyrodactylids, as predators are often infected with gyrodactylids closely related to those infecting their prey. For example the *Gyrodactylus wagneri* species complex (see Malmberg 1970) are principally found on cyprinids, but related species are found on predators sharing the same habitat. Furthermore, gyrodactylids from prey species are occasionally found on predators. Malmberg (1974) recorded a species normally found on cottids on *Salmo trutta*, and *G. macronychus* Malmberg, 1957 as well as *G. aphyae* Malmberg, 1957 and *G. phoxini* Malmberg, 1957, 2 species normally restricted to the minnow *Phoxinus phoxinus*, have been found on salmonids in the same river system (Mo 1983, 1988, Tanum 1983). *G. arcuatus* Bychowsky, 1933, a species which normally infects the stickleback *Gasterosteus aculeatus*, has also been found on salmon (Tanum 1983). In Nearctic freshwaters, *G. brevis* Crane et Mizelle, 1967, normally a parasite of a cyprinid (*Hesperoleucas navarroensis*), was originally described by Crane & Mizelle (1967) from the predatory trout *Salmo gairdneri* (= *Oncorhynchus mykiss*) (see Cone et al. 1983). This process may also occur in reverse. Scavenging on dead fishes may also form an important route of interspecific transmission, and the record of *G. salaris* from flatfish may be an example of this (see Mo 1987; Table 2).

### Parasite behaviour and transmission

Although gyrodactylid transmission has generally been regarded as a function of host behaviour only, parasite behaviour may also be very important, at least during host-host contact. Gyrodactylids inhabiting the gill chamber and other cryptic sites (e.g. *Gyrodactylus cryptarum* Malmberg, 1970 in the acoustico-lateralis canals) must presumably migrate onto the surface of the fish skin before transmission can occur during host-host contact. Even the action of the host response may involve a component of modified parasite behaviour when the gyrodactylids become detached from the host. For example *Gyrdicotylus gallieni* Vercammen-

Grandjean, 1960 lives in the mouth of *Xenopus laevis*, and accidental dislodgement would result in swallowing. The age structure of the parasite population suggests that this occurs rarely. However, Harris & Tinsley (1987) noted the synchronous appearance of living *G. gallieni* outside of the hosts 1 to 2 mo after infection, implying a migration of parasites out of the mouth, possibly for the purpose of transmission. Srivastava & James (1967) recorded *Gyrodactylus medius* Kathariner, sensu Srivastava et James, 1967, normally a gill parasite of the rockling *Onos mustela*, as occurring on the skin in heavy infections, which may also suggest migration by the parasite, and Cone & Cusack (1989) describe migrations of *Gyrodactylus colemanensis* on the host skin after infection. Finally Harris (1986, 1988b, 1989) recorded complex changes in parasite distribution and crowding during infections of *Gyrodactylus turnbulli* Harris, 1986 on guppies, which were probably due to migrations upon the host.

The parasites can discriminate between host species during transmission (Harris 1982, Bakke & Sharp 1990, Bakke et al. 1991b), probably using multiciliate 'spike' sensilla (Lyons 1969a, b) found only in gyrodactylids (Harris 1983) and which may be chemosensory (Lyons 1969b). Chemoreception forms an important part of monogenean transmission biology (Lyons 1969b, Llewellyn 1984) allowing gyrodactylids to recognise suitable hosts before transfer (Cone & Cusack 1989). Small diffusible molecules (e.g. urea) activate the swimming larvae of oviparous monogeneans (Kearn 1967, 1986), but are too generally distributed to allow host discrimination. However, the chemical composition of fish skin appears to be species-specific (Barry & O'Rourke 1959, O'Rourke 1961, Lubbock 1979) and contains sufficient chemical information to allow recognition of individuals by conspecifics (Bardach & Todd 1970). It could therefore produce chemoattractive cues suitable for use by the gyrodactylids.

#### TRANSMISSION, HOST SPECIFICITY AND THE EPIDEMIOLOGY OF *GYRODACTYLUS SALARIS* INFECTIONS

In Norway, *Gyrodactylus salaris* was first noted as a pathogen of *Salmo salar* during the mid-1970's (Johnsen 1978) and was thought to be an opportunist infecting already weakened fishes. Subsequently the parasite was thought to have been introduced with Baltic salmon stocks (Johnsen & Jensen 1986, Malmberg 1988). This origin for the parasite is disputed (Halvorsen & Hartvigsen 1989), although supported by differences in susceptibility between Baltic and Norwegian salmon (Bakke et al. 1990b, see Johnsen & Jensen 1991). The ecology of the Atlantic salmon

has been extensively modified by man, with large-scale changes in salmon population density and genetic structure (Anonymous 1990). As gyrodactylid population dynamics probably are unstable (May & Anderson 1978, Scott & Anderson 1984), host density and genetics may have a major effect on parasite population behaviour; it is therefore necessary to consider human influences on the host in relation to parasite translocation, transmission and parasite population growth. *G. salaris* can coexist on wild, restocked and farmed salmonids in the same watershed (Eken & Garnås 1989) and transmission between these hosts must be considered in assessing the epidemiology of the disease.

*Gyrodactylus salaris* principally affects salmon parr of 0+ to 3 yr in age. In suitable areas of river these fishes form large populations, within which individuals may be territorial (Kalleberg 1958, Saunders & Gee 1964, Symons 1976). Individuals do not move far from their territories (Saunders & Gee 1964) but intraspecific agonistic interactions would provide opportunities for host-host transmission of *G. salaris* during physical contact when nipping. However, most interactions between territorial parr would involve threat display rather than contact (J. Heggnes pers. comm.), indicating the importance of indirect transmission in the *Salmo salar*-*Gyrodactylus salaris* associations. In Norway during spring and summer, these infections increase, but in winter, when water temperature in Norwegian rivers are close to 0 °C and fish activity is reduced to a minimum, parasite populations decline although the parasite still can reproduce at this temperature (Jansen & Bakke 1991a).

The spatial and temporal patterns of parasite dispersal between populations and age-classes of salmon parr are uncertain. Adult salmon re-entering freshwater are initially uninfected but contract *Gyrodactylus salaris* as they swim through populations of infected parr. Infections may be contracted from detached parasites adhering to gravel and weeds in areas where epidemics on parr are occurring; alternatively, infected precocious males may transmit the parasite to adults during spawning (see Malmberg & Malmberg 1991). Adults swim rapidly and can cover 30 km in 2 d (L. P. Hansen unpubl.), so the potential of these fishes to spread infection is considerable. Smolts, passing through populations of parr on their way to the sea, are probably similarly important (Malmberg & Malmberg 1991). Pure transport hosts may also spread *G. salaris* between populations of parr within watersheds. Eels can sustain infections for several days (Bakke et al. 1991b) and could therefore transport the parasite considerable distances. This is probably also valid for *G. salaris* infections of the flounder *Platichthys flesus* (see Mo 1987). In these ways *G. salaris*, which

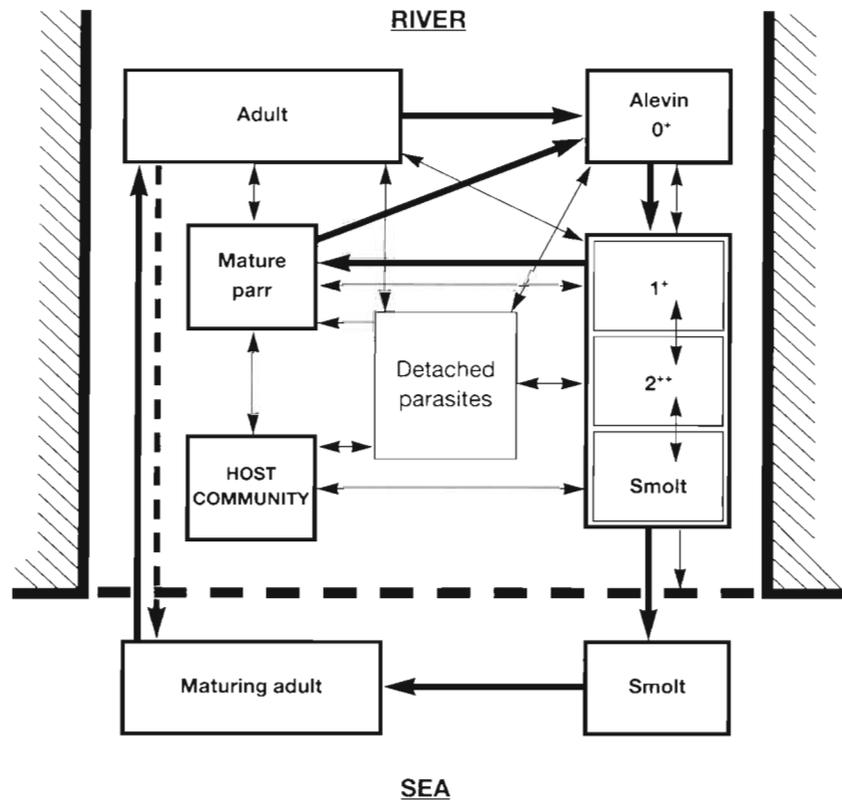


Fig. 4. *Gyrodactylus salaris*, *Salmo salar*. Circulation of *G. salaris* within the host community. Thick lines: life cycle of anadromous Atlantic salmon; thin lines: possible routes of circulation of *G. salaris* within the salmon river ecosystem. Epidemiological data on relative importance of the different salmon cohorts and routes, and seasonal dynamics of the system under natural conditions are generally lacking

cannot survive in sea water, may be also transferred between rivers through regions of brackish water, as they can endure up to 7.5‰ salt water for weeks (Soleng & Bakke 1991).

Possible transmission patterns of *Gyrodactylus salaris* within and between populations of salmon parr are summarised in Fig. 4. Rapid transmission within shoals of the new generation of parr in the spring, and the dissemination between parr populations of parasites by adult salmon, smolts and possibly eels and flounders, appear to be the most important features in Norway. The importance of other transmission routes remains unclear. We have no evidence of infection of salmon eggs, only evidence for infections of alevins, but the pathogenicity of *G. salaris* at this stage, and the importance of this age group as hosts of the parasite, are unknown. In order to understand the epidemiology of *G. salaris*, and to develop rational control strategies, the relative importance of all of these cohorts and possible routes of transmission will need to be investigated.

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