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A review of the biogeography and epidemiology of *Gyrodactylus salaris*

Odd Halvorsen
Rita Hartvigsen

NINA

NORSK INSTITUTT FOR NATURFORSKNING

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Gyrodactylus salaris Malmberg, 1957 er rapportert å være en introdusert parasitt i norske lakseelver som forårsaker stor dødelighet og truer laksepopulasjonene. Tiltak mot parasitten med sikte på utryddelse er basert på disse resultatene. Den biologiske isolasjon av den baltiske fra den øst-atlantiske laksestammen støtter antagelsen av Nord-Sverige/Baltikum som opprinnelig område for *G. salaris*. Sammenheng mellom påvist forekomst av *G. salaris* og utsatt fisk fra infisert svensk/finsk smolt, samt høy dødelighet av laks ved infeksjon, er tatt som indikasjon på at *G. salaris* er innført. Få undersøkelser av parasitter på frittlevende laks finnes, og naturlig utbredelse av parasittene er i hovedsak ukjent. Manglende observasjoner er følgelig utilstrekkelig bevis på manglende utbredelse. Videre forskning på taksonomi, forekomst og utbredelse av *G. salaris* er nødvendig. Nær beslektede parasitter finnes i hele utbredelsesområdet for frittlevende salmonider. Nær kontakt mellom atlantiske og baltiske vannsystemer i Nord-Skandinavia, samt lange tradisjoner med utsetting av laksefisk, innebærer at en geografisk barriere mot immigrasjon av *G. salaris* fra øst er usikker. Epidemiske utbrudd av infeksjon er ikke i seg selv bevis på en introdusert parasitt. *G. salaris* antas å være særlig tilpasset laks og er dermed ikke sammenlignbar med dokumenterte introduksjoner av parasitter til nye, taksonomisk forskjellige, verter. Eksperimentell forskning trengs på interaksjoner mellom *G. salaris* og hhv øst-atlantisk og baltisk laks. Sammenhengen mellom rapportert nedgang i laksepopulasjoner og epidemisk utbrudd av *G. salaris* er komplisert. Analyse tyder på at *G. salaris* rapporteres fra vassdrag noen tid inn i en nedgangsfase for laksepopulasjonene. Mer nøyaktige mål på utvikling av epidemien krever data for tetthet av parasitten i tillegg til prevalens. Eksperimentelt arbeid på populasjonsdynamikken til *G. salaris* er nødvendig. Foruten introduksjon av parasitten kan effekter av oppdrett og utsetting på laksens genetikk og demografi være alternative årsaker til epidemiske utbrudd av *G. salaris*.

Emneord: Parasitologi – Biogeografi – Epidemiologi – *Gyrodactylus-salaris – Salmo-salar*

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Abstract

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Gyrodactylus salaris Malmberg, 1957 is reported to be an introduced parasite into Norwegian salmon rivers causing gross mortality and threatening the salmon populations. Countermeasures aiming for extinction of the parasite are based on these results. The biological separation between the Baltic and East-Atlantic salmon stocks supports the assumption of Northern Sweden or the Baltic as the original distribution area of *G. salaris*. The relation between the registered occurrence of *G. salaris* and released salmon from infected Swedish/Finnish smolts, as well as a high mortality of salmon when infected, is taken as an indication that *G. salaris* has been introduced. Few studies of parasites of free-living salmon exist, and the natural distribution of its parasites is mainly unknown. Lacking observations are consequently inadequate proof of a lack of occurrence. Further research on the taxonomy, occurrence and distribution of *G. salaris* is needed. Closely related parasites exist over the entire distribution area of free-living salmonids. Near contact between Atlantic and Baltic water systems in Northern Scandinavia, as well as long traditions for the artificial release of salmonids, imply that a geographical barrier to the immigration of *G. salaris* from the east is uncertain. An epidemic is not in itself proof that a parasite has been introduced. *G. salaris* is assumed to be well adapted to salmon and hence does not conform to the documented introductions of parasites to new, taxonomically different, hosts. Experimental research is needed on the interactions between *G. salaris* and the East-Atlantic and Baltic salmon respectively. The relationship between the reported decline of salmon stocks and the epidemics of *G. salaris* is complex. Analysis indicates that *G. salaris* has been reported from rivers some time after a decline in the salmon stocks has been registered. More accurate measures for the development of the epidemics require data on density of the parasite as well as prevalence. Experimental work on the population dynamics of *G. salaris* is necessary. In addition to introduction of the parasite, effects of fish farming and release on the genetics and demographics of salmon may be alternative causes for the epidemics of *G. salaris*.

Key words: Parasitology – Biogeography – Epidemiology – *Gyrodactylus-salaris – Salmo-salar*

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Forord

Direktoratet for naturforvaltning opprettet i mai 1986 en arbeidsgruppe som skulle vurdere et fremtidig forskningsopplegg med det mål å redusere de negative virkningene av parasitten *Gyrodactylus salaris* på laksebestandene. Gruppen fikk bl.a. følgende mandat:

A. vurdere behovet for forvaltningsrettet forskning og grunnforskning på parasitten *Gyrodactylus salaris*, og dens forhold til fisk og miljø.

B. på bakgrunn av ovenstående, og vurdert i forhold til direktoratets handlingsplan for tiltak mot parasitten, foreslå ulike forskningsprosjekter og undersøkelser på *Gyrodactylus salaris*, som kan gi en større forståelse omkring parasittens biologi, samt muligheten til å minske dens sterkt negative innflytelse på laksepopulasjonene.

Gruppen fant behov for en bredere gjennomgang av relevant litteratur som basis for sitt arbeide, og forfatterne av denne rapporten ble bedt om å gjøre dette arbeidet i juli 1987. Rapporten er skrevet på engelsk med den målsetting at den skal tjene til å trekke den internasjonale fagekspertise inn i de videre drøftingene av problemene i forbindelse med *Gyrodactylus salaris*.

Preface

The Directorate for Nature Management appointed in May 1986 a committee to evaluate the need for further applied and basic research on the parasite *Gyrodactylus salaris* and its relationship to fish and the environment. The committee was also asked to propose research projects that would increase the insight into the biology of the parasite and to reduce its negative influence on the salmon populations. The committee found a need for a more extensive study of relevant literature to be carried out as basis for its work, and the authors of this review were asked to carry out this task in July 1987. It was decided that the report should be written in English so that it could be used as a basis for communication with the international expertise in the field.

Contents

1 Introduction

The first published account on *G. salaris* in a Norwegian salmon river is that of Johnsen (1978) who reported on the occurrence of *G. salaris*-type monogeneans on salmon in the River Lakselva in Misvær. According to Johnsen & Jensen (1985) the parasite had been found previously, in the early 1970's on rainbow trout in several fish farms, and it was recorded for the first time at the Sundalsøra Research Station for Salmonids in the summer of 1975.

Johnsen (1978) examined formalin preserved salmon fry and parr sampled by electrofishing at five stations in the River Lakselva. The sampling was carried out over a period of three years from 1975 to 1977. Johnsen found an increasing fraction of salmon infected on an increasing number of stations over the first two years. The last year only two salmon parr were caught, one at each of two stations, and they were both infected. No trout was found to be infected, and there was no clear reduction in its density.

Johnsen (1978: p 9) concluded that "it seems clear that the *Gyrodactylus* attack on the population of salmon parr is the main cause for the drastic reduction of the number of juvenile salmon. Since *Gyrodactylus* is a typical "weakness parasite" there must be some factors in the environment negatively influencing the salmon parr population. This weakening of the fish leads to the parasite attack. *Saprolegnia* infestation follows and the fish dies. These negative factors in the environment are not easy to point out".

Heggberget & Johnsen (1982) examined salmon fry and parr, trout, and charr from eight rivers in North and Mid Norway (the rivers Driva, Vefsna, Ranaelva, Beiarelva, Saltdalselva, Lakselva, Skjoma, and Skibotnelva situated between 65° and 70°N). The fish were collected by electrofishing, and the material was preserved in 40 % formaldehyde solution. Sampling was conducted between 1975 (1977) and 1980.

Salmon infected with *Gyrodactylus* sp were found in six of the eight rivers, Beiarelva and Skjoma being the parasite-free localities. Heggberget & Johnsen (1982) observed that the estimated densities of salmon and trout parr exhibited significant changes from one year to another, both in the rivers infected by *Gyrodactylus* and in rivers where *Gyrodactylus* were absent. They also pointed out that the results indicated that the fry were attacked in late summer or in the autumn, that there seemed to be little relationship between density of fish and the infection, and that an upstream spread of *Gyrodactylus* was indicated in three of the rivers. After having reviewed the literature Heggberget and Johnsen concluded that "the introduction of *Gyrodactylus* in north Norwegian rivers may have come from hatcheries with *Gyrodactylus* infections".

In 1980 a research project was established by the Directorate for Nature Management to investigate the "*Gyrodactylus*-problem". A concluding report based on the project and some additional research was published in 1985 (Johnsen & Jensen 1985), and a scientific article was published in 1986 (Johnsen & Jensen 1986).

Johnsen & Jensen (1986) reported that 212 Norwegian rivers had been examined for occurrence of *Gyrodactylus salaris*, and that the parasite had been found in 26 rivers and six salmon hatcheries along the coast from Troms in the north (70°N) to Sogn og Fjordane in the South (61°N). They concluded that the distribution of *G. salaris* was associated with the stocking of fish from infected hatcheries, and that the populations of salmon parr had been drastically reduced in the infected rivers. In later years catches of ascending salmon in these rivers had also sharply declined. Johnsen & Jensen (1986) concluded that *G. salaris* most probably was a recent introduction to Norwegian rivers, and that the primary management aim should be extermination of the parasite.

In October 1985 the Directorate for Nature Management published a plan for "measures to be taken against the salmon parasite *Gyrodactylus salaris*" (Handlingsplan for tiltak mot lakseparasitten *Gyrodactylus salaris* for 10-års perioden 1987 – 1996). The plan was based on two assumptions: 1) that *G. salaris* is a newly introduced parasite to Norway, and 2) that infection leads to gross (additive) mortality in wild salmon populations (because the parasite is an introduced pathogen). Parasite-induced losses to salmon production were estimated to be approximately 300 tons. The plan proposed to exterminate the parasite from Norwegian salmon rivers by killing off the existing host populations with rotenone and restocking with uninfected fish. Where rotenone for various reasons could not be used, it was proposed to hinder the return of spawning salmon to (parts of) the rivers to make the existing host population extinct in that way, and then to restock with uninfected fish.

It is the purpose of this review to consider the scientific basis for the conclusions drawn about the occurrence and effects of *G. salaris* in Norwegian salmon rivers, and to identify areas for further research where additional information may be critical for successful management of the salmon populations.

The assumption that the parasite is introduced has to a large extent been used to explain the epidemic, whereas the epidemic has been used as evidence of introduction. Such circularity in argument must be examined more closely. It is therefore important to consider these two phenomena separately, and to evaluate to what extent there is independent evidence available for each of them. A discussion of both problems must rest on the taxonomy of the group.

2 Taxonomy, host specificity, and biogeography

2.1 Taxonomy

More than 350 species have been described in the genus *Gyrodactylus* according to Mo (1983). The description and identification of species is based on the size and shape of the hard parts of the cirrus and particularly the opisthaptor. The morphology of the hard parts of the opisthaptor varies seasonally (Ergens 1981, Tanum 1983, Mo 1983). Species are allocated to species groups based on the morphology of the excretory system (Malmberg 1957, 1964, 1970).

G. salaris was described by Malmberg (1957) who grouped the species in the *G. wagneri*-complex, an allocation that apparently has been followed by all authors up to Malmberg (1987b). Malmbergs material (Malmberg 1957: Tabell II, p 68) consisted of 8 salmon parr each infected with more than 10 specimens of the parasite. Morphometric measurements were performed on one specimen of *G. salaris* only (Malmberg 1957: p 54).

Later Ergens (1961), Lucky (1963) and Rehulka (1973) each described *G. salaris* from separate material, and the species was reported found by Cankovic & Kiskarolj (1967), and Zitnan (1967 cited in Zitnan & Cankovic 1970), and Zitnan & Cankovic (1970).

According to Ergens (1983), who described and gave a key to *Gyrodactylus* from Eurasian freshwater Salmonidae and Thymallidae, the identification by Ergens (1961) of *G. salaris* was erroneous, and the species represented was *G. truttae* Gläser, 1974. Ergens (1983) obviously also regarded the parasite referred to by Zitnan & Cankovic (1970) as *G. salaris* to be *G. truttae*. Regarding *G. salaris* Malmberg, 1957 Ergens (1983: p 20) wrote "...., the author used for the species characterization the measurements of body, opisthaptor, pharynx, cirrus and individual hard parts of opisthaptor of a single specimen (holotype), though more specimens were available (Malmberg 1957, Table II, p. 68). From the formal point of view, this characterization fulfilled the general rules of the I.C.Z.N., but it could hardly be used for practical purpose, since one of the deciding characters, the exact shape of the hook proper of marginal hooks, was lacking. I succeeded in determining this character only during the reexamination of the type specimen which was kindly loaned to me by Dr. G. Malmberg from Stockholm".

Ergens (1983) also gave data on five specimens of *Gyrodactylus* from *Salmo trutta* morpha *fario* which he referred to as *Gyrodactylus* sp. About the identity of these specimens Ergens stated (p 24-25): "It is possible that this is a new hitherto undescribed species of the genus *Gyrodactylus*. This can be ascertained only after studies of a larger number of specimens and after the data on the general morphological and metrical variability of both *G. salaris* and *G. thymalli* are supplemented."

Tanum (1983) and Mo (1983) carried out extensive analysis of the variation in morphological and morphometric traits in *G. salaris* and *G. trutta* respectively. Tanums material of *G. salaris* was from salmon from Norwegian rivers and farms mainly on the west coast, but it also included some material lent to him by Malmberg. Mo's material of *G. truttae* came from salmon and trout from the river Sandviksvassdraget near Oslo. Because of the range of variation described in these two works, Mo (1983) concluded that the key of identification given by Ergens (1983) for *Gyrodactylus* on salmonids might be misleading, and that it was not suitable for the identification of *Gyrodactylus* on salmonids in Norwegian watercourses. Tanum (1983) concluded that Lucky (1963) and Rehulka (1973) were not dealing with *G. salaris* Malmberg, 1957. Mo (1983) suggested that Rehulka was dealing with *G. truttae* and that the three species that Ergens (1983) recorded from trout; *G. truttae*, *G. derjavini*, and *Gyrodactylus* sp may all belong to the same species, *G. truttae*.

Malmberg (1987b) pointed out that because of large morphological variation *G. salaris* was a problematic species, that it was difficult to distinguish from *G. thymalli* Zitnan, 1960, and that *G.* sp. Ergens, 1983 most likely was identical with *G. salaris*.

According to Malmberg (1987b) the original description of *G. truttae* by Gläser (1974) included two different species; *G. truttae* and a species closely related to or identical with *G. derjavini* Mikailov, 1975, and that *G. truttae* sensu Ergens, 1983 was not identical with *G. truttae* Gläser, 1974. Malmberg (1987b) was further of the opinion that the species in Rehulka (1973) (*G. salaris* Malmberg, 1957 sensu Ergens, 1961) could not be identified as *G. truttae*. According to Malmberg's (1987a) findings, *G. derjavini* or a closely related species is found on *Salmo trutta* and *Salmo gairdneri*, and a species similar to, but not identical with *G. derjavini* is found on salmon.

Malmberg (1987a) erected a new species group, the *G. salaris*-group to include *G. salaris* Malmberg, 1957; *G. thymalli* Zitnan, 1960; *G. brachymystacis* Ergens, 1978; *G. lenoki* Gussev, 1953; *G. asiaticus* Ergens, 1978; and *G. magnus* Konovalov, 1967.

2.2 Host specificity

Tanum (1983) investigated experimentally the ability of *G.salaris* to infect arctic charr (*Salvelinus alpinus*), anadromous and nonanadromous trout (*Salmo trutta*), and rainbow trout (*Salmo gairdneri*) by keeping them in tanks with infected salmon and then later separate them.

Tanum (1983) found that these other fish species became infected when kept with infected salmon, but that trout was less susceptible than charr and rainbow trout. When removed from the infected salmon, trout did not maintain the infection, while the infection on charr and rainbow trout persisted for the duration of the experiments (77 and 78 days). Tanum (1983) regarded this as a strong indication for reproduction of *G. salaris* on charr and rainbow trout.

Tanum (1983) also regarded the infection of trout with *G. salaris* in the river Røssåga as reflecting the ability of *G. salaris* to infect other fish than salmon under natural conditions. Mo (1987) reported *G. salaris* found on flounder.

2.3 Biogeography

2.3.1 Expanding areas: Immigration or research

A common problem in all biogeography is to separate true immigration from "new localities" which result from increased research efforts.

Awareness of this problem is important when dealing with fish parasites because experiences show that fish parasites are generally inconspicuous. The presence of even large ectoparasites of important fish species may not be known to fishermen or anglers, and certainly not to science if the locality has not been investigated.

The known distribution area of many freshwater fish parasites has expanded into and within Norway as the result of an increased research interest in this group since the 1950's (Vik 1954, 1957, 1963, Halvorsen 1970, 1971, Kennedy 1977).

The expansion of the known area in Norway of the freshwater fish leeches *Cystobranchus mammillatus*, *Piscicola geometra*, and *Acanthobdella peledina* may serve to illustrate this. These leeches are large ectoparasites several cm long compared to the half mm or so of *G. salaris* (Malmberg 1957). Still their occurrence in Norway was largely unknown until recently. The expansion of their known area resulting from the interest of biologists is illustrated in **Figure 1**.

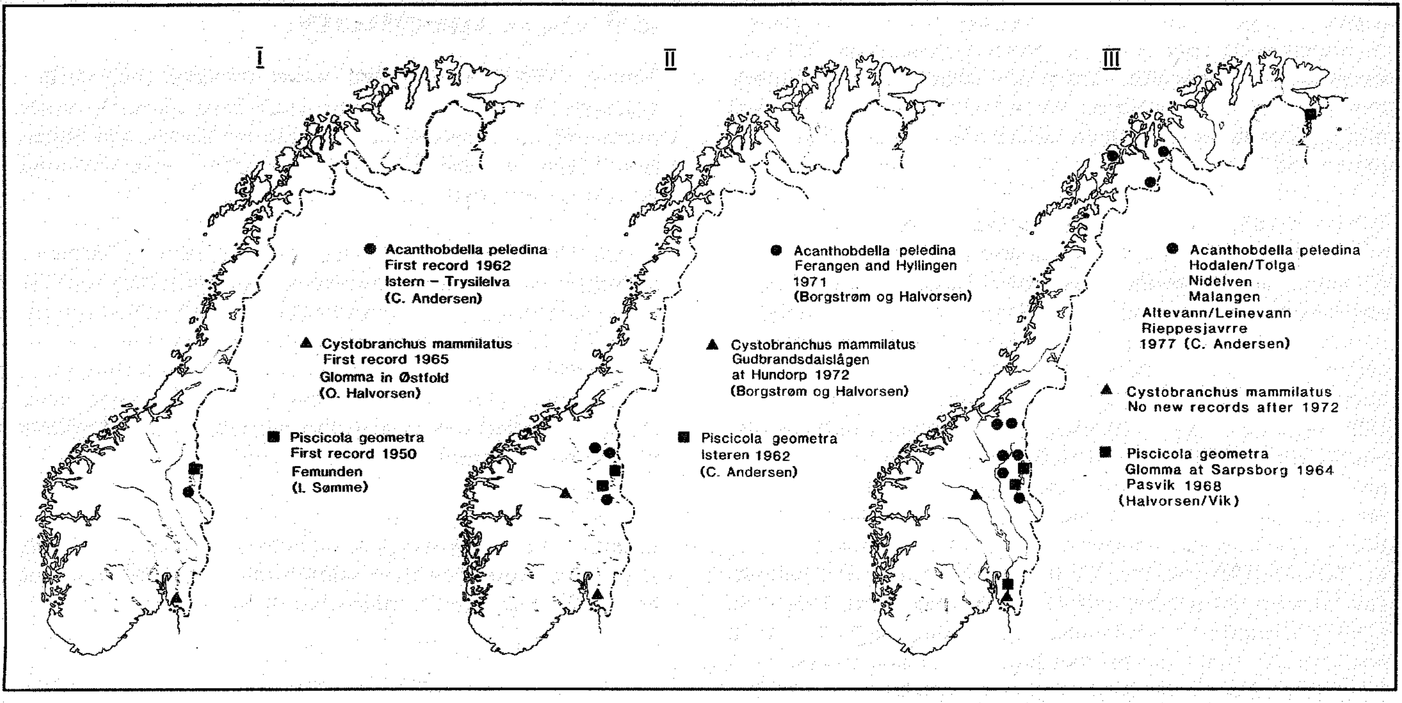

Figure 1
The expansion in the known geographic distribution in Norway of the fish leeches Acanthobdella peledina, Cystobranchus mammillatus, and *Piscicola geometra. Based on Andersen (1962, 1977), Borgstrøm & Halvorsen (1972), Halvorsen (1964, 1966), and Vik (1962).*

Prior to the discovery of *G. salaris* little work had been done on Monogenea from freshwater fishes in Norway. The two large species *Discocotyle sagittata* and *Diplozoon paradoxum* had been reported found by Huitfeldt-Kaas 1912, Bjerkan 1916, Brinkmann 1952, and Lien 1978 and Halvorsen 1969 respectively. Malmberg (1970) had reported *G. arcuatus* from three-spined stickleback and plaice in the Tromsø area, and Moen (1980) had found *G. arcuatus*, *G. branchius*, and *G. rarus* on three-spined and nine-spined sticklebacks near Oslo.

As a consequence of the research activity initiated in response to the discovery of *G. salaris*, *D. sagittata* and *G. arcuatus* have been recorded from more hosts and localities (Wilhelms 1983, Tanum 1983, Mo 1983), and *G. truttae*, *G. macronychus* and *G. aphyae* have been added to the list (Mo 1983).

As with the fish leeches mentioned above, the expansion in the known distribution area of *G. salaris* in Norway following Johnsen's (1978) report of its occurence could be explained as a result of an increased research interest in the species. This explanation has to be rejected before an alternative explanation of introduction and anthropochor spreading is made probable.

2.3.2 The age of the host-parasite system

The *Gyrodactylus*-problem in Norwegian salmon rivers has been considered only in a very short time perspective influenced by the recent description and discoveries of *G. salaris*. According to Llewellyn (1965) the remarkably high host specificity of the Monogenea is a very strong evidence that in general, speciation has taken place in correspondence with that of their hosts. The relationship between salmonids and their Monogenea may be as old as the salmonids themselves. Different opinions have been expressed, however, about details in the historical development of this relationship.

Bychowsky (1961) believed that the family Gyrodactylidae became separated somewhat earlier than the contemporary Salmonoidei, and these cannot be considered as having arisen later than the Paleocene period, the Osmeridae having separated as early as in the Cretaceous period. Bychowsky (1961) did not offer any suggestion about which group of fishes the origin of *Gyrodactylus* was linked to.

LLewellyn (1965) found indications that the protomonogenean stock had radiated into gyrodactylidean and entobdellid etc stocks before the Ordovician.

Malmberg's (1970) interpretation was that the genus *Gyrodactylus* seemed to be primarily fresh water, having infested species of Cyprinidae during two separate periods of its evolution: first in its early stages by *G.* (*Gyrodactylus*), second rather late in its evolution by *G.* (*Limnonephrotus*). Malmberg (1970) did not attach any geological time scale to this process.

According to Tchernavin (1939) the genus *Salmo* probably evolved during the Pleistocene, and the recent species of the family Salmonidae existed before the glaciation.

In view of these generally accepted understandings of the long history of both hosts and parasites, it seems necessary to consider the possible endemism of *G. salaris* in Norwegian salmon rivers in relation to the extent of isolation of these rivers from the rest of the palearctic distribution of *Salmo salar* in a time scale extending back to the glaciation.

2.3.3 The distribution and geographical structure of *Salmo salar*

Atlantic salmon (*Salmo salar*) is found along the coasts of the North Atlantic including the Baltic Sea. On the European side salmon is distributed from the Bay of Biscay in the south to the White Sea in the north-east.

The colonization by salmon of Norwegian rivers took place from the sea as the ice of the glaciation withdrew. Arctic charr, trout and three-spined stickleback colonized the Norwegian rivers both from the sea (west) and from the east through the Baltic, while all the other freshwater fishes found naturally in Norway immigrated from the east (Huitfeldt-Kaas 1918).

Ståhl (1987) found that there were at least three major genetically distinct and geographically separated groups of Atlantic salmon, the Western Atlantic, the Eastern Atlantic, and the Baltic Sea stock. The greatest genetic differences were found between populations of the West and the East Atlantic. The differentiation between the two continents was more than twice as great as that between the Eastern Atlantic and the Baltic populations. Today very few Baltic Atlantic salmon migrate into the Atlantic Ocean (Christensen & Larson 1979). However, in absolute terms (i.e. as measured by genetic distance) relatively little overall genetic differentiation appeared to have occurred among populations throughout the range of *S. salar* (Ståhl 1987).

Ståhl (1987) suggested that the North American and European populations of salmon diverged prior to or during the last glaciation. Each continent was then repopulated from refuge populations following the Pleistocene glacial recession.

Even if colonization from the west has been the main route of entry for salmon into Norwegian rivers, there are reasons to believe that also some immigration may have taken place from the Baltic in the east.

The Baltic went through several stages as the Pleistocene glacier withdrew. During early stages leading up to the Baltic Ice Lake (10 000 years ago) South Sweden was almost covered by the South Swedish Ice-Lake complex which drained to the west near Halmstad on the Swedish west coast (Lundqvist & Nilsson 1959).

During the Yoldia-Sea period the Baltic was directly connected to the Skagerrak over the area where the big lakes between Stockholm and Gothenburg are now situated. Vik (1971) believed that white-fish, pike, perch and several of the cyprinids may have reached rivers in South Norway via the brackish current set up from the Yoldia Sea along the east and south coast of Norway. A similar current may also have existed during the following freshwater period in the Baltic (the Ancylus Lake, 8 000 years ago) when the Baltic drained to the west through Storebelt.

From the time when the Baltic reached the configuration it has today (4 000 years ago) salmon has probably had a continuous distribution "river by river" from the Baltic, around South Sweden, up along the Kattegat and Skagerrak, and further along the Norwegian coast. Only in this century has salmon begun to dissappear from some of the rivers in South Scandinavia (Huitfeldt-Kaas 1918).

Compared to the southern Baltic, its northern region (Bothnian Bay) has seen less dramatic changes in shoreline level and drainage following the glaciation. When the shoreline reached its highest level in the Bothnian Bay in the Yoldia-Ancylus periods, it was situated almost half way up the present Torne River and Lule River watercourses (Lundqvist & Nilsson 1959). Even today, however, the divides between the water courses draining south into the Bothnian Bay and those draining west and north into the Norwegian Sea and the Barents Sea are not very distinct in many areas (**Figure** 2). Whitefish, perch, burbot, pike, grayling, and minnow have colonized the west- and north-draining watercourses in this region (Huitfeldt-Kaas 1918).

In the Kemi River and Torne River watercourses salmon migrate (or did before hydroelectric damming) more than 400 km up from the Bothnian Bay and reaches very close to watercourses draining west (Nordqvist 1906, Huitfeldt-Kaas 1918). As Huitfeldt-Kaas (1918) pointed out, it is possible to row a boat from the Bothnian Bay up the Kemi River, pull it over land a short distance into the Tana River and row to the Barents Sea.

In the Torne River catchment there are some continuous stretches of water across from the Bothnian Bay to the Norwegian Sea. A small lake near the border between Norway and Sweden drains both into the lake Kilpisjärvi (Torne River catchment) and the River Signaldalselva flowing into the Norwegian Sea. The larger Store Rostavann lake, also on the border, drains into the Torne River draining east and the Målselv River draining west. Up towards lake Kilpisjärvi salmon migrate to Naimakka about 60 km from the divide, and up to Rostonlinka near lake Store Rostavann by the divide (Nordqvist 1906).

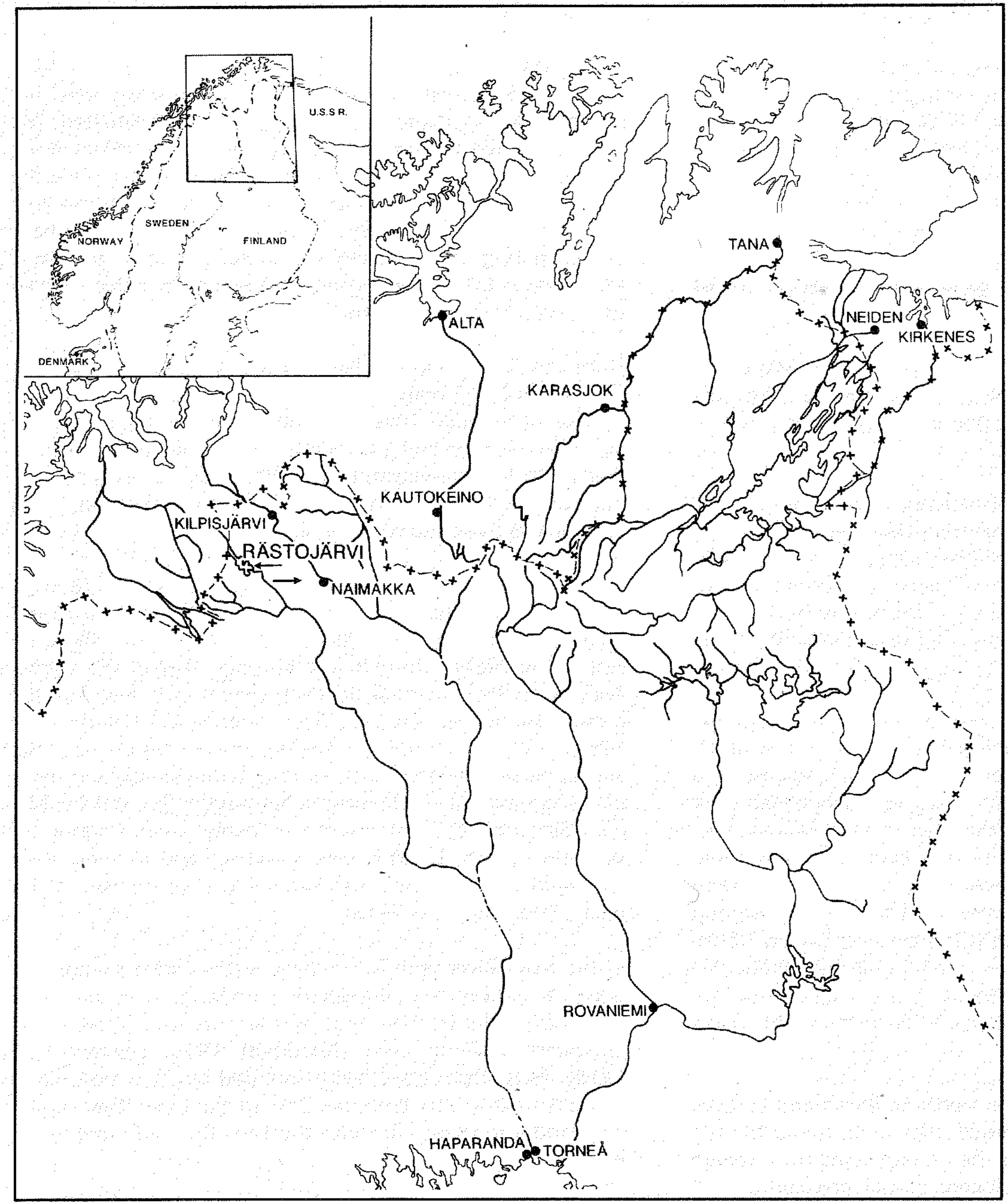

Figure 2
An outline of salmon rivers flowing to the Bothnian Bay and to the North East Atlantic in northern Fennoscandia.

2.3.4 Investigations of parasites of free-living *Salmo salar*

The ability to differentiate among true immigration, introduction, and new observations caused by research only rests heavily on the extent to which the geographical distribution of the species or group in question is known. Interpretation of the observations of *G. salaris* in Norwegian salmon rivers requires the consideration of all these factors.

There are about 15 investigations of parasites of *S. salar* that have resulted in standard published accounts. They are listed in Appendix I. About half of the investigations have been carried out in the Palearctic or include material from this subregion, the others are from the Nearctic.

Parasites identified as *Gyrodactylus* sp were found in 4 of the investigations, in the River Narova near Leningrad (Bauer 1957), in the River Almond in Scotland (Wootten & Smith 1980), in the Corrib catchment in Ireland (Connelly & McCarthy 1984), and in the Miramichi river system, New Brunswick (Hare & Burt 1975a,b). In addition, Pippy (1969) recorded *Gyrodactylus bychowski* on returning salmon at Greenland.

There are many indications that skin-dwelling *Gyrodactylus* is particularly difficult to detect when they occur in low numbers (endemic level). Harris (1985) could, for instance, describe one new species and record four new species for Britain after having examined five species of fish from Rogate, West Sussex. England is probably among the faunistically best described parts of the world, also for freshwater fish parasites, and this illustrates that *Gyrodactylus* tends to be overlooked. The same impression is given by Margolis' (1982) overview of the parasites of Pacific salmon. Margolis (1982) contains far fewer references to the Monogenea than any other of the helminth groups and the Protozoa. This may reflect either that they are really rare (few fish infected with low numbers) and/or that they are overlooked. Both possibilities point to the need for large samples to be able to detect the presence of *Gyrodactylus* on salmonids in natural waters.

Mo (1987) discussed the methodological problems in detecting *Gyrodactylus* and described procedures to be followed for improving chances of observation. He pointed out that one of the reasons for the rareness of observations is that *Gyrodactylus* dies and disappears shortly after the fish has been taken out of the water. Mo (1987) also underlined the need for an excellent dissecting microscope and light source to be able to detect the parasite. He also stated that a relatively large number of fish must be examined before one reasonably may assume that the parasite is not present in a wild population of fish or in a farm.

After having considered the purpose, material, and methods of the various other investigations, we suggest that only Thomas (1958) from Britain among the European investigations had the possibility to detect *Gyrodactylus* if present. Five of the North American investigations have been of such a design that *Gyrodactylus* may have been discovered if present (Appendix I).

2.3.5 The geographical distribution of records of *Gyrodactylus salaris* and related species

Outside Norway there is only one record of *G. salaris* on free-living salmon. This record is to be found in Ergens (1983) where he stated (p 21) "....... I came to the conclusion that the specimens from the skin of about 9-month-old *S. salar* caught in the Ladoga Lake in June 1972 (legit. E. A. Rumyantsev, unpublished results) can also be considered conspecific with *G. salaris*."

Campbell (1974) identified a parasite that was common on trout in the inflowing streams to Loch Leven, Scotland, as *Gyrodactylus salaris*, but this identification appears to have been generally rejected (e.g. Malmberg (1987a,b), and references to this record is only to be found in compiled checklists (Kennedy 1974). All other records or references to *G. salaris* outside Norway stem from the examination of cultured fish.

Malmberg's (1957) original description of *G. salaris* was based on material from the Hölle Laboratory in Jämtland, Sweden. Malmberg (1973) reported that *G. salaris* also occurred on salmon in hatcheries in Älvkarleö and Heden in Sweden, and on *S. trutta* in a Carphatian hatchery in the USSR. Malmberg (1987c) reported that "A comparative study was conducted of specimens of *G. salaris* Malmberg, 1957 from the host *Salmo salar* from the Hölle Laboratory (type locality) and from other fish farms in Sweden, Norway and Finland".

Malmberg (1987a,b) regarded *Gyrodactylus* sp of Ergens (1983) as most likely identical with *G. salaris*. For *Gyrodactylus* sp Ergens (1983) gave the following information (p 24)." Host, location, localities: *Salmo trutta* morpha *fario* L.; fins; Chernorecheskoye (Georgian SSR), the rivers Salgir and Angara (Crimea).". Ergens' (1983) material consisted of five specimens of the parasite.

Ergens (1983) gave from one to three localities for the other species of *Gyrodactylus* allocated to the *salaris*-group by Malmberg (1987a). These few localities are scattered across Eurasia from the Pacific in the east to Czechoslovakia and Lake Ladoga in the west.

Wootten & Smith (1980) identified parasites found on salmon in Scotland as *Gyrodactylus* sp. Malmberg (1987a,b) who retained *G. truttae* and *G. derjavini* in the *wagneri*-group after having split off the *salaris*-group from it, stated that according to his findings *G. truttae* parasitizes *Salmo trutta* in Great Britain, and that *G. derjavini* or a closely related species is found on the same host and on *S. gairdneri* in Sweden, Norway, Denmark and Italy. Further, according to Malmberg (1987a,b) *S. salar* in Scotland has a species similar to, but not identical with *G. derjavini*.

Ergens (1983) gave one locality at the Caspian Sea and one north of Afghanistan for *G. derjavini*, and several European localities for *G. truttae*, while Mo (1983) suggested that they were one species distributed from the Caspian sea to Norway.

2.3.6 Evidences of introduction

In addition to the epidemic outbreak, association between the presence of *G. salaris* and stocking from hatcheries with infection has been seen as evidence of introduction. Johnsen & Jensen (1986) concluded (p 238): " The first incident of mass infection by *G. salaris* in an Atlantic salmon population was thought to have been related to some changes in the environment of a river (Johnsen, 1978), it being assumed that *G. salaris* was commonly distributed among salmon parr populations in Norwegian rivers. Later investigations have proved this theory implausible. As shown by Fig 1, there seems to be an important connection between the occurrence of *G. salaris* in Norwegian rivers and deliveries of fish for river stocking from infested hatcheries. In all but three regions such deliveries have been made to at least one river. The rivers within each region are situated so close to each other that the occurrence of *G. salaris* in the neighbouring rivers may be explained as the result of spreading with fish through brackish water in the fjord area. The three regions containing *G. salaris* which have not been stocked with fish from infested hatcheries are region 1 Skibotnelva, region 3 Beiarelva and region 13 Vikelva/Aureelva. The occurrence of *G. salaris* in Skibotnelva seems to have been brought about by the dumping of smolts into the river from a Swedish smolt transport in 1975 (Gyrodactylus-prosjektet, 1983). Beiarelva is the neighbouring river to Lakselva (region 2) but the distance between their outlets is so great (80 km) that spreading through brackish water is unlikely: spreading across land from Lakselva in one way or another is a more probable explanation for the occurrence of *G. salaris* in Beiarelva.

No deliveries of fish from infested hatcheries are known in region 13. However, eyed eggs from infested hatcheries have been delivered to the region."

Further from Johnsen & Jensen (1986) (p 239): " The three documented cases where river stocking from infested hatcheries has not led to wide-scale occurrences of *G. salaris* in these rivers were in the rivers Forsåga, Hundåla and Bårdalselva / Baelva. In the R. Forsåga, fish were stocked directly into the sea and had no opportunity for ascending the river. On the Hundåla the place of stocking is unknown; however, the river is regulated for hydroelectric purposes, and water flow is low.

With the exception of region 1 and some uncertainty about region 13, the occurrence of *G. salaris* in Norway seems to be traced directly back to region 9 where it was first detected at a hatchery in this area in July 1975. How the parasite first arrived in this region is unknown. Infested fish seem to have been the primary agents of the further spreading of the parasite, but also eyed eggs, fish transport tanks and overland distribution by birds or fishermen may have been important factors".

Salmon fry and parr caught by electrofishing in the river Vefsna in the period (1975-1978) prior to the assumed introduction of *G. salaris* (1979, Heggberget & Johnsen 1982) had been preserved in formaldehyde and have been examined for infection by Johnsen & Jensen (1988). No parasites were found among salmon parr caught in 1975, 1976, and 1977, but on fish caught from 1978 and onwards.

2.4 Discussion

Llewellyn (1965: p 50) stated that: "Present-day monogeneans are for the most part permanent ecto-parasites on the skin and gills of fishes. They exhibit a remarkably high degree of specificity to their hosts (Bychowsky, 1957; Llewellyn, 1957a; Hargis, 1957), and while there is some evidence that "ecological specificity" does occur (Llewellyn and Kern, work in progress), nevertheless there is very strong evidence that in general, speciation has taken place in correspondence with that of their hosts." Llewellyn (1965) further regarded, in the Platyhelminthes in general, the degree of specificity to correlate with the age of the host - parasite relationship.

Malmberg (1957) pointed out that the species as well as the subspecies of *Gyrodactylus* were very host specific. Tanum (1983) concluded from his experiments that salmon clearly was the original host animal for *G. salaris*.

Until information to the contrary is available, this host - parasite relationship must be considered as being of considerable age, dating at least back to the beginning of deglaciation some 10 000 years ago. *G. salaris* or its predecessor may therefore have been present in the refuge population of salmon which repopulated both the East Atlantic and the Baltic Sea (Ståhl 1987).

The geographical distributions of hosts and their parasites do not overlap completely (Margolis 1982, Kennedy 1977), but the assumption about introduction at least demands a hypothesis about what is the natural area of distribution of *G. salaris*. Implicitly in published reports it appears as if Northern Sweden or the Baltic Sea is assumed to be this area. In one of the reports from the "*Gyrodactylus* project" (Anonymous 1983) it is stated that (p 11, our translation into English) "According to Professor Malmberg *G. salaris* occurs naturally in watercourses only north of Gävle." (Gävle is about 200 km north of Stockholm). Investigations followed to test the assumption that Swedish salmon are better adapted to *G. salaris* than Norwegian salmon (Anonymous 1983, Mo 1987). The preliminary experiments have not produced conclusive results.

The idea that *G. salaris* is endemic to the Baltic Atlantic salmon has probably resulted from (i) the fact that the parasite was originally described from a hatchery on the east coast of Sweden, and (ii) the degree of isolation between the Baltic and the East Atlantic salmon (Ståhl 1987). The former observation may reflect the unique situation that an expert on the Monogenea (Professor Malmberg, who first described *G. salaris*) has investigated the area. The latter observation may serve as a basis for a hypothesis, but not as proof. No other endemic helminth parasite appears to be known for the Baltic Atlantic salmon.

For *G. salaris* there is only one published observation of infection (on one fish?) in natural waters outside Norway (Ergens 1983). We do not know, however, whether the one fish from Lake Ladoga that Ergens (1983) examined belonged to a naturally reproducing population or a population maintained by stocking from hatcheries.

Based on the known occurrences of infection of "wild" salmon, Norwegian salmon rivers emerge as a possible nidus of infection with *G. salaris*. Another possible endemic locality may be Lake Ladoga, but the available information from this localty is very restricted.

Other localities given for the occurrence of *G. salaris* (Malmberg 1957, 1973, 1987c) are all hatcheries or farms. The international trade in living salmon has been considerable, and these occurrences of *G. salaris* may thus have resulted from introduction. Most of the information is given in abstracts from conferences (Malmberg 1973, 1987c), making evaluation of these occurrences difficult.

Because of the lack of relevant investigations, the absence of records of *G. salaris* from other parts of the European distribution area of *S. salar* may not be seen as proof that the parasite does not occur. In our opinion therefore, the natural area of distribution of *G. salaris* has to be regarded as not known.

Implications about the distribution of a species may be sought from the distribution of close relatives. Infection with *Gyrodactylus* on fish belonging to the genus *Salmo* has been recorded in localities that are scattered from the Crimea in the east to British Columbia and California in the west (Ergens 1983, Cone et al. 1983, and information given in Section 2.3.5 above). Before we discuss this aspect further, however, some comments on the taxonomy of *Gyrodactylus*, in particular those species parasitizing salmonids, are neccessary.

The taxonomy of *G. salaris* and related species is, as with much of helminth taxonomy, still in the preliminary stages. The taxonomy of *Gyrodactylus* is based on the morphology of certain hard parts, while host species is used implicitly or sometimes explicitly as an additional character. To the extent that morphometrica have been given, they have either been based on few (one) specimens, and/or have been sampled or treated so that statistical information has been lost. Identification can only be done with limited certainty based on published material. It appears that the various authors have quite different opinions as to the taxonomy of the group, and species delimitation can only be regarded as preliminary.

In an abstract from a conference Malmberg (1987a) erected the *salaris*-group containing several species of *Gyrodactylus* parasitizing salmonids, but not *G. trutta* and *G. derjavini*. Malmberg (1987a) also synonymized *Gyrodactylus* sp of Ergens (1983) with *G. salaris*. This seems to contradict a simultaneous view that *G. salaris* is host specific to *S. salar* as *G.* sp. was found on *Salmo trutta* morpha *fario* well outside the distribution area of *S. salar* (Ergens 1983).

Based on the information available in Ergens (1983), three of the species of Malmberg's (1987a) *salaris*-group (*G. asiaticus*, *G. brachymystacis*, and *G. lenoki*) are parasites of the lenok (*Brachymystax lenok*) which is found from northern Asia to Korea (Nelson 1984), while the two other (*G. magnus* and *G. thymalli*) are parasites of *Thymallus*. Malmberg's (1987a) grouping implies that the specific *Gyrodactylus* of *Salmo salar* is more closely related to species parasitizing another subfamily (Thymallinae) and the distant genus *Brachymystax* than to species parasitizing other members of the genus *Salmo* (*G. birmani*, *G. derjavini* and *G. truttae*) and the closely related genus *Salvelinus* (*G. birmani*). The validity of the *salaris*-group as defined by Malmberg (1987a) must therefore be substantiated, and in this connection experimental infection of grayling (*Thymallus thymallus*) may be of interest. In line with the generally accepted reasoning about the linked speciation of host and parasite in the Monogenea, we assume, however, for the time being that the members of *Gyrodactylus* parasitizing the genus *Salmo* are more closely related to each other than they are to other members of the genus.

Malmberg (1970) found that the *Gyrodactylus* faunas of Eurasia and North America were very different, and suggested that *G.(Limnonephrotus)* originated in Eurasia at a time when there was no connection with North America. Cone et al. (1983) considered on the other hand the similarity between the Eurasian and North American species of *Gyrodactylus* parasitizing salmonids to be a reflection of a common phylogenetic origin. They also concluded that the differences used to delimit the Eurasian *G. birmani*, *G. derjavini*, *G. truttae*, and *G. salaris* and the North American *G. salmonis* and *G. nerkae* should be confirmed by a single individual using one microscope, and that the true relationship of these species had to await a detailed comparison of parasite populations of northern hemisphere salmonids.

On this background the geographical scatter of the localities where *Gyrodactylus* has been found on members of *Salmo*, are taken to indicate that these closely related parasites are distributed within the entire distribution area of the host genus, and that verified absence in subareas within this has to be explained by local factors.

No explicit hypothesis seems to have been offered to explain why *G. salaris* should not be endemic on salmon in Norwegian rivers, but low tolerance to sea water in *G. salaris* appears to be implicit. This view probably further rests on the assumption that *G. salaris* is endemic to the Baltic Atlantic salmon.

Malmberg (1957) found that species of *Gyrodactylus* belonging to the *wagneri*-group were well adapted to brackish water in comparison with the *elegans*-group.

Mo (1987) did some preliminary experiments on the tolerance of *G. salaris* to salinity, but the interpretation of the results was difficult because the fish used in the experiments smoltificated. Mo (1987), however, suggested that the results gave reasons to believe that *G. salaris* may survive (for some time) on smolt which migrate in brackish water, and he gave examples of localities where *G. salaris* may have spread within fjord systems in that way, a view that Johnsen & Jensen (1986) adhere to. We believe that returning adult salmon may also take part in such a process. It has been shown that salmon returning to coastal waters move close to the surface (i.e., the most brackish water) and migrate in a near-random way along its general direction, thus bringing it in contact with several rivers and fjords (Westerberg 1982a,b, Vasshaug 1988).

Given that the age of the *G. salaris*-salmon system dates back at least to the beginning of the Pleistocene recession, both the prevailing conditions and the time available make it a reasonable hypothesis that *G. salaris* would have managed to invade the (now) Norwegian rivers through the process suggested by Johnsen & Jensen (1986) and Mo (1987) for present-day local invasion, even if the parasite was originally "trapped" in the Baltic Sea.

It is also noteworthy in this connection that *Salmo* in Scotland is infected with *Gyrodactylus*. The colonization of Scottish rivers appears much less probable, even on a long time scale, than the colonization of Norwegian rivers if sea water has been acting as a barrier.

Low tolerance to sea water would in any case only be a barrier to immigration along the southern coast of Norway. In the north, rivers flowing to the Baltic and to the Atlantic come very close together, as do the salmon populations. If *G. salaris* can be transported also on trout and charr which seems probable from Tanum's (1983) results, a spread of *G. salaris* across the present-day watershed seems very likely because trout as well as charr, grayling, and whitefish have crossed this barrier (Huitfeldt-Kaas 1918).

Anthropochor spreading, which Johnsen & Jensen (1986) suggested was the explanation for some of their observations, must also be considered here, as stocking of lakes with salmonids has a very long tradition (Ekman 1910, Huitfeldt-Kaas 1918), and transport of fish has most certainly taken place across the watershed over a long time. The river Skibotnelva in Norway where *G. salaris* has been found (Johnsen & Jensen 1986) has close proximity to the Torne watercourse in Sweden. Johnsen & Jensen (1986) believed that the occurrence of *G. salaris* in the River Skibotnelva had been brought about by dumping of smolts into the river from a Swedish smolt-transport in 1975. The Skibotn valley has historically, however, been an important route of trade between people living on the two sides of the watershed, and an avenue for Finnish and Swedish immigration into North Norway. As early as in the 18 century, there was a road connecting the two sides (Ytreberg 1980). In this perspective anthropochor spreading across the watershed seems likely at an earlier stage.

The fact that the East Atlantic salmon and the Baltic Atlantic salmon have been isolated to the extent that some genetic distance has developed (Ståhl 1987) does not negate the possibility of some exchange. Straying and anthropochor spreading of salmonids may still have sufficed to disperse the parasite even if it has not been extensive enough in salmon to prevent genetic separation.

The conclusion that *G. salaris* is an introduced species to Norwegian rivers have been explicitly based on its association with infected hatcheries (Johnsen & Jensen 1985, 1986). Johnsen & Jensen (1985) listed the 212 rivers examined by the *Gyrodactylus* project, but they did not give any details about the material and methods involved. Anonymous

(1982), however, gave sample sizes for 198 of the 212 rivers. Salmon were examined from 149 of these rivers, the other samples were of trout or charr. Of the 149 rivers where salmon were examined, *Gyrodactylus* was found in 17, which leaves 132 negative. Four of the samples from these negative rivers consisted of only one fish, 35 (23%) of them of less than 16 fish, and 60 (40%) of less than 31 fish. Mean sample size was 46 fish, and the largest sample from one river was 198 fish. It was pointed out above (2.3.4) that *Gyrodactylus* is difficult to detect, and in this connection the number of small samples represents a problem. Statistically, however, the assosiation between stocking and infection is significant.

Even if this association is very firm, it may have been caused by a quantitative dynamic relationship between an infection in both the "culture" and the "wild" system and not by introduction. Bauer et al. (1973) described how *Myxosoma cerebralis* appeared in new foci without any previous transport of fish, but as a result of large-scale fish breeding. The parasite which had occurred in small numbers in local fish increased in number in these populations as a result of fish farming and became "visible".

The geographical ranges of many helminths of fish have increased as a result of the intercontinental and transcontinental transportation of infected ornamental, sport, and food fish (Bauer & Hoffman 1976, McVicar 1975, Buchmann et al. 1987). Much information about the natural geographical distribution and the biology of any parasite is needed, however, before a conclusion about introduction can be reached. It is illustrative in this respect that Asian parasitologists (Chung et al. 1984) claim that *Pseudodactylogyrus* spp on eels were introduced from Europe, while European parasitologists (Buchmann et al. 1987) claim that the genus was introduced from Asia.

The Baltic Atlantic salmon may have parasites that are endemic to it, and the import of salmon smolt to Norway from Sweden and Finland has been extensive (Ståhl 1987, Ståhl & Hindar 1988). This, together with the connection between *G. salaris* and salmon farming leads to the hypothesis that the parasite has been introduced to Norway from the Baltic.

The old age of fish host - monogenean parasite relationships, the immigration history of salmon, the close neighbourhood between watercourses, and the long history of anthropochor spreading of salmonids leads to the hypothesis that *G. salaris* is endemic to Norwegian watercourses.

Fish parasites are patchily distributed among habitats within an area, i.e. a certain parasite may be found on a fish species in one lake or river but not necessarily in the neighbouring lake or river (Vik 1954,1957, Freeman & Thompson 1969, Kennedy 1977, 1978a, Margolis 1982). This means that the expectation is to not find *G. salaris* in all salmon rivers even if it is endemic in the area.

Neither of the two possibilities, endemism or introduction of *G. salaris* can be disproven by the available information. Nor do either of them receive overwhelming support. They therefore both remain valid hypotheses, and the question must be subjected to further research before conclusions may be reached.

3 Pathology

Representatives of the Monogenea, and in particular species within the genera *Dactylogyrus* and *Gyrodactylus* are common pathogens in fish culture, and are dealt with by most textbooks on fish diseases. Reichenbach-Klinke (1966), Amlacher (1970), Hoffman & Meyer (1974), Sinderman (1966), Roberts & Shepherd (1974) and Roberts (1978) are some examples. The same groups are also regularly dealt with in reviews on fish diseases. Examples are Sniszko (1970), Reichenback-Klinke (1975), Molnar (1987) and Paperna (1987).

There is a considerable amount of literature available that deals with Monogenea as disease organisms of fish, in particular for the Monogenea parasitizing carp. Literature dealing with Monogenea as disease organisms of salmonids is more scarce, probably reflecting the more recent emergence of salmonid farming.

Cone & Odense (1984) studied the attachment-site pathology of *G. salmonis* on *S. gairdneri* and four other species of *Gyrodactylus* on their respective fish hosts. They found that *G. salmonis*, unlike the other species, lodged its marginal hooks deep into the host epidermis and appeared to cause extensive fin damage and skin discoloration.

Cusack & Cone (1986) studied experimental infection of *Salvelinus fontinalis* fry with *G. salmonis*. They found that intensely infected fish had a thinner epidermis with fewer goblet cells than control fish. Internally the only obvious lesions involved the kidney where there was extensive tubular degeneration and necrosis. They hypothesized that attachment and grazing activity by *G. salmonis* can lead directly to death of fry through disruption of the osmotic permeability of the epidermis.

Cusack (1986) studied experimental infections of *Salmo gairdneri* with *G. colemanensis*, and found that the infection did not influence growth or survival of the host and produced no clinical signs of disease. Cusack (1986) concluded that both the species of host and parasite play an important role in the pathogenesis of *Gyrodactylus* infections.

We have not been able to find any published account of the pathology of *Gyrodactylus salaris*.

4 Epidemiology

4.1 Documentation of an epidemic outbreak of G. salaris in Norwegian salmon rivers: progress, effects, and causes

The documentation of an epidemic outbreak of *G. salaris* in Norwegian salmon rivers and evaluation of its cause and effects are primarily found in Johnsen & Jensen (1985, 1986). The bulk of the documentation consists of density estimates of salmon and trout fry (number of >1+/100 m^2) and data on the number of fish caught and number of fish infected. Fish densities were estimated by electrofishing and calculations were according to Zippin (1956).

The examination of watercourses with *G. salaris* varies much in quality according to Johnsen & Jensen (1985). In Johnsen & Jensen (1985) tables give the density of salmon and trout fry, and the number of fish caught and number infected are presented for 21 rivers. Accompanying figures show the density of salmon and trout fry >1+ for 5 rivers, and the density of salmon fry only for an additional 10 rivers. The sampling points for each river are about one year apart. Sampling has been carried out from May until October, but most of the samples are from August. The number of years sampled varies from 1 to 11 among rivers.

In Johnsen & Jensen (1986) the results from 5 rivers or watercourses (referred to as regions) are presented. One figure (Figure 2, p 236) shows the densities of juvenile salmon and trout in each river for a period of 8 to 11 years. Information about the infection is cursory, and only given in the text either as absolute numbers or percentages of fish infected.

According to Johnsen & Jensen (1986: p 239) the development in rivers with infection is characterized by a sudden decrease in salmon parr density during the first year after the beginning of the infection. The authors state that (p 239-240) "Overall, results of investigations so far indicate that infestation by *G. salaris* causes great reduction and near extermination of populations of salmon parr. .... Infestations in Norwegian rivers have been characterized by violent outbreaks, often with thousands of parasites on a single fish combined with fungus attacks resulting in the death of salmon parr."

In Johnsen & Jensen (1985) yearly data on number of fish caught and number infected are available for several rivers. We have calculated prevalences of infection in per cent from these data and listed them in **Table 1**. In most of the rivers where *G. salaris* has been recorded, the prevalence of infection is high to very high at most sampling points (**Table 1**), but in the river Steinkjærselva, for example, highest recorded prevalence is 33%.

The only data available for comparison are those of Bauer (1957), Hare & Burt (1975b) and Wootten & Smith (1980) who reported prevalences of infection of juvenile salmon with *Gyrodactylus* of 19.2, 0.27, and 19.2% respectively. The tendency in **Table 1** is towards prevalences much higher than this, which is an indication that the parasite populations in most of these rivers were in an epidemic state at these sampling points.

Of particular importance are the rivers where data on the density of salmon fry are also available prior to the first record of *G. salaris* in the river (Johnsen & Jensen 1985). This includes the rivers Skibotnelva, Rauma, Ranaelva, Istra, and the watercourses Vefsna and Beiarelva. Of these, Johnsen & Jensen (1986) did not include the Skibotnelva, Rauma, and Istra. Because of the importance of these rivers, the prevalence of infection and the density of young salmon in each year of sampling are shown separately in **Figure 3.**

Table 1. *Prevalence of infection (per cent) of salmon fry (mostly = 1+) with G. salaris in Norwegian rivers. Table numbers refer to Johsen & Jensen (1985). Percentages in brackets are based on less than 6 fish.* t_0 *= year when G. salaris was first recorded in the river.*

Locality	Table no.	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
I: Rivers with data on fry density prior to t_0											
Skibotnelva	2						100		86	100	
Beiarelva	7,8,9,10							15	57	80	100
Ranaelva	13			0	0	35	85	(100)	10	(100)	100
Vefsna	28,29				27	11	15	94	45		(100)
Rauma	46						0.9	36	79	99	(100)
Istra	47					0			32	67	
II: Rivers with data on fry density from t_0											
Lakselva	5	2.3	95	100	92		95		(100)	(100)	(100)
Steinkjærelva	32								25	33	
Figga	36								(71)	89	
Øksendalselva	40						100	100	(100)		
Batnfjordelva	42						99	95	100	67	100
Henseelva	44						99	75	(100)		
Valldalselva	49						(100)	100		(100)	
III: Rivers without data on fry density											
Bjerka	14						6	(100)	(0)		
Røssåga	16						95	100	92	(50)	93
Drevja	18							0	88		86
Fusta	20							83	89	8	40

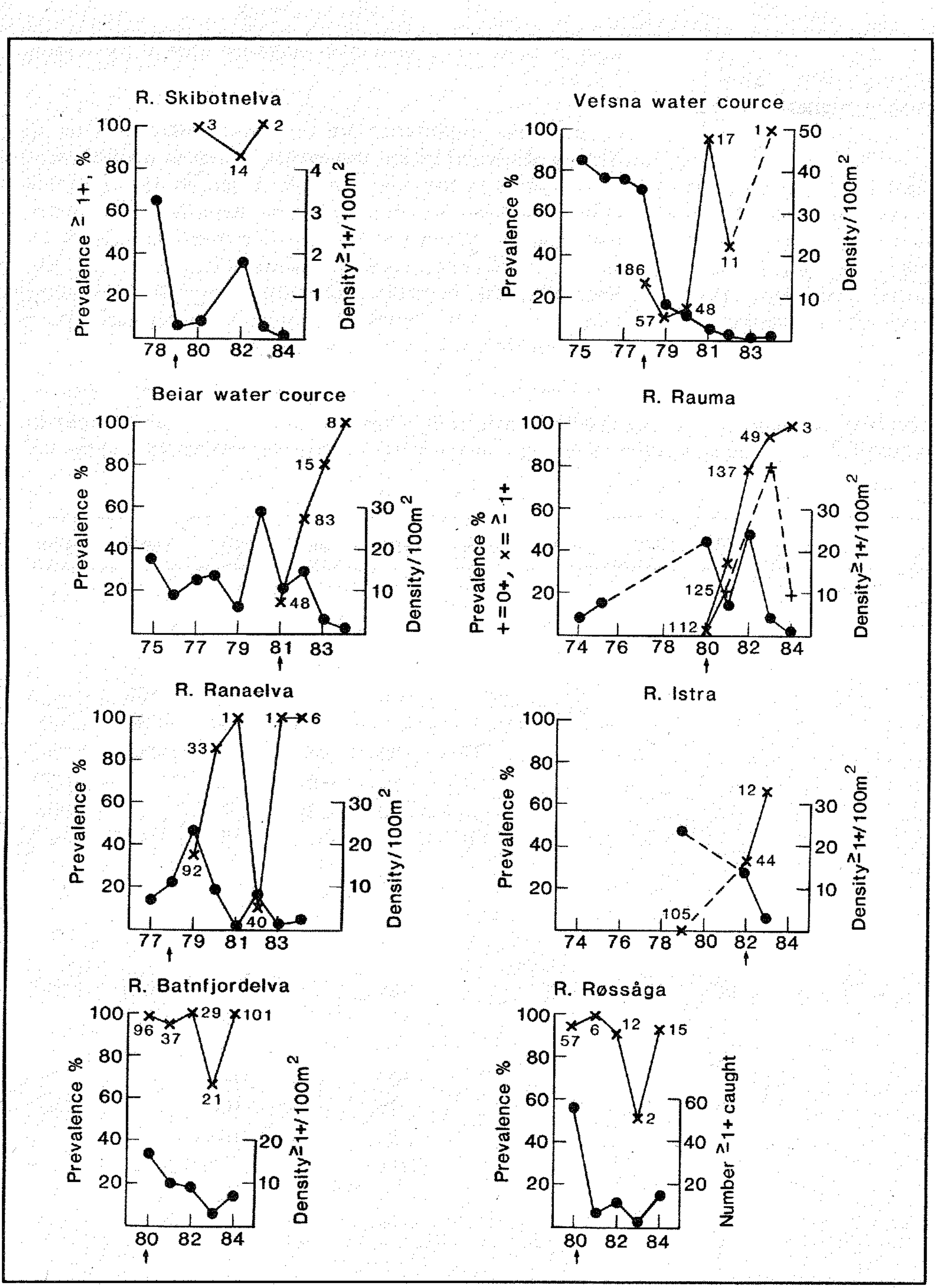

Figure 3
The density of young salmon and the prevalence (%) of infection with Gyrodactylus salaris in eight different rivers. Based on data from Johnsen & Jensen (1985).

The changes in the prevalences of infection with time (**Table 1, figure 3**) in the rivers Beiarelva and Rauma, and to some extent Lakselva, are as expected for the development of an epidemic outbreak, whereas this progression has not been caught in the rest of the data. Actually, the river Fusta, and to some extent the Røssåga, show the opposite trend.

A decrease in density of young salmon in the infected rivers and a reduction in the catches of ascending salmon in these rivers have been interpreted both as evidence for and effect of an epidemic outbreak (Johnsen & Jensen 1985, 1986). The most prominent trend in the results (**Figure 3**) appears to be a decrease in the density of young salmon with time, but in at least three rivers (Beiarelva, Rauma and Ranaelva), the decrease seems to follow a previous increase. A cause and effect relationship between the infection and the density is not easily deduced from these results when each river is presented separately.

In an attempt to elicit general trends in the results we have calculated the average yearly density of young salmon and the average yearly catch of ascending salmon in the infected rivers relative to the situation in the year when *G. salaris* was first observed in the river (year t_0) (**Figure** 4). I.e. the time scale is defined by t_0 and all years in all rivers that are, say, one year prior to the discovery of *G. salaris* become year $t_0 - 1$.

Average yearly densities of young salmon were calculated for rivers where estimates of density were also available prior to t_0, and the density in each river at t_0 was set to 100%.

If the size of the catch bear any relationship to infection with *G. salaris*, the effect of the infection must have been laid down while the fish lived in the river before migrating to the sea. We therefore transported the data on catches of adult salmon three years back in time and identified t_0 on this time scale. We further set the catch in each river at t_0 as 100%, expressed the catches in other years relative to this, and calculated the average catch over all infected rivers for each year before and after t_0. The data used for this procedure were obtained from Johnsen & Jensen (1985) and the results are presented in **Figure 4** together with the long-term records of salmon and trout catch from Norwegian rivers (Central Bureau of Statistics of Norway). Salmon catch is considered to be completely dominating in the latter statistic.

If the records of salmon catch are correlated with the size of salmon populations, they show the populations to have fluctuated considerably in size, but also to have generally increased since about 1945. During this growth phase, short time fluctuations seem to have been more erratic than in the previous part of the total period of records. From about 1968 to about 1978 the growth went through an eruptive phase culminating with a peak density around 1975 (**Figure 4**).

If records of catch in rivers with infection with *G. salaris* are transported back in time and treated as described above the population eruption is again apparent. The discovery of *G. salaris* (t_0), however, is situated rather late in the decline of the populations following the peak density (Figure 4). The same result is obtained when actual estimates of densities of young salmon in infected rivers are averaged in relation to t_0. *G. salaris* seems to have been discovered rather late in the declining phase of the eruption (**Figure 4**).

Johnsen & Jensen (1986: Figure 3) compared the total river fishing catches of salmon in Norway with the total catches of salmon in infected rivers for the period 1966-1984. Their figure demonstrated a very similar development in the catches from the two groups of rivers up to 1981, but from 1981 to 1984 the total catches in the infected rivers dropped by about 80% while that of all other rivers remained at a constant level.

As Figure 3 of Johnsen & Jensen (1986) dealt with total catches (the sum of catches in each river), this method may not have been very sensitive to the situation in rivers with relatively smaller catches. To dampen this effect we have considered the data on salmon catches from rivers separately for each county (**Figure 6**).

As shown in **Figure 5** the majority of the rivers with infection are located in the counties of Møre og Romsdal (II, 16 rivers) and Nordland (V, 8 rivers), while Sør-Trøndelag (III) and Nord-Trøndelag (IV) have no and 2 rivers with infection respectively. In Troms (VI) there is one and in Finnmark (VII) there are no rivers with infection.

Since 1975 salmon catches have decreased, but with considerable fluctuations, in Møre og Romsdal (II), and have also shown a tendency to decrease in Nordland (V) (**Figure 6**). This is, however, also the case for Sogn og Fjordane (I), and the most pronounced decrease has taken place in Finnmark (VII). Even if the most consistent decrease over the period appears to have taken place in Nordland (V) and Møre og Romsdal (II), the pronounced drop also in Finnmark (VII) makes it difficult to interpret the relationship between the decrease in catches and the occurrence of *G. salaris*.

Johnsen & Jensen's (1986) conclusions demand implicitly that the trend in catches from all other groups of rivers have developed differently from that of the rivers with infection. To test this assumption, we have summed the yearly catches from three groups of 20 randomly drawn rivers, and compared them with the rivers with infection with *G. salaris* (**Figure 7**). The general trend in all four groups of rivers is a decrease in catches over the period. The decrease appears to have been most consistent again in the rivers with infection, but because of the obvious random element involved in a procedure where samples of absolute values with large individual differences are involved, this may only be an indication of an additive parasite-induced effect in the rivers with infection.

The most detailed results available on the occurrences of *G. salaris* and salmon are from the river Vefsna (Johnsen & Jensen 1988). The catches of ascending salmon decreased from 6000-7000 kg in 1966-1968 to 2000-3000 kg in the period from 1968 to 1971, increased to 12000 kg in 1974 and decreased again, with some fluctuation, to 1000 kg in 1984 and 1985 (Johnsen & Jensen 1988: Figure 4).

From these data the situation in 1984-1985 does not appear

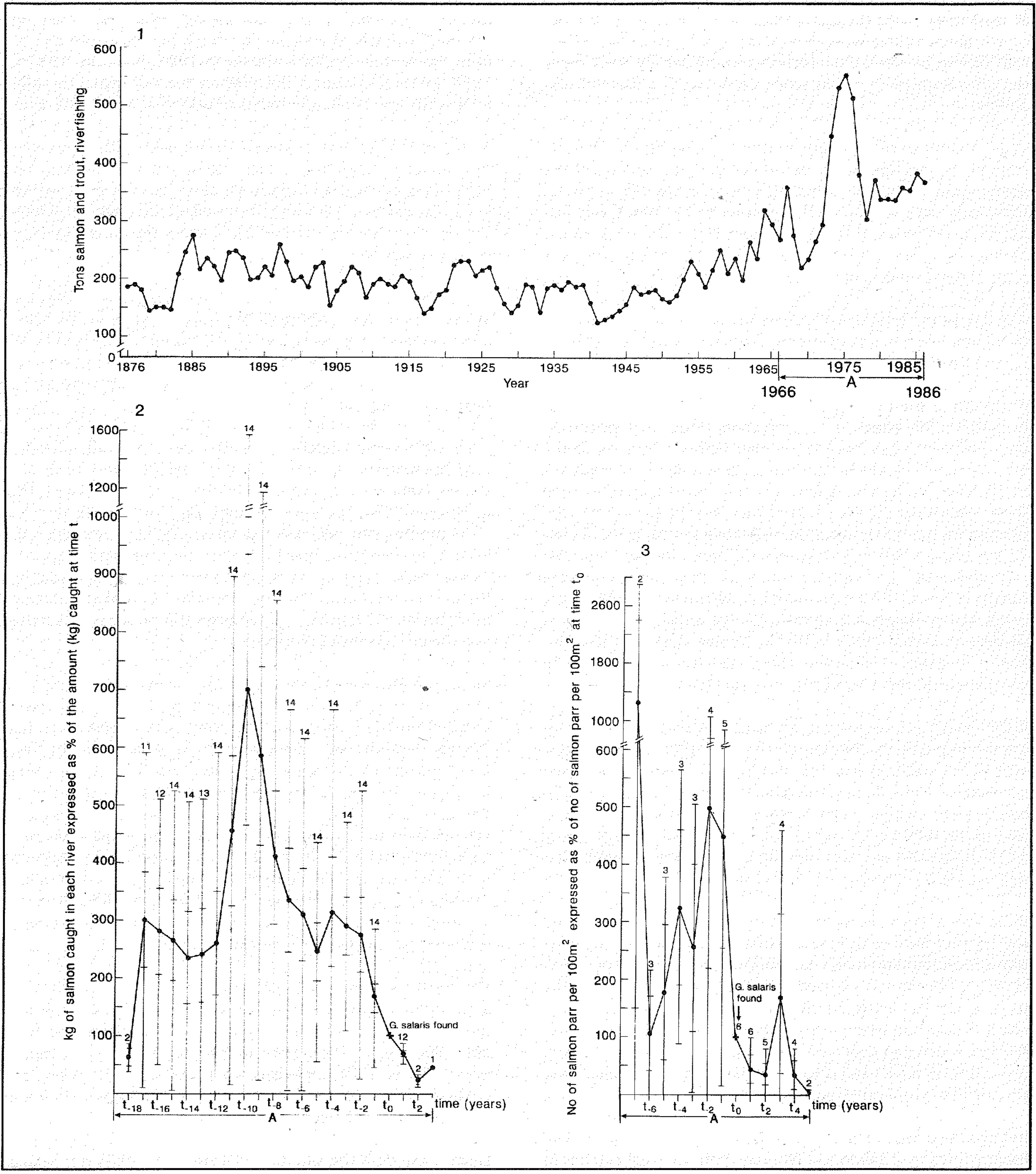
1
Tons salmon and trout, riverfishing
600
500
400
300
200
100
0
1876
1885
1895
1905
1915
1925
1935
1945
1955
1965
1975
1985
Year
A
1966
1986
2
kg of salmon caught in each river expressed as % of the amount (kg) caught at time t
1600
1200
1000
900
800
700
600
500
400
300
200
100
G. salaris found
t-18
t-16
t-14
t-12
t-10
t-8
t-6
t-4
t-2
t0
t2
time (years)
A
3
No of salmon parr per 100m2 expressed as % of no of salmon parr per 100m2 at time t0
2600
1800
1000
600
500
400
300
200
100
G. salaris found
t-6
t-4
t-2
t0
t2
t4
time (years)
A

Figure 4

1. The yearly recorded catches of salmon and trout in Norway 1876-1985.

2. The average amount (kg) of salmon caught in rivers with infection with Gyrodactylus salaris. Year of discovery of G. salaris in a river is t_0, and catch in a river that year is 100%. Numbers of rivers are given on the figure.

3. Average density of young salmon in rivers with infection with Gyrodactylus salaris. t_0 as in B. Density in a river that year is 100%. The numbers of rivers are given on the figure. Based on data from Johnsen & Jensen (1985).

to be dramatically different from that in 1968-1971. *G. salaris* was first discovered in 1978, so what emerges from this again is an eruption of the salmon population where the parasite appears after the decline phase of the host population has started. The trend in the density data for young salmon is a decline at least from the onset of sampling in 1975, as presented earlier (**Figure 4**).

Johnsen & Jensen (1986) concluded that it had been proven that the mass infestation by *G. salaris* was not related to some changes in the environment of a river as suggested by Johnsen (1978), and they imply that the outbreak is due to the parasite being introduced. Similar conclusions are found in Johnsen & Jensen (1985, 1988).

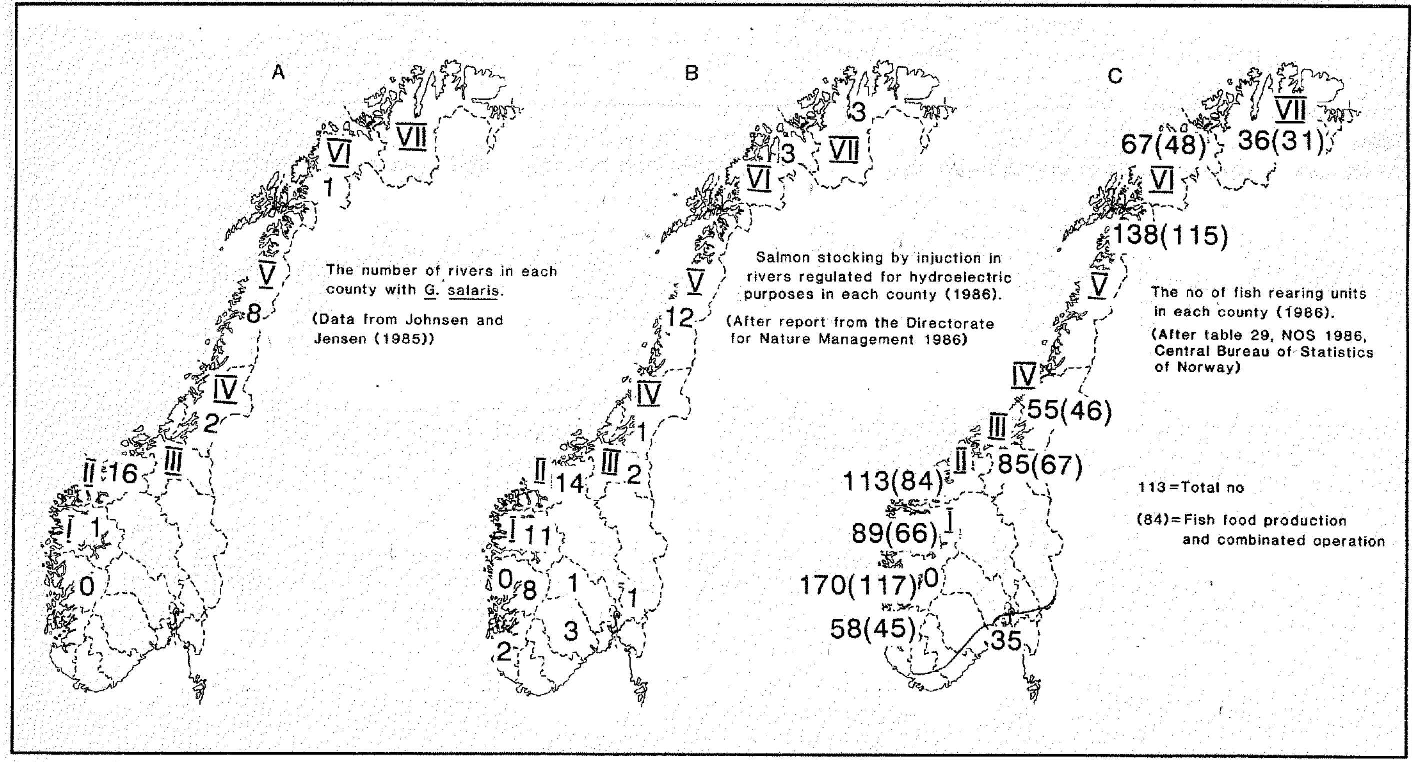

Figure 5

The number of rivers with Gyrodactylus salaris (A), salmon stocking by injunction (B), and number of fish farms (C) in each county from Rogaland (0) in the South to Finnmark (VII) in the North.

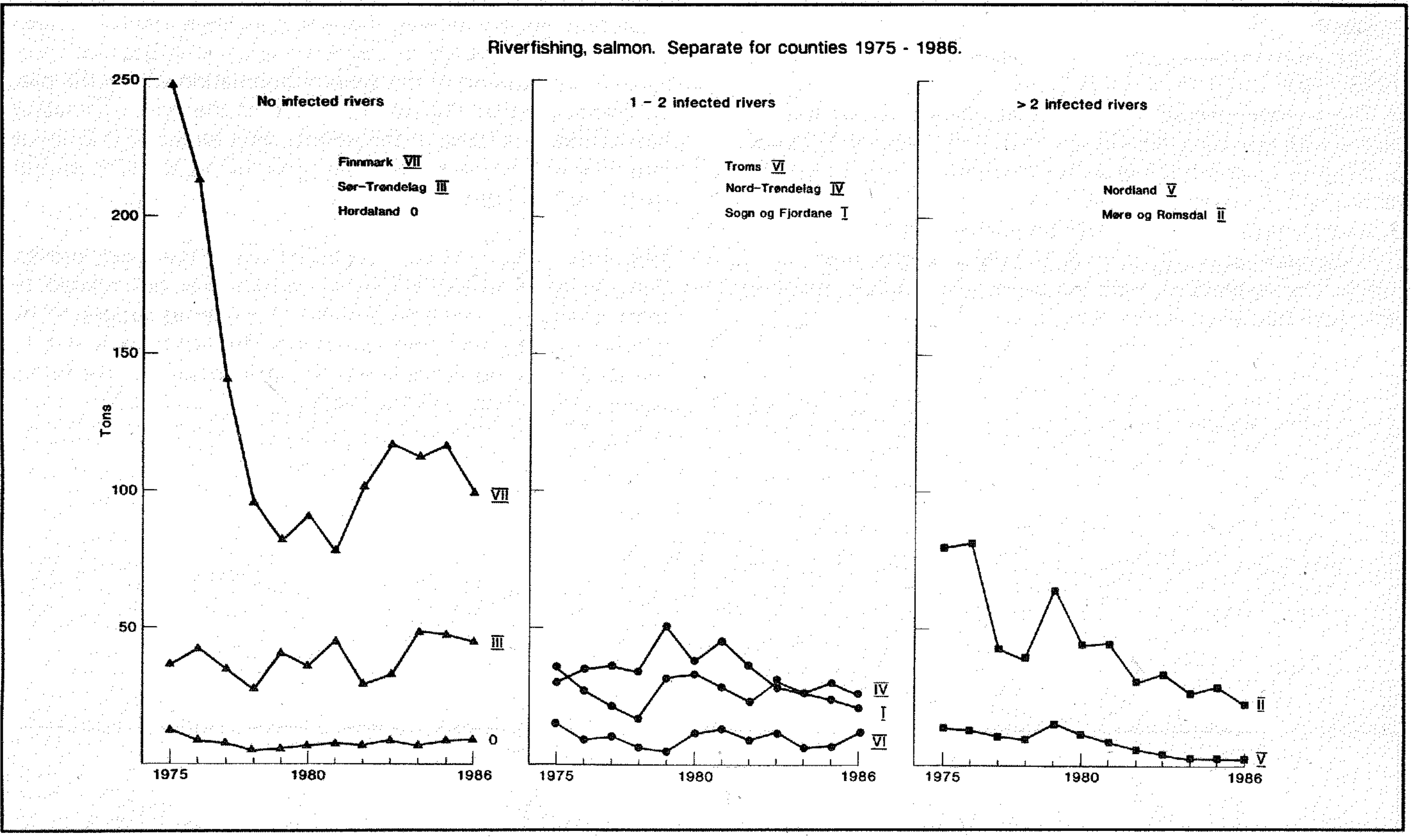

Figure 6
The amount of salmon caught in counties with no, one to two, and more than two rivers with Gyrodactylus salaris.

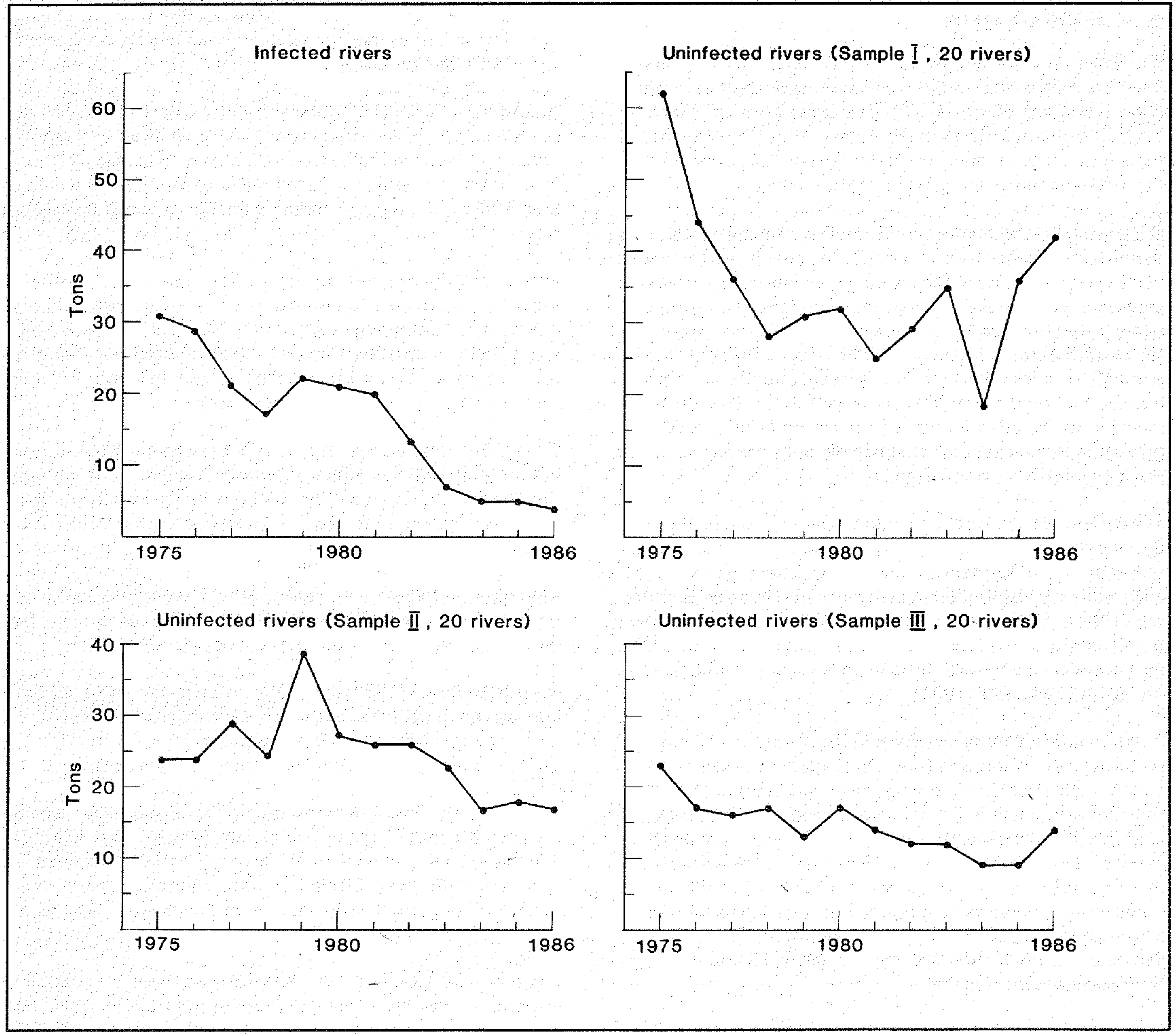

Figure 7
The amount of salmon caught in rivers with Gyrodactylus salaris compared with catches from three groups of 20 randomly drawn rivers without infection.

4.2 Discussion

The effect on a fish of infection with *G. salaris* most probably has close relationship to the number of parasites that it carries (worm burden) (Scott 1985). The prevalence of infection, which is some expression of the number of fish infected out of those examined, is, however, a poor descriptor of the interaction between the parasite and host populations.

Depending on the frequency distribution of parasite numbers per host, prevalence may or may not increase in an observable manner with increase in the parasite population, or an increase in prevalence may take place without any increase in worm burden per host (Anderson 1982). In experiments with *Gyrodactylus bullatarudis* on guppies Scott (1985) found that the parasite population quickly became highly overdispersed such that a few fish harbored the majority of the parasites. Prevalences of infection as recorded by Johnsen & Jensen (1985, 1986) can only serve to indicate that an epidemic outbreak has occurred in the *G. salaris* - salmon system.

More pertinent information could have been obtained by the use of a density approach; i.e. by calculating statistics that describe the worm burdens by their range, mean with variance, and frequency distribution as in Figure 3 of Halvorsen & Andersen (1984). Within such a framework, it is possible to analyze the dynamics of the host - parasite system much further than by a prevalence approach (Anderson & Gordon 1982, Scott & Anderson 1984, Lester 1984).

A step toward a density approach to the *G. salaris* - salmon system was taken by Johnsen & Jensen (1988) in analyzing the situation in the river Vefsna during the period 1975 to 1985. This together with the description of the increase in number of localities where *G. salaris* was found with time, make the development of an epidemic outbreak of disease in the River Vefsna more traceable. An actual growth in the size of the *G. salaris* population is, however, still poorly documented as Johnsen & Jensen (1988) really only had two size groups for worm burdens, i.e. less than and more than 10 (groups 3 and 4 differed from 2 only in other criteria).

Over the 11 years of the investigation from 1975 to 1985, Johnsen & Jensen (1988) caught 126, 200, 107, 102, 107, 78, 26, 30, 25, and 22 0-year fish. This indicates that there was a decrease in this age group of fish over the period, whereas the infection did not increase systematically after the first record in 1978.

Even if the relationship between the number of salmon spawning and the number of fry hatching is not a simple one, an alternative interpretation may be that the reduction in the density of 0-year fish reflects a reduction in the number of fry hatched as a result of the reduction in the number of salmon ascending to spawn. A decrease in spawning salmon started in 1975. If the decreasing size of the 0 year class is a result of fewer fish being born, this will, of course, subsequently lead to a decrease in the size of the older age classes.

According to Scott (1985) the substantial mortality caused by *G. bullatarudis* in its natural host may serve as an example of parasite-induced mortality that is capable of regulating the host population. Her results indicated that at guppy densities of less than 10/litre, the parasite reduced the host population by 50-60%.

Holmes (1982) regarded mortality due to disease as "compensatory" if it replaced other mortality (i.e. in demographic terms if they were "competing risks"), and "additive" if it acted in addition to other mortality. Holmes (1982) pointed out that one major viewpoint on the impact of parasites is that any mortality produced is almost entirely compensatory.

Scott (1985) also warned that even if her experimental studies indicated an additive effect of parasite-induced host mortalities, the difficulty in separating this from compensatory mortality makes it important to obtain field examples where other potential regulating factors are acting.

Mortalities induced by *G. salaris* after it went into epidemic growth may have interacted with decreasing recruitment by birth in causing a decrease in the host population.

Scott & Anderson (1984) in experiments with *Gyrodactylus bullatarudis* on guppies found that a linear model of the form

$$A = b + aM \qquad \text{(our notation)}$$

gave a crude approximation to the trend in the experiments.

A denotes the instantaneous rate of host mortality, which equals the parasite free mortality rate (b) plus an additional component proportional to the average parasite burden per host (M) where the coefficient of proportionality (a) is the per capita rate of parasite-induced host mortality defined as parasite/host/unit of time.

Based on the data available, this expression seems to capture important elements in the dynamics of the examined salmon populations. Further research aimed at estimating the components of the equation will be important for understanding the relative importance of each.

4.2.1 The relationship between transmission and extinction

One central enigma that emerges in attempts to understand the parasite - host dynamics of *G. salaris* in Norwegian salmon rivers is the transmission of the parasite in relation to extinction of the host population.

It is generally understood that *Gyrodactylus* normally is transmitted from one fish to another through direct contact (Scott & Anderson 1984, Mo 1983, Johnsen & Jensen 1985). When transmission is by contact between hosts, the proportion of hosts infected with time will grow in a sigmoid way, and the rate at which new cases arise will follow a roughly bell shaped curve. As the density of the host population increases, the development of an epidemic occurs more rapidly. The net rate of parasite transmission is always greater in dense populations than sparse ones (Anderson 1982).

When transmission is by contact at hosts, the density of the host population must be above certain limits for the parasite to persist, or for an epidemic to occur. Limits to parasite population growth become even more apparent if there is parasite-induced host mortality. The dynamics of this type of host - parasite systems has been analyzed both theoretically, in experiments, and in field investigations.

Scott & Anderson (1984) studied the population dynamics of *Gyrodactylus bullatarudis* within laboratory populations of the fish host *Poecilia reticulata*. In a prevalence framework, they found that for an "epidemic" to occur, the density of susceptible hosts must exceed a critical value X_T where

$X_T = (b + a + g)/K$ (our notation)

The parasite is only able to persist within the host population provided that the following condition is satisfied

$I/b > X_T$

(I is host immigration rate, b is parasite free host mortality rate, X_T is the critical threshold density of host population for the persistence of the parasite population, a is infection-induced mortality rate, g is recovery rate from infection, and K is infection rate).

Prevalence model predictions were poor mimics of observations (Scott & Anderson 1984), but they were useful indicators of the complexity involved. Important points in our connection are that X_T is predicted to be proportional to a and inversely proportional to K.

Scott & Anderson (1984) estimated X_T to be 6 guppies/5 l of water for experiments run at 25°C with *G. bullatarudis* in 5 l of water in 10-l aquarium. An aquarium of 10 l may have a bottom area of about 500 cm^2, in which case X_T equals 30 000 fish/100 m^2. This is much higher than the density of young salmon estimated in Norwegian salmon rivers (Johnsen & Jensen 1985, 1986).

In a theoretical study Anderson (1980) found that a parasite with reproduction directly on the host may cause the extinction of the host and hence itself if the inequality

$r > c - (u + a + b)$ (our notation)

is not met. (r is rate of increase of the host population, c is the rate of direct multiplication per parasite per unit of time, u is parasite death rate, a is parasite induced host death rate, and b is parasite free host death rate.) This means that the intrinsic rate of growth of the host population, r, must be greater than the net rate of population growth of the parasite on the host if the host and parasite are to avoid extinction. Parasite multiplication and parasite-induced host death rate work in opposite directions in the interaction. In the model on which this result is based, the rate of direct parasite reproduction had to lie in a narrow window of parameter values if host and parasite extinction were to be avoided.

This model also gives an approximation to the conditions that have to be met for certain outcomes of the interaction to occur. The model assumed, however, a random distribution of parasite numbers on hosts, and will therefore not represent any actual system very accurately.

The most studied infection which has a number of principal similarities to the *G. salaris* - salmon system as described by Johnsen & Jensen (1985, 1986) is the viral infection of foxes which causes rabies. The rabies virus is contained in the saliva of the rabid fox and is normally transmitted by bite. Therefore a contact between a rabid and a susceptible fox is necessary for the transmission of the disease. Few, if any, foxes recover once the virus is established in the host (Anderson et al. 1981, Källen et al. 1985).

Obviously, if the mortality rate is higher than the transmission rate, the infection cannot persist. For the transmission rate to be higher than the mortality rate, the density of the fox population must be above a "threshold density".

Anderson et al. (1981) expressed this "threshold density" as

$X_T = (p+a)(d+a)/tp$ (our notation)

(1/p is the average latent period, a is average per capita birth rate of foxes, d is death rate of rabid foxes, and t is transmission coefficient). Källen et al. (1985) formulated this critical fox density as

$S_c = u/K$ (our notation)

(1/u is life expectancy of an infected fox, K is the transmission coefficient).

In both formulations there is an inverse relationship between parasite-induced death rate and transmission.

Both theory as well as experiments and field observations show that for a population of directly transmitted parasites to persist, or to grow, the host population must be above a certain density. Extinction of host and parasite population is theoretically possible under certain conditions. Empirical evidence suggests, however, that parasite-induced host mortality will reduce host density to a stable constant value or stable cycle as described by Anderson et al. (1981) for rabies. There is an inverse relationship between parasite-induced host mortality and transmission in relation to limit conditions for the persistence of the parasite or the development of an epidemic. The more pathogenic a parasite is, the lower will be its prevalence in the host population (Anderson et al. 1981).

In Norwegian salmon rivers *G. salaris* apparently has a very high pathogenicity leading to extinction but also a transmission rate leading to prevalences of 100% in declining host populations where density becomes very low. This does not fit easily into the framework of the theoretical, experimental and field studies referred to above. The fact that salmon parr are territorial (Folmar & Dickhoff 1980) increases this problem further. This suggests that there is a severe lack of knowledge about some factor(s) relating to transmission biology and parasite - host population growth and interaction in the *G. salaris* - salmon system.

In some cases it has been found that *Gyrodactylus* spp. in fish culture may be transmitted via the bottom of the tank or the pond (Lewis & Lewis 1970). Mo (1983) suggested that *G. truttae* could be transmitted via the substrate in the river, and Scott & Anderson (1984) found that *G. bullatarudis* could transmit from dead to living guppies. Behaviour traits in the guppy may make transmission from dead fish even more efficient than direct transmission.

For these types of transmission to alter, in principle, the relationship between pathogenicity and transmission, they have to occur commonly, and the free-living stage has to be long lived. Lester & Adams (1974a) found that *G. alexanderi* had a longevity of 28 days on *Gasterosteus aculeatus* at 15°C, whereas the parasite lived not more than 4 days when removed from the fish. Scott (1982) found a longevity of about 7 days for *G. bullatarudis* on guppies at 25°C, whereas Scott & Anderson (1984) recorded a longevity of about 1 day for the parasite on dead fish.

Johnsen & Jensen (1988) reported that *G. salaris* spread upstream in the river Vefsna, and within two years from the first finding the parasite had colonized the entire 126 km section of the river where salmon is found. This colonization had occurred via 14 salmon ladders that are unlikely to have been climbed by presmolt salmon. Johnsen & Jensen (1988) therefore suggested that the parasite had been carried by adult salmon.

If *G. salaris* may be carried by adult salmon, which does not seem unlikely, this may serve to resolve to some extent the dilemmas encountered. It is therefore important to investigate the role adult salmon play in the biology of *G. salaris*. Further investigations of the role of trout and charr in the parasite's biology are also needed.

Most freshwater fish parasites demonstrate seasonality in some population dynamic trait (Chubb 1977). There are indications that the prevalence of *G. salaris* on salmon and trout increases during the autumn (Anonymous 1983). Lester & Adams (1974a) demonstrated that demographic rates in *G. alexandri* were temperature sensitive, and Scott & Nokes (1984) found the same for *G. bullatarudis*. Further research on *G. salaris* must therefore take seasonality into account, both in the field and in the laboratory.

For a better understanding of the population dynamics of the *G. salaris* - salmon system, quantification of birth, death and transmission rates of the parasite are needed. The studies of Lester & Adams (1974a,b) on *G. alexanderi*, and of Scott (1982), Scott & Anderson (1984) and Scott & Robinson (1984) on *G. bullatarudis* provide models for this kind of work of a standard that is unusual within fish parasitology.

4.2.2 Possible causes for the *G. salaris* epidemic in Norwegian salmon rivers

When *G. salaris* was first recorded on salmon in the river Lakselva in 1975, Johnsen (1978) speculated that the incident was related to some changes in the environment. Heggberget & Johnsen (1982) reported infection in five more rivers, and formulated two theories: (i) that the fish were weakened by environmental factors, (ii) that *G. salaris* was introduced from infected salmon hatcheries in Scandinavia (Johnsen & Jensen 1986). Johnsen & Jensen (1986) stated that investigations subsequent to Johnsen (1978) had proven implausible the theory that mass infestation by *G. salaris* was related to some changes in the environment of a river. Johnsen & Jensen (1988) stated that environmental factors have been ruled out as a cause of the problem. In Johnsen & Jensen (1985, 1986, 1988) the epidemic of *G. salaris* is explained as a consequence of introduction.

Epidemics, which are rapid growth in parasite populations, may be caused by introductions, or for endemic parasites, by changes in the environment, the host population, or the parasite population, or by combinations of these factors. We will discuss these possibilities in relation to the *G. salaris* epidemic.

4.2.2.1 Introduction of the parasite

As with free-living species, introduction of a parasite species into a new area may result in rapid growth of the introduced population in the establishment phase. There are many examples of epidemics following introduction (Elton 1958, Soulé & Wilcox 1980).

Many of the infectious diseases of man like smallpox and malaria were introduced to America from Europe and Africa and their establishment in the aboriginal population is believed to have had far-reaching demographic and historical consequences (McNeill 1976).

In other mammals well-known examples include the introduction from the Old World to Africa of paramyxovirus causing rinderpest (Plowright 1982, Fowler 1985) and from South America to Australia and Europe of myxoma virus of rabbits (Ross 1982, Goodfrey 1985).

An often quoted example among fish parasites is the introduction of the monogenean *Nitzschia sturionis* parasitizing *Acipencer stellatus* in the Caspian Sea to the Aral Sea where it resulted in high mortality of *Acipenser nudiventris* (Bauer & Hoffman 1976). The fungus *Aphanomyces astaci* imported from North America has decimated the European crayfish *Astacus astacus* (Vik 1969, Håstein & Unestam 1972).

It is questionable, however, whether such examples are relevant for understanding the *Gyrodactylus salaris* - salmon situation as suggested by Johnsen & Jensen (1985). Most of them describe intercontinental transfer of parasites into host populations that were taxonomically different. Also, when the transfer was intracontinental as in the case of *N. sturionis*, the new host population belonged to a different species. In the case of *G. salaris* and salmon, we are investigating the relationship of a parasite to its specific host within the natural area of distribution of this host. Even if current data indicate that European populations of Atlantic salmon are substructured into two major genetic groups corresponding to the geographical regions of the Eastern Atlantic and the Baltic Sea, recognition of these groups even as "races" appears to be unjustified (Ståhl 1987).

Even if introductions may lead to epidemics, not all of them appear to do so, and it may even be questionable that it happens in the majority of cases. Hoffman (1970) found that at least 48 species of freshwater fish parasites had become established on other continents through transfer of infected fish, and several examples are referred also by Hoffman (1976) and Bauer & Hoffman (1976). Most of the translocated parasites have continued to be a disease problem in hatcheries and farms after translocation, but except for *N. sturionis* it remains unclear how many of them that have become established and have caused epidemics in natural fish populations.

Myxosoma cerebralis, for example, is believed to have been introduced to North America from Europe. It causes disease in hatcheries, but has rarely been detected in wild salmonids (Hoffman 1970).

It was pointed out in Section 2.3 Biogeography, that within an area of endemic distribution, the occurrence of parasites is often patchy. We believe this reflects a dynamic relationship between local colonization and extinction (Hanski 1982). The (re)colonization of a patch may be seen as an introduction, even if it is not caused by man.

Kennedy (1981a,b, 1985, 1987) and Kennedy & Burrough (1981) studied the population dynamics of parasites that colonized a small lake (Slapton Ley) in the south-west of England. The parasites *Ligula intestinalis*, *Tylodelphis calvata* and *T. podicipina* which have fish as intermediate hosts, were introduced in the lake in 1973, 1973 and 1976 respectively by *Podiceps cristatus* when the bird started (or resumed) breeding in the lake. *L. intestinalis* had a pronounced effect on the dynamics of the fish populations, whereas there was no evidence that *T. clavata* or *T. podicipina* induced host mortality (Kennedy 1985).

As with free-living animals, the size of parasite populations fluctuates over time. Unfortunately even fewer parasite populations than free-living populations have been monitored over any extent of time, so data showing the actual magnitude of fluctuation are scarce.

In Slapton Ley Kennedy (1985) observed that the populations of *Diplostomum spathaceum* and *Acanthocephalus clavula* underwent pronounced and dramatic changes over a period of 11 years of study, and the infrapopulation of the latter in perch probably became extinct. The data of Kennedy & Rumpus (1977) for the infection of dace with *Pomphorhynchus laevis* in the River Avon over a period of 8 years show, on the other hand, only small fluctuations. MacKenzie (1987) published records of the prevalence of two cestodes, one in mackerel and one in herring over a period of five years. Within this period, the prevalence of the mackerel parasites varied from about 17% to zero, and of the herring parasite from about 12% to about 1%.

Epidemics occur in both vertebrate and invertebrate host populations (Holmes 1982, Pence et al. 1983, Kummeneje 1974, Halvorsen et al. 1980, Steen & Rhebinder 1986, Lessios et al 1984). And even if the process does not express itself as an epidemic, infection-induced mortality may be high. Stout & Cornwell (1976) calculated that disease accounted for 85% of nonhunting mortality in waterfowl.

According to Sindermann (1970), mass mortalities of marine, estuarine, and anadromous fishes are common, even though many such events may escape scientific attention. There are, however, some cases that are well documented.

Outbreaks of the fungus *Ichthyophonus hoferi* in herring in the western North Atlantic have been known since 1898, the most recent occurred in the Gulf of Saint Lawrence in 1954-1955 when an estimated one half of the herring population was killed by the disease (Sindermann 1970).

Another example given by Sindermann(1970) is that of *Vibrio anguillarum* in eels where outbreaks have been recorded in European waters at intervals since 1718.

Paperna et al. (1984) recorded mass mortalities from infection of large individuals with the monogenean *Benedenia monticelli* in wild populations of *Liza carinata* from lagoonal habitats in the Gulf of Suez.

Outbreaks of *Schistocephalus solidus* in fresh-water sticklebacks have been observed (Vik 1954 and references therein). Wisniewski (1932) and Huitfeldt-Kaas (1927) reported epidemics caused by *Cyathocephalus truncatus* which infect salmonids, and outbreaks of diphyllobothriasis in salmonids have been reported from both Europe and North America (references in Halvorsen & Andersen 1984).

Epidemics of parasites have been recorded in connection with introduction of parasites to new areas as well as in endemic populations. Introductions may or may not lead to epidemics. There is not a simple and constant relationship between the two phenomena. Fish with large burdens of *Gyrodactylus* that may cause disease and death have been observed under natural conditions where there was no suspicion of introduction (Malmberg 1957). An epidemic outbreak can therefore not alone be used as evidence that *G. salaris* is introduced. And introduction is not necessarily the only possible cause of the epidemic.

4.2.2.2 Changes in the environment

Many Norwegian rivers have been regulated for the production of hydroelectricity. One purpose of such regulation is to change the yearly rhythm in the waterflow of the river. Regulation may also change several other abiotic factors in a river, and thus alter it as a habitat. Heggberget & Johnsen (1982) considered the possibility of connections between the *G. salaris* epidemic and regulation of rivers, but this kind of connection did not appear to be present.

Johnsen (1978), when discussing the possible causes of the *G. salaris* outbreak in the river Lakselva, reported that some agricultural and domestic pollutants were disposed in the river, and that a greater part of the riverbed was overgrown by algae, mostly *Didymosphenia geminata*. A possible role of habitat changes through pollution in the *G. salaris* epidemic has not been further discussed.

Anonymous (1988) reported on the pollution of Norwegian fjords. Five out of the 10 most polluted fjords are situated south and east of the part of the coast where *G. salaris* was reported found by Johnsen & Jensen (1986). The 5 remaining worst polluted fjords were Årdalsfjorden, Sundalsfjorden, Orkdalsfjorden, Vefsnfjorden, and Ranafjorden. Of the 14 regions listed as positive for *G. salaris* by Johnsen & Jensen (1986), 7 are directly associated with these strongly polluted fjords.

Pollution in these cases was caused by heavy metals as well as organic compounds, and it may be worth investigating if this may render returning salmon more vulnerable to *G. salaris* in the river systems.

4.2.2.3 Changes in the parasite populations

Malmberg (1987c) speculated that isolation of *G. salaris* populations on fish farms, and extreme temporary reductions in the size of such populations by antiparasitic treatment, may result in genetic drift involving enhanced pathogenicity.

4.2.2.4 Changes in the host populations

The data which have been reviewed above seem to indicate that there was a growth in the Norwegian salmon population from about 1945 with an eruptive development around 1975. On the average, the density of young salmon in the rivers with recorded infection with *G. salaris* went through a phase of rapid increase prior to the discovery of the parasite in the river. The parasite was discovered some time into the decline phase of the eruption.

It has been described above how the persistence and growth of populations of parasites with direct transmission is dependent on the density of the host population. From this it may be seen that an increase in host density alone may cause epidemic growth in the parasite population. Based on established epidemiological knowledge, an unavoidable hypothesis is therefore that the *G. salaris* epidemic has been caused by an increase in the density of salmon.

When permission is granted to regulate a salmon river for the production of hydroelectricity, stocking with young salmon is usually inducted to compensate for the effect of regulation (**Figure 5**). In addition, fish stocking is also carried out by local land owners and angling clubs.

In 1986, smolt originating from stocking represented only a small fraction (0.01 - 3%) of descending fish in the counties of Finnmark (VII, **Figure 5**), Troms (VI), Nord-Trøndelag (IV), and Sør-Trøndelag (III). In Nordland (V), Møre og Romsdal (II), Sogn og Fjordane (I) and Hordaland (O), smolt originating from stocking was estimated to make up 28, 23, 12 and 21% respectively. In rivers strongly influenced by regulation, fish from stocking may be more numerous than those from natural reproduction (Ståhl & Hindar 1988).

Stocking appears to have been widely applied to the rivers where infection with *G. salaris* has been recorded (Anonymous 1981, Johnsen & Jensen 1985, 1986). As an illustration, **Figure 5** shows the number of rivers with recorded infection and the number of rivers where there is stocking by injunction in each county from Hordaland in the south to Finnmark in the north. The counties of Møre og Romsdal (II) and Nordland (IV) have the highest score for both variables.

The apparent regional co-occurrence of stocking and *G. salar-*

is justify a further discussion of factors connected with stocking which may be of epidemiological significance.

Presumably stocking increases the density of young salmon in a river. The reared fish are also normally released in one or a few places, and for at least some time the density will be particularly high in these localities. If stocking works in accordance with intentions, it will increase fish density, and therefore be of epidemiological significance as discussed above.

In addition to the density effect, stocking may also have a time effect if reared fish are released at a time which departs from the input to the salmon population through natural birth processes.

Scott & Anderson (1984) and Scott (1985) found that in the absence of continual addition of susceptible guppies, *G. bullatarudis* was unable to persist. In experiments with a continual input of hosts, parasite populations persisted over the timespan of observations, but the character of population fluctuations was dependent upon the rate of input.

The age of the young salmon used for stocking may also be of epidemiological significance as larger worm burdens presumably will develop on larger fish. Stocking with parr, and particularly smolt, is not uncommon and may have increased (Anonymous 1981, Ståhl & Hindar 1988). Stocking may therefore represent a demographic as well as a numerical push in the direction of growth in the parasite population.

Stocking may also influence the behaviour of the fish population. Returning salmon originating from stocking have a much higher tendency to stray than salmon that originate from natural breeding (Stabell 1984). Young reared salmon used for stocking may also show less tendency to space out, hide and become territorial. All this may influence the possibility of parasites like *G. salaris* to transmit.

Salmon, *Salmo salar*, occurs in genetically separated populations even within geographically very small areas (Ståhl 1987). Ståhl & Hindar (1988) found that in Norwegian rivers, salmon occurred in genetically different populations both within and among rivers.

Stocking with young salmon bred in hatcheries may alter the genetic structure of the young segment of the salmon populations. Ståhl & Hindar (1988) found that unintended genetic differences also developed in a hatchery where the intention was to preserve the local landlocked salmon population. In some other hatcheries intentional selection is performed to "improve" the stock (Refstie 1986).

During recent years, fish for stocking have been delivered from a limited number of larger hatcheries, and a hatchery with programs for selection has been among the main suppliers of fish for stocking (Anonymous 1981, Johnsen & Jensen 1986). Even where local hatcheries are operated, the composed genetic structure of the natural populations are not allowed for when the parent fish are collected either from the rivers or from the sea (Ståhl & Hindar 1988).

In many rivers, smolt from stocking outnumber those from natural breeding, and on a regional basis they may make up more than 20% of the smolt cohort (Ståhl & Hindar 1988). It is conceivable then, that stocking may alter the genetic structure of this cohort from that which natural breeding alone would have generated. As fish originating from stocking return to spawn, one would expect this process to be enforced.

Madhavi & Anderson (1985) studied experimentally the susceptibility of 4 inbred strains of guppy to infection with *G. bullatarudis*. They recognized 3 broad categories of susceptibility among guppies: (i) resistant hosts on which the parasite either failed to establish or failed to reproduce, (ii) moderately susceptible hosts on which the parasite population built up by reproduction but the host slowly recovered and the parasite was eliminated, and (iii) highly susceptible hosts on which the parasite population grew rapidly and the infection resulted in host death. Working on the same host - parasite system, Scott (1985) reported similar results.

In two strains of fish in the experiments of Madhavi & Anderson (1985) the majority of fish were resistant, while in two other strains the majority were susceptible. The susceptible strains were characterized by higher average worm burdens, longer duration of infection and greater parasite-induced host mortality when compared with the resistant strains. Madhavi & Anderson (1985) concluded that genetic factors undoubtedly were involved in the determination of resistance/susceptibility traits. Resistance appeared to be a dominant character, but the results did not suggest that a single locus controlled the character.

Stocking may also be a significant factor in the *G. salaris* epidemic by changing the genetic structure of the salmon populations.

Mainly because of the high densities of fish, many parasites become more abundant in hatcheries and farms than in natural habitats. In this way hatcheries and farms may also become breeders of parasites. These parasites are mostly endemic, but may not have been recorded in the local natural populations, either because of lack of investigations or because they occur at low abundance (Bauer et al. 1973). Håstein & Poppe (1986) listed some 40 infectious diseases recorded from cultured salmon in Norway. Only a few of these were previously known as salmon parasites in Norway, but most of them are probably endemic. In addition to the possibility that *G. salaris* has been introduced and spread via hatcheries in connection with stocking, one has to consider the possible effect of stocking with fish that are more infected than the natural population even if the parasite should be endemic.

Stocking with heavily infected fish will increase the parasite suprapopulation. If parasite population growth takes place in the absence of density dependent constraints, this may increase the rate of growth of the parasite population ($dN/dt = rN$), i.e. act as a push towards an epidemic development.

In experiments with *G. bullatarudis* and guppies Scott (1985) found that the net transmission increased with parasite burden, i.e., the number of parasites moving onto the uninfected fish increased with the parasite burden of the infected fish. Scott (1985) also pointed out that the ability of a guppy to recover from infection with *G. bullatarudis*, in addition to being genetic, was also likely to be a function of the initial infection dose. Because of the immediate exponential growth in parasite numbers that occurs, Scott (1985) regarded it as probable that all fish would succumb if infected with a large enough inoculum.

It is therefore possible that, even if *G. salaris* is an endemic species, stocking with heavily infected fish may have increased the growth of the parasite population and caused the epidemic outbreak.

The international trade with young salmon has increased with the growth of the salmon farming industry. According to Ståhl & Hindar (1988) there were about 27 million salmon smolt in salmon farms in 1986, which they estimated to be 4 times the number of smolt both naturally born and introduced by stocking in the salmon rivers. Further, according to Ståhl & Hindar (1988), in 1986 about 2 million smolt were imported to Norway from Finland and Sweden (i.e. salmon of the genetically separate Baltic Sea stock). The "Introduction Hypothesis" implicitly explains the *G. salaris* as a consequence of such import (Johnsen & Jensen 1986).

The salmon farming industry has also had other impacts on the natural populations of salmon in addition to those resulting from stocking. A considerable number of salmon escape from the farms, and many of these migrate into the rivers and this may be of epidemiological significance.

Gausen (1988) examined 54 salmon rivers from the county of Nord-Trøndelag (IV) in the north to Rogaland in the south, and found escaped farmed salmon on 23 (43%) of these. Escaped farmed salmon made up 13% of the 615 fish examined in the investigation. About 90% of the escaped fish were sexually mature. According to Gausen (1988) there was a connection between the number of escaped farmed salmon on the rivers, and the number of farms in the area.

Ståhl & Hindar (1988) estimated that escaped farm fish made up about 10% of the Norwegian river stock in 1986, and that they made up about 5% of the salmon spawning on the rivers that year.

The introduction of escaped salmon into "wild" salmon rivers has a number of effects which may be of epidemiological significance. Density, demography, behavior, and genetic structure of the local salmon populations may be altered (Ståhl & Hindar 1988, Skjervold 1988) much in the same direction as by stocking. The sum of the epidemiological effects of farming and stocking may therfore be considerable. In this connection it is interesting that the counties of Nordland (V) and of Møre og Romsdal (II) have many fish farms and many rivers with stocking as well as many rivers with *G. salaris* (**Figure 5**).

5 Conclusion

There is a clear need for further research on the taxonomy of *Gyrodactylus* of salmonids including descriptions of variation in characters in relation to host species, locality, and season. Morphometrical data sampled and treated as statistics of population parameters, despite their obvious importance, are lacking. Biochemical techniques should be applied (Rollinson & Southgate 1985).

There is presently no adequate basis for describing the geographical distribution of any species of *Gyrodactylus* parasitizing salmonids, including *G. salaris*, due to insufficient investigation and taxonomic uncertainty. There is no biogeographic basis for deciding whether *G. salaris* has recently been introduced to Norway. An investigation of the parasites of salmonids, including *Gyrodactylus*, in watercourses of northernmost Scandinavia, where several fish species have crossed the divide, would be of particular biogeographical interest. A premature conclusion about geographical origin of *G. salaris* may obscure or hinder research on important aspects of the *G. salaris* - salmon problem. Lack of such knowledge resulting in poor management could be deleterious to the salmon population. The occurrence of *G. salaris* over time and in relation to the age of salmon needs to be described in detail within a density framework. Such an approach is necessary for a better documentation and understanding of the host - parasite interaction of this system, and the magnitude of parasite induced host mortality. The role of adult salmon, and of trout and charr, in the transmission of the parasite needs further attention. Demographic traits and pathology of *G. salaris* can be elucidated through experimental work and is required to understand this dynamic system.

Stocking and salmon farming are the causal factors if *G. salaris* is a recently introduced parasite. But even if *G. salaris* is an endemic species, stocking and farming may play a significant role in causing epidemic outbreaks. This possibility must be examined.

In relation to the risk of epidemic outbreaks of communicable diseases generally, the management of the salmon populations should aim for preservation of the genetic heterogeneity of local populations and avoidance of artificial and biologically unfounded increase in salmon population density.

6 Sammendrag

Gyrodactylus salaris Malmberg, 1957 er rapportert å være en introdusert parasitt i norske lakseelver, hvor den forårsaker stor dødelighet og truer eksistensen av laksepopulasjonene. Tiltak mot parasitten er basert på disse resultatene og har som mål å utrydde den. Hensikten med denne rapporten er å gi en oversikt over litteraturen om *G. salaris* og holde denne opp mot relevant zoogeografisk, økologisk og parasittologisk litteratur for å identifisere mulige behov for videre forskning.

Implisitt i publiserte rapporter synes det som om Nord-Sverige og/eller Baltikum er antatt å være det opprinnelige området til *G. salaris*. Isolasjonen av den baltiske stammen av laks fra den øst-atlantiske stammen kan være en biologisk basis for denne hypotesen. Muligheten for at parasitten er innført til norske elver understøttes av at det er en sammenheng mellom den påviste forekomsten av *G. salaris* og utsetting av fisk fra infiserte klekkerier som har importert laksesmolt fra Finland og Sverige. Videre er det tatt som bevis for at parasitten er innført at den forårsaker omfattende dødelighet i laksepopulasjonene.

Det finnes svært få undersøkelser av parasitter hos frittlevende *Salmo salar*, og spesielt er undersøkelser som inkluderer de små monogenene iktene svært få. Det naturlige utbredelsesområdet for de ulike parasittene hos laks, inkludert *G. salaris*, er derfor i hovedsak ukjent. Forekomsten av en parasitt i et område vil ikke bety at den vil finnes i alle vertspopulasjoner innenfor området. Negative lokaliteter, særlig når de er basert på undersøkelser av få fisk, kan derfor ikke uten videre bli sett på som bevis for introduksjon til de positive lokalitetene.

Videre forskning er nødvendig på taksonomi, forekomst og utbredelse av *Gyrodactylus* på laks og beslektede arter. De taksonomiske undersøkelsene burde også inkludere biokjemiske metoder.

Den vide geografiske spredningen av de få lokalitetene der det er påvist infeksjoner på frittlevende salmonider med *Gyrodactylus*, synes å indikere at nært beslektede parasitter finnes i hele utbredelsesområdet for disse vertene.

I det nordlige Skandinavia er vannskillet mellom vassdrag som renner østover ut i Østersjøen og vestover ut i Atlanteren svært smale. I noen tilfeller er skillet dannet av vann som har avrenning begge veier. Utsetting av laksefisker har en svært lang historie i dette området. Også sik og harr, som er av østlig opprinnelse, finnes på begge sider av vannskillet. Laks går fra Østersjøen helt opp til bare kort avstand fra vannskillet i flere elver. Det må derfor undersøkes nærmere hvorvidt det smale vannskillet faktisk har fungert som barriere for immigrasjonen av *G. salaris* inn i elvene som renner vestover, dersom parasitten er av østlig opprinnelse. En hypotese om en baltisk opprinnelse av *G. salaris*, og en begrensning av dens utbredelse til dette området opptil tidspunktet for moderne lakseoppdrett, må også vurderes i forhold til den høye alderen forholdet mellom fiskene og deres monogene parasitter er antatt å ha. At disse vert - parasitt systemene er så gamle, fører til at man må anta at assosiasjon mellom laksen og dens monogene parasitter går tilbake til tiden før immigrasjonen av laks inn i Østersjøen og Nord-Atlanteren etter siste istid for bare noen tusen år siden.

Selv om det finnes noen velkjente eksempler på at introduserte parasitter har forårsaket stor dødelighet i populasjoner som ikke har vært i kontakt med parasitten tidligere, kan man stille spørsmål ved hvorvidt dette er regelen når man tar i betraktning omfanget spredning av parasitter må antas å ha i dag. Epidemiske utbrudd er i seg selv ikke noe bevis for at parasitten er innført. De fleste dokumenterte eksempler på at introduksjon har ført til epidemier refererer til parasitter som har kommet i kontakt med nye verter som er taksonomisk forskjellige fra deres opprinnelige verter. *G. salaris* er antatt å være spesielt knyttet til laks, så situasjonen tilsvarer ikke de eksempler som oftest refereres. Forskningen bør utføres for å sammenligne interaksjonen mellom *G. salaris* og henholdsvis øst-atlantisk og baltisk laks. Dette vil kreve en eksperimentell tilnærming.

De epidemiske utbrudd av *G. salaris* i norske lakseelver er blitt dokumentert ved bruk av prevalens (%) som mål på infeksjonen av ung laks, i tillegg til endringer i tetthet av lakseunger i elvene og statistikk over årlige fangster av laks i lokal og nasjonal målestokk. Nøyaktigheten av tetthetsestimater er bestandig et problem. Forholdet mellom rapporterte mengder av fanget laks hvert år og den faktiske populasjonsstørrelsen er sannsynligvis også svært komplisert. Gitt at tilgjengelig fangststatistikk har en slik nær sammenheng med størrelsen av laksepopulasjonen som publiserte rapporter antar, viser vår analyse at *G. salaris* oftest blir rapportert funnet i elvene noen tid inn i en nedgangsfase i laksepopulasjonene etter en fase av eruptiv vekst. En sammenligning mellom grupper av elver med og uten kjent forekomst av *G. salaris* indikerer at laksepopulasjonene har avtatt betydelig også i mange elver hvor *G. salaris* ikke er påvist. Estimater av den faktiske, additive dødelighet forårsaket av *G. salaris* vil derfor trenge betydelig forbedring. Til dette formål, og for å gi en sterkere vitenskapelig basis for å kunne evaluere utviklingen av epidemien, trengs det data for tettheten av parasitten (intensitet) i tillegg til prevalens. Eksperimentelt arbeid på grunnleggende populasjonsdynamiske trekk hos *G. salaris* er også nødvendig.

Det finnes flere faktorer i tillegg til en eventuell introduksjon som kan ha forårsaket epidemiske utbrudd av *G. salaris* i lakseelvene. Laksepopulasjonene i de områdene hvor utbrudd av *G. salaris* er blitt rapportert, har vært underlagt en lang rekke av endringer både av genetisk og demografisk art i sammenheng med utsetting og oppdrett. Mange av disse endringene kan ha forandret laksepopulasjonene på en slik måte at epidemiske utbrudd av parasitter blir mer sannsynlige enn i naturlige populasjoner som kan være både genetisk og demografisk mer heterogene.

7 Summary

Gyrodactylus salaris Malmberg, 1957 has been reported to be an introduced parasite into Norwegian salmon rivers where it causes gross mortality and threatens the existence of the salmon populations. Measures taken against the parasite are based on these results, and aim at its eradication. The purpose of this report is to review the literature on *G. salaris* and to relate it to the relevant zoogeographical, ecological, and parasitological literature to identify possible needs for further research.

Implicitly in published reports it appears as if northern Sweden and/or the Baltic Sea is assumed to be the area of origin of *G. salaris*. The isolation of the Baltic Sea stock of salmon from the Eastern Atlantic stock could be a biological basis for this hypothesis. The possibility that the parasite has been introduced into Norwegian rivers is supported by the association between the occurrence of *G. salaris* and stocking of rivers with fish from infected hatcheries. Salmon smolt from Finland and Sweden have been imported to such hatcheries. It has also been regarded as a proof of introduction that the parasite causes extensive mortality in the salmon populations.

There are very few investigations of the parasites of free-living *Salmo salar*, and in particular are investigations including the small monogeneans very scarce. The natural distribution area of the various parasites of salmon, including *G. salaris*, may therefore not be indicated with any degree of certainty. The occurrence of a parasite in an area does not normally imply that it may be found in all host populations within this area. Negative localities, particularly when they are based on the examination of few fish, are therefore difficult to use as proof of introduction.

Further research is needed on the taxonomy, occurrence and distribution of *Gyrodactylus* infecting *Salmo* and related genera. The taxonomic research should also involve biochemical methods.

The wide geographic scatter of the few records that exist of infections of free-living salmonids with *Gyrodactylus* seems to indicate that closely related parasites are distributed within the entire area of distribution of these hosts.

In northernmost Scandinavia the divide between watercourses draining east into the Baltic Sea and west into the Atlantic is very narrow. In some cases the divide is formed by lakes draining both ways. Anthropochor spreading of salmonids has a very long history in this area, and *Coregonus* and *Thymallus* which are of eastern origin are found on both sides. Salmon ascend from the Baltic Sea to a relatively short distance from the divide in several rivers. It has to be examined more closely if this narrow divide actually has served as a barrier for the immigration of *G. salaris* into the rivers draining west if the parasite is of eastern origin. A hypothesis about a Baltic origin of *G. salaris* and a restriction of its distribution to this area until the time of modern salmon farming has also to be considered in relation to the old age that the associations between fish hosts and their monogenean parasites are believed to represent. This would lead to the expectation that the association between the salmon and its monogenean parasites was formed prior to the immigration of salmon into the Baltic Sea and the North Atlantic following the last glaciation only a few thousand years ago. Even if there are some well known examples of introduced parasites causing gross mortality, it appears questionable if this is the rule when the possible magnitude of present-day anthropochor spreading of parasites is considered. Most documented examples also refer to parasites affecting hosts that are taxonomically different from their endemic host(s). *G. salaris* is believed to be a specific parasite of salmon, so the situation is in no case analogous to the examples most often quoted. An epidemic outbreak is not in itself proof of introduction. Research should also be carried out to compare the interaction between *G. salaris* and East Atlantic and Baltic Sea salmon respectively. This would call for an experimental approach.

The progress of the epidemic outbreak of *G. salaris* in Norwegian salmon rivers has been documented by the use of prevalence data on infection of young salmon, changes in the density of young salmon on the rivers, and statistics on the yearly catches of salmon on local or national scale. The accuracy of density estimates is always a problem. The true relationship between reported amounts of salmon caught each year and the actual population size is probably very complicated. Granted that the available data bear the relationship to salmon population size as published reports imply, our analysis show that *G. salaris* typically has been reported found in rivers some time into a decline phase of the salmon population following a phase of eruptive growth. A comparison of groups of rivers with and without known occurrence of *G. salaris* indicate that the salmon populations have declined considerably also in many rivers where *G. salaris* is not known to occur. Estimates of the actual additive mortality caused by *G. salaris* may need considerable refinement. For this purpose, and to give a firmer scientific basis on which to evaluate the progress of the epidemic, density data on the occurrence of the parasite are needed in addition to prevalence data. Experimental work on the basic population dynamic characteristics of *G. salaris* is called for.

Factors that may be alternative explanations to introduction of the parasite as a cause of the epidemic are discussed. It is observed that the salmon populations in the regions where *G. salaris* has been reported in Norway have been subjected to a number of changes of both genetic and demographic nature in connection with stocking and farming. Many of these changes may have altered the salmon populations in a way that makes epidemic outbreaks of parasites more likely than in the natural genetic and demographic more heterogenous populations.

8 Literature

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Appendix

Appendix 1: Investigations of parasites of S. salar from natural watercourses that have resulted in standard published accounts.

Reference	Location	Material	Sample size	Method +/-	Monogenea	G. salaris	Comments
Sandeman & Pippy 1967	Newfoundland, Canada	Salmon parr	23	+	D. salmonis	-	
		Salmon smolts	2	+	-	-	
		Salmon grilse	14	+	-	-	
		Salmon adults (landlocked)	27	+	D. salmonis	-	
Threlfall & Haneck 1970	Avalon Peninsula, Newfoundland, Can.	Salmon grilse	3	+ fresh	-	-	
Hicks & Threlfall 1973	Labrador coast, Canada	Salmon grilse	35	+	D. sagittata	-	
		Salmon smolts	4	+		-	
		Salmon parr	21	+	D. sagittata	-	
Haneck & Molnar 1974	Metamek river, Quebec, Can.	Salmon	18	+ fresh	D. sagittata	-	
Hare & Burt 1975a	Miramichi river system, Canada	Salmon juv.	1710	+	Gyrodactylus sp. D. sagittata	-	
Hare & Burt 1975b	Trout brook, New Brunswick, Canada	Salmon juv.	375	+ fresh	Gyrodactylus sp.	-	
Chinniah & Threlfall 1978	Labrador, Can., reservoir	Salmon adults (landlocked)	5	+/- fresh/frozen	D. sagittata	-	
Cone & Ryan 1984	Newfoundland, Can., lake	small (< 151 mm)	7	-	D. sagittata	-	
		med. (151-200 mm)	12	- frozen	D. sagittata	-	
		large (> 200 mm)	4	-	D. sagittata	-	
Pippy 1969	Newfoundland, Can., several loc.	Salmon smolts	474	- frozen	-	-	
	Labrador, Can.	Salmon smolts	34	-	-	-	
	Prince Edward Island, Can.	Salmon smolts	50	-	-	-	
	Nova Scotia, Can.	Salmon smolts	123	-	-	-	
	New Brunswick, Can., several loc.	Salmon smolts	278	-	-	-	

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Appendix 1 (cont.)

Reference	Location	Material	Sample size	Method +/-	Monogenea	G. salaris	Comments
	Maine, USA	Salmon smolts	53	-	-	-	
	North American rivers	Salmon grilse 1 year at sea	41	-	-	-	
		Salmon 2-3 years at sea	440	-	-	-	
	Greenland	Salmon 1 year at sea	97	+	G. bychowski	-	
	West Greenland	Salmon post-grilse	88	-	-	-	
	England rivers several loc.	Salmon smolts	152	-	-	-	
	Ireland rivers	Salmon smolts	283	-	-	-	
	Scotland rivers	Salmon smolts	168	-	-	-	
	SW England	Salmon 2 years at sea	32	-	-	-	
Bauer 1957	River Narova, Leningrad, USSR	Salmon juv.	200	+	Gyrodactylus sp.	-	Stocked river
Wooten & Smith 1980	River Almond, Scotland	Salmon parr	42	+	Gyrodactylus sp.	-	
Connelly & McCarthy 1984	Corrib catchment, Ireland	Salmon	24	+/- fresh/frozen	Gyrodactylus sp. D. sagittata	-	
Kennedy 1978	North Norway	Salmon smolts	30	-	-	-	
		Salmon adults	45	-	-	-	
Kennedy 1969	River Exe W Brittain	Salmon smolts	50	-	-	-	
		Salmon adults	98	-	-	-	
Thomas 1958	River Teify West Wales	Salmon smolts	274	+	- Not recorded	-	
Vik 1964	River Røssåga Norway	Salmon smolts	23	-	-	-	
		Salmon adults	2	-	-	-	
Margolis 1958	North America	Salmon	?	?	?	?	
Chubb 1967	British Isles	Salmon parr	?	?	?	?	

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