GYRODACTYLIDAE ET GYRODACTYLOSE DES SALMONIDAE

G. MALMBERG

Department of Zoology, Stockholm University - S-106 91 STOCKHOLM, Sweden

RESUME

Vingt et une espèces de *Gyrodactylus* de Salmonidae arrangées en six groupes sont présentées. Les observations concernant ces espèces dans les milieux naturels et en pisciculture sont résumées. Sur la base de données générales relatives aux espèces de *Gyrodactylus* en milieu naturel en Scandinavie et Baltique, les observations biologiques, écologiques et comportementales de *G. salaris* Malmberg, 1957 et *G. derjavini* sensu MALMBERG et MALMBERG (1987) des salmonidae sauvages des rivières norvégiennes et suédoises sont présentées.

La viviparité unique, la reproduction asexuée et sexuée et le pouvoir de reproduction chez les *Gyrodactylus* sont développés. La Gyrodactylose à *G. salaris* est abordée en milieu naturel, dans les rivières norvégiennes et en pisciculture, en Suède et au Danemark. L'étude ultrastructurale des blessures causées par *G. salaris* ainsi que les résultats expérimentaux sur les espèces norvégiennes et canadiennes sont présentés. La distribution géographique naturelle des Salmonidae, les modifications liées à l'homme et à l'activité économique ainsi que les Salmonidae élevés sont revus.

La présence de six groupes d'espèces de *Gyrpdactylus* en Amérique du Nord et Eurasie est discutée en fonction de la distribution géographique des espèces hôtes. Il est souligné qu'une propagation intercontinentale des espèces de *Gyrodactylus* de Salmonidae a dû être impossible à cause de leur origine limnique d'une part et de la salinité élevée des océans atlantique et pacifique d'autre part.

Les exigences micro et macro environnementales des espèces sont discutées dans les conditions naturelles et les variations saisonnières, préférendums et tolérances du parasitisme sont signalés. L'effet des conditions de pisciculture sur les espèces de *Gyrocactylus* sont discutées : la capacité reproductrice et de propagation ainsi que la spécificité — stricte dans la nature — peuvent être influencées. Une dérive génétique peut résulter de nouvelles formes pathogènes. Ainsi les piscicultures peuvent agir comme des centres de développement et de propagation des *Gyrodactylus*. La truite Arc en Ciel, *O. mikiss* est indéniablement l'unique nouvel hôte potentiel pour nombre d'espèces de *Gyrodactylus*.

En conclusion, il est recommandé de poursuivre sur les stocks de Salmonidae, des études concernant leur résistance aux *Gyrodactylus* pathogènes, d'étudier de manière comparative les blessures causées par différentes espèces de *Gyrodactylus*, d'étudier leur viviparité si spécifique , ainsi que les intéractions complexes des conditions micro et macro environnementales.

GYRODACTYLIDAE AND GYRODACTYLOSIS OF SALMONIDAE

G. MALMBERG

Department of Zoology, Stockholm University - S-106 91 STOCKHOLM, Sweden

SUMMARY

21 *Gyrodactylus* species, described from salmonids are presented, arranged in six *Gyrodactylus*-groups (Table I, Figs. 6-8). Findings of the species in fish farms and/or natural waters are summarized (Table II). With data from *Gyrodactylus* species in natural waters in

Scandinavia and in the Baltic as a background, biological, ecological and behavioural observations in natural waters of *G. salaris* Malmberg, 1957 and *G. derjavini* sensu MALMBERG et MALMBERG (1987) in Swedish and Norwegian rivers with wild salmon are presented. The unique viviparity, asexual and sexual reproduction and the reproductivity in *Gyrodactylus* are emphasized. Gyrodactylosis on salmonids in natural waters and fish farms is dealt with, e.g. the *G. salaris* gyrodactylosis in Norwegian rivers and in Swedish and Danish salmonid farms. The ultrastructure of wounds caused by *G. salaris* and results from Norwegian and Canadian experiments with *Gyrodactylus* species on salmonids are presented. The natural geographical distribution of salmonids, distribution by man, and economics, including culturing of salmonid species are reviewed.

With regards to the geographical distribution of the salmonid host species, the presence of the six *Gyrodactylus* species groups within North America and Eurasia (Figs. 1, 2) is discussed. It is stressed that an intercontinental spreading of *Gyrodactylus* species on salmonids might have been impossible, because of their limnique origin and the high salinity of the Atlantic and the Pacific Oceans. Macro-, micro- and mixed environmental demands of *Gyrodactylus* species in natural waters are discussed and the presence of host and parasite related seasonal variations, preferences and tolerances pointed out (Fig. 3). Influences upon *Gyrodactylus* species by fish farm conditions are dicussed: reproductive and spreading capacity, as well as a strict host specificity present in natural waters, may be influenced; genetic drift may result in new pathogenetic forms. Thus fish farms may act as culturing and spreading centra for *Gyrodactylus* species (Fig. 5). The rainbow trout, *O. mykiss*, is stressed as a unique, "new" host for a number of *Gyrodactylus* species. In conclusion it is recommended: further studies on salmonid stocks concerning differences in resistance to a pathogenetic *Gyrodactylus* species, comparative studies of wounds (Fig. 4) caused by different *Gyrodactylus* species, studies of the unique viviparity and the complicated interactions between macro- and microenvironmental conditions in *Gyrodactylus*.

1. INTRODUCTION

Culturing a fish species may result in "culturing" its ectoparasite species. The infestation may arrive via the water supply of the fish farm and/or via the routine shipments of fish. Then the infested farm may become a "spreading centrum" for the ectoparasites. Other farms may be infested via fish transports, and via the waste water from a farm; ectoparasite species may be spread to a water recipient (Fig. 5). Thus spreading of parasites between fish farms has to be expected and farmers must be ready to treat fish against ectoparasite, e.g. *Ichtyobodo* and *Gyrodactylus*.

Certainly there is a frequent spread of *Gyrodactylus* species from fish farm to fish in natural waters. Unless the spread would cause gyrodactylosis to wild fish, the infestation would scarcely be discerned. In spite of the fact that fish farming has a long history, - salmonids have been cultured for more than 100 years, - spreading of gyrodactylosis from farms to wild fish was unknown until 1975. This year, a central Norwegian salmonid farm developed problems with a severe gyrodactylosis on salmon parr. Later the same year, a severe gyrodactylosis was established on salmon parr in two geographically distributed Norwegian rivers. In course of time, it was established that the disease was caused by *G. salaris* Malmberg, 1957 and a correlation was shown between the outbreak of gyrodactylosis in an increasing number of rivers and the stocking of these rivers with parr from the infested central salmonid farm. The gyrodactylosis was fatal. After about two years of infestation the salmon parr populations in the rivers were drasticly diminished, in turn influencing the number of ascending adult salmon. Thus angling and the fishery of one of the most important salmonids were badly influenced. An annual loss of almost one fifth of the total fishing catch of salmon in Norway was estimated (DOLMEN, 1987).

The unique gyrodactylosis in rivers made matters worse. The natural reproduction of salmon was increasingly threatened by pollution of waters (industrial discharge, acid rain) and by water obstructions built for hydroelectric purposes. Salmonid farming was developing intensively, not only for compensating the natural reproduction in influenced rivers, but also for supplying smolt for the enormous cage-rearing of salmon in salt water for consumption. In both cases routine shipments of salmonids could spread *G. salaris* within Norway. Furthermore, between about 1965-85 the Norwegian cage-farming industry was to a large degree depending on smolts from Sweden and Finland, and these smolt import could imply an "import" of *G. salaris.* Various measures were taken for preventing spreading of *G. salaris* into and within Norway and great economic, scientific and practical efforts were initiated to overcome the pest (MEHLI et DOLMEN, 1986; JOHANSEN et JENSEN, 1991).

In other parts of the Northern hemisphere salmonid farming was also developing. Frequent trading and transports of farmed salmonids implied a risk of spreading *G. salaris* and caused fear of its gyrodactylosis. The knowledge about *Gyrodactylus* species and their distribution, however, was small and the fear for *G. salaris* inspired parasitological investigations on salmonids. Thus in Norway, salmon and trout were investigated (TANUM, 1983; MO, 1983). CONE *et al.* (1983) analysed and reviewed North American gyrodactylids on salmonids, ERGENS (1983) analysed and described *Gyrodactylus* species on salmonids in Eurasian freshwaters and LUX (1990) contributed with new data about gyrodactylids on salmonids in Germany. In the discussion on spreading of *G. salaris*, the Baltic area became a burning question and Swedish salmonid farms and rivers were investigated (MALMBERG et MALMBERG, 1991) and *Gyrodactylus* species from Finnish salmonid farms were discriminated (RINTAMÄKI, 1989; MALMBERG et MALMBERG, in press). Furthermore, several experimental studies on host-parasite relationships were performed (e.g. CONE et CUSACK, 1988; JANSEN, 1989; BAKKE *et al.*, 1992b). From a biogeographic and epidemiological point of view, HALVORSEN et HARTVIGSEN (1989) made a critical examination of recent and earlier data on *G. salaris.*

In the present paper for the International Symposium on Monogenea ISM II, results on gyrodactylids of salmonid, published during the last 15 years or so are compiled. Although the family Gyrodactylidae consists of several genera the present paper is delimited to species of the genus *Gyrodactylus* (Table I). Findings of *Gyrodactylus* species on salmonids in fish farms and natural waters are presented. The species are arranged in species-groups and drawings of their taxonomically important species characters are comparatively presented (Figs. 6-8). Biological and ecological characters of gyrodactylids, with special reference to gyrodactylids on salmonids is shortly presented. Salmonidae and salmonids are used in a broad sence. A summary presentation of salmonid aquaculture in the world, is given (Table II). On this basis salmonid - gyrodactylid relationships and spreading of *G. salaris* and other *Gyrodactylus* species will be dicussed (Figs. 3, 5).

2. MATERIAL AND METHODS

For the salmonid field investigations, most fish were captured by means of electrofishing, kept, transported, killed and investigated in accordance with MALMBERG (1970, p. 8, 9). If possible, slides were made of at least 10 *Gyrodactylus* specimens per host species, per locality, per visit (MALMBERG et MALMBERG, 1991). Each *Gyrodactylus* specimen was fixed in vivo between slide and cover glass in ammonium picrate-glycerin (MALMBERG, 1957; 1970). The slides were labeled in accordance with (MALMBERG, 1970, p. 12). For the species discrimination, comparative studies of slides from my *Gyrodactylus* collection (in the Section of Invertebrate Zoology, Swedish Museum of Natural History) and borrowed slides of a few *Gyrodactylus* species were used. Drawings of anchors, ventral bars and marginal hooks were made by means of a phase contrast microscope (ocular 10x ; objective 90x, oil immersion) and a drawing prism (for the equipment, see MALMBERG, 1970).

The drawings were compared to similar drawings published by other authors. For this purpuse, the latter drawings were redrawn at a certain magnification by means of a Liesgang Antiskop (Germany) equipment: the scale bar of a published drawing was made equal to the scale bar for my own drawings via the microscope (Figs. 6-8). All drawings were then compared in an illuminated bench (MALMBERG, 1970). The method cannot replace a comparison of *Gyrodactylus* specimens based on drawings made via the same microscope. It is sufficient, e.g. for getting the proportions of different parts of an anchor but not for the comparison of more detailed parts, e.g. marginal hooks sickles. The marginal hooks in Figs. 6b and 7a, b may be an example.

Fins of *G. salaris* infested salmon parr specimens (Sundalsøra, Norway) were fixed for scanning electron microscopy (SEM) in a cold solution of 2.5 % glutaraldehyde in 0.1 M sodium cacodylate buffer, post fixed for 1 h in a cold 1% solution of osmium tetroxide, dehydrated in ethanol and acetone, transferred to acetone, critical-point dryed (Balzers) and coated with gold in a sputtering device (Balzers). A Zeiss Novascan 30 was used for the SEM investigations.

3. GYRODACTYLIDAE

The gyrodactylids are parasitic platyhelminths belonging to the class Monogenea, or haptor worms. At the rear end these parasites have an adhesive locomotory organ (haptor/opisthaptor), armed with hooks. The Gyrodactylidae includes several genera. Most species are ectoparasites on fish and have a body length of about 0.5-1 mm. The majority of species belongs to the genus *Gyrodactylus*. *G. elegans* Nordman, 1832 was the first species described. Today more than 350 species are known, of which about 20 are known to parasitise salmonids.

3.1. The genus *Gyrodactylus* : species discrimination, subgenera and species groups

The species discrimination in *Gyrodactylus* is mainly based on the haptoral hooks. Thus the precise shape (phase contrast microscopy) of marginal hooks (especially the marginal hook sickle), anchors and ventral bar provide the "species formula" (Figs. 6-8). Species of a subgenus have a common type of protonepridial system (MALMBERG, 1970). Species within a subgenus, having common types of anchors and ventral bars can be arranged in species groups (MALMBERG, 1964; 1970).

Table 1 presents the characteristics of six species groups with species parasitizing salmonids.

3.2. Subgenera of *Gyrodactylus* species on salmonids

G. salaris and *G. derjavini* sensu MALMBERG et MALMBERG (1987) belong to the subgenus *Gyrodactylus (Limnonephrotus)* Malmberg, 1964. Their protonephridial systems lack bladders and lateral flames in the main canals; their pharynx has long pharyngeal processes. This is also valid to *G. nerkae* (see Table I) and most likely also the closely related species *G. salmonis*. Other species, below presented under the *G. salaris*- and the *G. wageneri*-groups, presumably belong to the *G. (Limnonephrotus)*. According to KIKUCHI (1929) the protonephridial system of *G. japonicus* lacks excretory bladders. This may imply that this species and the other two species of the *G. japonicus*-group are members of the *G. (Limnonephrotus)*. *G. taimeni* and *G. bolonensis*, the *G. taimeni*-group, however, might belong to another subgenus (Table I).

Because of the characteristic shape of its anchors and ventral bar, *G. colemanensis* certainly is a member of the *G. arcuatus*-group. The member of this group have a protonephridial system with lateral flames in the main canals and small excretory bladders. In 1970, in the U.S.A, I studied the protonephridial system of fresh water members of the *G. arcuatus*-group (Table I).

Remark. *G. avalonia* Hanek et Threlfall, 1969 is most likely a member of the *G. arcuatus*-group and *G. brevis* Crane et Mizelle, 1967, certainly a member of the subgenus *G. (Gyrodactylus)*. Although the two species are described from salmonids, they are not included here because of their "accidental" presence on salmonids (see CONE *et al.*, 1983).

3.3. Geographical distribution of *Gyrodactylus* species on salmonids

Since the early beginning, salmonid farmers had problems with gyrodactylosis. Because the treatment could be performed without any species discrimination of the parasite, the infesting pathogen was simply called *G.* sp. (or incorrectly *G. elegans*; see CONE *et al.*, 1983; ERGENS 1983). Furthermore, because of taxonomic problems species of several faunistic investigations were incorrectly discriminated (MALMBERG, 1964). Consequently, knowledge about the presence of *Gyrodactylus* species on salmonids in fish farms and natural waters is still rather small. Further investigations are urgently needed to increase our knowledge of the natural distribution of *Gyrodactylus* species on salmonids (HALVORSEN et HARTVIGSEN, 1989).

3.4. Biology, ecology and behaviour of *Gyrodactylus* species

3.4.1. *Gyrodactylus* species in Scandinavian waters and in the Baltic area

G. salaris Malmberg, 1957 was the first species described from a salmonid host *(S. salar)* within the Baltic region. The original material of the species was obtained already in September 1952. In 1958, *G. derjavini* sensu MALMBERG et MALMBERG was found on *S. trutta* within the Atlantic region of Sweden. The studies of *G. salaris* and the *G. derjavini* in question, were included in a project dealing with *Gyrodactylus* species within different geographical areas of North-Western Europe (northern Norway - northwestern Germany), and was performed between the years 1951 and 1969. The *Gyrodactylus* fauna of the Baltic area was compared to other areas of the project. Taxonomy, morphology, ecology and behaviour of about 85 *Gyrodactylus* species from fish species in fresh, brackish and salt water were discerned and the same methods (including the microscopic equipment) was used for the study (MALMBERG, 1964; 1970). Results regarding *Gyrodactylus* species were obtained: presence in different types of fresh water, presence in brackish and salt waters, seasonal fluctuations, species specificity, organ specificity, temporary hosts, influence by "wrong hosts" in mixed samples of fish species, infestation intensity of fish of different size and age, influence of macroenvironmental change, spreading behaviour, spreading capacity, active and passive spreading. It was established that *G. salaris* and *G. derjavini* belongs to G. *(Limnonephrotus)*, and that the members of this subgenus are present only in fresh and brackish water (salinity approx. 5.5-6 ‰). This long-range investigation on *Gyrodactylus* species in the Baltic region is of a special interest to the discussion on *G. salaris*, its presence and spreading within Scandinavia.

3.4.2. *G. salaris* and *G. derjavini* sensu MALMBERG et MALMBERG on salmonids in Swedish rivers with wild salmon.

MALMBERG et MALMBERG (1991) investigated *S. salar* and *S. trutta* in Swedish rivers with wild salmon, i.e. a river with a salmon population based on natural reproduction. 9 rivers containing the Baltic stock (Baltic area) and 6 containing the Atlantic stock (Atlantic area) were investigated. *G. salaris* was found on *S. salar* in 3 rivers of both areas.

The highest intensity of infestation was repeatedly found in one of the rivers within the Atlantic area. In November 1991, precocious males in this river were more infestated (maximal intensity approx. 800-1.000) than other salmon parr, simultaneously investigated (MALMBERG et MALMBERG, in press). In September, 1992, in another branch of the same river system, ALENÄS (1992) found two yearlings (4.4 and 4.8 cm) of Atlantic salmon parr with 900 and 1.300 *G. salaris* specimens, respectively. Repeated investigations on migrating smolts from this river system, from a second river with the Atlantic stock, and from a northern river with a Baltic stock indicated an increased intencity of infestation (highest intensity approx. 815). No investigations hiherto have revealed mortal infestation, but a balanced *G. salaris* situation in the infested Swedish rivers.

G. derjavini sensu MALMBERG et MALMBERG was found on *S. trutta* within the Baltic region, in two of the southern rivers and in one more river in mid-Sweden. In the last river a trout parr had about 130 *G. derjavini* specimens. Within the Atlantic region, *G. derjavini* sensu MALMBERG et MALMBERG was found on *S. trutta*, in one of the rivers with wild salmon and in two additional rivers. The species was also found on *S. salar* in rivers with wild salmon: two rivers within the Baltic and one river within the Atlantic region. Within the northern half of Sweden, *G. derjavini* was not found in natural waters (MALMBERG et MALMBERG, 1991).

3.4.3. *G. derjavini* sensu MALMBERG et MALMBERG and *G. salaris* in Norwegian rivers.

In a southern river in eastern Norway, MO (1983; 1992) studied *G. derjavini* sensu MALMBERG et MALMBERG on *S. trutta* and *S. salar*. The infestation intensity varied between 1 and 3.500 on *S. trutta* and 1 and 95 on *S. salar*. The prevalence and abundance on both fish increased during the spring and summer and decreased during the autumn and winter. *G. salaris* was not present in this river.

MO (1992) also studied *G. salaris* on *S. salar* in a more northern river in Western Norway. The lowest intensity of infestation was found in the winter following a period of two-three months with water temperatures just over 0°C. In the early autumn on yearling and older parr, about 1.150 and 4.400 specimens could be found, then the abundance decreased. The infestation intensity of *G. salaris* on salmon parr varied between one and 12.500. Most parasites were found on the dorsal fin (about 35 %) and on the pectoral fins (27%).

JENSEN et JOHNSEN (1992) found that salmon parr from the river Lakselva (N Norway) were infested with between 1 to 10625 specimens of *G. salaris*. At an intensity of infestation of less than 100 specimens, the dorsal fin was the principal site of attachment and at an intensity of over 1000 specimens, the body was also infested. JANSEN et BAKKE (1992) found that during the summer the infestation of *G. salaris* on salmon parr in the river Lierelva (SE Norway) increased more rapidly on 0+ specimens than on 1+ specimens. The difference was presumed to depend on an increased resistance with increasing age of the parr.

3.5. Viviparity, reproductive capacity, asexual and sexual reproduction

3.5.1. Development of oviparous and gyrodactylid monogeneans

Most monogeneans are oviparous. Generally, the eggs are produced, encapsuled, released or attached to the substratum. The eggs of most species develops into a ciliated larva (oncomiracidium), which after leaving the egg will have to find its way to a specific host. On the host the ciliation is lost, and by creeping as a leech the larva must find the way to a specific organ (often gill filaments). There it will develop into an adult.

The gyrodactylids are viviparous. The fertilized egg develops in the uterus of the parent by means of a unique cleaving process, resulting in a number of embryos developing one inside the other. When the outermost embryo is developed to a full-grown worm, it is born carrying the other worm anlages in its own uterus. The innermost embryo is still an egg, ready to start its cleavage (TURNBULL, 1956; BYCHOWSKY, 1961; BRAUN, 1966).

After a birth, the parent´s uterus is empty and a new, fertilized egg will enter its uterus, and the development of embryos inside each other may start again.

The new-born worm will immediatly attache to its host. Thus, compared with an oncomiracidium, a new-born *Gyrodactylus* is excepted from the hazardous swimming needed to find a suitable host.

3.5.2. Reproductive capacity

Comparative studies of *Gyrodactylus* species in natural waters indicated a different reproductive capacity (MALMBERG, 1970). Laboratory experiments on the viviparity of *Gyrodactylus* likewise indicate species differences. The fertilized egg entering the uterus may give rise to three (TURNBULL, 1956) or four (BYCHOWSKY, 1961; BRAUN, 1966) embryos (one inside the other) before the outermost one will be born as a full-grown worm.

The birth rate was found to depend on the macroenvironmental temperature. Birth could happen between 18, 24 or 36 hours (TURNBULL, 1956; SCOTT, 1982; SCOTT et NOKES, 1984). BRAUN (1966) found that after the birth of the outermost embryo/worm the innermost egg continued the cleavage: via the birth of different generations, one single original egg could give rise to at least 12 full-grown worms.

GLÄSER (1969) presumed the life-span of a *Gyrodactylus* to be about 12-15 days. Other estimations are about 30 days. SCOTT (1982) found that the *Gyrodactylus* species in his experiment had “an average fecundity of 1-68 offspring during its expected life-span of 4-20 days”. Most likely, the-life span of a *Gyrodactylus* specimen is species connected. It may also be dependent on macroenvironmental conditions, e.g. the water temperature.

3.5.2. Asexual and sexual reproduction

Gyrodactylids are hermaphrodites. The female reproductive organs develop before the male reproductive organs (protogyny). Thus a new-born worm is prevented from copulation and cannot contribute to cross fertilization until its male reproductive system is full-developed. The new-born worm, developed from the fertilized egg, represents together with the two or three worm anlages in its uterus a first, sexually reproduced generation. When the second or third of these worm anlages, respectively is fully-developed and borned the egg/embryo in its uterus may continue the cleavage processe and parthogenetically give rise to a number of new asexual reproductions (BRAUN, 1966). Thus a population of *Gyrodactylus* species on a host specimen may consist either of sexual and asexual reproduced specimens, or a mixture of such specimens.

HARRIS (1989) studied the interaction between population growth and sexual reproduction and discussed the importance of copulation, insemination and cross-fertilization. He found that copulation especially occured between worms sitting crowded in supra-populations (large intensity of infestation), but not between few specimens on a host. He concluded that a supra-population was the result of asexual reproduction and presumed that prolonged sexual reproduction in such populations could result in strains with novel combinations of traits, implying specimens with drug resistance, altered host specificity and pathogenicity.

4. GYRODACTYLOSIS

Presumably, different *Gyrodactylus* species influence the host epithelium differently (CONE et ODENSE, 1984). The marginal hooks of the gyrodactylid cause small wounds. The pharynx, however, may cause much larger wounds by resolving the host epithelium (Fig. 4a). This is the case with *G. salaris*. In specimens of the Norwegian Atlantic salmon the latter wounds seem to have a problematic healing (Fig. 4b). Furthermore, the wounds may lead to secondary infestation by bacteria and fungi.

Most likely only certain species are pathogenic, depending on species differences concerning, e.g. reproductive capacity, spreading capacity and macroenvironmental demand. Initially, the organ specificity of a *Gyrodactylus* species may delimit the gyrodactylosis to a certain part of the body, e.g body surface, the fins or the gill filaments (JENSEN et JOHNSEN, 1992).

4.1. Gyrodactylosis in natural waters

On fish in natural waters, specimens of one or more host specific *Gyrodactylus* species may be present. The intencity of infestation may differ, depending on species-connected capacities. In natural waters, mass-infestation by gyrodactylids is rare (MALMBERG, 1957). A pathogenic, mortal infestation on fish locked in rook-pools was observed by PETRUCHEVSKY et SHULMAN (see MALMBERG, 1970). ERGENS (1983) described a mortal gyrodactylosis caused by *G. derjavini* Mikailov, 1975, in rivers in Azerbaidzhan and Tadzhikistan; specimens of *Salmo trutta caspius* and *S. trutta oxianus* were killed by the parasite. Most threatening is the *G. salaris* gyrodactylosis on salmon parr in Norwegian rivers.

4.1.1. The gyrodactylosis on salmon parr in Norwegian rivers.

In 1975, a central salmonid farm in Sundalsøra at the River Driva (SW Trondheim), Norway developed severe problems with gyrodactylosis on salmon parr (the Norwegian Atlantic stock). At this time, farmers in Norway were unfamilar to *Gyrodactylus* and gyrodactylosis. I was asked to make a species discrimination, and studies of received specimens indicated an infestation by *G. salaris* (see JOHNSEN, 1978). In Swedish farms, *G. salaris* infestations of the salmon parr (the Baltic stock) was successfully controlled by means of formalin. The same method was tried in Sundalsøra, but found to be ineffective (VASSVIK, 1976).

In August 1976, salmon parr in a northern Norwegian river were found to suffer from a severe *G. salaris* gyrodactylosis. In course of time, this gyrodactylosis was establish in several other Norwegian rivers, among them the river receiving the waste water from the Sundalsøra farm. Then a correlation was shown between compensatory stocking with salmon parr, mainly from Sundalsøra, and an outbreak of gyrodactylosis in the stocked rivers.

For coping with the *Gyrodactylus* problem and preventing the spread of the gyrodactylosis within Norway, different means were taken. Thus in 1983, *G. salaris* was declared a notifiable disease. Infested fish farms were localized and treated against *Gyrodactylus*. For preventing the spread of the parasite by migrating salmon, barriers were built between infested lower and uninfested upper parts of a number of river systems. In order to clean rivers from *G. salaris*, all fish populations of suitable rivers were exterminated by means of rotenon. The rivers were then recolonised by ascending adult salmon (JOHNSEN et JENSEN, 1991).

Furthermore, a number of scientific programs were initiated. Thus more than 200 rivers were investigated (TANUM, 1983; HALVORSEN et HARTVIGSEN, 1989) and at the end of 1989 *G. salaris* was registered in 34 rivers and in about 35 hatcheries, scattered throughout the country (JOHNSEN et JENSEN, 1991). Running experimental investigations on *G. salaris* were also initiated in Oslo (TANUM, 1983; BAKKE *et al.*, 1992b).

In the majority of the *G. salaris* infested rivers the mass-infestation or gyrodactylosis correlated a drastic diminishing of the salmon parr reproduction. Consequently, a reduced number of adult salmon were ascending for spawning in the infested rivers. In turn, this caused a drastic reduction of the Norwegian fishing catch in both the sea and rivers. Thus the annual loss during the last twenty years is estimated at about one fifth of the total salmon fishing catch (DOLMEN, 1987).

4.1.2. *Gyrodactylus* and gyrodactylosis in salmonid farms

On fish in confinement gyrodactylosis is common. In a short time, an initial low infestation may turn into a severe infestation which has to be treated (see for example SCHÄPERCLAUS, 1991; THONEY et HARGIS Jr., 1991; SANTAMARINA *et al.*. 1991; SCHMAL, 1991; TOJO *et al.,* 1992).

4.1.2.1 *Gyrodactylus* and gyrodactylosis in North American salmonid farms

The earliest information about gyrodactylosis in salmonid farms are from the USA. Thus in 1899, young specimens of *Salvelinus namaycush* in a salmonid farm in Maine (NE USA) were found to be heavily infested and suffering from a severe gyrodactylosis. Furthermore, a general infestation (but not gyrodactylosis) was also established on "wild fish" in the stream at the farm (WARD et WHIPPLE, 1918; VAN CLEAVE, 1921). "Wild fish" might refer to *S. namaycush.* If so, the report represents one of the earliest descriptions of *Gyrodactylus* on salmonids in natural waters.

From the first five decades of this century, there are several reports on gyrodactylosis in North American salmonid farms. None of the pathogens, however, received a correct species discrimination. On the whole, the first adequate description of *Gyrodactylus* on a salmonid host is *G. colemanensis* Mizelle et Kritsky, 1967. The host was *Oncorhynchus mykiss* (Syn. *Salmo gairdneri)* and the locality a fish farm in California. About 15 years later, CONE *et al.* (1983) reviewed the *Gyrodactylus* species on salmonids in Canada and USA. For their presentation they used specimens collected from wild and cultured salmonid fish across the North American continent and made a comparative taxonomic analysis of the specimens. Obviously, most specimens were from farms, rather few from natural waters. In the collection, only five species were recognized. Three of them seem to be specific to salmonid hosts : *G. nerkae* Cone, Beverley-Burton, Wiles, McDonald, 1983, *G. salmonis* Yin et Sproston, 1948 and *G. colemanensis* Mizelle et Kritsky, 1967. Most likely, the remaining two species : *G. avalonia* Hanek et Threllfall, 1969 and *G. brevis* Crane et Mizelle, 1967 were accidentally present on the salmonids, while they are excluded from the present paper.

4.1.2.2. *G. salaris* and gyrodactylosis in Swedish salmonid farms

Between 1951 and 1960, the Salmon Research Institute had a salmonid farm and a laboratory, the Hölle Laboratory, at the river Indalsälven (N Sweden). The laboratory was the Swedish research centre for salmonid reproduction. The institute was moved but the farm is still present. The farm water was (is) taken from the river, which flows into the Baltic. Salmon (the Baltic stock) and trout were (are) cultured.

In 1952, salmon parr in the farm had a *Gyrodactylus* infestation. On formalin fixed specimens from this infestation, the species *G. salaris* Malmberg, 1957 was described. In 1957, live specimens of *G. salaris* from the Laboratory were studied and the structure of the protonephridial system and the unusual wide range of variation of the parasite's opisthatoral hard parts were studied (MALMBERG, unpublished; see also TANUM, 1983, Fig. 11). In April 1954, the salmon parr at the farm of the Hölle Laboratory were also infested by *G. salaris.* Most troughs were stocked with parr of the Baltic stock, but two troughs were stocked with parr of the land-locked Atlantic stock from the River Gullspångsälven (falling into the Lake Vänern). All parr in the farm had the same farm conditions. It was found, however, that the parr of the Atlantic stock was more vulnerable to, and more difficult to treat against *G. salaris* than the parr of the Baltic stock. In March 1990, the salmon parr in the Hölle farm were likewise infested with *G. salaris.* In June 1992, however, no specimens of *G. salaris* were found in the farm (unpublished).

For the time 1961-1985, annual reports from the Salmon Research Institute of Sweden presented seven years, when *Gyrodactylus* was found on salmon in Swedish farms. No species discrimination was performed, but most likely *G. salaris* was the infesting species. Whether or not the parasite caused gyrodactylosis was not presented (MALMBERG et MALMBERG, 1991).

In Sweden, the summer 1988 was hot and dry. A salmonid farm at the River Mörrumsån (SE Sweden) had some water supply problems and also a problematic gyrodactylosis on the salmon (the Baltic stock). Unfortunately, no species discrimination was performed (personal communications). In November the same year, however, it was established, that parr from the farm harboured *G. salaris.* The River Mörrumsån belongs to one of the investigated rivers with wild salmon and *G. salaris* (see MALMBERG et MALMBERG, 1991).

MALMBERG et MALMBERG (in press) investigated salmonid farms and found *G. salaris* on 5 out of 12 investigated farms within the Baltic region and in 2 out 6 investigated farms within the Atlantic region.

4.1.2.3. *G. derjavini* sensu MALMBERG et MALMBERG in Swedish and Danish salmonid farms

In 1958, for the first time the above species was found on *S. trutta* in a small river in mid-Sweden (Atlantic region). In 1972, the same species was found in a small river and also in a fish farm receiving its water supply from the river. In the farm, the species was present on *O. mykiss*, *Salvelinus alpinus* and *Salvelinus fontinalis* (*S. trutta* was not investigated; MALMBERG et MALMBERG, 1991). According to the farmer, *Gyrodactylus* never caused problems to the farm.

In 1972, the species was also found in three Danish farms with *O. mykiss*. In one of them, the rainbow trout was mass-infested by the parasite (MALMBERG, 1973). According to the farmer, the rainbow trout were regularily treated for preventing gyrodactylosis.

MALMBERG et MALMBERG (in press) reported *G. derjavini* from 2 out of 12 investigated farms in the Baltic and in 1 out 6 farms in the Atlantic region.

5. *Gyrodactylus* on salmonids in laboratory experiments

5.1. Experimental investigations with *G. salaris* in Norway.

Since the begining of the 1980s, host-parsite relationships of *G. salaris* have been intensively studied in Norway. BAKKE et JANSEN (1992) found that *G. salaris* under laboratory conditions can live and reproduce (apart from *S. salar*) on *S. trutta*, *O. mykiss*, *Salvelinus alpinus*, *Salvelinus namaycush*, *Salvelinus fontinalis* and *Thymallus thymallus*, but not on *Coregonus lavaretus*. According to BAKKE *et al.* (1990a) *G. salaris* can reproduce neither on *Lampreta planeri* (Bloch), *Rutilus rutilus* (L.) nor *Perca fluviatilis* L.; and according to BAKKE et SHARP (1990) not on *Phoxinus phoxinus* (L.). On a basis of laboratory experiments, BAKKE *et al.* (1991) and BAKKE *et al.* (1992a) concluded that also in natural waters *O. mykiss* and *Salvelinus fontinalis* could be a suitable hosts for *G. salaris* and transmit the parasite to other fish species.

JANSEN (1989) found that the life-span of *G. salaris* was longer at 2.6°C (maximally 34 days) and shorter at 19.9°C (4.5 days). *G. salaris* gave birth to more worms between 6.6°C and 13.0°C (average 2.4 worms) than at other temperatures. The birth rate increased with increased temperature. SOLENG et BAKKE (1991) found that a population of *G. salaris* could survive "for days" in water of a salinity of 10‰, and "for months" in 7.5‰.

BAKKE *et al.* (1990b) found that salmon parr of the Neva stock (Baltic salmon stock) demonstrated both an innate and an aquired resistance towards *G. salaris*, in contrast to parr of the Norwegian Atlantic stock, which was higly susceptible. According to JANSEN *et al.* (1991) the growth of a *G. salaris* infra-population was continuously slower on parr of the Neva stock than on parr of the Norwegian Atlantic stock. BAKKE et MacKENZIE (1992) experimentally infested salmon parr of the Atlantic stock from two rivers in Scotland and one in Norway, with *G. salaris* from naturally infested Norwegian salmon parr. Infestation intencities of 1.600 to maximally approx. 4.000 *G. salaris* were recorded on all three stocks. They found that the Scotish as well as the Norwegian stock of the Atlantic salmon were sensitive to *G. salaris*.

5.2. Exprimental investigations with *G. salmonis* and *G. colemanensis* in Canada

CONE et COSACK (1988) studied the infestation of *G. salmonis* and *G. colemanensis* at a fish farm in Nova Scotia (SE Canada). At this farm *O. mykiss* was obtained annually from another farm, while *Salvelinus fontinalis* was constantly kept at the farm. They presumed that the two *Gyrodactylus* species were repeatedly introduced by the routine shipments of salmonids and by specimens of *S. salar* and *S. fontinalis* that were frequently entering the farm via the water supply (a river). On S. fontinalis, the two *Gyrodactylus* species showed behavioural differences : *G. colemanensis* clinged delicately to the edges of the fin, while *G. salmonis* infested all the body, except the fin edges, and embedded its marginal hooks deep into the skin. Both species were most abundant at a water temperature of 8°C or less. The intensity of infestation generally decreased with host age. A mixed infestation was subsequently changed: first into a *G. salmonis* infestation then into a *G. colemanensis*, and then again into a *G. salmonis* infestation. No infestation caused gyrodactylosis.

At an experimental infestation of *O. mykiss* with *G. colemanensis* in the same farm, CUSACK (1986) found no clinical sign of disease. Neither did the infestation influence growth or survival of the host specimens. In this case *G. colemanensis* was transferred from yearlings of *Salvelinus fontinalis*. CONE et ODENSE (1984) studied the attachment-site of five *Gyrodactylus* species, among them *G. salmonis* on fingerlings of *O. mykiss*. The fingerlings were obtained from a fish farm in Idaho (NW USA) and were heavily infested. *G. salmonis* differed from the remaining four *Gyrodactylus* species in lodging the marginal hooks deep into the host skin of *O. mykiss*, and seemed to cause extensive fin damage and skin discoloration. The fingerlings had from less than 15 to more than 40 worms. Bacteria present on *G. salmonis* were presumed to cause a secondary infestation of the host. CUSACK et CONE (1986) experimentally infested fry of *Salvelinus fontinalis* with *G. salmonis*. The infestation caused mortality. Changes of epidermis and in the kidney were observed. The parasitic activity was presumed to cause disruption of the osmotic permeability of the host epidermis and finally the death of the fry.

6. SALMONIDAE

Members of the following genera are included : *Salmo, Oncorhynchus, Salvelinus, Hucho, Brachymystax, Plecoglossus, Thymallus, Coregonus, Osmerus, Hypomesus*.

6.1. Distribution of salmonids

Naturally, the salmonids are distributed within the Northern Hemisphere (Table II; Fig. 2). Several species are characterized by a pronounced ability to develop local forms. Species of the genus *Salmo* occur on both sides of the Atlantic Ocean while members of the genus *Oncorhynchus* are present on both sides of the Pacific Ocean. Several salmonid species have been distributed to new areas by man (Table II).

6.1.1. *Salvelinus*; natural distribution and species distributed by man

Natural distribution : The Arctic charr, *Salvelinus alpinus* (L.) is the most northerly found salmonid species and has a circumpolar distribution. Thus the same species is present in the northern parts of both the Eurasian and the North American continents. The original distribution of the brook charr/trout, *S. fontinalis* Mitchill and the canadian charr, *S. namaycush* (Walbaum) is the northeastern and northern parts of North America, respectively.

Species distributed by man : *S. fontinalis* and *S. namaycush* were introduced to Europe, e.g. Scandinavia for culturing. In certain areas they may reproduce in natural waters. *S. fontinalis* were introduced to the Falkland Islands.

6.1.2 *Salmo*; natural distribution and species distributed by man

Natural distribution : The species *Salmo salar* L. is originally present in eastern North America, in Greenland and in western Eurasia (Fig. 2). It consists of three major, genetically distinct groups: the Western Atlantic salmon stock (Canada, NE USA), migrating between the northeast coasts of America and southeastern Greenland; the Eastern Atlantic salmon stock (W Scandinavia), with groups of stocks migrating between Scotland-northeastern England, France and southeastern Greenland and other groups of stocks migrating along western Norway, to Scotland, to southeastern Norway and to the White Sea; the Baltic salmon stock, migrating to and growing up in the southern Baltic.

Salmo trutta : the original distribution area of *Salmo trutta trutta* L. mainly covers that of the Eastern Atlantic and the Baltic salmon stocks together (Fig. 2). *Salmo trutta fario* L., however, originally belongs to mid-European fresh waters. Another subspecies is present in eastern Europe and around the Black Sea. A third subspecies, *S. trutta caspius* L., is distributed in an area around and north of the Caspian Sea and a forth species is mainly present in the most northwestern part of Africa, in Corsica, Sardinia, Greece, Cyprus and southern parts of Turkey.

Species distributed by man : *S. salar* has been introduced to the Southern Hemisphere and is presently cultured in Chile, in the Falkland Islands and in Australia. *S. trutta* has been intruduced to the North American continent and is cultured in Canada and USA. On the Falkland Islands introduced specimens have established anadromous populations.

6.1.3. *Oncorhynchus*; natural distribution and species distributed by man

Natural distribution: The native range of the rainbow trout, *O. mykiss* (Walbaum) was the eastern Pacific Ocean and western fresh waters from northwest Mexico to rivers in Alaska (Fig. 2). *Oncorhynchus gorbuscha* (Walbaum) and *O. keta* (Walbaum) are distributed in northeastern

Eurasia and northwestern North America. *O. masu* (Brevoort) is distributed along the Asiatic shores from Korea and Japan to the Kamchatka Peninsula.

Species distributed by man : *Oncorhyncus mykiss*, the rainbow trout is widely spread by man. In North America, it is widely introduced outside its natural range. Possibly in 1874, the spread within USA was initated. In 1887, it was introduced into Newfoundland, and in 1895 into the Great Lakes, Canada. At the end of the 19th centuary, the rainbow trout was introduced from North America in form of eggs to Japan and Europe. Since the introduction in 1877 to Japan, an import has continued (OGAWA, 1986). Already by the 1890s, the species was cultured in Denmark and during the first 30 years or so of this centuary, Denmark was exporting rainbow trout to a farm in Central Sweden (KÄLLEFALL, TIDAHOLM; comm. pers.). Today the species is cultured in North America, South-America, the Falkland Islands, Europe (see also Table II), southern Asia, Japan, Hawaii, Australia, New Zealand, Tasmania and Africa. Thus farming has made the rainbow trout the most widely spread salmonid.

6.1.4. Other salmonids; natural distribution

Brachymystax lenok (Pallas) is distributed in Siberian rivers from the River Ob to the River Kolyma and is common in the Amur River. It never enters saline waters.

Hucho taimen (Pallas) is distributed in Eurasia from the Volga and Pechora rivers in the west to the Amur water basin in the east.

Plecoglossus altivelis Temmick et Schlegel is an anadromous species present in Japan, Taiwan, Korea and east China. The adults descend the river and spawn in the river mouth. The alevins migrate into the sea and feed there for one year, before returning to the river.

Thymallus thymallus (L.) has a west-Eurasian distribution, but there are forms or subspecies in eastern parts of Russia and Siberia. *Thymallus arcticus* (Pallas) is present both in Kamchatka and in northern parts of North America.

Hypomesus olidus (Pallas), an osmerid, inhabits the Asiatic coast of the Pacific Ocean and the eastern part of the Arctic Ocean. *H. olidus* bergi Taranetzis lives in the lakes of Sakhalin and the rivers of eastern Siberia and the Amur basin (NIKOLSKII, 1961).

Coregonus : the genus is present in northern Eurasia and northern North America. *C. pidschian* (Gemlin) occur from Alaska through Siberia to north- and mid-Sweden. *C. lavaretus* (L.) is distributed from Scotland through northern Russia, *C. nasus* from Scandinavia to Kamchatka.

6.2. Life cycles of salmonids

The majority of salmonid species spend the first part of their life cycle in running fresh water. Many species have both stationary and anadromous forms and spawn in the autumn or early winter in rivers. In late winter or early spring time, the youngest specimens (alevins) start their life in the river. The length of development is temperature and food dependant. In nature, the development of e.g. anadromous forms of *S. salar* L. and *S. trutta* L., trough fry and parr into smolts, differs from one to several years. In spring time or early summer, the smolt leaves the river. Generally, in Scandinavia, this development is shorter (one to two years) in more southern rivers and longer (three years or more) in northern rivers.

6.3. Economics and human influences on salmonids

Several salmonid species are highly prized as sport fishes. Salmonids have traditionally been an important food fish, and their fishery has always been of great economic value. Furthermore, since the begining of the 1970s a salmonid food industry has developed intensively and increased the economics even more. During the last centuary, however, the existence of salmonids has gradually been threatened. In fresh waters, environmental changes, e.g. pollution, acidification, water obstructions for hydroelectric purposes, have diminished the original distribution or caused extinction of many salmonid species.

In salt and brackish water, increased catches, for example, for the the Baltic salmon, have drastically diminished the number of adults, ascending their specific rivers for spawning (MONTÉN, 1988; ACKEFORS *et al.*, 1991). Some of the ascending adults may reach their spawning areas (if present), other adults are caught and used for the brood stock for parr/smolt production for either restocking purposes or for the aquaculture industry. The farming is partly perfomed for compensating a diminished or vanished natural river reproduction, caused by waters regulated for hydroelectric purposes. In this case, smolts are released into the sea. Large numbers of the cultured salmon smolts, however, are used for an intensive food production in cages, mainly in salt and brackish water. The use of only a relatively small brood stock in salmonid cultivation threatens to diminish the genetic basis of the original, natural variability of the salmon (ACKEFORS *et al.*, 1991).

6.4. Cultivation of salmonid species

Salmonid cultivation (Table II) is a rather young industry. In U.S.A., Japan and Central Europe, it started at the latter end of the 19th centuary. Initially, ponds were mainly used, e.g. in Europe for culturing brown trout, *Salmo trutta* L., rainbow trout, *Oncorhynchus mykiss* (Walbaum) and brook trout/charr, *Salvelinus fontinalis* Mitchill. The farming was aimed at food production, but also for producing young stages of salmonids to be released in natural waters. In connection with the latter type of farming an intensive rearing of parr and smolt was developed, using troughs or basins with circulating, running water and mostly with a very large density of individuals. Since the early 1950s this type of farming (MONTÉN, 1988) has been used for producing large amounts of parr and smolts for compensatory purposes (e.g. *S. salar* and *S. trutta*), and since the mid-1970s, for cage rearing, (especially *S. salar* and *O. mykiss*).

Local forms of salmonid species may be farmed. Thus, in Canada at least three and in U.S.A more than seven *Oncorhynchus* species are cultered and in Japan *O. masu*, *O. rhodurus* and *Plecoglossus altivelis* are farmed.

6.4.1. Salmonid aquaculture in Scandinavia

In Denmark, already in the 1890s, an advanced pond cultivation of rainbow trout for consumption was developed.

In Sweden, at the beginning of this centuary, pond cultivation of salmonids was started. According to MONTÉN (1988), in Sweden cultivation of *Salmo salar* is older than rainbow trout farming. Between 1864 and 1867, in distant parts of Sweden, the first farms for salmon egg production were built. During the 1900s, fry of *S. salar* and *S. trutta* was produced, initially in ponds. Around 1950, all over Sweden, more than 100 farms were producing fry of *S. salar*, *S. trutta*, *Salvelinus alpinus*, *Thymallus thymallus*, *Coregonus lavaretus* and *C. albula*. During the years 1947-51 the present, intensive production of smolts was developed. The main part of this farming is intended as compensation for a diminished natural reproduction (ACKEFORS *et al.*, 1991). Several local populations of trout, as well as Atlantic and Baltic salmon are farmed. During the 1970s and the 1980s live, cultured salmon and rainbow trout were exported to Norway.

Finland has a large aquaculture industry for *O. mykiss* (all parts of the country). The Baltic stock of *S. salar* is also farmed. During the 1970s and the 1980s, live, cultured salmon and rainbow trout were exported to Norway.

In Norway, *S. salar* and *O. mykiss* are likewise cultured. Since the 1950s salmon smolts have been produced for compensatory stocking of regulated rivers. In the middle of the 1960s, the technique of the present Norwegian cage-rearing was developed. Today, this method of salmon cultivation in salt water is the largest in the world. Yearly, hundreds of ton are exported, for example to U.S.A., France and Germany (MALMBERG, 1989). For the first ten years or so, however, the Norwegian farmers were depending on the import of smolts from Sweden and Finland (HANSEN et BAKKE, 1989). Salmon and rainbow trout smolts were imported. Thus during the years 1973-76, the Norwegian imports from hatcheries of the Swedish State Power Board was totalled 560.000 smolts of Baltic salmon stock (MONTÉN, 1988). In 1986, the import from Finland and Sweden was about 2 million smolts, ("i.e. salmon of the genetically separated Baltic Sea stock"; see HALVORSEN et HARTVIGSEN, 1989).

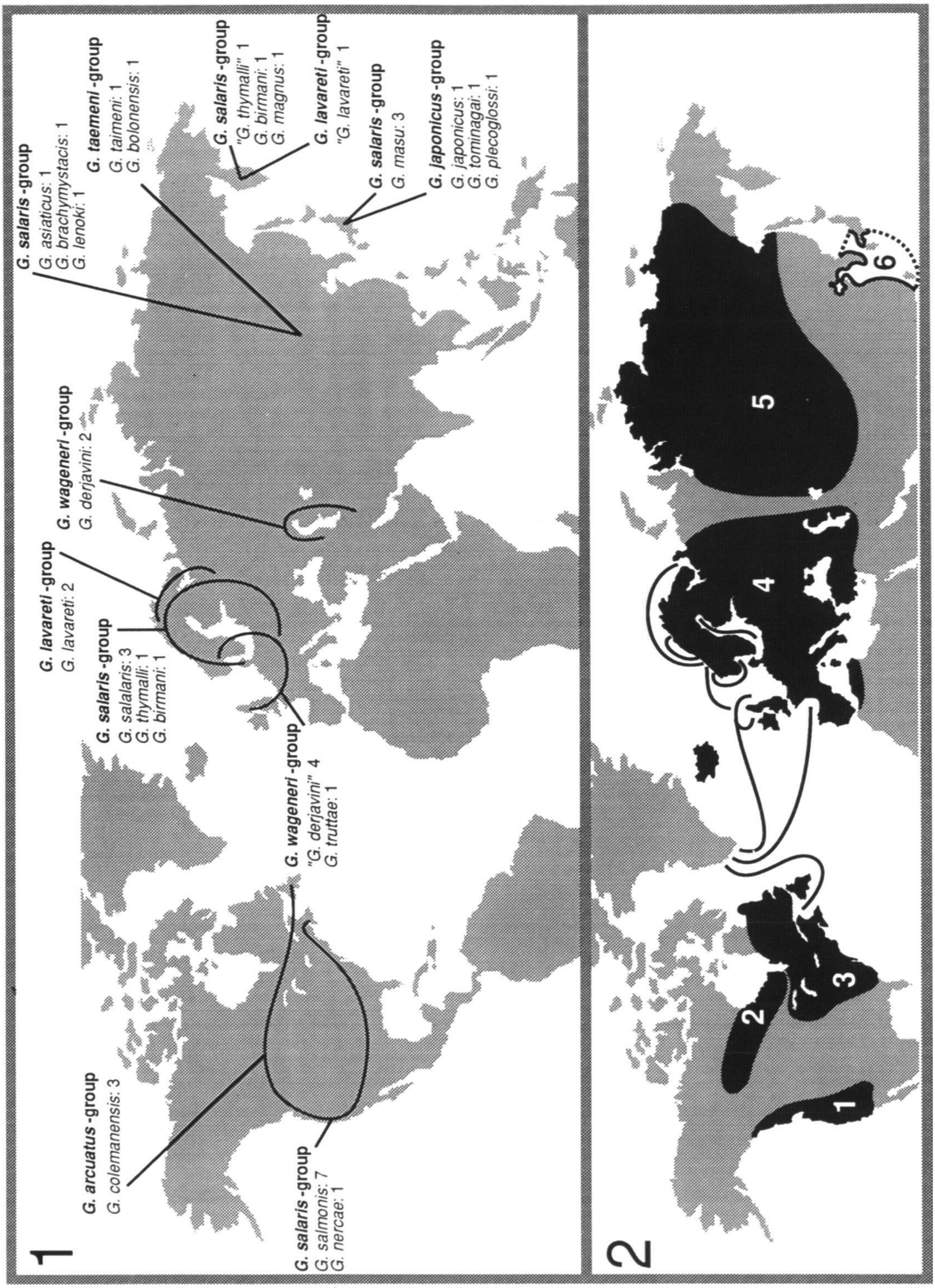

Fig. 1 : ***Gyrodactylus*-groups and *Gyrodactylus* species on salmonids: findings of species in different parts of the Northern Hemisphere. The figure after a species name indicates the number of host species/subspecies, reported.**

Fig. 2 : Migration routes for adult specimens of *Salmo salar* between feeding grounds and spawning areas.
Approximate geographical distribution of: 1. *Oncorhynchus mykiss*, 2. *Salvelinus namaycush*, 3. *Salvelinus fontinalis*, 4. *Salmo trutta*, 5. *Brachymystax lenok*, 6. *Plecoglossus altivelis*.

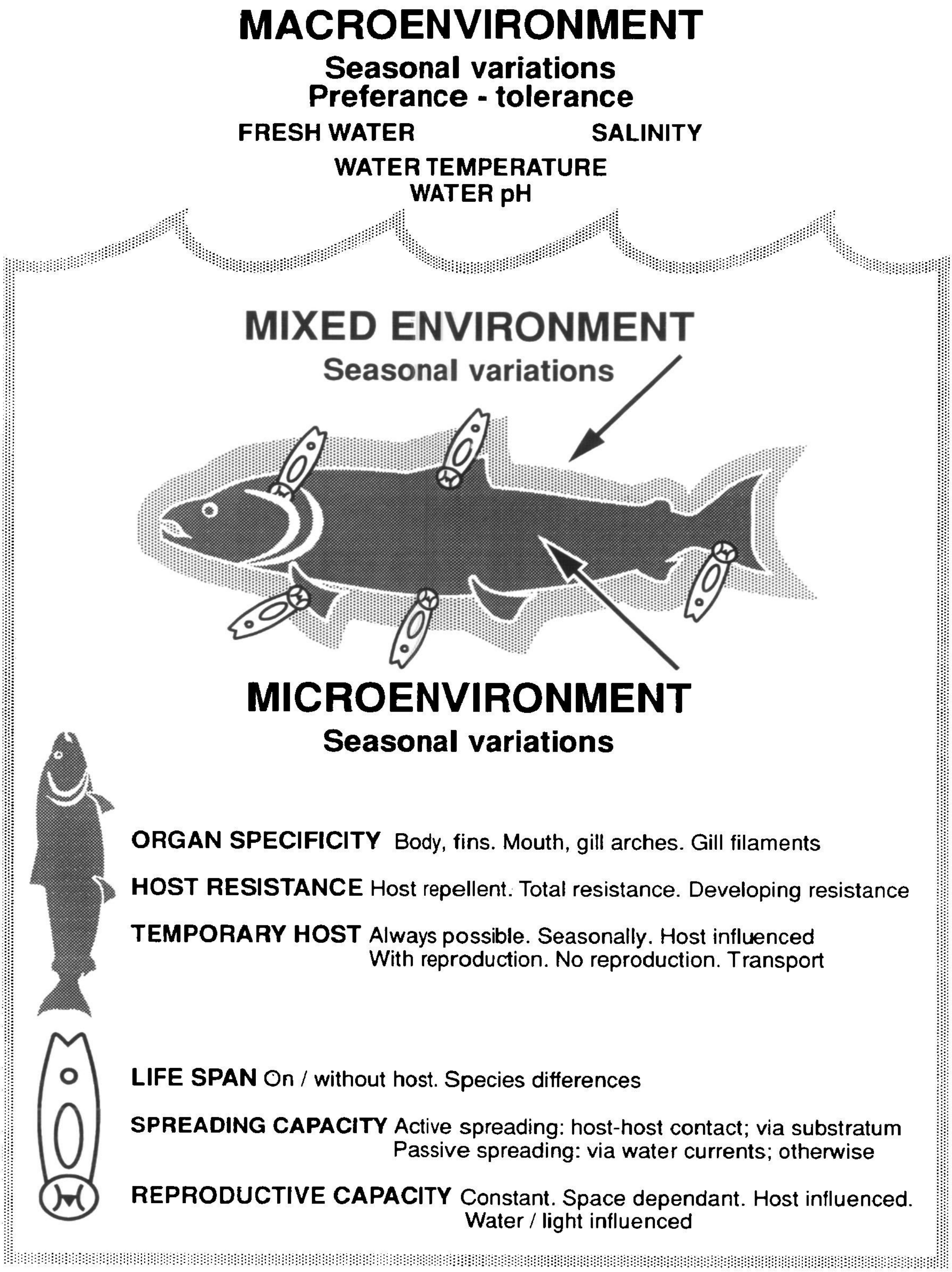

Fig. 3 : Diagramatic presentation of life span, spreading and reproduction in *Gyrodactylus* and the dependance of *Gyrodactylus* species on host and environmental conditions. Different interactions of the macro- and microenvironments and conditions in the mixed environment closed to the fish body decides the opportunities for a *Gyrodactylus* species to live and reproduce on a fish species.

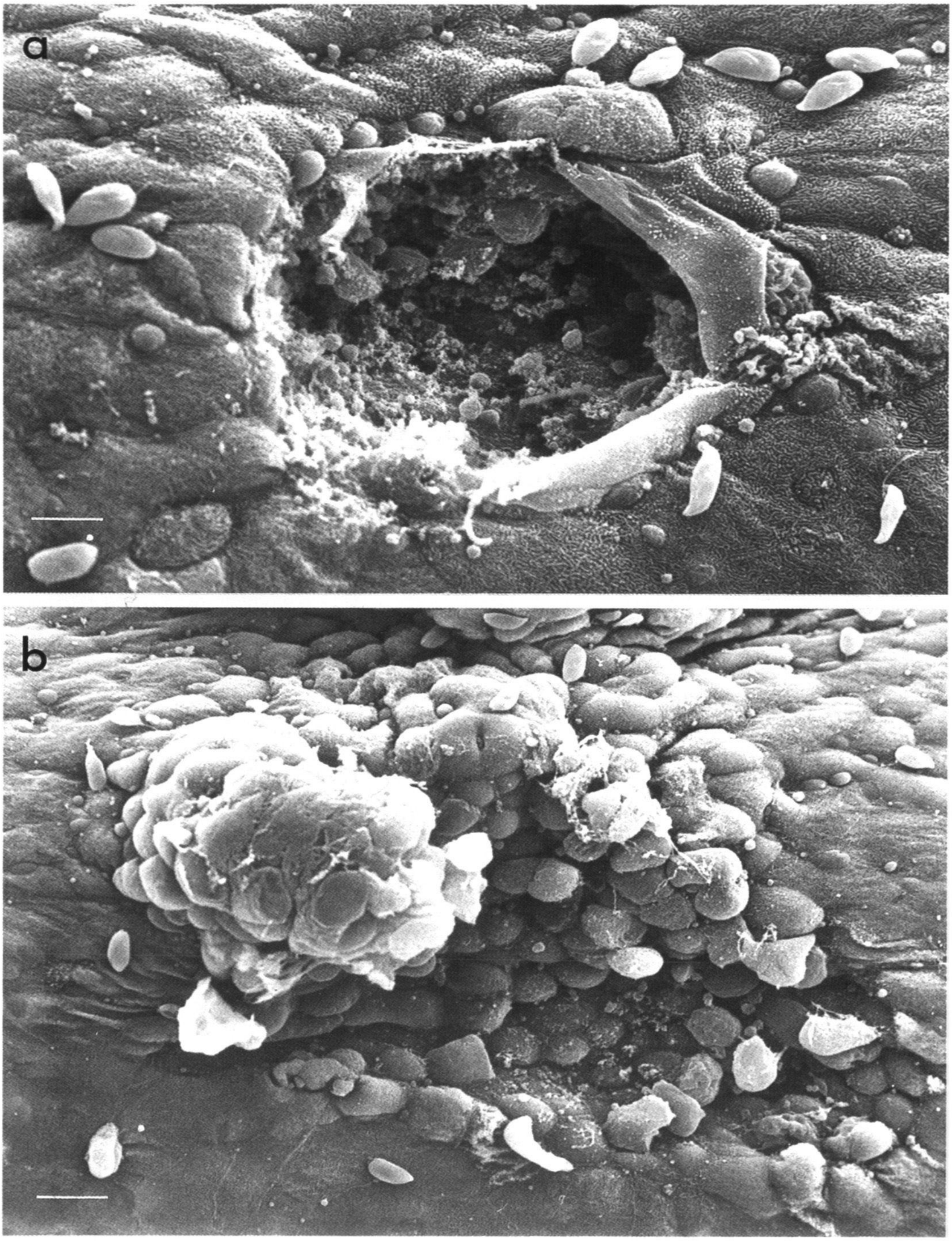

Fig. 4 : Scanning electron micrographs of a fin of *Salmo salar* L, the Norwegian Atlantic stock; parr specimen from a salmonid farm (Sundalsøra, Norway): - a. (from MALMBERG, 1987c) wound caused by the pharynx of *G. salaris* Malmberg, 1957. - b. a healing wound on the fin in 4a. Note the boil-like accumulation of cells. (Specimens of *Icthyobodo* are visible in both micrographs). Scale bars: a. 0.01 mm; b. 0.02 mm.

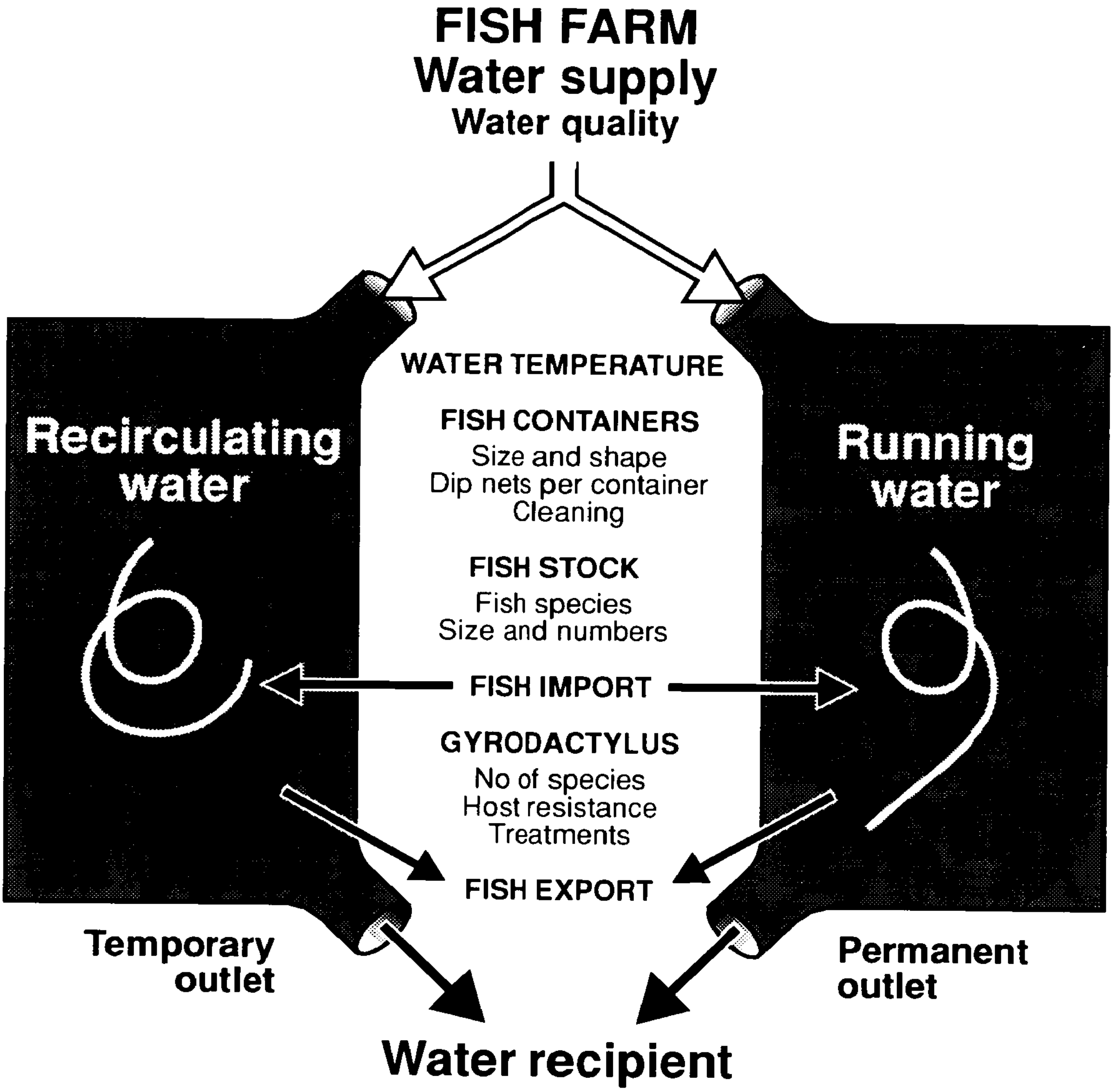

Fig. 5 : Diagramatic presentation of environmental conditions, connected to two types of fish farms. Common conditions in the middle. Establisment, "culturing" and a further spreading of a *Gyrodactylus* infestation is differently favoured in the two farms (see the text; Gyrodactylosis).

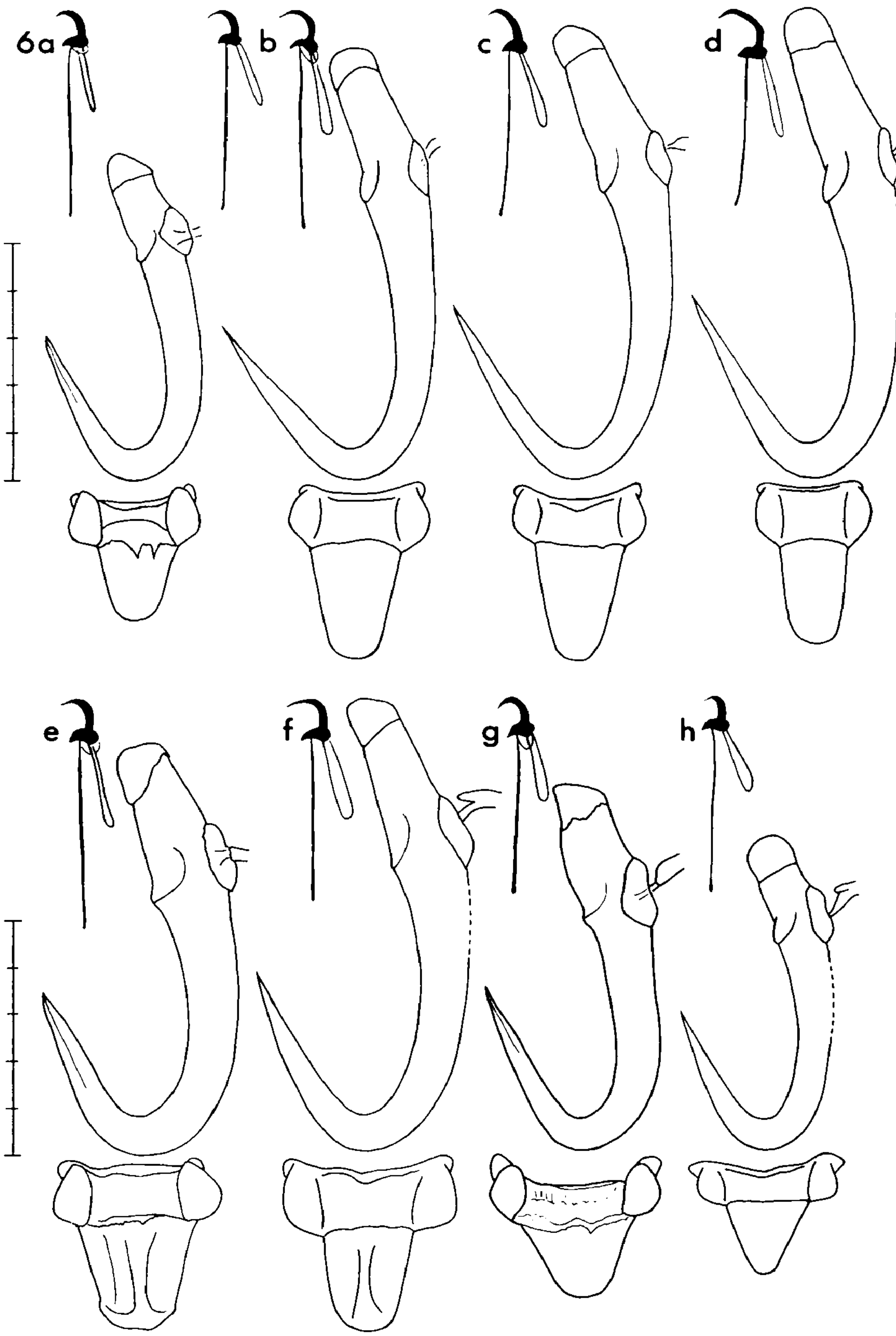

Fig. 6 : *G. salaris*-group, marginal hooks, anchors, ventral bars: - a-d Subgroup 1, - a. *G. salaris* Malmberg, 1957, anchor and ventral bar of the holotype, marginal hook from another specimen on *Salmo salar*, Hölle Laboratory 12-14.12.1957, 15. - b. *G. brachymystacis* Ergens, 1978, left marginal hook, anchor, ventral bar redrawn after ERGENS, 1983, right marginal hook from a CSAV, Helminthologie, specimen No Coll.M-236, 18.4.1966. - c. *G. lenoki* Gussev, 1953, redrawn after ERGENS, 1983. - d. *G. asiaticus* Ergens, 1978, redrawn after ERGENS, 1983. - e, f. Subgroup 2: - e. *G. thymalli* Zitnan, 1960 from CSAV, Helminthologie, specimen A, Cerna 25.4.1988. - f. *G. magnus* Konovalov, 1967, redrawn after ERGENS, 1983. - g, h. Subgroup 3: - g. *G. masu* Ogawa, 1986 from specimen TL. Bl.7.2cm, Jan.13,1978. - h. *G. birmani* Konovalov, 1967, redrawn after ERGENS, 1983. Scale bar: 0.05 mm.

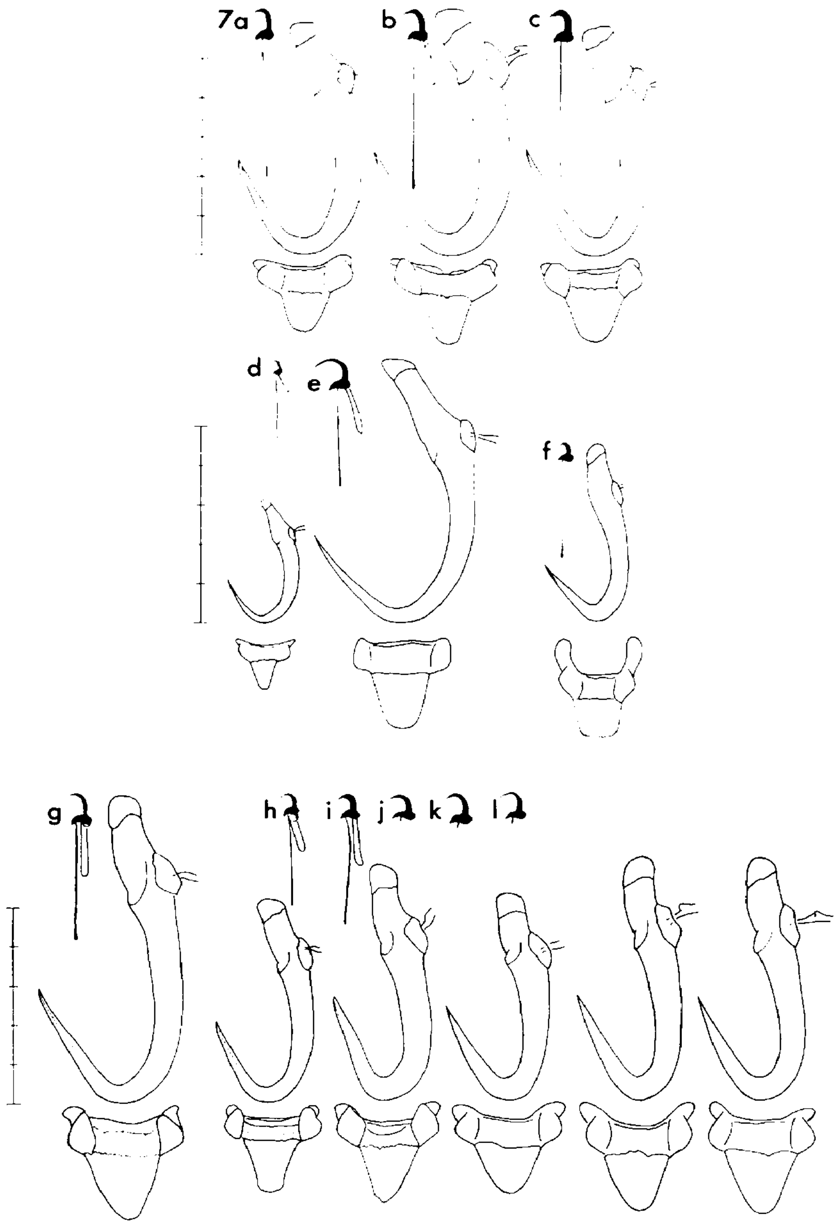

Fig. 7 : - a-c. *G. salaris*-group, subgroup 3 (continued); - d, e. *G. taimeni*-group; - f. *G. arcuatus*-group; - g *G. lavareti*-group; - h-l. *G. wageneri*-group, marginal hooks, anchors, ventral bars:

- a, b. *G. nerkae* Cone et al., 1983: - a. redrawn after CONE *et al.*, 1983, - b. from a specimen on *S. fontinalis*, Leetown Hatchery, 31.8.1970, F8. - c. *G. salmonis* Yin et Sproston, 1948, redrawn after CONE *et al.*, 1983. - d. *G. bolonensis* Ergens et Yukhimenko, 1975, redrawn after ERGENS et YUKHIMENKO, 1975. - e. *G. taimeni* Ergens, 1971, redrawn after ERGENS, 1983. - f. *G. colemanensis* Mizelle et Kritsky, 1967, redrawn after CONE *et al.*, 1983. - g. *G. lavareti* Malmberg, 1957, paratype, 14.7.1955.4h/f. - h. *G.* sp. from *Osmerus eperlanus*, The Baltic, Nämdö 19.8.1960.1ph. - i. *G. derjavini* sensu MALMBERG et MALMBERG, 1987 from *S. trutta*, Tidaholm 12-13.1.1958.4f. - j. *G.* sp. Ergens, 1992, (Syn. *G. truttae* Gläser, 1974, Fig. 6b), redrawn from ERGENS, 1992. - k. *G. derjavini* Mikailov, 1975, redrawn from ERGENS, 1992. - l. *G. truttae* Gläser, 1974 (Syn. *G. truttae* Gläser, 1974, Fig. 6a) holotype, redrawn after ERGENS, 1992. Scale bar: 0.05 mm.

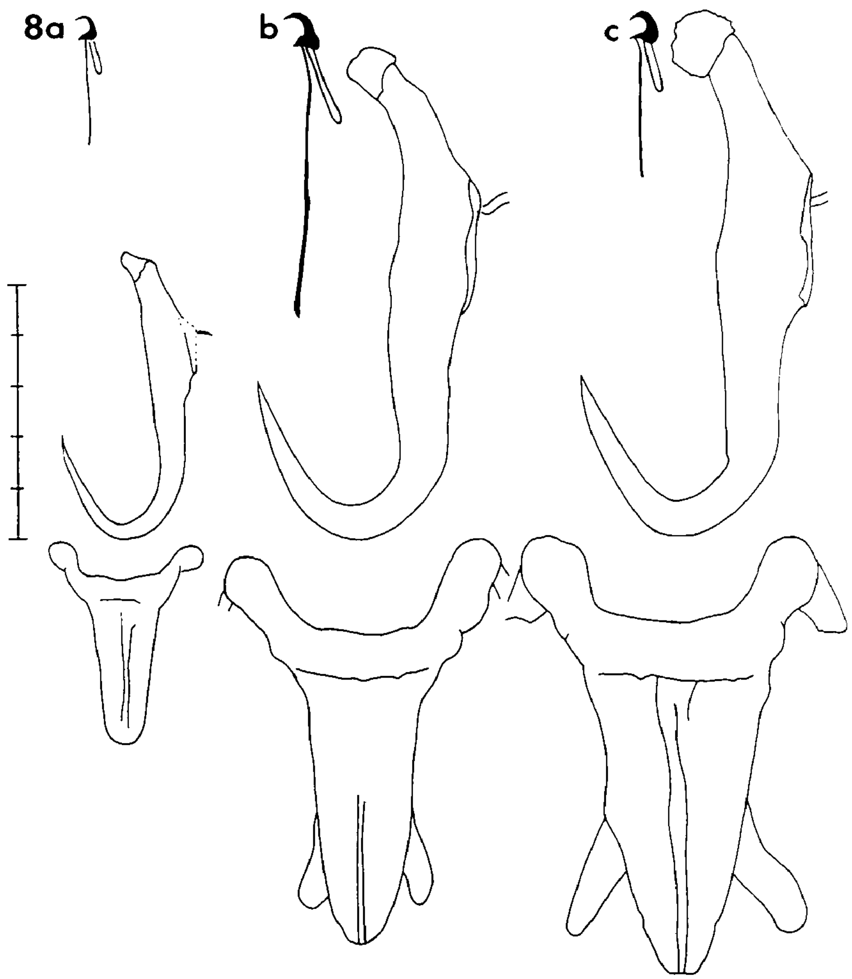

Fig. 8 : - a-c. *G. japonicus*-group, marginal hooks, anchors, ventral bars, redrawn after OGAWA et EGUSA, 1978: - a. *G. plecoglossii* Ogawa et Egusa, 1978. - b. *G. japonicus* Kikuchi, 1929. - c. *G. tominagai* Ogawa et Egusa, 1978. Scale bar: 0.05 mm.

TABLE I

Gyrodactylus species on salmonids in the world.

***G. salaris*-group** (Fig. 6, 7a-c)

The most typical species have comparatively robust anchors with diverging anchor roots, a rather short and broad ventral bar with broad, rounded ends, small processes, and a less triangular ventral bar membrane than in the *G. wageneri*-group. The group can be divided into three subgroups:

Subgroup 1: including the most typical members of the *G. salaris*-group: *G. salaris* Malmberg, 1957, *G. brachymystacis* Ergens, 1978, *G. lenoki* Gussev, 1953 and *G. asiaticus* Ergens, 1978.

Subgroup 2: including *G. thymalli* Zitnan, 1960 and *G. magnus* Konovalov, 1967, with typical anchors and a ventral bar similar to, but more robust, than that in subgroup 1.

Subgroup 3: including *G. masu* Ogawa, 1986, *G. birmani* Konovalov, 1967, *G. nerkae* Cone, Beverley-Burton, Wiles, McDonald, 1983 and *G. salmonis* Yin et Sproston, 1948 with typical anchors but a ventral bar similar to that in the *G. wageneri*-group: a rather long bar with a more or less triangular ventral bar membrane.

Subgroup 1

***G. salaris* Malmberg, 1957** (Fig. 6a)

Opisthaptoral hard parts exhibiting an unusually large range of variation (see TANUM, 1983, MO, 1991c, 1991d, 1991e). Syn. *G. sp.*, ERGENS (1983).

Hosts, localities, location:

Salmo salar L.: Sweden, Finland, Norway, Germany, Russia; on fins and skin.

Salmo trutta L.: Ukraine, Crimea, Georgia; on skin and fins.

Oncorhynchus mykiss (Walbaum): Sweden, Norway, Finland, Denmark, Germany, Spain; on skin and fins.

***G. brachymystacis* Ergens, 1978** (Fig. 6b)

See also ERGENS, 1971; 1978.

Host, locality, location:

Brachymystax lenok (Pallas): Mongolia; on fins.

***G. lenoki* Gussev, 1953** (Fig. 6c)

See also ERGENS, 1971; 1978.

Host, localities, location:

Brachymystax lenok (Pallas): Amur river system, Mongolia; on fins and gills.

***G. asiaticus* Ergens, 1978** (Fig. 6d)

See also ERGENS, 1971; 1978.

Host, locality, location:

Brachymystax lenok: Mongolia; on gills and fins.

Subgroup 2

***G. thymalli* Zitnan, 1960** (Fig. 6e)

Species similar to *G. salaris*, but anchors and ventral bar more robust and ventral bar probably more similar to that of G. *magnus*.

Hosts, localities, location:

Thymallus thymallus L.: Czechoslovakia, Germany, Norway (MO, 1991b), Sweden?; on fins and skin.

Remark. ERGENS (1983) confirmed KONOVALOV's (1967) finding of *G. thymalli* on fins of *Thymallus arcticus grubei* n. *mertensi* in Kamchatka.

***G. magnus* Konovalov, 1967** (Fig. 6f)

Species redescribed by ERGENS (1971). Ventral bar seems to be similar to that of *G. thymalli*.

Hosts, localities, location:

Thymallus arcticus grubei n. *mertensi* Valenciennes; Kamchatka; on fins.

T. arcticus (Pallas): Mongolia; on fins.

Subgroup 3

***G. masu* Ogawa, 1986** (Fig. 6g)

Hosts, locality, location:

Oncorhynchus masu (Brevoort), *O. rhodurus* Jordan et McGregor,

O. mykiss (Walbaum): Japan; on fins, skin, gill filaments, gill arches.

***G. birmani* Konovalov, 1967** (Fig. 6h)

Species redescribed by ERGENS (1983)

Host, locality, location:

Salvelinus alpinus (L.): Kamchatka, Norway (MO, 1991b); on fins.

***G. nerkae* Cone, Beverley-Burton, Wiles, McDonald, 1983** (Fig. 7a, b)

Hosts, localities, location:

Oncorhynchus nerkae (Walbaum): British Columbia (Cultus Lake); on skin

Salvelinus fontinalis (Mitchill): West Virginia; on fins

***G. salmonis* Yin et Sproston, 1948** (Fig. 7c)

Hosts, localities, location:

Oncorhynchus clarki (Richardson): British Columbia; on fins and skin.

Oncorhynchus kisutch (Walbaum): British Columbia; on skin.

Oncorhynchus aguabonita Jordan: California; on skin.

Oncorhynchus mykiss (Syn. *Salmo gairdneri*): West Virginia, Arkansas, Idaho, Montana, British Columbia; on skin and fins.

Salmo salar L.: Nova Scotia; on skin.

Salmo trutta L.: North Carolina; on skin.

Salvelinus fontinalis (Mitchill): Nova Scotia; on skin and fins.

***G. lavareti*-group** (Fig. 7g)

Anchor roots diverging but all the anchor more gracile than in the *G. salaris*-group. *G. lavareti* Malmberg, 1957 is a member of this group.

G. lavareti **Malmberg, 1957** (Fig. 7g)

Hosts, locality, location:

Coregonus lavaretus L.: Sweden, Russia (Karelia); on fins, skin.

Oncorhynchus mykiss (Walbaum): Sweden, Finland; skin, fins.

Remark. In 1992, I re-examined type specimens of *G. lavareti* and could identify specimens found in Sweden and Finland on *O. mykiss* and presented as *G. sp.* (MALMBERG et MALMBERG, 1987; 1991) as specimens of *G. lavareti.*

G. lavareti **sensu KONOVALOV (1967)**

Host, locality, location:

Coregonus nasus (Pallas): Kamchatka; on gills.

Remark. ERGENS (1983) re-examined specimens in KONOVALOV's (1967) collection and found differences. This may imply that *C. nasus* is parasitised by a separate species, very similar to *G. lavareti.*

***G. wageneri*-group** (Fig. 7h-l)

Anchors often shorter than in the *G. salaris*-group and anchor roots mostly not diverging; ventral bar with small distinct processes and a triangular ventral bar membrane.

Remark. On salmonids there are at least three very similar species : *G. truttae* Gläser, 1974, *G. derjavini* Mikailov, 1975 (see ERGENS, 1983) and *G. derjavini* sensu MALMBERG et MALMBERG (1987); (see also MALMBERG,1987; 1989; MALMBERG et MALMBERG, 1991; MALMBERG et MALMBERG, in press). ERGENS (1992) redescribed *G. truttae* Gläser, 1974, fig 6a, and informed that *G. derjavini* sensu MALMBERG et MALMBERG (see below) is not identical with *G. derjavini* Mikailov, but probably identical with the species in Gläser's description of *G. truttae*, fig. 6b (see also MALMBERG, 1987) and probably also with *G. salaris* sensu REHULKA (1973). There are small differences between the size and shape of marginal hook sickles and the size of the anchors of the three species.

G. truttae **Gläser, 1974** (Fig. 7 l)

See also GLÄSER (1974; fig. 6a). ERGENS (1992) redescribed the species.

Host, localities, location:

Salmo trutta L.: Germany; on fins;

Scotland, Czechoslovakia, Poland; on skin and fins

G. derjavini **Mikailov, 1975** (Fig. 7 k)

ERGENS (1983) redescribed the species.

Hosts, localities, location:

Salmo trutta caspius (Kessler) and *Salmo trutta oxianus* Kessler:

Azerbaidzhan, Tadzhikistan; on skin, fins, gills.

Remark. Specimens sent me by Dr. B. JALALI (Iran) from fins of *S. trutta caspius* in the Iranian part of the Caspian Sea, are most likely specimens of *G. derjavini* Mikailov.

G. derjavini **sensu MALMBERG et MALMBERG (1987)** (Fig. i)

See also MALMBERG et MALMBERG,1991; MALMBERG et MALMBERG, in press; MALMBERG,1987b; 1989. This species is also identical with *G. truttae* sensu MO (1983) and presumably with *G.* sp., ERGENS (1992); (Fig. 7j).

Hosts, localities, location:

Salmo trutta L.: Sweden, Norway, Denmark, Italy, Poland, Germany; on skin and fins.

Oncorhynchus mykiss (Walbaum): Sweden, Denmark, Scotland, Italy, Poland; on skin and fins.

Salmo salar L.: Sweden, Norway; on skin and fins.

***G.* sp., MALMBERG et MALMBERG (1991)** (Fig. 7h)

Host, localities, location:

Osmerus eperlanus L.: Sweden and Finland (brackish water); on fins and in mouth.

***G. taimeni*-group** (Fig. 7d, e)

The anchors of *G. taimeni* Ergens, 1971 and *G. bolonensis* Ergens et Yukhimenko, 1975 are dorsally convex; their ventral bar neither of a *G. salaris* nor of a *G. wageneri* type; but of a *G. rarus* type; see MALMBERG, (1970). This indicates that the two species neither belongs to the *G. salaris*-group nor to the *G. wageneri*-group.

Remark. Although the type of protonephridial system of the two species is unkown, the species are provisionally grouped together.

***G. taimeni* Ergens, 1971** (Fig. 7e)

Host, locality, location:

Hucho taimen (Pallas): Mongolia; on gills.

***G. bolonensis* Ergens et Yukhimenko, 1975** (Fig. 7d)

Host, locality, location:

Hypomesus olidus (Pallas): Mongolia; on gills.

***G. japonicus*-group** (Fig. 8)

Species with dorsally concave anchor shafts and diverging anchor roots; ventral bar comparatively short with large, diverging processes and a long, pointed ventral bar membrane, in some species with a pair of large postero-lateral processes.

Hitherto, the *G. japonicus*-group is only found in Japan. The group has the following members: *G. japonicus* Kikuchi, 1929, *G. tominagai* Ogawa et Egusa, 1978 and *G. plecoglossi* Ogawa et Egusa, 1978.

***G. japonicus* Kikuchi, 1929** (Fig. 8b)

Species redescribed by OGAWA et EGUSA (1978)

Host, locality, location:

Plecoglossus altivelis Schleg.: Japan; on skin, fins and gills.

***G. tominagai* Ogawa et Egusa, 1978** (Fig. 8c)

Host, locality, location:

Plecoglossus altivelis Schleg.: Japan; on fins.

***G. plecoglossi* Ogawa et Egusa, 1978** (Fig. 8a)

Host, locality, location:

Plecoglossus altivelis Schleg.: Japan; on fins.

***G. arcuatus*-group** (Fig. 7f)

Species with rather small anchors with short, dorsally concave anchor roots; ventral bar with prominent, anteriad processes. *G. colemanensis* Mizelle et Kritsky, 1967, repeatedly reported as a parasite on salmonid hosts in North America, is the only species of the group on salmonids, hitherto.

***G. colemanensis* Mizelle et Kritsky, 1967** (Fig. 7f)

The species was originally described from *Oncorhynchus mykiss* (Walbaum), (Syn. *Salmo gairdneri* Richarson; see SMITH et STEARLEY, 1989) in California. CONE *et al.* (1983) re-examined the species and added more hosts and localities.

Hosts, localities, location:

Oncorhynchus mykiss (Walbaum): California, Arkansas, Newfoundland; on skin

Salvelinus fontinalis (Mitchill): Nova Scotia, Ontario; on skin

Salmo trutta L., *Salvelinus namaycush* (Walbaum), *Salvelinus fontinalis* x *Salvelinus namaycush*: Ontario; on skin

TABLE II.

Aquaculture of salmonids and presence of *Gyrodactylus* species on salmonids in fish farms and natural waters in the world.

Here presented data on distribution of salmonids and of salmonids within different aquaculture sectors are mainly taken from ADCP: Aquaculture Development and Coordination Programme (1988, 1989), MUUS et DAHLSTRÖM (1968), NIKOLSKII (1961), COOK (1984) and HAMMAR (1989).

1. NORTH AMERICA

CONE *et al.* (1983) could establish only three species, specific to salmonid hosts in North America: *G. nerkae*, *G. salmonis* and *G. colemanensis*.

1.1. CANADA

1.1.1. Aquaculture

At least three *Oncorhynchus* species, including *O. mykiss*, *S. trutta* and *S. salar* are cultured.

1.1.2. *Gyrodactylus* species

See CONE *et al.* (1983).

***G. nerkae* Cone, Beverley-Burton, Wiles, McDonald, 1983**

Fish farm: farm in Nanaimo, British Columbia (NW North America)

Natural water: on *O. nerkae* in lake in British Columbia.

***G. salmonis* Yin et Sproston, 1948**

Fish farms: two farms on Vancouver Island on *O. clarki* and on *O. mykiss*, respectively ; one farm on Nova Scotia (SE Canada) on *Salvelinus fontinalis*.

Natural waters: three rivers on Vancouver Island (NW Canada), on *O. clarki*, *O. kisutch* and *O. mykiss*, respectively.

Remark. This species has been found on widly scattered localities in both the eastern and the western half of North America.

***G. colemanensis* Mizelle et Kristky, 1967**

Fish farms: one farm in Newfoundland (E Canada); one farm with *Salvelinus fontinalis* in Nova Scotia (SE Canada); one farm in Ontario (E Canada); one farm in Ontario with *S. trutta*, *Salvelinus namaycush* and *S. fontinalis* x *S. namaycush*.

Natural waters: -

1.2. U S A

1.2.1. Aquaculture

More than seven, native *Oncorhynchus* species, among them *O. mykiss* (the rainbow trout), *Salvelinus fontinalis*, *Salmo trutta* and *S. salar* are cultured.

1.2.2. *Gyrodactylus* species

See CONE *et al.* (1983).

***G. nerkae* Cone, Beverley-Burton, Wiles, McDonald, 1983**

Fish farm: on *O. mykiss* and *Salvelinus fontinalis* in the hatchery of Eastern Fish Disease Laboratory, Leetown, West Virginia (E USA); own studies in 1970.

Natural waters: -

***G. salmonis* Yin and Sproston, 1948**

Fish farms: on *O. mykiss* in: one farm in Montana (NW USA), one farm in Idaho (NW USA), one farm in Arkansas (SW central USA), one farm in North Carolina (E USA).

Natural waters: -

Remark. According to CONE *et al.* (1983), this species has been found on widly scattered localities in both the eastern and the western half of North America.

***G. colemanenis* Mizelle et Kritsky, 1967**

See MIZELLE et KRITSKY (1967); CONE *et al.*, (1983).

Fish farms: on *O. mykiss* in one farm in California (SW USA) and in one farm in Arkansas (SW central USA).

Natural water: Navarro River, California (SW USA).

2. SOUTH AMERICA

2.1.1. Aquaculture

O. mykiss is farmed in 11 countries: Argentina, Bolivia, Brazil, Chile, Colombia, Costa Rica, Mexico, Panama, Peru, Uruguay, Venezuela.

S. salar is farmed in Chile and on the Falkland Islands.

2.1.2. *Gyrodactylus* species

Fish farms: -

Natural waters: -

3. ASIA

3.1. JAPAN

3.1.1. Aquaculture

Cultured salmonid species are: *O. masu*, *O. rhodurus*, *Plecoglossus altivelis*; *O. mykiss* (since 1877).

3.1.2. *Gyrodactylus* species

G. japonicus Kikuchi, 1929 on *Plecoglossus altivelis* is the first described Japanese species. KIKUCHI (1929) presented no locality. In 1978, on material from the same host, OGAWA et EGUSA redescribed *G. japonicus* and described two more species, *G. tominagai* and *G. plecoglossi*. The three species are closely related (the *G. japonicus*-group) and of a type, hitherto not found outside Japan. A fourth Japanese species is *G. masu* Ogawa, 1986.

Remark. OGAWA et EGUSA (1978) obtained the host specimens of *P. altivelis* from the Lake Biwa and transferred them for culturing to two fish farms. Later on, specimens of the three *Gyrodactylus* species were collected from the cultured host specimens. They presumed that the *P. altivelis* specimens were infested by the three *Gyrodactylus* species already in the Lake Biwa.

***G. japonicus* Kikuchi, 1929**

***G. tominagai* Ogawa et Egusa, 1978**

***G. plecoglossi* Ogawa et Egusa, 1978**

Fish farms: all three species on *Plecoglossus altivelis*.

Natural water: all three species on *Plecoglossus altivelis* in Lake Biwa?

G. masu **Ogawa, 1986**

Fish farms: Okutama Branch, Tokyo Met. Fish. Exp. Stn.: on *O. masu* and *O. mykiss*. Chitose Branch, Hokkaido Salmon Hatchery: on *O. masu*. Kitoh Village, Tokushima Pref.: on *O. rhodurus*.

Natural waters: -

3.2. KOREA

3.2.1. Aquaculture

O. mykiss is farmed.

3.2.2. *Gyrodactylus* species

Fish farms: -

Natural waters: -

3.3. KAMCHATKA

3.3.1. Aquaculture

3.3.2. *Gyrodactylus* species

KONOVALOV (1967) described *G. magnus* from *Thymallus arcticus* and *G. birmani* from *Salvelinus alpinus*. He also reported *G. lavareti* from *Coregonus nasus* and *G. thymalli* from *Thymallus arcticus*. ERGENS (1983) redescribed the two first species and presented results from studies of slides of the two remaining species.

G. magnus **Konovalov, 1967**

G. birmani **Konovalov, 1967**

G. lavareti **sensu KONOVALOV (1967)**

G. thymalli **Zitnan, 1960**

Fish farms: -

Natural waters: all four *Gyrodactylus* species were collected on host specimens from natural waters: *G. magnus* on *Thymallus arcticus*; *G. birmani* on *Salvelinus alpinus*; *G. lavareti* sensu KONOVALOV on *Coregonus nasus*; *G. thymalli* on *Thymallus arcticus*.

3.4. MONGOLIA

3.4.1. Aquaculture

3.4.2. *Gyrodactylus* species

GUSEV (1953) described *G. lenoki* from the salmonid *Brachymystax lenok*. ERGENS (1978) described *G. asiaticus* and *G. brachymystacis* from the same host. ERGENS (1971) described *G. magnus* from *Thymallus arcticus* and *G. taimeni* from *Hucho taimen*. ERGENS et YUKHIMENKO (1971) described *G. bolonensis* from *Hypomesus olidus* (Osmeridae).

G. lenoki **Gusev, 1953** on *Brachymystax lenok*.

G. asiaticus **Ergens, 1978** on *Brachymystax lenok*.

G. brachymystacis **Ergens, 1978** on *Brachymystax lenok*.

G. magnus **Konovalov, 1967** on *Thymallus arcticus*.

G. taimeni **Ergens, 1971** on *Hucho taimen*.

G. bolonensis **Ergens et Yukhimenko, 1971** on *Hypomesus olidus*

Fish farms: -

Natural waters: all six *Gyrodactylus* species were found in natural waters, *G. lenoki*, *G. asiaticus*, *G. brachymystacis* on *Brachymystax lenok*, *G. magnus* on *Thymallus arcticus*, *G. taimeni* on *Hucho taimen* and *G. bolonensis* on *Hypomesus olidus*.

3.5. TADZHIKISTAN, AZERBAIDZHAN

3.5.1. Aquaculture

3.5.2. *Gyrodactylus* species

***G. derjavini* Mikailov, 1975**

ERGENS (1983) redescribed the species on material from the River Kura (type locality), Azerbaidzhan, and the River Kafirnigan, Tadzhikistan.

Fish farms: -

Natural waters: on *S. trutta caspius* in the River Kura; on *S. trutta oxianus* in the River Kafirnigan.

3.6. IRAN

3.6.1. Aquaculture

S. trutta and *S. salar* are farmed.

3.6.2. *Gyrodactylus* species

***G. derjavini* Mikailov, 1975**

ERGENS (1992) gave drawings of the species.

Fish farms: -

Natural water: on *S. trutta caspius* in the River Sardab.

3.7. ISRAEL, LEBANON, SYRIA, TURKEY

3.7.1. Aquaculture

O. mykiss is farmed.

3.7.2. *Gyrodactylus* species

Fish farms: -

Natural waters: -

4. AFRICA

4.1. MOROCCO

4.1.1. Aquaculture

O. mykiss is farmed.

4.1.2. *Gyrodactylus* species

Fish farms: -

Natural waters: -

5. EUROPE

O. mykiss (about 1880, introduced as fertilized eggs from North America) is farmed all over Europe; in about 30 countries: Albania, Austria, Belgium, Bulgaria, Cyprus, Czechoslovakia, Denmark, England, Faeroes, Finland, France, Germany, Greece, Hungary, Iceland, Ireland, Italy, Latvia, Netherlands, Norway, Poland, Portugal, Russia, Scotland, Spain, Sweden, Switzerland, Yugoslavia.

5.1. GEORGIA, SOUTH RUSSIA, CRIMEA, UKRAINA

5.1.1. Aquaculture:

See above, *O. mykiss*.

5.1.2. *Gyrodactylus* species

ERGENS (1992) gave drawings of *G. derjavini* from a fish farm in South Russia. ERGENS (1983) gave drawings of a *G.* sp. from Georgia and the Crimea.

***G. derjaini* Mikailov, 1975**

Fish farm: on *S. trutta caspius*, South Russia.

Natural waters : -

***G.* sp., ERGENS (1983)**

This species is most likely identical to *G. salaris* Malmberg.

Fish farm: on *S. trutta fario*, in Georgia.

Natural waters: on *S. trutta fario*, in two rivers in the Crimea.

***G. salaris* Malmberg, 1957**

Fish farms: -

Natural water: on *S. trutta fario*, River Seret, SW Ukraina.

Remark. In MALMBERG (1973) the locality was said to be a Carpathian hatchery; read: a Carpathian river. Specimens were obtained from Dr. O. KULAKOVSKAYA, Lvov; 1960.

5.2. NORTHWESTERN RUSSIA

5.2.1. Aquaculture

See above, *O. mykiss*.

5.2.2. *Gyrodactylus* species

ERGENS (1983) reported *G. salaris* from the Lake Ladoga and *G. lavareti* from Karelia. MITENEV (1989) reported *G. thymalli* in two rivers on the Kola Peninsula. MO (comm. pers.) informed about *G. salaris* in rivers falling into the White Sea.

***G. salaris* Malmberg, 1957**

***G. lavareti* Malmberg, 1957**

***G. thymalli* Zitnan, 1960**

Fish farms: -

Natural waters: *G. salaris* Malmberg, 1957 on *S. salar*; *G. lavareti* Malmberg, 1957 on *Coregonus lavaretus*; *G. thymalli* Zitnan, 1960 on *Thymallus thymallus*.

5.3. CENTRAL EUROPE

5.3.1. Aquaculture

See above, *O. mykiss*.

S. trutta is cultured in e.g. Czechoslovakia, Germany, Poland.

S. salar is cultured in e.g. England, Ireland and Scotland.

Salvelinus fontinalis is cultured in e.g. Czechoslovakia and Poland.

5.3.2. *Gyrodactylus* species

ERGENS (1983; 1992) reported *G. thymalli*, *G. truttae* and *G.* sp. from Czechoslovakia, Germany and Yugoslavia. LUX (1990) reported *G. truttae*, *G. salaris* and *G. thymalli* from Germany; PROST (1991) discussed *G. derjavini* and *G. truttae* in Poland; LULLU *et al.* reported *G. truttae* from Latvia; SANTAMARINA *et al.* (1991) and TOJO *et al.* (1992) worked with *G. salaris* (discrimination by G. MALMBERG) in Spain. On material from Dr. K. MOLNAR, 1977, I discriminated specimens of *G. derjavini* sensu MALMBERG et MALMBERG from Italy.

***G. salaris* Malmberg, 1957**

Fish farms: on *O. mykiss* in Germany and Spain.

Natural waters: on *S. trutta fario* in Germany.

***G. thymalli* Zitnan, 1960**

Fish farms: on *O. mykiss* in Germany.

Natural waters: on *Thymallus thymallus* in Czechoslovakia and Germany.

***G. truttae* Gläser, 1974**

Fish farms: on *O. mykiss* in Germany and Latvia (?).

Natural waters: on *S. trutta fario* in Germany and Czechoslovakia, Yugoslavia, in Poland on *S. trutta trutta*.

G. derjavini **Mikailov, 1975**

Fish farms: -

Natural waters: on *S. trutta fario*, *S. trutta*, *O. mykiss* and *Salvelinus fontinalis* in Poland.

G. derjavini **sensu MALMBERG et MALMBERG (1987)**

Fish farms: on *O. mykiss* in Italy and Spain; on *S. trutta fario* in Italy.

Natural waters: -

5.4. SCOTLAND

5.4.1. Aquaculture

See above, *O. mykiss*.

5.4.2. *Gyrodactylus* species

MALMBERG (1987) reported *G. truttae* (specimens from Dr. E. TURNBULL, 1959). WOOTTEN et SOMMERVILLE (1989) reported *Gyrodactylus* spp. SHINN *et al.* (1992) reported about studies in British watercourses: 70 sample sites of *Gyrodactylus*, were collected from *S. salar*, *S. trutta*, *O. mykiss*, *Salvelinus alpinus*.

G. truttae **Gläser, 1974**

Fish farms: - see below, *G.* spp.

Natural waters: on *S. trutta*.

G. **spp., WOOTTEN et SOMMERVILLE (1989)**

Fish farms: on *Salmo salar* and *O. mykiss*.

Natural waters: on *S. salar*, *S. truttae*, *O. mykiss*.

Remark. The *Gyrodactylus* species on *S. salar* is probably different to that on the two other species.

5.5. FAEROES, ICELAND

5.5.1. Aquaculture:

S. salar and *O. mykiss* are cultured.

5.5.2. *Gyrodactylus* species

Fish farms: -

Natural waters: -

5.6. DENMARK

5.6.1. Aquaculture

Since the 1890s, an advanced pond cultivation of rainbow trout for consumption is performed.

5.6.2. *Gyrodactylus* species

MALMBERG et MALMBERG (1991) reported *G. derjavini* sensu MALMBERG et MALMBERG and *G. salaris*.

G. derjavini **sensu MALMBERG et MALMBERG (1987)**

Fish farms: on *O. mykiss* in three geographically distributed localities.

Natural water: on *Salmo trutta*.

G. salaris **Malmberg, 1957**

Fish farms: on *O. mykiss* in one of the three fish farms (above).

Natural water: -

5.7. SWEDEN

5.7.1. Aquaculture

Since the beginning of 1900, pond cultivation of salmonids; that of *Salmo salar*, older than rainbow trout farming. Around 1950, all over Sweden, more than 100 farms producing fry of

S. salar, *S. trutta*, *Salvelinus alpinus*, *Thymallus thymallus*, *Coregonus lavaretus* and *C. albula*; since about 1950 an intensive production of salmon smolt. Several local populations of trout and of the Atlantic and the Baltic salmon are farmed.

5.7.2. *Gyrodactylus* species

MALMBERG et MALMBERG (1991; 1992) reviewed Swedish findings of gyrodactylids on salmonids and reported the following species: *G. salaris*; two *G.* sp. of the *G. salaris*-group, one on *Thymallus thymallus* and another on *O. mykiss*; *G. lavareti*; one *G.* sp. of the *G. wageneri*-group on *Osmerus eperlanus*. 17 rivers and 18 fish farms were investigated (MALMBERG et MALMBERG, 1992).

Remark. In 1992, I identified the *G.* sp. on *O. mykiss* as *G. lavareti*.

***G. salaris* Malmberg, 1957**

Fish farms: on *S. salar* in 5 farms within the Baltic region and 2 within the Atlantic region; on *O. mykiss* in 2 farms within the Atlantic region.

Natural waters: on *S. salar* (the Baltic form) in 3 geographically distributed rivers; on *S. salar* (the Atlantic form) in 2 different river systems; - all five rivers with a natural reproduction of salmon parr. On *S. trutta* (one isolated specimen in one of the investigated rivers).

***G. sp., G. salaris*-group**

Fish farms: -

Natural water: on *Thymallus thymallus*, one isolated specimen (similar to *G. thymalli*) in a lake in NW Sweden.

***G. lavareti* Malmberg, 1957**

Fish farm: on *O. mykiss* in one farm in SW Sweden (see above).

Natural water: on *Coregonus lavaretus* in a lake in NW Central Sweden (type locality).

***G. derjavini* sensu MALMBERG et MALMBERG (1987)**

Fish farms: on *S. trutta* in two geographically distributed farms; on *O. mykiss*, *Salvelinus alpinus* and *Salvelinus fontinalis* in a third, more westerly farm.

Natural waters: on *S. trutta* in 6 rivers in the southern half of Sweden; on *S. salar* in two rivers with Baltic salmon and one river with Atlantic salmon.

***G.* sp., *G. wageneri*-group**

Fish farms: -

Natural water: on *Osmerus eperlanus* in the Baltic (brackish water; approx. 5-6 ‰) at one Swedish locality.

5.8. Finland

5.8.1. Aquaculture

O. mykiss is farmed in all parts of Finland; *S. salar* of the Baltic salmon stock also farmed.

5.8.2. *Gyrodactylus* species

RINTAMÄKI (1989) studied *G. salaris* in a fish farm in Northern Finland. MALMBERG et MALMBERG (1989) reported *G. salaris* from Northern Finland and the Finnish Archipelago (Åbolands Skärgård), brackish water.

Remark. MALMBERG et MALMBERG (1987; Fig: No 9) presented a species from *O. mykiss* in Finland. In 1992, I identified this species as *G. lavareti*.

***G. salaris* Malmberg, 1957**

Fish farms: on *Salmo salar*, one of the farms in brackish water (salinity about 5 ‰).

Natural waters: -

***G. lavareti* Malmberg, 1957**

Fish farms: on *O. mykiss*.

Natural waters : -

G. **sp.,** ***G. wageneri*-group**

Fish farms: -

Natural water: on *Osmerus eperlanus* in the Baltic (brackish water; approx. 5-6 ‰) at one Finnish locality.

5.9. NORWAY

5.9.1. Aquaculture

E.g. *S. salar* and *O. mykiss* are cultured.

5.9.2. *Gyrodactylus* species

TANUM (1983) and JOHNSEN et JENSEN (1991) reported *G. salaris*. MO (1983) reported *G. truttae* syn. *G. derjavini* sensu MALMBERG et MALMBERG. MO (1991a) reported *G. salaris*, *G. derjavini*, *G. birmani* and *G. thymalli*.

G. salaris **Malmberg, 1957**

Fish farms: on *S. salar* in about 35 farms.

Natural waters: on *S. salar*, Atlantic stocks in about 35 (out of more than 210 investigated) rivers, scattered over Norway.

G. derjavini **sensu MALMBERG et MALMBERG (1987)**

Fish farms: -
Natural waters: on *S. trutta* in SE Norway

G. birmani **Konovalov, 1967**

Fish farms: -

Natural waters: on *Salvelinus alpinus*.

G. thymalli **Zitnan, 1960**

Fish farms: -

Natural waters: on *Thymallus thymallus*.

7. DISCUSSION

Gyrodactylus species on salmonids; taxonomic problems

The morphological discrimination of *Gyrodactylus* species is based on the differences in shape between marginal hooks, anchors and ventral bars. These species characters are likewise a good basis for studies of infraspecific variations (MALMBERG, 1970). Studies of *G. salaris* revealed an unusually large range of variations of the species characters (TANUM, 1983), which may be an effect of "culturing" and genetic drift (MALMBERG, 1987a). Although to a less extent, similar variations seem to be present also in *G. derjavini* sensu MALMBERG et MALMBERG. Furthermore, under fish farm conditions, a *Gyrodactylus* species may adapt to a "wrong host". Thus *G. salaris* and the above *G. derjavini* can live and reproduce on *Oncorhynchus mykiss*. At least in the case of *G. salaris*, this adaptation seems to have resulted in a special form of *G. salaris* (see MALMBERG, 1973; MALMBERG et MALMBERG, 1987; MO, 1991d), which form seems to have the capacity to spread to wild salmon parr in natural waters (MO, 1991d). A "cultured" form may remind of related/similar species, e.g. the "*O. mykiss form*" of *G. salaris* reminds of *G. thymalli*. For the species discrimination such forms may be a problem, which can only be solved by comparative studies of the range of variation of *Gyrodactylus* specimens from fish farms and natural waters.

Distribution of species groups of *Gyrodactylus* on salmonids

In this paper, 21 species of *Gyrodactylus* are pesented and arranged into six species groups. The six *Gyrodactylus*-groups are found within different areas of the Northern Hemisphere (Fig. 1): hitherto the *G. japonicus*-group is only found in Japan, the *G. arcuatus*-group only in North America, the *G. taimeni*-group only in central Asia (Mongolia). The *G. wageneri*-group is distributed within Europe, including an area around the Black Sea and the Caspian Sea. The *G. lavareti*-group is found in western as well as in eastern areas of Eurasia, while the *G. salaris*-group is differently represented in areas all over the Northern Hemisphaere.

The three species of the *G. japonicus*-group (Fig. 1) are probably specific to *Plecoglossus altivelis*, an anadromous salmonid, which lives in waters of Taiwan, Korea and eastern China. The species is the only representative of the genus *Plecoglossus*, that might form a separate branch of salmonids (DOROFEUEVA et al., 1981; GORDON et SANFORD, 1987). The host specificity and the co-evolution between host and parasite common in the genus *Gyrodactylus* may imply that the *G. japonicus*-group not will be found outside the distribution area of *P. altivelis*. A restricted, host related distribution may also apply to the *G. taimeni*-group. Its two representatives, *G. taimeni* and *G. bolonensis* are not related to any *Gyrodactylus* species described from salmonids. *Hucho taimen* lives within the eastern half of Eurasia and the osmerid *Hypopmesus olidus*, the fresh water smelt, has an eastern Asian distribution. Its *Gyrodactylus species, G. bolonensis* is quite different to the *G.* sp. found on *Osmerus* eperlanus in the Baltic (Figs. 7d, h).

Generally, in fresh water, the *G. arcuatus*-group seems to have more representatives within the North American continent than in Eurasia (MALMBERG, 1970) and a number of North American *Gyrodactylus* species of this group are described from unrelated fish species. From this point of view, it seems likely that a member of the *G. arcuatus*-group, *G. colemanensis* also could adapt to a North American salmonid. Hitherto, however, the species is not found on a specific host in natural waters. Furthermore, on salmonids in farms the species seems not to cause disease (CUSACK, 1986; CONE et CUSACK, 1988). Thus the species in fish farms may use salmonids as temporary hosts.

Generally, in Europe, the *G. wageneri*-group has several representatives, many of them parasitizing unrelated fish species. The group does not seem to be present on salmonids in northern areas of Europe (MALMBERG et MALMBERG, 1991). Otherwise, the presence of the *G. wageneri*-group on salmonids correlates the distribution of species and subspecies of *Salmo trutta*, i.e. Europe, including areas around the Black Sea and the Caspian Sea (Figs. 1, 2).

Hitherto the *G. lavareti*-group is found on *Coregonus lavaretus* in western Europe and on *C. nasu* in Kamchatka (Table 1). The coregonids are distributed over the northern half of Eurasia and North America. Further investigations will reveal whether or not the *G. lavareti*-group also has representatives on coregonids in natural waters in North America.

The *G. salaris*-group can be divided into three subgroups (Table I). *G. thymalli*, a representative of the subgroup 2, is found on fish of the genus *Thymallus* in Europe and in Kamchatka. The subgroup 3, likewise has a representative in Europe (Norway) and in Kamchatka, i.e. *G. birmani*, on *Salvelinus alpinus*. In both cases, the presence of the parasites may depend on a coincident distribution of parasites and hosts within the Eurasian continent. The two fish genera are also present in northern North America, but hitherto no *Gyrodactylus* species of the subgroup 3 are described from that area.

Findings of the remaining members of the *G. salaris*-group indicate quite disparate distributions of the group (Fig. 1). Thus *G. masu* of the subgroup 3 is only described from *O. masu* in Japan, *G. nerkae* and *G. salmonis* of the same subgroup are only found in North America and *G. salaris*, *G. brachymystacis*, *G. lenoki* and *G. asiaticus* of the subgroup 1 are hitherto only found in Eurasia. The last three species are described from the primitive (DOROFEYEVA *et al.*, 1981) salmonid genus *Brachymystax*, distributed in central Asia (Mongolia). *G. salaris* (subgroup 1) in turn, is found in natural waters on *Salmo trutta* in the Ukraine, on *Salmo salar*, in the Baltic area and in Norway. Hitherto *G. salaris* is not reported from natural waters in western Europe, including the British Isles, and not from natural waters in eastern Asia or North America. *Salmo salar* is distributed on both sides of the Atlantic Ocean. From this point of view, a coincident distribution of *G. salaris* would have been possible. A natural spreading of *G. salaris* with adult host specimens over the Atlantic Ocean, however, might have been completely impossible because of the high salinity of the macroenvironment. The close relationship between *G. salaris* and other members of subgroup 1 (Fig. 6 a-d), in turn and possibly also the finding of *G. salaris* in natural water in the Ukraine, indicates that *G. salaris* once spread from central Asia, westwards to the Baltic area of Europe. Probably, early developmental stages of the Baltic after the last Glacial Period permitted a certain spread of the species over Sweden to the Swedish West-Coast, but a further spreading to Norway was stopped by the Scandinavian Mountains (MALMBERG et MALMBERG, in press; see also NORRMAN, 1992). Most likely, during the first half of the 1970s, this natural barrier was overcome by means of antrophocoric spreading (salmonid transports; MALMBERG, 1989).

With one exception (*G. colemanensis*), all members of *Gyrodactylus* on salmonids might be limnic species. Thus the Atlantic and the Pacific Oceans may have prevented spreading of these *Gyrodactylus* species in between the Eurasian and the North American continents. On sticklebacks (*Gasterosteus*), members of the *G. arcuatus*-group are present on both sides of the northern Atlantic ocean. Thus *G. colemanensis* of the *G. arcuatus*-group could be presumed to endure spreading on adult salmon from North America via Greenland to Europe. This seems not to have happend. Furthermore, the present findings in fish farms in different areas of North America may indicate that the species is restricted to fresh water (see above).

Environmental conditions

As an ectoparasite, a *Gyrodactylus* species is constrained to microenvironmental conditions (generally an epithelium of the host) and the macroenvironment (the mutual environment of the host and the gyrodactylid). Because of the small body size (approx. 0.5-1.0 mm), however, a *Gyrodactylus* species is also dependent on the conditions in a mixed environment, i.e. the environment close to external parts of the host (Fig. 3). The latter environment is influenced by different kinds of exchange between the host and the macroenvironment. All three environments may exhibit seasonal variations.

Comparative morphological investigations during different times of the year revealed seasonal variations and differences between species regarding preference and tolerance to macroenvironmental conditions (MALMBERG, 1970), e.g. regarding the water salinity (fresh and salt water species). Macroenvironmental conditions may exclude a *Gyrodactylus* species from an environment that is fully adequate or endurable for its host. This applies e.g. to the *Gyrodactylus* species of fresh and salt water species living in the Baltic area with a salinity of approx. 5 ‰. The "hard" brackish water environment also seems to diminsh the opportunities to use temporary hosts, compared to what may be possible on the same hosts in fresh and saltwater, respectively. An oligotrophic fresh water seems also to be problematic or exclude certain *Gyrodactylus* species (MALMBERG, 1970). Macroenvironmental conditions may be the reason why no *Gyrodactylus* species were found on salmonids in certain Swedish rivers and may also explain the absence of *Gyrodactylus* in certain investigated salmonid farms

(MALMBERG et MALMBERG, 1991). The changing of macroenvironment by the host may cause the death or a gradual disappearance of the specimens of some of its *Gyrodactylus* species. Thus the fresh water species *G. salaris* will disappear in salt water. Under farmed conditions, in waters of a salinity of approx. 5 ‰, the parasite can survive and probably also reproduce (MALMBERG et MALMBERG, 1991). Temporarily, it can endure a higher salinity (SOLENG et BAKKE, 1991), but its narrow salt water tolerance will result in seaward migrating smolts, becoming free from *G. salaris*. Reinfestation of the adults in the ascending river may contribute to a further spread of the parasite.

A *Gyrodactylus* species on its wild salmonid host may exhibit seasonal variations in infestation intensity. These variations may relate to environmental conditions. The fact, that in salmonid farms gyrodactylosis mostly is limited to a certain period of the year may likewise depend on environmental conditions. Thus in northern Sweden *G. salaris* gyrodactylosis seems to correlate to the moderate increase in water temperature during early springtime (MALMBERG et MALMBERG, 1991). The difference between infestation intensity on small fertile males (precocious males) and smolts compared to other salmon parr in a river indicates a more complicated procedure. Probably the hormonal changes associated with precocious maturation in male parr in early winter, and in smoltification during spring may influence the reproductive capacity of *G. salaris*, and increase the population size on such parr specimens. Infested precocious males and smolts may act as important spreaders of *G. salaris* within a river system (MALMBERG et MALMBERG, in press).

Host specificity

Investigations of natural waters within the Eurasian area indicate that teleostean fish species may have one or more host specific *Gyrodactylus* species. The host specificity can be inexorable : a "wrong host" is repellent for a number of *Gyrodactylus* species. Other *Gyrodactylus* species may survive for a short time on an "accidental host" and still others can use one or more temporary hosts, e.g. for their spreading (MALMBERG, 1970). In Swedish rivers, *G. salaris* was rarely found on *Salmo trutta*. During the warmer part of the year, in southern rivers, however, *G. derjavini* sensu MALMBERG et MALMBERG was often present on parr specimens of *S. salar*. It seems likely, that *G. derjavini* can use *S. salar* as a transport host and that this capacity increases the spreading opportunities of the parasite to other specimens of *S. trutta*, its true host.

Fish farming

Fish farms (Fig. 5) may be favourable to certain *Gyrodactylus* species and contribute to their spreading. Few specimens of *Gyrodactylus* on individuals of stocked fish, wild fish entering the farm via the water supply (CONE et CUSACK, 1988), or even detached worms in the water intake may give rise to large populations of *Gyrodactylus* in a farm. The unnaturally large density of fish in the tanks will favour the development of a *Gyrodactylus* population. Backets and nets used for more than one tank may favour spreading within the farm. Via the waste-water from a farm, wild fish in the water recipient may subsequently become infested by *Gyrodactylus*. The presence of one or more harmless *Gyrodactylus* species in a farm may not attract notice and as long as the fish remains healthy, the presence of a pathogenic species may probably not be observed. Only 8 of the 21 species presented in this paper were found in salmonid farms. Four of the eight species: the three species of the *G. japonicus*-group and *G. masu* of the *G. salaris*-group, seem to cause no problem in farms (OGAWA et EGUSA, 1978; OGAWA, 1986). Of the remaining four, *G. colemanensis* may give rise to mass-infestation. Hitherto, however, only three : *G. salaris*, *G. salmonis* and *G. derjavini* sensu MALMBERG et MALMBERG are known to cause gyrodactylosis on farmed salmonids.

Under farmed conditions, the rainbow trout, *Oncorhynchus mykiss* is a unique temporary host : in North America it harbours other species of *Gyrodactylus* than found in Europe (MALMBERG et MALMBERG, 1987). In Sweden, *G. salaris*, *G. lavareti* and *G. derjavini* sensu MALMBERG et MALMBERG can survive and reproduce on rainbow trout. In only one northern Swedish farm, however, was *G. derjavini* found (MALMBERG et MALMBERG, 1991) and in cages in the Lake Enare, northern Findland only *G. lavareti* and *G. salaris* was registrated (see below). In natural waters in Finland and northern areas of Sweden and Norway, *G. derjavini* has to date never been found. This may imply that natural waters in northern parts of Europe do not belong to the distribution area of the species. Furthermore, in Swedish farms, none of the three species seem to be harmful to *O. mykiss*. In the southern Denmark, however, farmed *O. mykiss* was treated against *G. derjavini* gyrodactylosis (MALMBERG et MALMBERG, 1991). The mean annual water temperature is higher in Denmark than in the other three countries. Thus the pathogenity of the parasite may be influenced by the water temperature, i.e. only in farms with a certain water temperature, *G. derjavini* sensu MALMBERG et MALMBERG may be pathogenetic to the "wrong host" *O. mykiss*.

In North American fish farms, *G. colemanensis* seems to live and reproduce successfully on several salmonid species. This seems also to be valid to *G. salmonis*. In laboratory experiments (CONE et ODENSE, 1984; CUSACK, 1986; CUSACK et CONE, 1986; CONE et CUSACK, 1988), however, *G. salmonis* was pathogenic to the experimental host, *Salvelinus fontinalis*, while infestations by *G. colemanensis* caused no clinical sign. This may imply that *G. salmonis* (*G. salaris*-group) is a true salmonid parasite, while *G. colemanensis* (*G. arcuatus*-group) is not specific to salmonids. Probably *G. colemanensis* is secondarily spread from a non-salmonid fish species, and under farm conditions it can adapt and successfully live and reproduce on several salmonids without causing gyrodactylosis.

Generally, confined fish live in an unnaturally delimited macroenvironment. The delimitation may favour certain *Gyrodactylus* species. In a field experiment (unpublished), *Phoxinus phoxinus* (L.) was kept for several month in a fish-chest. The *Gyrodactylus* fauna on the confined fish was followed and compared to the fauna on wild *P. phoxini*, captured during the experiment within the same area. At the end of the experiment, a rare species of *Gyrodactylus* was rather common in the fish-chest but during the experiment no time on wild specimens. Furthermore, during the spawning time of *Perca fluviatilis* L., several specimens were kept in a fish-chest. After a month or so the fish in the chest was intensively infested by a host specific *Gyrodactylus* species, until that time not found on wild specimens within that area. The two experimental results apply to fish farmed in cages in a natural water. It is most likely that *Gyrodactylus* infested salmonids in a cage farm, e.g. salmon parr in fresh water (lakes), sooner or later will suffer from gyrodactylosis. Furthermore, there is a risk that in time, the fish will become infested by fish in the surrounding water. Even good water exchange in the cages may not compensate for the confined cage conditions. In a fish farm with running water, however, an increased water current may help the neutralizing of a gyrodactylosis by causing attachment problems to infesting *Gyrodactylus* specimens. In an infested farm with recirculating water, however, an increased water current will have no treating effects.

Threats against salmonid stocks by *Gyrodactylus* species

Only 2 species, *G. derjavini* Mikailov, 1975 and *G. salaris* Malmberg, 1957, out of the 21 species presented in this paper are known to cause gyrodactylosis on salmonids in natural waters. *G. derjavini* Mikailov can cause death to specimens of *S. trutta caspius* and *S. trutta oxianus* in rivers in Azerbaidzhan and Tadzhikistan (ERGENS, 1983). There is no information, however, about economics caused by the species. For preventing a possible spread of this *G. derjavini* gyrodactylosis, fish transports might be avoided from the infested areas to uninfested areas with trout in a similar macroenvironment.

The salmon in rivers of the Swedish West-Coast belong to the Atlantic Salmon stock. Hitherto, *G. salaris* has been found in only two of these rivers. Here, however, even the highest registrated intensity of infestation is lower than the intensities found in Norwegian rivers, but higher than any intensity found in infested rivers within Baltic region (Baltic salmon stock). The intermediate situation of the Atlantic salmon in western Sweden may depend on a less developed resistance to *G. salaris*, compared to the resistance of the Baltic salmon (MALMBERG et MALMBERG, in press). Macroenvironmental conditions, e.g. the annual mean temperature, may also have an influence. Generally, the above Swedish rivers with the Atlantic salmon stock are more southerly situated than Norwegian rivers and the higher annual mean temparature in these Swedish rivers may decrease the pathogenesis of *G. salaris*. This would imply, that *G. salaris* would cause less severe infestations than in Norway on Atlantic salmon stocks in natural waters with a higher annual mean temperature than in Scandinavia.

Fear for a further spread of the *G. salaris* epidemics came recently true : *G. salaris* gyrodactylosis seems to have now spread to salmon parr in Russian rivers falling into the White Sea (T.A. MO, comm. pers.). The distribution area of the Norwegian Atlantic Salmon stock includes the White Sea and this stock has a low resistance to *G. salaris*. The background of the "Russian *Gyrodactylus* story" seems to be as follows. In 1990, it was feared that rainbow trout, *O. mykiss* in cages in Lake Enare, northern Finland, were infested by *G. salaris*. It was established, however, that the rainbow trout harboured another species (discriminated by me as *G. lavareti*). Later on, new samples revealed that farmed *O. mykiss* in Lake Enare harboured both *G. lavareti* and *G. salaris* (determination T. A. MO, comm. pers.). Still later on, it became known, that live *O. mykiss* specimens from Lake Enare had been exported to the White Sea area (MO, comm. pers.). Presumably, the exported *O. mykiss* were infested and after being stocked in river systems in the White Sea area, they spread the *G. salaris* epidemic to the local salmon. Such a spread reminds of the spreading of *G. salaris* to the River Drammenselva in southeastern Norway. There infested *O. mykiss* specimens, escaping from cages in a lake in the river system, might have spread the *G. salaris* gyrodactylosis to salmon populations downstream of the lake. Measures are urgently needed to prevent spreading of the epidemic to the salmon in adjacent northern fresh waters, e.g. the important Teno River in northern Norway.

8. CONCLUSIONS

The Norwegian catastrophy caused by *G. salaris* drew attention to gyrodactylids on farmed salmonids and the disastrous spread of a pathogenic *Gyrodactylus* species to an economically important salmonid in natural waters. Increased studies have considerably increased our knowledge about gyrodactylids on salmonids. Certainly, one of the most important results obtained by these studies is the establishment of a greater resistance to *G. salaris* for specimens of the Baltic Salmon stock (River Neva) than for specimens of the Norwegian Atlantic Salmon stock (BAKKE *et al.*, 1990b ; BAKKE et MacKENZIE, 1992). If further investigations will prove that this resistance is genetically based (JANSEN *et. al.*, 1991), genetic manipulation and selection of salmon specimens may be a useful tool in the atempt to restore salmon rivers suffering from *G. salaris* gyrodactylosis (BAKKE et MacKENZIE, 1992).

The unique viviparity in *Gyrodactylus*, makes possible an enormous reproductive capacity, at least in certain species, and only one specimen of such a species may in a short time result in a huge population. In fish farms, genetic drift within isolated populations of such a *Gyrodactylus* species may result in changed forms with an increased pathogenity (MALMBERG, 1987a). Then, spread of such a pathogenetic form to natural waters, with an insufficiently resistant host stock, may cause mortal gyrodactylosis. However, *Gyrodactylus* species seem to differ in reproductive capacity. The reproductive capacity in turn, may be influenced by the host's condition and/or hormonal status. Further studies of processes behind the gyrodactylid viviparity may reveal opportunities to influence the reproductive capacity of pathogenetic species.

On fins of *S. salar* of the Norwegian Atlantic stock, the pharynx, but not the opisthaptor of *G. salaris* caused distinct wounds, which seemed to have problematic healing (Fig. 4). Similar studies on specimens from both Atlantic and Baltic stocks, with gyrodactylosis are of interest: the healing process may reflect the varying resistence present in different salmon stocks. Comparative SEM studies of tracks after the opisthaptor and the pharynx of *G. salaris* and other pathogenetic and non pathogentic species will yield information concerning the effects on the host epithelium by different *Gyrodactylus* species.

Investigations from the field and in the laboratory indicate a complicated interaction between the macro- and the microenvironment of *Gyrodactylus* species. Probably, the different resistance to *G. salaris* between Swedish and Norwegian populations of the Atlantic stock is more complicated than a different degree of immunity. Macroenvironmental conditions may also have an influence. Investigations on geographical distribution and seasonal variations, together with long-term experimental studies of macroenvironmental preferences in actual species may reveal micro-and macroenvironmental relations of interest to the control of pathogenetic *Gyrodactylus* species.

However, the spread of *Gyrodactylus* species to salmonids in natural waters can be effectively obstructed : by a better control of *Gyrodactylus* species in connection with fish farming; by preventing the escaping of fish from cages in natural waters ; by cleaning waste water from fish farms ; by treatment of fish before transportation; by treatment of fish before stocking of farmed fish in natural waters.

9. Acknowledgements

A large part of the work was carried out at the Department of Zoology, Stockholm University, and I wish to express my gratitude for the facilities placed at my disposal.

I am grateful to BIBBI MAYRHOFER at the Department of Zoology, Stockholm who kindly made the maps and illustrations of this paper by means of computo-graphics and to Dr. IAN MAYER at the same institute for his linguistic revision. Dr. RADIM ERGENS, Czechoslovakia and Dr. KAZUO OGAWA, Japan kindly loaned me slides of *Gyrodactylus* species from salmonids. Dr. ALAIN LAMBERT, France kindly made the French résumé.

Most of the field investigations were performed together with my wife, Fil.lic. MARIANNE MALMBERG. I also wish to thank all people who assisted with the field work. The field investigations were supported by grants from the Swedish National Board of Fisheries.

10. REFERENCES

ACKEFORS H., JOHANSSON N., WAHLBERG B., 1991. The Swedish compensatory programme for salmon in the Baltic : an action plan with biological and economic implications. *ICES mar. Sci. Symp., 192*, 109-119.

ADCP : AQUACULTURE DEVELOPMENT AND COORDINATING PROGRAMME, 1988, 1989. A regional survey of aquaculture sectors, Rep. 88, 89, rom.

ALENÄS I., 1992. Sammanställning av elfisken, Falkenbergs Kommun 1992 (in Swedish), Miljö-och Hälsoskyddskontoret, Falkenberg, *Rapport*, 3, 1-12.

BAKKE T.A., HARRIS P.D., JANSEN P.A., 1992a. The susceptibility of *Salvelinus fontinalis* (Mitchill) to *Gyrodactylus salaris* Malmberg (Platyhelminthes; Monogenea) under expe rimental conditions. *J. Fish. Biol., 41*, 499-507.

BAKKE T.A., HARRIS, P.D., JANSEN P.A., HANSEN L.P., 1992b. Host specificity and dispersal strategy in gyrodactylid monogeneans, with particular reference to *Gyrodactylus salaris* (Platyhelminthes, Monogenea). *Dis. Aquat. Org., 13*, 63-74.

BAKKE T.A., JANSEN P.A., 1992. *Gyrodactylus salaris* (Monogenea) on salmonoid fish : host specificity, resistance and susceptibility, *in* Pathological Conditions of Wild Salmonids. SOAFD Marine Laboratory, 6-8 May 1992, Aberdeen.

BAKKE T.A., JANSEN P.A., BRABRAND Å., 1990a. Susceptibility and resistance of brook lamprey, *Lampreta planeri* (Bloch), roach, *Rutilus rutilus* (L.) and perch, Perca *fluviatilis* L. to *Gyrodactylus salaris* Malmberg (Monogenea). *Fauna norv. Ser. A, 11*, 23-26.

BAKKE T.A., JANSEN P.A., HANSEN L.P., 1990b. Differences in the host resistance of Atlantic salmon, *Salmo salar* L., stocks to the monogenean *Gyrodactylus salaris* Malmberg, 1957. *J. Fish. Biol., 37*, 577-587.

BAKKE T.A., JANSEN P.A., KENNEDY C.R., 1991. The host specificity of *Gyrodactylus salaris* Malmberg (Platyhelminthes, Monogenea): susceptibility of *Oncorhynchus mykiss* (Walbaum) under experimental conditions. *J. Fish. Biol., 39*, 45-57.

BAKKE T.A., MacKENZIE K., 1992. Comparative susceptibility of native Scottish and Norwegian stocks of Atlantic salmon, *Salmo salar* L., to *Gyrodactylus salaris* Malmberg: Laboratory experiments *in* CM 1992/M:32, Session O. Anadromous and Catadromous Fish Committee. Internat. Council. Exploration. Sea, 1-7.

BAKKE T.A., SHARP L.A., 1990. Susceptibility and resistance of minnows, *Phoxinus phoxinus* (L.) to *Gyrodactylus salaris* Malmberg, 1957 (Monogenea) under laboratory conditions. *Fauna norv. Ser., 11*, 51-55.

BRAUN F., 1966. Beiträge zur mikroskopischen Anatomie und Fortplanzungsbiologie von *Gyrodactylus wageneri* v. Nordmann, 1832. *Z. ParasitKde, 28*, 142-174.

BYCHOWSKY B.E., 1961. Monogenetic trematodes. Their systematics and phylogeny. Am. Inst. Biol.Sci. Publ., Stockholm,627 p.

CONE D.K., BEVERLEY-BURTON M., WILES M., McDONALD T.E., 1983. The taxonomy of *Gyrodactylus* (Monogenea) parasitizing certain salmonid fishes of North America, with a description of *Gyrodactylus nerkae* n.sp. *Can. J. Zool., 61*, 2587-2597.

CONE D.K., CUSACK R., 1988. A study of *Gyrodactylus colemanensis* Mizelle and Kritsky, 1967 and *Gyrodactylus salmonis* (Yin and Sproston, 1948) Monogenea parasitizing captive salmonids in Nova Scotia. *Can. J. Zool.*, 66, 409-415.

CONE D.K., ODENSE P.H., 1984. Pathology of five species of *Gyrodactylus* Nordmann, 1832 (Monogenea). *Can. J. Zool., 62*, 1084-1088.

COOK P.H., 1984. Directional information from surface swell: some possibilities. 79-101 *in* McCleave J.D., Arnold G.P., Dodson J.J., Neill W.H. Mechanisms of migration in fishes. Plenum Press, New York, London, 574 p.

CRANE J.W., MIZELLE J.D., 1967. Studies on monogenetic trematodes. XXXI. Five new species of *Gyrodactylus* from California fish. *J. Parasitol., 53*, 270-273.

CUSACK R., 1986. Development of infections of *Gyrodactylus colemanensis* Mizelle and Kritsky, 1967 (Monogenea) and the effect on fry of *Salmo gairdneri* Richardson. *J. Parasit., 72*, 663-668.

CUSACK R., CONE D.K., 1986. *Gyrodactylus salmonis* (Yin and Sproston, 1948) parasitizing fry of *Salvelinus fontinalis* (Mitchill). *J. Wildlife Dis., 22*, 209-213

DOLMEN D., 1987. *Gyrodactylus salaris* (Monogenea) in Norway ; infestations and management. in STENMARK A., MALMBERG, G., Parasites and diseases in natural waters and aquaculture in Nordic countries, 63-69, Naturhistoriska Riksmuseets Reprocentral, Stockholm.

DOROFEYEVA Y.A., ZINOVYEV Y.A., KLYUKANOV V.A., RESHETNIKOV Y.S., SAVVAITOVA K.A., SHAPOSHNIKOVA G.K., 1981. The present state of research into the phylogeny and classification of Salmonoidei. *Ichthyol., 20*, 1-19.

ERGENS R., 1971. Dactylogyridae and Gyrodactylidae (Monogenoidea) from some fishes fom Mongolia. *Folia parasit., 18*, 241-254.

ERGENS R., 1978. Two new species of *Gyrodactylus* (Monogenoidea) from Mongolian *Brachymystax* lenok (Pallas). *Folia parasit., 25*,79-81.

ERGENS R., 1983. *Gyrodactylus* from Eurasian freshwater Salmonidae and Thymallidae. *Folia parasit., 30*, 15-26.

ERGENS R. 1992. Redescription of *Gyrodactylus truttae* Gläser, 1974 (Monogenea : Gyrodactylidae) from *Salmo trutta fario* L. (Clupeiformes: Salmonidae). *Folia parasit., 39*, 201-206.

ERGENS R., YUKHIMENKO S.S., 1975. Two new species of the genus *Gyrodactylus* Nordmann, 1832 (Monogenoidea) from fishes of the River Amur. *Folia parasit., 22*, 177-179.

GLÄSER H-J., 1969. Die *Gyrodactylus*-Arten des Karpfens in der Deutschen Demokratischen Republik. *Dt. Fischerei Ztg., 16*, 372-380.

GLÄSER H-J., 1974. Sechs neue Arten der *Gyrodactylus*-wageneri-Gruppe (Monogenea, Gyrodactylidae) nebst Bemerkungen zur Präparation, Determination, Terminologie und Wirtsspezifität. *Zool. Anz., 192*, 56-76.

GORDON J.H., SANFORD C.P.J., 1987. The phylogenetic position of the Plecoglossidae (Teleostei, Salmoniformes), with comments on the Osmeridae and Osmeroidei *in* Kullander, S.O., Fernholm, B. Proceedings, V Congress of European Ichthyologists, 17-30, Stockholm 1985. Swedish Museum of Natural History, Stockholm.

GUSEV A.V., 1953. Report on monogenetic trematodes of Amur fishes (in Russian). *Trudy zool. Inst. Leningr., 13*, 127-136.

HALVORSEN O., HARTVIGSEN R., 1989. A review of the biogeography and epidemiology of *Gyrodactylus salaris. NINA, Utredning, 2,* 1-41.

HAMMAR J., 1989. Freshwater ecosystems of polar regions: vulnerable resources. *AMBIO, 18*, 6-22.

HANEK G., THRELFALL W. 1969. Monogenetic trematodes from Newfoundland, Canada. 1. New species of the genus *Gyrodactylus* Nordmann, 1832. *Can. J. Zool., 47*, 951-955.

HANSEN L.P., BAKKE T.A., 1989. Flukes, genetics and escapees. *Atlantic Salmon J., autumn 1989*, 26-29.

HARRIS P.D., 1989. Interactions between population growth and sexual reproduction in the viviparous monogenean *Gyrodactylus turnbulli* Harris, 1986 from the guppy, *Poecilia reticulata* Peters. *Parasitology, 98*, 245-251.

JANSEN P.A., 1989. Overlevelse og reproduksjon hos *Gyrodactylus salaris* Malmberg, 1957 (Platyhelminthes, Monogenea) pa atlantisk laks, *Salmo salar* L., i relasjon til temperatur. (in Norwegian). Thesis/Hovedfagsoppgave i Akakultur, 1-63, Zool. Mus., Oslo.

JANSEN P.A., BAKKE T.A., 1992. Epidemiology of *Gyrodactylus salaris* Malmberg on Atlantic salmon *Salmo salar* L. : 1. Field studies in a southeasatern Norwegian river. *in* Pathological Conditions of Wild Salmonids. SOAFD Marine Laboratory, 6-8 May 1992, Aberdeen.

JANSEN P.A., BAKKE T.A., HANSEN L.A., 1991. Resistance to *Gyrodactylus salaris* Malmberg, 1957 (Monogenea) in *Salmo salar*: a genetic component. *Bull. Scand. Soc. Parasit., 1*, 50.

JENSEN A.J., JOHNSEN B.O.,1992. Site specificity of *Gyrodactylus salaris* Malmberg, 1957 (Monogenea) on Atlantic salmon (*Salmo salar* L.) in the river Lakselva, northern Norway. *Can. J. Zool., 70*, 264-267.

JOHNSEN B.O., 1978. The effect of an attack by the parasite *Gyrodactylus salaris* on the population of salmon parr in the river Lakselva, Misavaer in Northern Norway. *Astarte, 11*, 7-9.

JOHNSEN B.O., JENSEN A.J., 1991. The *Gyrodactylus* story in Norway. *Aquaculture, 98*, 289-302.

KIKUCHI H., 1929. Two new species of Japanese trematodes belonging to Gyrodactylidae. *Annotnes. zool. jap., 12*, 175-186.

KONOVALOV S.M., 1967. Monogenetic suckers of fishes of Kamchatka (in Russian, English summary). *Parazitologiya, 2*, 137-143.

LULLU A.V., VISMANIS K.O., BAKHTINA G.B., 1989. Etiological agents of rainbow trout *Salmo gairdneri* in fish tanks *in* BAUER, O., Parasites of freshwater fish of North-West Europe, 86-88, Internat. Symp. Soviet-Finish Coop., Inst. Biol. Acad. Sci. Karelia, Petrozavodsk. Zool. Inst. Acad. Sci. Leningrad.

LUX E., 1990. *Gyrodactylus salaris* - Parasitierung von Salmoniden, ein diagnostisches-taxonomisches Problem in Bernoth, E-M., Hoffman, R. Tagung der Fachgruppe, "Fischkrankheiten" in Verbindung mit der EAFP/deutsche Sektion European Association of Fish Pathologists, 87-98, Deutsche Vet.med. Gesellschaft e.V., Giessen.

MALMBERG G., 1957. On the occurence of *Gyrodactylus* on Swedish fishes. (In Swedish, with description of species and a summary in English). *Skr. söd. Sver. Fisk För Årsskr., 1956*, 19-76.

MALMBERG G., 1964. Taxonomical and ecological problems in *Gyrodactylus* (Trematoda) Monogenea *in* ERGENS, R., RYSAVY, B., Parasitic worms and aquatic conditions, 203-230, Czechoslovak Academy of Sciences, Prague.

MALMBERG G., 1970. The excretory systems and the marginal hooks as a basis for the systematics of *Gyrodactylus* (Trematoda, Monogenea). Ark. Zool. (2), 23, 1-235.

MALMBERG G., 1973. *Gyrodactylus* infestations on species of *Salmo* in Danmish and Swedish hatcheries. *Norwegian J. Zool., 21*, 325, 326.

MALMBERG G., 1987a. Increased intraspecific divergence in *Gyrodactylus salaris* resulting from genetic drift in fish farm populations. *Information, 19*, Åbo Akad., 33.

MALMBERG G., 1987b. *Gyrodactylus salaris* Malmberg, 1957 and *G. truttae* Gläser, 1974 - two problematic species. *Information,* **19**, Åbo Akad., 34.

MALMBERG G., 1987c. *Gyrodactylus* - en haptormask av ekonomiskt intresse för fiskodlare (in Swedish). *Vattenbruk, 2,* 15-20.

MALMBERG G., 1989. Salmonid transports, culturing and *Gyrodactylus* infections in Scandinavia *in* BAUER, O., Parasites of freshwater fish of North-West Europe, 88-104. Internat. Symp. Soviet-Finish Coop., Inst. Biol. Acad. Sci. Karelia, Petrozavodsk. Zool. Inst. Acad. Sci. Leningrad.

MALMBERG G., MALMBERG M., 1987. *Gyrodactylus* in salmon and.rainbow trout farms *in* Stenmark, A. and Malmberg, G., Parasites and diseases in natural waters and aquaculture in Nordic countries, 199-204, Naturhistoriska Riksmuseets Reprocentral, Stockholm.

MALMBERG G., MALMBERG M., 1991. Investigations for *Gyrodactylus* on salmonids in natural waters and fish farms during the periods 1951-72 and 1986-May 1991. (in Swedish, legends and summary in English). *Information, 2,* Inst. Freshwater. Res., Swedish Nat. Board Fish., Drottningholm, 1-30.

MALMBERG G., MALMBERG M., (in press). Species of *Gyrodactylus* (Platyhelminthes, Monogenea) on salmonids in Sweden. *J. Fish Res.*

MEHLI S.A., DOLMEN D., 1986. Handlingsplan for tiltak mot lakseparasiten *Gyrodactylus salaris* for 10-års perioden 1987-1996. (in Norwegian). Direktoratet for Naturforvaltning (DN), Fiskekontoret, ISBN 82-7072-046-1. Trondheim, 1-42.

MITENEV V.K., 1989. Ecologic and geographic peculiarities of Monogenea in the Kola Subarctic zone. in BAUER, O., Parasites of freshwater fish of North-West Europe, 105-111, Internat. Symp. Soviet-Finish Coop., Inst. Biol. Acad. Sci. Karelia, Petrozavodsk. Zool. Inst. Acad. Sci. Leningrad.

MIZELLE J.D., KRITSKY D.S., 1967. Studies on monogenetic trematodes. XXXIII. New species of *Gyrodactylus* and a key to the North American species. *Trans. Am. microsc. Soc., 86,* 390-401.

MO T.A., 1983. *Gyrodactylus truttae* Gläser, 1974 på ørret, *Salmo trutta* L. og laks, *Salmo salar* L. in Sandviksvassdraget: Taksonomi og infeksjonsforhold. (in Norwegian). Thesis/Hovedfagsoppgave i spesiell zoologi, parasitologi, 1-85. Zoologisk Museum, Universitetet i Oslo.

MO T.A., 1991a. *Gyrodactylus salaris* - en patogen parasitt for norsk laks (in Norwegian). *Fellesnr. Naturforvaltning/Biolog, 1,* 25-28.

MO T.A., 1991b. Seasonal variations of opisthaptoral hard parts of *Gyrodactylus salaris* Malmberg, 1957 (Monogenea: Gyrodactylidae) on parr of Atlantic salmon *Salmo salar* L. in the River Batnfjordselva, Norway. *Systematic Parasiol., 19,* 231-240.

MO T.A., 1991c. Variations of the opisthaptoral hard parts of *Gyrodactylus salaris* Malmberg, 1957 (Monogenea : Gyrodactylidae) on rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) in a fish farm, with comments on the spreading of the parasite in south-eastern Norway. *Systematic Parasitol., 20,* 1-9.

MO T.A., 1991d. Variations of the opisthaptoral hard parts of *Gyrodactylus salaris* Malmberg, 1957 (Monogenea : Gyrodactylidae) on parr of Atlantic salmon *Salmo salar* L., in laboratory experiments. *Systematic Parasitol., 20,* 11-19.

MO T.A., 1992. Seasonal variations in the prevalence and infestation intensity of two *Gyrodactylus* species on salmonids in Norwegian rivers, *in* Pathological Conditions of Wild Salmonids. SOAFD Marine Laboratory, 6-8 May 1992, Aberdeen.

MONTÉN E., 1988. Fiskodling och vattenkraft (in Swedish). Vattenfall, Stockholm, 245 p.

MUUS B.J., DAHLSTRÖM P., 1968. Sötvattensfisk och fiske i Europa (in Swedish). P.A. Norstedt & Söners Förlag, Stockholm, 224 p.

NIKOLSKII G.V., 1961. Special ichthyology. Israel Prog. Sci. Trans., Jerusalem, 538 p.

NORDMANN von A., 1832. Mikrographische Beiträge zur Naturgeschichte der wirbellosen Thiere, I. Berlin, 118 p.

NORRMAN J.O., 1992. Ett hav bildas och lever vidare - Östersjöns fysiska geografi (in Swedish) pp. 21-28 *in* Naturvetenskapliga Forskningsrådets Årsbok 1992, Risbergs Tryckeri AB, Uddevalla.

OGAWA K., 1986. A monogenean parasite *Gyrodactylus masu* sp. n. (Monogenea: Gyrodactylidae) of salmonid fish in Japan. *Bull. Jap. Soc. Sci. Fisheries, 52*, 947-950.

OGAWA K., EGUSA S., 1978. Seven species of *Gyrodactylus* (Monogenea: Gyrodactylidae) from *Plecoglossus altivelis* (Plecoglossidae), *Cyprinus carpio* (Cyprinidae) and *Anguilla* spp. (Anguillidae). *Bull. Jap. Soc. Sci. Fisheries, 44*, 613-618.

PROST M. 1991. Fish Monogenea of Poland. IX. Two species of *Gyrodactylus* from Salmonidae. *Acta parasit. pol., 36*, 109-114.

REHULKA J., 1973. Remarks on the occurrence of *Gyrodactylus salaris* Malmberg, 1957 sensu Ergens, 1961 (Monogenoidea: Gyrodactylidae). *Acta Soc. Zool. Bohemosolov, 37*, 293-295.

RINTAMÄKI P., 1989. *Gyrodactylus salaris* at a fish farm in Northern Finland *in* BAUER, O., Parasites of freshwater fish of North-West Europe, 123-130, Internat. Symp. Soviet-Finish Coop., Inst. Biol. Acad. Sci. Karelia, Petrozavodsk. Zool. Inst. Acad. Sci. Leningrad.

SANTAMARINA M.T., TOJO J., UMBEIRA F.M., QUINTEIRO P., SANMARTIN M.L., 1991. Anthelmintic treatment against *Gyrodactylus* sp. infecting rainbow trout Oncorhychus mykiss. *Dis. aquat. Org., 10*, 39-43.

SCHMAHL G., 1991. The chemotherapy of monogeneans which parasitize fish: a review. *Folia Parasitol., 38*, 97-106.

SCHÄPERCLAUS W., 1991. Fish diseases, Vol. II, Oxonian Pr. Pvt. Ltd., New Delhi, 597-1398 p.

SCOTT M.E., 1982. Reproduction potential of *Gyrodactylus bullatarudis* (Monogenea) on guppies (Poecilia rfeticulata). *Parasitology, 85*, 217-236.

SCOTT M.E., NOKES D.J., 1984. Temperature-dependant reproduction and survival of *Gyrodactylus bullatarudis* (Monogenea) on guppies (*Poecilia reticulata*). *Parasitology, 89*, 221-227.

SCOTT M.E., ROBINSON M.A., 1984. Challenge infections of *Gyrodactylus bullatarudis* (Monogenea) on guppies, *Poecilia reticulata* (Peters), following treatment. *J. Fish Biol., 24*, 581-586.

SHINN A.P., SOMMERVILLE C., GIBSON D.I., 1992. The discrimination of *Gyrodactylus* species and their distribution in British salmonids *in* Pathological Conditions of Wild Salmonids. SOAFD Marine Laboratory, 6-8 May 1992, Aberdeen.

SMITH G.R., STEARLEY R.F., 1989. The classification and scientific names of rainbow and cutthroat trouts. *Fisheries, 14*, 4-20.

SOLENG A., BAKKE T.A., 1991. Experimental studies on the salinity tolerance of *Gyrodactylus salaris* Malmberg, 1957 (Monogenea). *Bull. Scand. Soc. Parasit., 1*, 79.

TANUM K., 1983. Studier av taksonomi og vertsforhold hos *Gyrodactylus*-arter på laksefisk av slektene *Salmo og Salvelinus* i Norge (in Norwegian). Thesis/Hovedfagsoppgave i spesiell zoologi, parasitologi, 1-99, Zoologisk Museum, Universitetet i Oslo.

THONEY D.A., HARGIS Jr., W.J., 1991. Monogenea (Platyhelminthes) as hazards for fish in confinement. *Annual Rev. Fish Diseas.* 133-153.

TOJO J., SANTAMARINA M.T., UBEIRA F.M., ESTEVEZ J., SANMARTIN M.L., 1992. Anthelmintic activity of benzimidazoles against *Gyrodactylus* sp. infecting rainbow trout *Oncorhynchus mykiss. Dis. aquat. Org., 12*, 185-189.

TURNBULL E.R., 1956. *Gyrodactylus bullatarudis* n.sp. from *Lebistes reticulatus* Peters with a study of its life cycle. *Can. J. Zool., 34*, 583-594.

VAN CLEAVE H.J., 1921. Notes on two genera of ectoparasitic trematodes from fresh-water fishes. *J. Parasit., 8*, 33-39.

WARD H.B., WHIPPLE G.C., 1918. Fresh-water biology. J. Wiley & Sons, Inc. New York, p. 374.

VASSVIK V. 1976. Sjøvann og kunstig fremstilt saltvann til behandling ved ektoparasitt/soppangrep på settefisk (in Norwegain). *Norsk Vetrinærtidskr., 88*, 181, 182.

WOTTEN R., SOMMERVILLE C., 1989. *Gyrodactylus* in wild and cultured Scottish salmonids. *Information, 20*, Åbo Akad., 44.

YIN W-E., SPROSTON N.G., 1948. Studies of the monogenetic trematodes of China: Parts 1-5. Part. 1 An examination of some forms of *Gyrodactylus elegans* Nordmann, and a description of a new subspecies from Chinese goldfish. *Sinensia, 19*, 57-85.

ZITNAN R., 1960. *Gyrodactylus thymalli* sp. nov. from the fins of the grayling (*Thymallus thymallus* L.) (in German, English summary). *Helminthologia, 2*, 266-269