Parasites in cultured and feral fish

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Abstract

Parasites, causing little apparent damage in feral fish populations, may become causative agents of diseases of great importance in farmed fish, leading to pathological changes, decrease of fitness or reduction of the market value of fish. Despite considerable progress in fish parasitology in the last decades, major gaps still exist in the knowledge of taxonomy, biology, epizootiology and control of fish parasites, including such ‘evergreens’ as the ciliate Ichthyophthirius multifiliis, a causative agent of white spot disease, or proliferative kidney disease (PKD), one of the most economically damaging diseases in the rainbow trout industry which causative agent remain enigmatic. Besides long-recognized parasites, other potentially severe pathogens have appeared quite recently such as amphizoic amoebae, causative agents of amoebic gill disease (AGD), the monogenean Gyrodactylus salaris which has destroyed salmon populations in Norway, or sea lice, in particular Lepeophtheirus salmonis that endanger marine salmonids in some areas. Recent spreading of some parasites throughout the world (e.g. the cestode Bothriocephalus acheilognathi) has been facilitated through insufficient veterinary control during import of fish. Control of many important parasitic diseases is still far from being satisfactory and further research is needed. Use of chemotherapy has limitations and new effective, but environmentally safe drugs should be developed. A very promising area of future research seems to be studies on immunity in parasitic infections, use of molecular technology in diagnostics and development of new vaccines against the most pathogenic parasites. ©1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Fish are an indispensable source of proteins for humans, notwithstanding their importance as an object of sport fishery and pets in the case of ornamental fish. Development

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of aquaculture during the last decades has resulted in much greater attention being paid to problems posed by parasites and their importance for fishery leading to constraints in the productivity of aquaculture (Kennedy, 1994a). Besides direct losses caused by mortality, parasites may have considerable impact on growth and behaviour of fish, their resistance to other stressing factors, susceptibility to predation, etc.; their presence may also reduce marketability of fish (Crowden and Boom, 1980; Brassard et al., 1982; Lom and Dyková, 1992; Williams and Jones, 1994; Kumaraguru et al., 1995; Woo, 1995).

Important progress in fish parasitology has been achieved in the last years and several comprehensive textbooks dealing with fish parasites have recently appeared (Lom and Dyková, 1992; Moravec, 1994; Pike and Lewis, 1994; Williams and Jones, 1994; Woo, 1995). Nevertheless, there remain numerous problems to be solved. Due to space limitations, only a few selected parasites of each major groups of fish parasites, i.e. protozoans, myxosporeans, helminths and parasitic crustaceans, will be dealt with in more detail in the present paper and some contemporary research activities and topics of possible future interest will also be briefly discussed.

2. Pathogens of cultured and feral fish: present state and perspectives

2.1. Protozoa

Protozoans undoubtedly represent one of the most important groups of pathogens which negatively affect the health state of cultured and feral fish. There are a number of protozoan parasites long recognized as causative agents of severe diseases such as flagellates of the genus *Piscionodinium*, *Ichthyobodo necator*, or *Amyloodinium* pathogenic to freshwater and marine fish, respectively, *Trypanoplasma salmositica* affecting all species of Pacific salmon on the west coast of North America, or *Cryptocaryon irritans*, a ciliate parasitic in tropical marine fish, sometimes named ‘saltwater ich’, accounting for significant economic losses in mariculture, including food and ornamental fish (Nigrelli and Ruggieri, 1966; Lom and Dyková, 1992; Moravec, 1994; Pike and Lewis, 1994; Williams and Jones, 1994; Woo and Poynton, 1995; Berland, 1997). However, other protozoans have recently appeared as serious pathogens e.g. the microsporidium *Loma salmonae*, previously considered relatively non-pathogenic to salmonids in fresh waters but now recognized as a cause of high morbidity and mortality in Pacific and Chinook salmons in Canada (Lom and Dyková, 1992; S. Poynton, personal communication). In the following paragraphs, two protozoan parasites will be discussed in more detail: the ciliate *Ichthyophthirius multifiliis* as an example of a well-known and important pathogen, and amphizoic amoebae as a newly emerged veterinary problem which requires much attention by fish parasitologists.

2.1.1. *Ichthyophthirius multifiliis*

This long-time-recognized parasite occurs in tropical, subtropical and temperate zones. Ichthyophthiriasis or ‘white spot disease’ is one of the most serious diseases of fish in fresh waters. Considerable losses caused by mortality or decreased yield in non-lethal infections have been reported from cultures of carp, rainbow trout, tilapia, eel, channel catfish as well
as ornamental fish (Ling et al., 1991; Lom and Dyková, 1992; Matthews, 1994; Buchmann and Bresciani, 1997). Besides occurrence in cultured fish, outbreaks have also been reported from feral fish populations in rivers, water reservoirs and lakes (see Matthews, 1994).

The parasite invades the skin and gills, in heavy infections eyes, buccal epithelium and tongue (Lom and Dyková, 1992). Its pathogenetic effects are heavy damage to gill and skin tissues and resulting impairment of the osmotic balance. In addition to the primary effect of the parasite, secondary bacterial infections are often associated with the white spot disease (Hines and Spira, 1974a; Lom and Dyková, 1992; Matthews, 1994).

Transmission of *I. multifiliis* in nature is very effective and rapid which contrasts with low effectivity of laboratory maintenance and losses of isolates of *I. multifiliis* after a few (maximum 50–60) cycles (Ekless and Matthews, 1993; Matthews et al., 1996). It is speculated that senescence of laboratory isolates might be related to sexual reproduction, although there is no evidence yet about this type of reproduction (Matthews, 1994; Matthews et al., 1996).

Control of the disease is based largely on use of chemical treatment as formalin, mala-chite green, chloramine T and toltrazuril (Cross and Hursey, 1973; Farley and Heckmann, 1980; Schmahl et al., 1989, 1992; Matthews, 1994) but such treatments of food fish can be questionable (Bernoth, 1991). Elimination of free-living stages as tomites or theronts by repeated changes of water and sediment in cultures can decrease population density of the parasite.

Although immunity to *I. multifiliis* has been known for a long time (Hines and Spira, 1974b; Clayton and Price, 1992), there is still no simplistic explanation of protective immunity against white spot disease (Woo, 1987; Matthews, 1994). Recent research is focused on studies of mechanisms of immunity against *Ichthyophthirius* infection and on development of new control measures such as immunization or development of vaccines (Goven et al., 1980; Ling et al., 1991; Cross and Matthews, 1992; Sin et al., 1992, 1994, 1996; Matthews, 1994).

### 2.1.2. Amphizoic amoebae

Some free-living amoebae may change their mode of life and become harmful. Pathogenic potential of these so called amphizoic amoebae is rather high and several outbreaks of diseases associated with amoebic infections, several in cultures of salmonids, have been reported (Sawyer et al., 1974; Daoust and Ferguson, 1985; Kent et al., 1988; Bullock et al., 1994; Bryant et al., 1995). Amoebic gill disease (AGD) has become a significant problem in salmonid aquaculture and AGD due to a species of *Paramoeba* in sea-caged Atlantic salmon and rainbow trout in Tasmania has been considered as the most serious infectious disease (Roubal et al., 1989; Munday et al., 1990; Bryant et al., 1995; Findlay et al., 1995).

Free-living amoebae that may become pathogenic for fish include members of the genera *Acanthamoeba*, *Cochliopodium*, *Naegleria*, *Thecamoeba*, *Vahlkampfia* and *Paramoeba*, the members of the latter genus undoubtedly being of the greatest veterinary importance (Sawyer et al., 1974; Kent et al., 1988; Roubal et al., 1989; Munday et al., 1990; Findlay et al., 1995). Currently, cases of gill amoebic infections of other fish than salmonids have also been reported, e.g., in European catfish (*Silurus glanis*) or turbot (Nash et al., 1988; Dyková et al., 1995, 1998; Paniagua et al., 1998).
The initial phase of amoebic infection of gills is similar: necrosis of epithelial cells, subsequent hypertrophy and hyperplasia of cells in contact with amoebae and fusion of secondary lamellae. This phase is followed by desquamation of the epithelium, local disturbances of blood circulation and progressive changes represented by inflammation (Dyková et al., 1995). All the above mentioned changes result in decrease or loss of gill respiratory surface area.

The present increase of recorded amoebic infections in fish may be related to improvement of diagnostic methods, in particular culture methods. If infections are old and material is not fresh, it may be difficult or impossible to isolate amoebae from gills; microbial flora is often dominant in the late phase of infection and the primary infection agent is not isolated (Dyková et al., 1995).

Control of amoebic diseases is rather problematic and effective measures are still unavailable, although amoebic gill disease of salmonids may be controlled by the use of repetitive freshwater baths (Findlay et al., 1995). One of the most promising avenues is to stimulate development of local immunity and resistance of reinfected fish (Munday et al., 1990; Bryant et al., 1995; Findlay et al., 1995) but further investigations are needed in the area of immunology, including studies of potential immunostimulants which might enhance immunity against amoebic infections, and future preparation of vaccines.

2.2. Myxozoa

Within fish parasitology, the area of research of myxosporeans (Myxozoa) attracts much research interest at this time. The application of modern molecular technology has revolutionized understanding of this group and confirmed its placement in the Metazoa, possibly to Bilateria (Anderson et al., 1998). The occurrence of the two-host life cycle involving fish and invertebrates such as tubificid worms is now well accepted. Myxosporea includes a number of important fish pathogens such as Myxobolus cerebralis, a causative agent of whirling disease with highest losses in cultures of salmonids in North America, multivalvulids of the genus Kudoa or Unicapsula seriolae that cause myoliquefaction (‘milky flesh’) in marine teleosts, or Ceratomyxa shasta, a dangerous pathogen provoking severe problems in cultured and wild populations of salmonids off the western coast of North America (Lester, 1982; Langdon, 1991; Lom and Dyková, 1992; R.A. Heckmann, personal communication). In the following paragraph, one of the most mysterious diseases caused by myxosporeans, proliferative kidney disease, will be mentioned.

2.2.1. Proliferative kidney disease (PKD)

This disease with serious consequences for cultured fish raises presently problems not only in farmed but also feral trout populations in Europe and North America (Lom and Dyková, 1992; Hoffmann and El-Matbouli, 1994).

The causative agent of PKD, named ‘PKX’, is still undetermined although it has been demonstrated that it is a myxosporean (Kent and Hedrick, 1985a, b; Kent and Hedrick, 1986; Clifton-Hadley and Feist, 1989). Kent et al. (1993, 1994) postulated the hypothesis that the PKX is a developmental stage of Sphaerospora oncorynchi.
PKX-cells, which represent multinuclear developmental stages similar to *Sphaerospora* forms in various organs outside the final site of spore production (Lom et al., 1983, 1985; Hedrick et al., 1986; Baska and Molnár, 1988), can be detected especially in the kidney and spleen (Kent and Hedrick, 1986; Hoffmann and El-Matbouli, 1994). The disease is induced by an intense defence reaction of the host elicited by the parasite (Lom and Dyková, 1992).

It is assumed that salmonids are not the original hosts of the agent of PKD because formation of spores has not been observed (Kent and Hedrick, 1985a). Other fish such as stickleback or cyprinids have been supposed to be the original hosts despite lack of convincing evidence (Feist, 1988; Hedrick et al., 1988; Bucke et al., 1991; Hoffmann and El-Matbouli, 1994).

Diagnosis of the disease is largely based on demonstration of PKX cells in histological sections of tissues (Hoffmann and El-Matbouli, 1994). More sensitive diagnostic methods are being developed, e.g., lectin binding, monoclonal antibodies, PCR or sequencing of DNA coding antigens (Castagnaro et al., 1991; Adams et al., 1992; Saulnier et al., 1996; Saunier and de Kinkelin, 1996, 1997). Control of this disease remains unsatisfactory, but antibiotics (fumagilin) may prevent PKD when given prophylactically and malachite green bath was found to be successful in suppressing PKD (Hoffmann and El-Matbouli, 1994). Prevention of contact of salmonids with other fish in the critical period (April to June) is also recommended (Lom and Dyková, 1992).

2.3. Helminths

Infections with helminths are quite common in both feral and cultured fish (Petrushevski and Shulman, 1961; Williams and Jones, 1994) and some helminths may cause veterinary problems in cultures (Bauer, 1961). There is a variety of helminth parasites recognized as pathogens of cultured and feral fish: eye or blood flukes (the genus *Diplostomum* and the family Sanguinicolidae, respectively), which may become pathogenic in feral and cultured fish populations, monogeneans as *Dactylogyrus extensus*, *D. vastator*, *D. lamellatus*, *Gyrodactylus katharineri* and *G. cyprini* in cultures of cyprinid fish, *G. luciopercae* pathogenic to pikeperch, *G. colemanensis* and *G. derjavini* to rainbow trout, *G. ictaluri* to *Ictalurus punctatus*, species of *Pseudodactylogyrus*, newly appearing pathogenic parasites in farmed eels, or *Diplectanum aequans*, one of the most important pathogens in farmed sea bass, the caryophyllidean tapeworm *Khawia sinensis*, recently imported from East Asia to Europe, or the ‘cod-worm’ (or ‘seal worm’), the anisakid nematode *Pseudoterranova decipiens*, causing great economic losses, in particular in Canada (Petrushevski and Shulman, 1961; Smith, 1972; Molnár, 1974; Lester, 1977; Lester and Huizinga, 1977; Sharriff et al., 1980; Hoffman et al., 1985; Iqbal and Sommerville, 1986; Buchmann et al., 1987; Sapolzhnikov, 1988; Cognetti-Varriale et al., 1992; Berland and Fagerholm, 1994; Chappell et al., 1994; Hoole, 1994; Kirk and Lewis, 1994; Buchmann and Bresciani, 1997; Cecchini et al., 1998; M. Gelnar, personal communication).

Three species of helminths will be dealt with in more detail as examples of how insufficient preventive control of exported fish stocks has enabled rapid emergence and subsequent wide distribution of some fish pathogens into new areas.
2.3.1. Gyrodactylus salaris

The most famous monogenean parasite in the last years is undoubtedly Gyrodactylus salaris, which eliminated several salmon populations in Norwegian rivers and caused significant losses in farms. The history of spreading of G. salaris and its detrimental effect on native fish should serve, as was stated by Mo (1994, p. 46), ‘as an object lesson of how a presumed harmless organism may become a pathogen if it is introduced to new areas where the host lacks effective responses against it.’

This viviparous, ectoparasitic monogenean with high reproductive capacity is a major problem in farmed and wild salmon in Norway. It is assumed that G. salaris was introduced to Norwegian waters recently, probably in the 1970s, with salmon parr from a hatchery in Sweden where the parasite had occurred (Johnsen and Jensen, 1986; Bakke et al., 1990; Mo, 1994). In most localities in Norway, G. salaris spread quickly infecting in two months about 90% of the salmon parr population. Migration of salmon pre-smolt between rivers via fjords and possibility of spreading of G. salaris by fish eggs probably facilitated rapid spreading of the parasite as well (Lund and Heggberget, 1992; Mo, 1994). The presence of the parasite resulted in considerable decline in salmon parr density—to about 50% two years after G. salaris introduction and to 2–4% after 5–7 years (Johnsen and Jensen, 1986; Mo, 1994).

Control measures involve replacing populations of salmon with parasite-free stocks after application of rotenone which kills all the fish in the river. Using this drastic method, the parasite has been eradicated from more than half of the localities where it previously occurred (Mo, 1994). However, the most important aim for veterinarians and fish farmers at present should be to take all possible measures to prevent introduction of the parasite to new regions. Laboratory experiments with Scottish stocks of Atlantic salmon have indicated possibly disastrous consequences of introducing G. salaris into new areas (MacKenzie and Mo, 1994).

2.3.2. Bothriocephalus acheilognathi

Regarding expansion to new regions, this pseudophyllidean cestode, named ‘Asian fish tapeworm’, occupies the most prominent position among metazoan parasites. Indigenous in East Asia (Japan and China), it has been disseminated throughout the world in association with grass carp import and man-made introduction of poeciliid and other fish. It was first introduced into the ex-USSR and East Europe in the 1960’s and now occurs in most countries of Europe, including the British Isles (Andrews et al., 1981; Scholz and Di Cave, 1993). It was imported to Mexico in 1965 with grass carp from China (López-Jiménez, 1981) and it was first reported from the USA by Hoffman (1980); into the West of the USA it was imported by bait minnows. The cestode soon appeared in South Africa (Brandt et al., 1981) and recently in Australia (Dove et al., 1997).

The Asian tapeworm is pathogenic to carp fry causing mortalities (Bauer et al., 1973; Scott and Grizzle, 1979; Hoole and Nisan, 1994). In new areas it may endanger local, often endemic fish by its occurrence (Font and Tate, 1994; Font, 1997; A. Dove, personal communication). It has been able to adapt to a wide spectrum of new, often phylogenetically unrelated fish hosts. For example, in Mexico B. acheilognathi was found during 25 years in as many as 15 species of 4 families (Centrarchidae, Atherinidae, Cyprinidae and
Goodeidae); in addition, it was reported from an amphibian (*Ambystoma dumerili*) (García-Prieto and Osorio-Sarabia, 1991). Rapid and wide spreading of *B. acheilognathi* to new regions, including isolated oceanic islands or subterranean sinkholes (cenotes), has also been facilitated by introductions of exotic fish, mainly poeciliids, to new regions for mosquito control (Font and Tate, 1994; Scholz et al., 1996; Font, 1997). Intermediate hosts of *B. acheilognathi* are planktonic copepods of the families Cyclopidae and Diaptomidae (Körting, 1975) which are present in most freshwaters.

2.3.3. *Anguillicola crassus*

The dracunculoid nematode *Anguillicola crassus* is a specific parasite of eels (*Anguilla* spp.), presumably native to South East Asia. It was originally described from cultured imported European (*A. anguilla*) and native Japanese (*A. japonica*) eels in Japan, where it does not represent a veterinary problem (Kuwahara et al., 1974). It has never been found in the feral eel populations in Japan, where another species, *A. globiceps*, occurs (Moravec and Taraschewski, 1988; Nagasawa et al., 1994).

The nematode was introduced into Europe, probably via re-exportation of European eel (*A. anguilla*) maintained in Japan or from other countries of East Asia (China or Taiwan, F. Moravec, personal communication). In Europe, it was first reported from Germany in 1982 becoming established over almost all of Europe within 10 years (Moravec, 1992). Soon after its appearance in Europe, the parasite affected natural and farmed eel populations, with the greatest outbreaks, attributed to this nematode being reported from Balaton Lake in Hungary (Molnár et al., 1993, 1994). Nematodes localized within the swimbladder degrade haemoglobin and influence other haematological parameters, with negative consequences for the respiratory capacity of infected eels (Boon et al., 1990a, b; Höglund et al., 1992; Molnár, 1993; Würtz et al., 1996).

The basic life cycle of the parasite involves only one intermediate host, a planktonic crustacean such as a cyclopid or diaptomid copepod or an ostracod (Petter et al., 1989; De Charleroy et al., 1990; Kennedy and Fitch, 1990; Moravec et al., 1993, 1994). However, most eels do not feed largely on copepods or other planktonic crustaceans, and numerous animals may be incorporated into the life cycle of *A. crassus* to facilitate transmission and to enable spreading in new areas. Third-stage larvae, infective for eels, have been found in as many as 33 species of prey (coarse) fish, serving as paratenic hosts (Haenen and van Banning, 1991; Moravec and Konecny, 1994; Szekely, 1995). In addition to prey fish, invasive larvae of *A. crassus* were found in experimentally infected tadpoles and invertebrates such as aquatic molluscs or larvae of water insects (Megaloptera, Odonata, Trichoptera) (Moravec and Konecny, 1994; Moravec, 1996; Moravec and Škoriková, 1998).

Current research in anguillicolosis is directed mainly towards problems of parasite control, including factors influencing regulations in parasite–host systems, and studies of relationships between *A. crassus* infection and susceptibility of parasitized eels to stress factors (see Ashworth, 1994). Despite a lack of any effective treatment, the veterinary interest of anguillicolosis in Europe seems to be decreasing rather than rising when compared to the first years following its introduction. However, this nematode has been recently imported to the east coast of the USA (Johnson et al., 1995; Fries and Williams,
and it is possible that it may prove to be a potential danger for eels in North America.

2.4. Parasitic crustaceans

Although parasitic crustaceans are not as numerous as protozoans or helminths, some of them are important pathogens and diseases caused by them may result in considerable economic losses. The parasitic copepods *Ergasilus sieboldi* or *Lernaea cyprinacea* may provoke veterinary problems in cultures of cyprinid fish whereas *Lernaeocera branchialis* is probably the most serious metazoan parasite of cod (*Gadus morhua*) (Boxhall and Defaye, 1993; Alston and Lewis, 1994; Berland, 1997). This ectoparasite affects reproduction of infected fish causing delayed gonad development and sexual maturity, and a negative influence on food conversion efficiency, resulting in a significant effect on the condition factor, lower growth ratio in small cod and a loss of weight up to 20–30%, and may cause mortality associated with blood loss, open lesions and possibly occlusion of vessels or aorta (Mann, 1952; Templeman et al., 1976; Möller, 1983; Khan, 1988; Khan and Lee, 1989; Khan et al., 1990; Jones and Taggart, 1998). However, the most important group among parasitic crustaceans are undoubtedly sea lice.

2.4.1. Sea lice

Sea lice is the term used to describe several species of ectoparasitic copepods of the genera *Lepeophtheirus* and *Caligus* that parasitize cultured fish and may cause diseases with damage to the epidermis and in severe cases death through osmoregulatory failure or secondary infections (Boxhall and Defaye, 1993; Berland, 1997). *Lepeophtheirus salmonis* is now recognized as one of the most serious pathogens of marine farmed Atlantic salmon (Jónsdóttir et al., 1992; Boxhall and Defaye, 1993; Ritchie, 1997). This species and *Caligus elongatus* have economic impact on farmed salmonids in the northern hemisphere (Canada, Scotland, Ireland, etc.); other caligids pathogenic to cultured or wild fish are *C. patulus*, *C. orientalis*, *C. epidemicus*, and *Pseudocaligus apodus* (Boxhall and Defaye, 1993; Roubal, 1994).

Formaldehyde, malathion and natural compounds show either poor efficacy or unsuitable therapeutic margins. Pyrethroids are at present the most used therapeutic against sea lice in Norway where more than 400 000 tonnes of salmonids were produced in 1998. Diflubenzuron and teflubenzuron added to feed are also used in significant amounts. Carbaryl and diflubenzuron are efficacious but the compounds make them unsuitable due to undesirable environmental toxicological characteristics (Roth et al., 1993). Despite these problems, chemotherapy remains an important component of control strategies. As appropriate sea lice control strategies appear to be prevention of cross-contamination by avoiding overlaps of salmon generations in cultures or biological control by stocking locally obtained wrasse (cleaner-fish of the family Labriadae) into cages when salmon first go into the sea cages (Costello, 1993). Development of vaccines against sea lice is also a perspective area of control of these parasites (Boxhall and Defaye, 1993; Jenkins et al., 1994).
3. Fish parasites and humans

In addition to the negative impact on health of feral and cultured fish, some fish parasites can also be of medical importance. Medical problems are caused mainly by those parasites, which infective stages (third-stage larvae of nematodes, metacercariae of trematodes, plerocercoids of tapeworms) are localized in the flesh of fish. Humans might acquire infection after consuming raw or poorly-cooked fish meat. As an example, anisakid nematodes (*Anisakis*, *Pseudoterranova*), the spirurid nematodes of the genus *Gnathostoma*, small liver and intestinal flukes (*Opisthorchis*, *Clonorchis*, *Heterophyes*, *Haplorchis*, *Stellantchasmus*) or *Diphyllobothrium* tapeworms can be mentioned (Oshima, 1972; Smith and Wootten, 1978; Berland and Fagerholm, 1994; Williams and Jones, 1994; WHO, 1995; Berland, 1997).

The presence of parasites may also have negative impact on the marketability of fishery products (Arthur et al., 1982). Losses caused by the presence of anisakid larvae in fish flesh are estimated to reach several millions of dollars in the Atlantic coast of Canada (Bonnell, 1994). Multivalvulid myxosporeans as *Kudoa thyrsites* or *K. musculoliquefaciens* have detrimental effect on commercial value of fish products because they macerate flesh and thus reduce economic income (Lom and Dyková, 1992).

Besides these negative effects, the occurrence of some fish parasites may provide useful information suitable for population studies of fish, including stock separation, migration and recruitment (Sherman and Wise, 1961; Arthur, 1997). Parasites have been most successfully used in studies on ecology of salmonids, in particular anadromous Pacific species of *Oncorhynchus* (MacKenzie, 1987; Arthur, 1997). Fish parasites have also been studied as possible indicators of water quality, with special attention being paid to water pollution. Numerous papers have dealt with this aspect (see Khan and Thulin, 1991 and MacKenzie et al., 1995 for review), but the topic is far beyond the scope of the present contribution.

4. Concluding remarks and perspectives

Fish parasites are an integral part of water ecosystems and they are common in natural and cultured populations of fish. In natural conditions, most parasites do not tend to severely injure their hosts and cause mortalities which affect the population size at detectable levels. It is very difficult to estimate the actual harm to fish caused by the presence of parasites; if this is uneasy in cultured fish, it is almost impossible in feral fish populations. It should also be emphasized that the presence of a parasite does not necessarily imply manifestation of a disease. Diseases caused by parasites are much more frequently manifested in cultured fish, which suffer from artificial conditions and numerous stress factors that influence their ability to effectively protect themselves against parasitic infections. In aquaculture, some parasites are able to reproduce rapidly and heavily infect a large proportion of farmed fish which may lead to diseases with significant economic consequences.

An important aspect of effective control of fish diseases caused by parasites is reliable diagnostics (see des Clers, 1993), preferably in early phases of a disease, enabling the application of adequate prophylactic measures and treatment and prevention of serious out-
breaks. Besides classical methods of diagnostics based on postmortem examination, new, non-destructive methods, which avoid killing fish, should be more widely used and further developed. Many problems remain unsolved in diagnostics of important pathogens such as amoebae or PKX and in species identification of members of all major groups of fish parasites, i.e., protozoans (e.g., species of *Trichodina*), myxosporeans (species of *Myxobolus*), helminths (*Gyrodactylus* species in salmonids or eye flukes of the genus *Diplostomum*) and crustaceans (identification of life cycle stages of parasitic copepods).

Standard taxonomical methods and identification based primarily on morphological features represent an important basis for species diagnosis. Nevertheless, new methods and techniques should be developed in order to facilitate determination, particularly in those groups of fish pathogens, where morphology cannot provide sufficient data for species distinguishing as in blood flagellates or larvae of anisakid nematodes. The use of scanning and transmission electron microscopy is inevitable for further progress in distinguishing genera and species of numerous protozoans such as diplomonadids of the genera *Spironucleus* and *Hexamita*. Recent results based on molecular approaches are very promising. For example, species-specific DNA probes have enabled us to distinguish morphologically similar taxa of *Gyrodactylus* or differentiate *Cryptobia salmositica* from other North American *Cryptobia* species (Cunningham et al., 1995a, b; Cunningham, 1997; Li and Woo, 1996). Techniques based on lectin detection, monoclonal antibody staining and PCR primers have provided valuable data on PKX (Marin de Mateo et al., 1993, 1996; Sitjà-Bobadilla and Woo, 1994; Saulnier and de Kinkelin, 1997).

There is still a high demand for improved methods to control fish parasites. Effective drugs for treatment are often available, but there are some limitations of their use because of parasite resistance, toxicity of chemicals and persistence of chemical residues. Moreover, many drugs previously widely used in fish farming such as malachite green, flibol or ditrifon are now prohibited as environmentally undesirable. Preventive measures in fish parasite control, including effective quarantine (see des Clers, 1993), are often ignored resulting in much higher costs necessary to eliminate pathogenic parasites once outbreaks have occurred. Import of infected fish and man-made introduction of parasites into new areas also cause serious problems (Kennedy, 1994b).

Studies on immunity of fish infected with parasites, their susceptibility to parasitic infections, development of immuno-chemotherapy strategies (conjugating a therapeutic drug to a monoclonal antibody) and preparation of vaccines against the most dangerous pathogens represent other perspective areas of future research in fish pathogen control (Burkart et al., 1990; Buchmann et al., 1991; Ling et al., 1993; Jenkins et al., 1994; Matthews, 1994; Forward and Woo, 1996; Li and Woo, 1995, 1997; Feng and Woo, 1996, 1997a, b; Ardelli and Woo, 1997; Buchmann and Uldal, 1997; Woo, 1998, 1999).

In some countries such as Hungary, intensity of fish culture has dropped over the last years due to high costs of fish feed. This has had a positive effect on the health status of farmed fish: diseases that existed as a consequence of intensive culturing have vanished (K. Molnár, personal communication). However, this is not, of course, the ideal way of reducing the negative impact of parasites on cultured fish. It is obvious that much more should be known about life cycles, transmission and epizootiology of fish parasites. This knowledge would enable us to apply more adequate control measures to prevent losses caused by the pathogens. As an example of relatively simple but effective control measures
based on good knowledge of transmission patterns and biology, a substantial reduction of eyeflue infection in rainbow trout in a farm in Northern Ireland can be mentioned (Field and Irwin, 1994).

Further advances in understanding aspects of biology of fish pathogens, in particular protozoans such as *I. multifiliis* or flagellates, can be brought about by the ability to maintain them in culture. Alternative methods of fish parasite control should also be developed and more widely applied. All this will enable an increase in fish production without significantly augmenting costs to control fish pathogens. It is hoped that fish parasitologists, veterinarians and fish farmers from all countries will successfully cooperate and thereby contribute to further advancements of fishery in the future.

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