



Looking fish in the eye - cataract as a problem in fish farming

Looking fish in the eye - cataract as a problem in fish farming

TemaNord 2009:515

© Nordic Council of Ministers, Copenhagen 2009

ISBN 978-92-893-1838-9

Print:

Cover:

Layout:

Cover photo:

Copies: 50

Printed on environmentally friendly paper

This publication can be ordered on www.norden.org/order. Other Nordic publications are available at www.norden.org/publications

Printed in Denmark



Nordic Council of Ministers

Store Strandstræde 18
DK-1255 Copenhagen K
Phone (+45) 3396 0200
Fax (+45) 3396 0202

Nordic Council

Store Strandstræde 18
DK-1255 Copenhagen K
Phone (+45) 3396 0400
Fax (+45) 3311 1870

www.norden.org

Nordic co-operation

Nordic cooperation is one of the world's most extensive forms of regional collaboration, involving Denmark, Finland, Iceland, Norway, Sweden, and three autonomous areas: the Faroe Islands, Greenland, and Åland.

Nordic cooperation has firm traditions in politics, the economy, and culture. It plays an important role in European and international collaboration, and aims at creating a strong Nordic community in a strong Europe.

Nordic cooperation seeks to safeguard Nordic and regional interests and principles in the global community. Common Nordic values help the region solidify its position as one of the world's most innovative and competitive.

Content

Preface	7
Summary	9
1. Introduction.....	11
1.1 General background	11
1.2 Main objectives of the LFITE-project.....	13
1.3 Overview of study subjects and methodological approach	13
1.4 Collaboration.....	14
2. Cataract prevalence	17
2.1 Cataract occurrence in farmed salmonids.....	17
2.2 Cataracts observed in the wild	22
3. Factors predisposing salmonid fishes to cataracts	25
3.1 Rearing environment.....	25
3.2 Genetics underlying cataracts.....	31
4. Individual performance	39
4.1 Foraging ability.....	39
4.2 Avoidance of predation	41
4.5 Maturation	42
4.4 Performance in the wild	43
5. Conclusions and recommendations.....	45
References	47
Sammandrag	53
Preface	55
Summary	57

Preface

This report is based on a joint Nordic research project “Looking fish in the eye – cataract as a problem in fish farming” (LFITE), which received funding from the Nordic Council of Ministers (the Nordic Working Group of Fishery Research, NAF) 2005–2007. During past years, increasing numbers of farmed salmonids have been observed to suffer from cataracts that can lead to impaired vision, and ultimately, to total blindness of the fish. Therefore, the project’s aims were to

- Update information on the prevalence of cataract in hatchery (and wild) populations of salmonid fishes in the Nordic countries.
- Elucidate factors important in influencing cataract development.
- Cast new light on consequences of cataract to performance of the fish in the hatchery and to stocked fish in the wild.

The project was carried out by scientists from Finland, Sweden and Norway.

The report summarizes what is known of cataract prevalence in salmonids in the participating countries based on literature and new data gathered from hatchery and wild-caught fish under the LFITE-project. This section is followed by a presentation of case studies conducted during the project with special attention to environmental (biotic) and genetic factors potentially important in cataract formation. Investigation into the influence of cataract on individual performance is also covered. Finally, conclusions and recommendations regarding possible lines of future actions are made.

Summary

Salmonid fishes are nowadays subject to extensive aquaculture in the Nordic countries with the aim to produce food for human consumption and, on the other hand, to enhance endangered populations by stocking of captive-propagated fish. Stocking is also conducted to underpin fisheries.

The initiation of this joint Nordic project was an outcome of the observation that increasing frequencies of cataracts have been diagnosed in farmed salmonids during past years. Cataract is a pathological condition of the eyes where the normally transparent eye lens turns opaque to a varying degree. Cataract has proven a pronounced problem in modern fish farming because it leads to impaired eyesight and even total blindness of the fish. In Norway, the Atlantic salmon industry has suffered from monetary losses owing to reduced growth and increased mortality of the fish due to cataracts. In addition to economics, concern has also arisen over the potential role of this eye disease in the failure of stocking programs. The occurrence of cataracts in farmed fish is also an ethical issue of animal welfare.

Of the Nordic countries, Norway has been the leading quarter in research on the causes of cataracts owing to the need to solve this problem that has been noticed to prevail in the economically significant Atlantic salmon farming. Therefore, information of factors underlying cataract development in salmon has started to accumulate during past years. However, there still are gaps in our knowledge on the causes of cataract as well as on its consequences. Furthermore, quantitative information on the severity of the problem in the other Nordic countries than Norway is largely lacking. Through co-operation between the Nordic countries Finland, Sweden and Norway it was possible to make progress in filling these gaps in our knowledge.

The available information on cataract occurrence in salmonids in the participating Nordic countries was updated with new data gathered during the project on the prevalence of cataract in hatchery populations of salmonid fishes in Finland and Sweden. Wild-caught fish were also included in the research. Cataracts appeared relatively common in all the six salmonid species included in the surveys but the exact prevalence and severity (coverage of eye lens) were variable being most notably related to the exposure to *Diplostomum* spp. parasite. This result is clearly a contrast to those of Norwegian studies in which nutritional imbalance and environmental (abiotic) factors have generally been established as primary explanatory causes for cataract development. New information on the occurrence of cataracts in wild fish was also gained during the project.

The research on the causes of cataracts concentrated on proximate biotic factors, parasite and pathogen infestation, as well as on the role of genetic predisposition, and progress was achieved in the course of the project in the understanding of the potentially significant role of these factors in cataract development. Based on short-term experimental work, new light was shed also on the relationship between fish performance and the occurrence of cataract. Individual energy metabolism and *Diplostomum* spp. infection and consequently parasite-induced cataracts were found to be interrelated, and cataracts were furthermore found to clearly influence both foraging and risk of predation in controlled experimental conditions. In addition, cataracts appeared to influence also the breeding biology of the fish by slowing down the female maturation process. Long-term research was also commenced on cataract occurrence and individual performance to clarify the dependency between these two phenomena more thoroughly.

Given that *Diplostomum* spp. parasites appear to play such an important role in cataract development in freshwater fish hatcheries (at least in Finland and Sweden), it is highly recommended that expedient means available for preventing or minimising the incidence of the parasite in the hatchery conditions are brought into play widely by the fish farmers. Attention should also be paid to efficient actions preventing infectious bacterial diseases that may predispose the fish to cataracts. In breeding programs and commercial aquaculture, selection against cataracts may be considered as an applicable measure to diminish cataract prevalence and severity and the growth and survival problems associated with them. When hatchery propagation and rearing is carried out for conservation purposes selection should be used on no account. The project also recommends that examination of cataracts should be included as a standard practice in fish farming, and stocking programs particularly. This will help in discerning when there is a need to take requisite actions.

1. Introduction

1.1 General background

Captive-propagated fish are increasingly being used all over the world for food production as well as for enhancing and re-establishing self-sustaining populations for conservation and fisheries purposes. The Nordic countries make no exception to this pattern. For example, Atlantic salmon *Salmo salar* aquaculture in Norway is nowadays intensive having great economic value. In Finland, on the other hand, many of the endangered fish populations have been taken to the hatchery to save them from extinction. The hatchery-reared fish are used as live gene banks and the broodstocks are generally used also for producing parr and smolts for restocking.

It has become clear that a transfer from wild to captive environment, which exposes the fish to both biological and physical conditions that they would not experience in their natural surroundings (Price 1999) may be accompanied with a number of challenges (Huntingford 2004). The abnormal artificial conditions as such and genetic deterioration of the fish, often associated with captive rearing (Allendorf and Waples 1995, Fleming et al. 2000), may for instance predispose the fish to various deficiencies and disorders (Kihlslinger & Nevitt 2006, Tiira et al. 2006).

One significant symptom of the problems caused by the artificial conditions appears to be the occurrence of eye diseases, such as cataract (Figure 1), in the farmed fish (Wall 1998). Cataract is defined as opacification of the eye lens or its capsule (Hargis 1991).

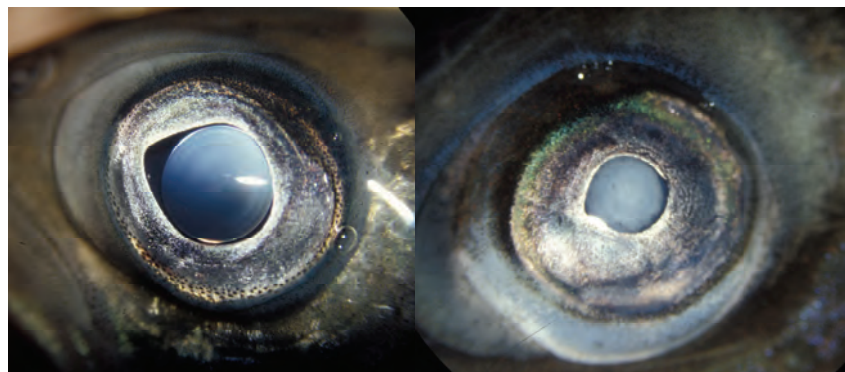


Figure 1 A healthy eye of a salmonid on the left and an eye with cataract on the right (photographs by E. Bjerkås). Fish lens is spherical with a regular transparent protein structure when healthy. Opacity (cataract) develops when structural changes in the lens fibers occur (Midtlyng et al. 1999).

Owing to the development of cataract in the lens, less light is transmitted onto the retina and vision is impaired, or even lost (Shariff et al. 1980, Bjerkås and Sveier 2004). Cataract may be a permanent destruction of lens fibres and proliferation of lens epithelium or it may appear as a reversible opacity of the lens owing to disturbances in the osmotic homeostasis of the lens (Iwata et al. 1987, Hargis 1991).

It is well established that multiple nutritional and environmental factors may lead to cataractogenic changes in the eye lens of fish and thus to primary cataracts that are not associated with previous or concurrent disease or infection. Such factors include, e.g., nutritional imbalance (Hargis 1991, Wall 1998, Waagbø et al. 2003, Bjerkås and Sveier 2004, Breck et al. 2005), changes in water temperature and salinity (Iwata et al. 1987, Bruno and Raynard 1994, Bjerkås and Bjørnstad 1999, Bjerkås et al. 2001, Breck and Sveier 2001), toxic detergents (Fraser et al. 1990), exposure to UV-light (Cullen et al. 1994) and excess oxygen in the water (Waagbø et al. 2008). Also rapid growth has been identified as a cataract-causing factor (Bjerkås et al. 1996, Ersdal et al. 2001). However, cataracts that are secondary to intraocular infection or inflammation also occur in many animal species, probably arising from inflammatory mediators in the aqueous humour that interfere with normal lens metabolism (Hendrix 2007). Secondary cataracts have been shown to be induced, e.g., by infections of the digenean trematode eye flukes *Diplostomum* spp. (e.g., Ashton et al. 1969, Shariff et al. 1980, Chappel et al. 1994, Chappell 1995, Karvonen et al. 2004a, 2004b), that are among the commonest parasites in freshwater fish causing outbreaks in fish farms (Stables and Chappell 1986, Valtonen and Gibson 1997). Multiple factors may also act in concert in predisposing the fish to cataract development (Bjerkås and Sveier 2004).

Cataracts have this far raised concern mainly in the context of cultivation of fish for human consumption because of their negative effect on growth and survival of the farmed fish (Ersdal et al. 2001, Breck and Sveier 2001, Karvonen and Seppälä 2008). The direct annual costs related to cataract were estimated as nearly 28 million € annually for Atlantic salmon in Norway alone a few years ago (Menzies et al. 2002). However, when it comes to captive propagation and subsequent release of the hatchery-reared fish, monetary losses are not the only concern. Of great significance is also the potential failure of stocking programs because of a poor performance and survival of the released fish owing to a multitude of reasons related to hatchery propagation and rearing (Einum and Fleming 1997, 2001, McGinnity et al. 1997, Fleming et al. 2000), among them potentially cataract (Kincaid & Elrod 1991). Furthermore, producing and stocking fish with phenotypic deficits cannot be considered ethically acceptable for animal welfare reasons.

1.2 Main objectives of the LFITE-project

The initiative of the LFITE-project, introduced in this report, emerged from the observation that during past years, increasing numbers of hatchery-reared fish have been reported to suffer from cataracts (e.g., Wall 1998, Midtlyng et al. 1999). However, knowledge about cataracts in farmed fish appeared to differ between the Nordic countries. To gain more understanding about the severity of the problem at present, there was a need to update information about the current situation, especially for Finland and Sweden.

Research on the causes of cataract has been extensive during the past years in Norway (e.g., Bjerkås and Bjørnstad 1999, Bjerkås et al. 1996, 2001, Breck and Sveier 2001, Waagbø et al. 2003, 2008, Bjerkås and Sveier 2004, Breck et al. 2005) where farming of Atlantic salmon for food has great economic importance. However, a lack of basic knowledge on some factors, such as genetics, potentially significant in cataract development, necessitated their further scrutinising. Furthermore, the little that was known of the consequences of cataract in terms of individual performance, excepting perhaps growth, emphasized the importance of investigating also this phenomenon in more detail.

The key objective of the LFITE-project has been to fill in gaps that we have in knowledge of cataract. Three main sub-goals were set for the project:

- To compile up-to-date information on the prevalence of cataract in hatchery populations of salmonid fishes in the Nordic countries.
- To illuminate roles of genetic and environmental (biotic) factors in cataract development.
- To cast new light on consequences of cataract for the fish in the hatchery and for those stocked in the wild.

1.3 Overview of study subjects and methodological approach

Although cataracts occur in a number of fish species (e.g., Bjerkås et al. 1998, 2000, Deng & Wilson 2003), Atlantic salmon has been the main research target on cataracts to date. It was therefore considered important to include different species and populations in the research in order to better assess whether cataract poses a more general problem in aquaculture in the Nordic countries nowadays. The project concentrated on salmonid fishes because of their general importance in the Nordic countries in commercial aquaculture. Salmonids were chosen as research targets also because of the extensive utilisation of hatchery propagation and rear-

ing of different salmonid species and their local populations for conservation and restocking.

The target species (and their migration forms, or morphs) of this project were Arctic charr *Salvelinus alpinus*, lake trout *Salvelinus namaycush*, Atlantic salmon (anadromous and landlocked *S. salar* m. *sebago*), sea trout *Salmo trutta* m. *trutta*, brown trout *S. trutta* m. *lacustris*, European grayling *Thymallus thymallus* and rainbow trout *Oncorhynchus mykiss*.

A combination of research methodologies was adopted during the project. The project has compiled available information on the occurrence of cataract in the Nordic countries involved in the project. In addition, the project has applied a comparative approach and produced new information on cataract prevalence in hatchery stocks of especially Arctic charr in Finland and Sweden. Data on cataract prevalence from other species were also gathered. These approaches were complemented by experimental work in aquaria, hatchery conditions and semi-natural outdoor pools as well as in nature for studying the causes and consequences of cataracts. The use of a range of research facilities has made it possible to gain the most benefits of controlled experiments in the captive conditions and to expose individuals also to conditions they normally would be confronted with in the wild.

The investigation of eyes was carried out for anaesthetised fish using slit-lamp microscopy (KOWA sl-15 slit lamp microscope; Kowa Ltd., Tokyo, Japan), which enables detailed observation of lesions in the eye without the need to kill the fish. The occurrence of the cataract in the lens was recorded. In addition, the severity of the cataract (the area of lens covered by cataract) was assessed on a scale of 0 to 4 following the categorisation by Wall and Bjerkås (1999), with score 0 referring to a healthy lens and score 4 to a lens of which 75%–100% is concealed by cataract, or the coverage percentage as such was directly used.

1.4 Collaboration

Though the main goals of fish farming may differ between the Nordic countries, cataract causes a common threat to achieving them. In addition to the research carried out during this project, one of the basic objectives was to promote and enhance collaboration between Nordic researchers and experts and together concentrate on the problem of cataract in order to be able to make use of the wide knowledge as well as different situations in Nordic fish farms.

The project has been carried out by a multidisciplinary group of scientists from Finland, Norway and Sweden. The manifold experience of the project collaborators enabled combining ecological, parasitological, physiological and genetic approaches in the research to achieve the goals

of the project. Furthermore, the cooperation was considered (and found to be) of great use in spreading the produced information to fish farming in the Nordic countries. In addition to the project group *per se*, other scientists have contributed to the project subtasks.

Project group:

Ellen Bjerkås, professor, Norwegian School of Veterinary Sciences, Norway
Eva Brännäs, professor, Swedish University of Agriculture, Sweden
Nina Peuhkuri, senior scientist, Finnish Game and Fisheries Research Institute (FGFRI), Finland (project coordinator)
Jorma Piironen, senior fisheries biologist, FGFRI, Finland
Craig Primmer, professor, University of Turku, Finland
Jouni Taskinen, professor, University of Jyväskylä, Finland

Main collaborators:

Hannu Huuskonen, senior researcher, University of Joensuu, Finland
Antti Kause, principal research scientist, MTT, Agrifood Research Finland, Biotechnology and Food Research, Finland
Erling-Olaf Koppang, associate professor, Norwegian School of Veterinary Sciences, Norway
Irma Kolari, fisheries biologist, FGFRI, Finland
Hanna Kuukka-Anttila, researcher, University of Helsinki, Finland (present occupation: senior officer, Finnish Food Safety Authority (EVIRA), Finland)
Andreas Lindén, researcher, University of Helsinki, Finland
Eila Seppänen, researcher, FGFRI, Finland
J. Albert Vallunen, researcher, University of Turku, Finland
Ari Voutilainen, researcher, University of Joensuu, Finland

The project has received funding from the Nordic Council of Ministers (the Nordic Working Group of Fishery Research, NAF) in 2005–2007.

2. Cataract prevalence

The chapter introduces data on cataract prevalence in salmonids gathered during the LFITE-project with accompanied information on what is known of cataract prevalence in salmonid fishes in the Nordic countries mainly based on published literature. Because of the scanty data on cataract occurrence in the freshwater fish hatcheries common in Finland and Sweden, surveys on several hatcheries were conducted in these countries. In addition, data on cataract prevalence were gathered along with separate experimental studies. Fish were also sampled from the wild and screened for the occurrence of cataract for comparative purposes. All the target species listed above were included in the research.

2.1 Cataract occurrence in farmed salmonids

In our survey at eight Finnish fish hatcheries on five salmonid species (Atlantic salmon, sea trout and brown trout, Arctic charr, European grayling, lake trout; $n = 4172$ fish) of varying age (from 0+ to 7 years, mostly 1–4 years old) and originating from 27 populations (1–6 pop. per species) all the studied species were found to suffer from cataracts (N. Peuhkuri, H. Kuukka-Anttila, I. Kolari, A. Lindén in prep.; Figure 2). The frequency of cataract-bearing fish (cataract observed in either or both eyes) in the studied hatchery groups varied from 0 to 100% (50 fish per group sampled with just a few exceptions). In only six out of the total of 79 sampled groups no cataracts were found. None of the examined 0+ fish were found to have cataracts yet, whereas cataracts were observed in all groups of fish older than one year.

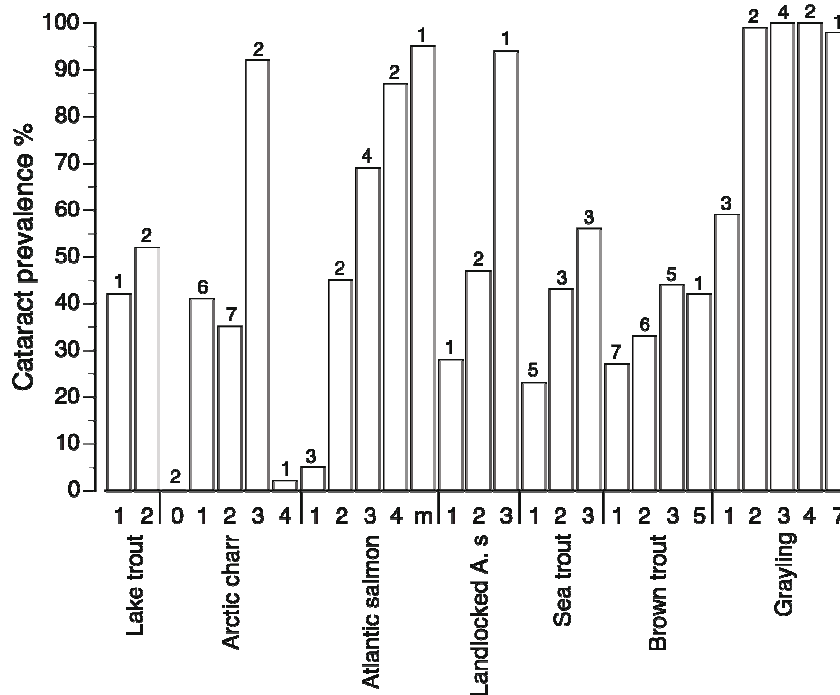


Figure 2 Cataract prevalence in sampled hatchery groups of a given age class (age is indicated below each bar; m = mixed group consisting of fish older than four years) shown for the different salmonid species/migratory forms. Groups representing fish of the same age are pooled for each species/migratory form sampled from different hatcheries (the number of sampled groups is indicated above the bars).

Our survey results of cataracts in Arctic charr and European grayling appear qualitatively congruent with cataract incidences found in Finnish freshwater hatcheries in Arctic charr (Pylkkö et al. 1996), and recently, also in European grayling (Pylkkö et al. 2006). In the first, and only, published study (in Finnish) prior to the commence of the LFITE-project on cataract prevalence in hatchery-reared fish in Finland Pylkkö et al. (1996) found cataracts to be common in Arctic charr eyes, depending, however, on the hatchery and population. In general, cataract prevalence per eye in the studied one-year-old Arctic charr varied from 3 to 89% and in the two-year-old charr from 12 to 100%. All two-year old Arctic charr were found to have cataractogenic changes in their eyes in a couple of hatcheries. Furthermore, a follow-up study conducted with one hatchery strain showed cataractogenic changes already 10 weeks after hatching. Lake trout and brook charr *Salvelinus fontinalis* were also included in the study and Pylkkö et al. (1996) found brook charr to be the least cataracted (only 2% of the examined eyes of 1-year-old brook charr had cataracts, whereas the corresponding figure for the lake trout was 31%). Pylkkö et al. (1996) concluded that the *Salvelinus* species included in their study are likely to have strong genetic predisposition to develop non-parasitic cataracts with the local hatchery conditions influencing the development process. Interestingly enough, in the three hatcheries where *Diplostomum* spp. were found in the eyes of

the fish, the fish in better condition were more often infected compared to fish in poorer condition (Pylkkö et al. 1996). In the research of grayling, Pylkkö et al. (2006) reported over 60% of the studied 480 0+ fish to have non-parasitic cataracts. The cataracts were however rather small (<10% of the eye lens covered). We did not have 0+ grayling in our own study but the incidences of non-parasitic cataract found in older grayling (nearly 100% of fish having cataracts in most of the sampled groups) suggest that also 0+ fish likely had had cataracts.

Hughes (1985) reported that cataracts developed simultaneously in both eyes when induced by nutritional deficiencies. It is thus unlikely that nutritional factors have played a central role in cataract formation in the sampled fish in our investigation because cataracts either occurred only in one eye or both eyes were opaque to a varying degree. Other factors are more likely to be important in underlying the eye opacities found during our survey.

Like found by Pylkkö et al. (1996, 2006), the cataract scores observed in our investigation were in general rather low such that in only a few cases the median value of the cataract score (calculated as the sum of both eyes, only fish having cataracts included) in a sampled group was 5 or higher than that (cataract bilateral and covering a minimum of 46% of the combined lens area). The result, nevertheless, suggests that at least in a small proportion of the sampled fishes cataracts were severe enough to significantly impair vision (Bjerkås et al. 2003).

Diplostomum spp. were found in five of the eight hatcheries and parasite-induced cataracts thus prevailed in the studied stocks. However, cataracts were rather common also in hatcheries where the parasite did not appear, although the prevalence of cataract in the sampled groups appeared to increase when the parasite was present (N. Peuhkuri, H. Kuukka-Anttila, I. Kolari, A. Lindén in prep.; Figure 3).

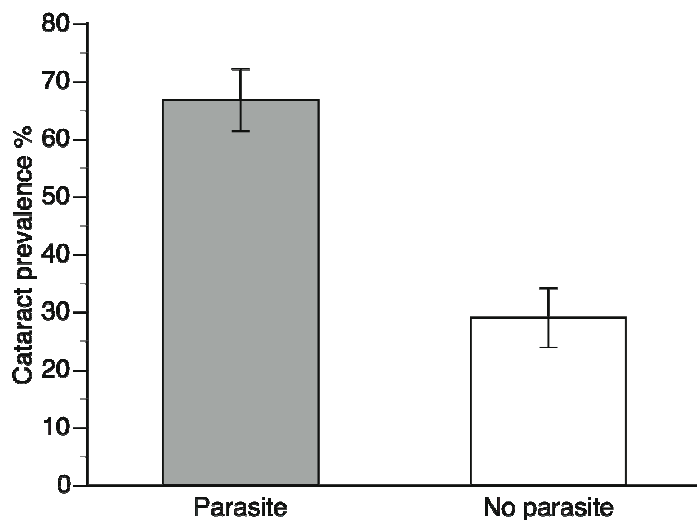


Figure 3 Cataract prevalence (mean $\pm$ SE) in groups of salmonids exposed ($n = 43$) and not exposed ($n = 36$) to *Diplostomum* spp. in the different hatcheries. The species/migratory forms and age groups are pooled in the figure.

The present project was the first attempt to systematically survey the frequency of cataract in Swedish fish farms. Cataract, or blindness, in fish has mainly been mentioned when surveying parasites in fish but the incidences have not been evaluated further. To our knowledge, no published data exist on the frequency of cataracts in farmed (or wild) salmonids in Sweden, not even in the grey literature.

Five main Arctic charr producing hatcheries were included in our survey in Sweden. Ten strains of charr with age mainly ranging from 0+ to 3+ were checked for cataracts. The hatchery history of the fish differed from a number generations under selection in the hatchery to wild-caught fish. The cataract prevalence per investigated hatchery group ranged from 0 to 90% ($n = 30$ sampled fish per group with one exception of 90 fish per group; H. Kuukka-Anttila, E. Brännäs, N. Peuhkuri in prep.), which is in accordance with the view of fish farmers and the Swedish Fish Health Institute that the frequency of cataract is variable between fish farms. According to these stakeholders, unpredictable year-to-year variation has also been detected and cataract has not been considered as a major problem but rather a local and temporal one in fish farming, at least partly caused by *Diplostomum* spp..

Our findings suggested cataract prevalence in Swedish Arctic charr to be lower compared to Finnish charr both when the fish in the rearing groups were exposed to *Diplostomum* spp. and when the parasite was not found in the eyes (average cataract prevalence per sampled group under parasite exposure and without parasite burden in Sweden approx. 47% and 23%, respectively, and in Finland, 72% and 32%, respectively). According to the Swedish fish farmers, cataracts appear to be more common in older fish in Arctic charr farms with a broodstock, probably due to longer period of exposure to parasites and eye damage in general.

A difference between Finnish and Swedish charr, which may partly relate to the lower *Diplostomum* spp. prevalence observed in Swedish charr, was apparent in the size of the lens area that cataracts covered. The charr in the Swedish hatcheries had somewhat smaller cataracts than those in Finland. Given that this appeared to be the case also when *Diplostomum* spp. were not observed, we cannot exclude the effect of strain on the differences between Finnish and Swedish hatchery charr given that the Swedish charr originated from different populations and their hatchery history differed from charr studied in Finland. There is some indication of genetic factors influencing susceptibility to non-parasitic cataract (Kincaid and Elrod 1991, Ersdal et al. 2001), but to the best of our knowledge, parasite-induced cataracts have not earlier been studied in this respect.

In one rainbow trout stock, reared in old earth-bottom raceways in Finland, we found all the investigated individuals (969 fish of age 2+) to suffer from cataracts (Kuukka et al. 2009). *Diplostomum* spp. were common in the eyes of the fish and the cataract was classified as parasite-induced. The cataracts were severe, with the average score pooled for both eyes being 7.50 (range 4–10). It should be noted that in addition to the conventional scale from 0 to 4 (Wall and Bjerkås 1999) also a score of 5 was used in this study, indicating a totally ruined eye where the normal eye anatomy could not be seen. Our observation is in line with the finding of rainbow trout being vulnerable to *Diplostomum spathaceum* infestation (Betterton 1974, Wootten 1974, but see Speed and Pauley 1984 for opposite results) and the following cataracts and other ocular changes after a chronic infection being massive (Shariff et al. 1980).

The project included also eye investigation of fish to be stocked in nature. A survey of 2-year-old smolts of landlocked Atlantic salmon ($n = 3990$) and brown trout ($n = 3987$) prior to their stocking indicated that in salmon, there was cataract in either or both eyes in 36% of the studied fish, whereas in brown trout the corresponding figure was 46%. The cataracts were generally small (less than 20% of the lens covered) and in most cases, they were accompanied with *Diplostomum* spp. infection. A notable finding was that in a vast number of fish, the lens was dislocated which may reflect a chronic *Diplostomum* spp. infection (Shariff et al. 1980). A similar exploration of 2-year-old anadromous Atlantic salmon smolts ($n = 1987$) from another hatchery revealed 76% of the fish to have cataracts in either or both of their eyes. In those fish that had cataracts ($n = 1510$), the opaque area covered approx. 30% of the eye lens. Again, *Diplostomum* spp. infection was clearly related to cataract occurrence. The fate of these individually tagged fish in nature is followed making use of the recapture statistics collected by FGFR1.

Mainly the causes of cataract have been under intensive investigation in Norway (e.g., Bjerkås and Bjørnstad 1999, Bjerkås et al. 1996, 2001, Breck and Sveier 2001, Waagbø et al. 2003, 2008, Bjerkås and Sveier

2004, Breck et al. 2005) but there exists also some published information on cataract prevalence in farmed (sea-caged) Atlantic salmon. A study by Ersdal et al. (2001) carried out in 49 different seawater sites along the coastline of Norway revealed cataracts in all the investigated salmon groups and high overall prevalence of cataract: 83% and 79% in fish transferred to sea during spring and autumn, respectively. In the spring entry group, differences in cataract formation were found between some of the studied strains that had been under selective growth-rate-based breeding, suggesting for genetic differences in susceptibility to cataracts directly or via genetic differences in growth patterns (Ersdal et al. 2001).

2.2 Cataracts observed in the wild

The Finnish Arctic charr population, suffering from both parasite-induced and non-parasitic cataracts in the hatchery, is unfortunately so endangered that despite our endeavours, we have not been able to sample wild fish for eye examination and comparison with hatchery fish.

However, our sampling of juvenile Atlantic salmon and sea trout (0+ and 1+ or 2+ fish) caught by electrofishing from south-eastern Finland revealed 65% of salmon (414 fish caught in total) and 84% of trout (111 fish caught) to have parasite-induced cataracts in their eyes (H. Kuukka-Anttila, A. Saura, N. Peuhkuri unpublished). In salmon, the prevalence of cataract in 0+ fish was on average as high as in the older fish (Figure 4). In sea trout, in contrast, fish of the younger age class had more cataracts than their older conspecifics whose cataract prevalence was equivalent to that of Atlantic salmon in both age groups (Figure 4). When compared to hatchery fish of similar age and originating from the same river, the cataract incidences in the wild-caught and hatchery fish were approximately similar, with the exception of the 0+ sea trout from the wild having more cataracts than the three hatchery groups available for comparison. The cataracts were generally small, just like they were also in the equivalent groups sampled in the hatchery.

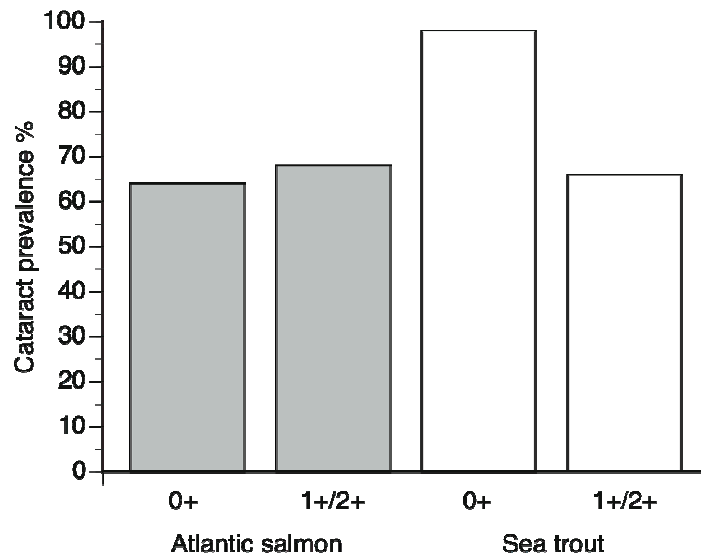


Figure 4 Cataract prevalence in wild-caught Atlantic salmon and sea trout shown separately for 0+ and older (1+ & 2+) fish.

The prevalence of cataracts observed in fish from the wild may be explained by the behaviour of the fish. The newborn salmon and trout are exposed to parasite infection in the shallow and slow-running water where the fish spend their early life. When the fish grow older they presumably move to forage to areas with higher water current and thus lower exposure to parasites. The infection has occurred at early life stage with no or just a few parasites entering the lenses later on. That young sea trout by their nature swim in a lower water current compared to Atlantic salmon (Riley et al. 2006) and are thus more exposed to parasites at early stages may have resulted in their higher cataract prevalence. Furthermore, given that at least some of the largest fish were of hatchery origin based on the signs of erosion in their fins, it is possible that cataract prevalence in the older trout reflects more of that as found in the hatchery. Bjerkås et al. (2003) studied cataracts in salmon postsmolts caught from the wild (Norwegian Sea) and they reported that all the 191 fish showed lens opacities. In 188 salmon, the cataracts were bilateral and they were considered as osmotic in contrast to the parasite-induced cataracts found in the Finnish salmon and trout. Bjerkås et al. (2003) suggested that the cataracts found in the postsmolts were of such magnitude (average cataract score 5.4 combined for both eyes) that they reduced vision.

Our gillnet sampling of larger sea trout (average body mass 990 g) during their feeding migration in the Finnish southeast coastal area, Gulf of Finland, has revealed 43% of the fish (147 fish caught in total so far) to have cataracts. Given that the stocked sea trout are not generally tagged it is not certain whether the fish originated from the wild or were of hatchery origin. Thus far, the cataracts have in each case, however, been very small, not exceeding coverage of 5% of the lens. At the present stage, it is not possible to explicitly conclude whether this might be due

to poorer survival of fish with more severe cataracts, or alternatively, to repaired lens damage occurred at early life, later on (at the time of catching from the sea) seen as tiny, deep cataracts (Fraser et al. 1990). Sampling of the trout in the sea as well as of young (wild and stocked) fish will be continued.

3. Factors predisposing salmonid fishes to cataracts

Because the research on the causes of cataract has to date mainly concentrated on nutritional and environmental (abiotic) factors with less attention having been paid, e.g., to the possible genetic basis of the susceptibility to cataract (but see Kincaid and Elrod 1991, Ersdal et al. 2001 for exceptions), one aim of the current project was to gain more understanding on different factors potential in predisposing the fish to cataract formation and study their importance in more detail. Emphasis was mainly put on biotic elements of the rearing environment as well as genetic factors.

3.1 Rearing environment

Based on our survey on cataract prevalence we aimed at identifying factors related to the conditions in the hatcheries potentially underlying cataract formation. It turned out to be impossible in practice to trace back the whole rearing history (including all the changes of rearing tanks and group compositions, rearing temperatures, feed rations, diseases etc.) of the fish in most cases. Furthermore, because different species and/or their strains were generally reared in different hatcheries, modelling the effect of hatchery on cataract formation in different species/populations was infeasible. Therefore, a general model including several factors potentially influencing cataract prevalence and severity could not be constructed. Instead, separate models were conducted for each species/migratory form and there appeared indication of *Diplostomum* spp. eye fluke being important in cataract development (N. Peuhkuri, H. Kukka-Anttila, I. Kolari, A. Lindén in prep.). Interestingly, the main causes of cataracts have proved to be very different in the studies conducted in Norway (e.g., Bjerkås and Bjørnstad 1999, Bjerkås et al. 1996, 2001, Breck and Sveier 2001, Waagbø et al. 2003, 2008, Bjerkås and Sveier 2004, Breck et al. 2005), whereas parasite infection has rarely been evoked as the underlying factor for cataracts there.

3.1.1 Parasite infection

The cataract-inducing *Diplostomum* spp. eye flukes are ubiquitous parasites of freshwater and brackish water fish (Valtonen & Gibson 1997, Valtonen et al. 1997). The parasite reproduces sexually in the intestine of fish-eating birds such as seagulls. After a release via bird faeces to the

water, the miracidia larvae hatched from the eggs of the parasite infect lymnaeid snails. The parasite reproduces asexually in the snail from which free-swimming cercariae larvae are released in the water. The emersion of the cercariae is temperature-dependent, usually occurring at greater numbers only after the water temperature has reached 10 °C (Stables and Chappell 1986, Lyholt and Buchmann 1996, McKeown and Irwin 1997). The cercariae contact the fish by chance (Höglund 1991, Karvonen et al. 2003), penetrate fish surface and migrate to the eye lens where they form metacercariae (Ashton et al. 1969, Chappell et al. 1994). The temporal window for a successful attachment of the *Diplostomum* spp. cercariae on the fish host in natural conditions is likely very short due to the avoidance behaviour of the fish (Karvonen et al. 2004c). Indeed, *Diplostomum* spp. cercariae appear able to infect the fish within an extremely short duration of exposure, namely 5 sec, as was shown by our experiments (Voutilainen and Taskinen 2009). The metacercarial infection in the lens may lead to varying degrees of reduced vision, ultimately total blindness, through metabolic excretions and destruction of the lens structures by the parasite (Shariff et al. 1980). A recent study with rainbow trout has shown parasite-induced cataract development to be related to *Diplostomum* spp. infection intensity in the lens (Karvonen et al. 2004a).

The role of *Diplostomum* spp. infection in cataract formation in Arctic charr
Although cataracts seemed to increase in frequency in hatcheries where the parasite was found in our hatchery survey (Figure 2), we cannot exclude other possible differences among the hatcheries as factors influencing our results. The level of infection by *Diplostomum* spp. eye flukes is likely to vary between years depending on the environmental conditions favourable to the avian and snail hosts, and to the release of the miracidia and cercaria larvae from them, respectively. The differences in cataract prevalence found in our survey between the rearing groups may thus partly reflect year-to-year differences in the level of *Diplostomum* spp. quantities in the water supply (see, e.g., Marcogliese et al. 2001, Sangster et al. 2004). Furthermore, it was not always possible to differentiate between parasite-induced and non-parasitic cataract in the hatcheries where *Diplostomum* spp. occurred. It was therefore considered necessary to clarify the role of the parasite in cataract development in a controlled experiment in which the exposure to *Diplostomum* spp. eye flukes would differ between experimental groups, with all else being equal. We considered Arctic charr as a good candidate for the study because of the variation in susceptibility of this species to cataracts found in the different hatcheries (Pylkkö et al. 1996, own hatchery survey).

A one-year rearing experiment with eight replicated groups of Arctic charr from a common hatchery stock in non-filtered (normal water supply) and filtered water (eye flukes filtered out) showed cataracts to be more common in non-filtered water where fish were exposed to natural

Diplostomum spp. infection via the incoming water supply (N. Peuhkuri, I. Kolari, H. Kuukka in prep.). In non-filtered water, cataract prevalence ranged from 40 to 61%, whereas in filtered water, prevalence appeared notably lower (range 3–13%). The result confirmed our deduction of the importance of parasite infection in cataract development, at least in Arctic charr.

Energy metabolism and parasite infection

Short-term challenges to the immune system, such as an exposure to parasites (Shingawa et al. 2001), have been shown to elevate metabolic rate presumably caused by the activation of immune system, as elicited, e.g., by *Diplostomum* spp. infection in rainbow trout (Whyte et al. 1987, Höglund and Thuvander 1990). This notion is supported by Laitinen et al.'s (1996) finding of an immediate simultaneous increase in heart and ventilation rates in brown trout when exposed to *Diplostomum* spp. eye flukes.

To unravel the energetic costs of *Diplostomum* spp. infection an experimental infection of Arctic charr young with the eye flukes was carried out and metabolic costs of an acute (defined as the first 24 h post-exposure hours) and chronic (10 weeks later when the cataracts had already been formed in the eyes) infection were studied (Voutilainen et al. 2008). Although the mean mass-specific hourly oxygen consumption rate of infected charr was slightly higher than that of the control fish (average 7.3 vs. 7.0 $\mu\text{mol O}_2 \text{ h}^{-1} \text{ g}^{-1}$, respectively) in the acute infection group, the difference was not significant. Energetically the acute increase in the fish energy consumption caused by *Diplostomum* spp. infection was however negligible because of its very short duration. In chronic infection, the mean hourly oxygen consumption of the infected fish was significantly higher than that of the control fish (7.7 vs. 5.8 $\text{O}_2 \text{ h}^{-1} \text{ g}^{-1}$, respectively). In the latter measurement, difference in the oxygen consumption between the groups remained fairly constant throughout the measurement period, except in darkness, when the healthy-eyed charr increased their oxygen consumption rate unlike the cataract-bearing individuals (Figure 5). The increase in oxygen consumption of the healthy-eyed fish at the onset of dark period may reflect their normal response to nocturnal conditions in wild, e.g., an increase in activity when the visual predators do not be a severe threat. If this is so, an absence of the normal behaviour of cataract-bearing fish may lead to differences in performance in wild.

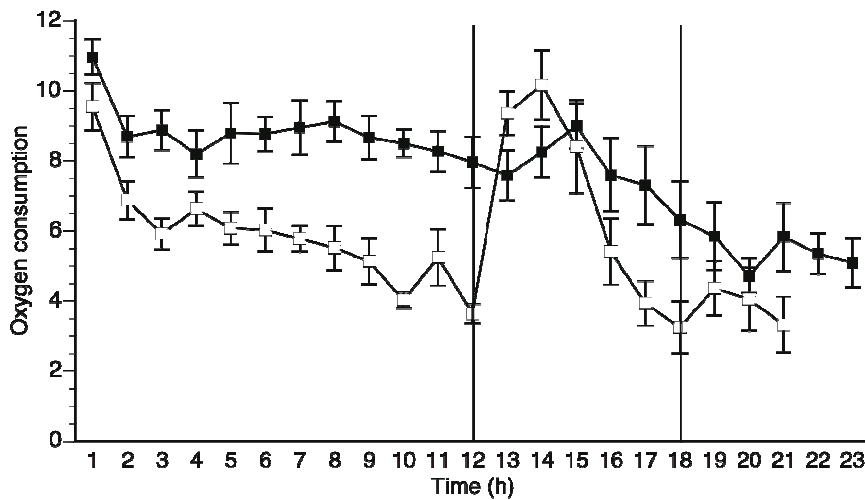


Figure 5 Mean ($\pm$ SE) oxygen consumption ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) of infected (black squares) and control (white squares) Arctic charr 10 weeks after an exposure to *Diplostomum* spp., i.e. in the chronic stage of infection. The onset and the end of the dark period is indicated by the two vertical lines. (Redrawn from Voutilainen et al. 2008)

Interestingly, when full-sibs from the same hatchery population of Arctic charr were tested for the relationship between standard metabolic rate (SMR), considered as the minimum rate of metabolism needed for the maintenance of critical physiological functions (Priede 1985, Jobling 1994), and chronic infection under natural exposure to the parasite, charr with parasite-induced cataracts had lower SMR than healthy fish (Seppänen et al. 2009; Figure 6). Furthermore, an enlargement of both spleen and liver were observed in the infected cataract-bearing fish as compared to the healthy fish (Seppänen et al. 2009).

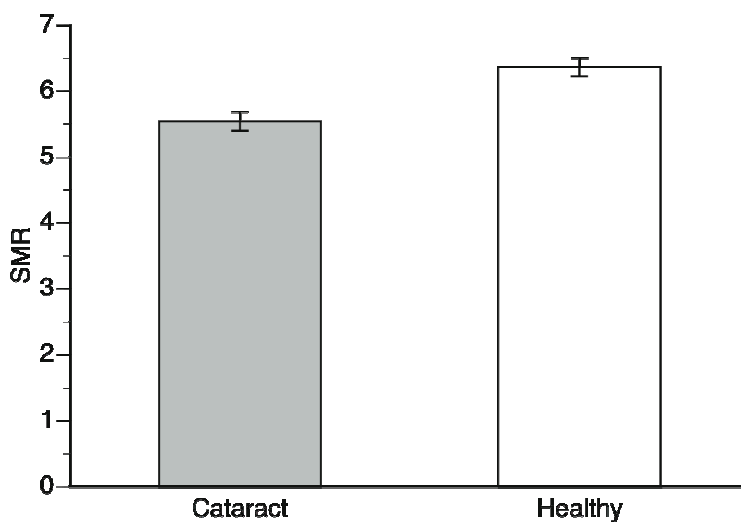


Figure 6 Standard metabolic rate [mean ($\pm$ SE) oxygen consumption, $\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$] of charr with parasite-induced cataract (chronic infection) and charr with healthy eyes. (Redrawn from Seppänen et al. 2009)

The lowered SMR together with enlarged liver in cataract-bearing fish suggests that chronic *Diplostomum* spp. infection harmed fish energy metabolism resulting in fatty liver, disturbed energy utilization and depressed rate of standard metabolism. The liver colouration in the infected fish also suggested for fat accumulation (E. Seppänen unpublished). Hence, chronic *Diplostomum* spp. infection did not directly cause energetic costs on Arctic charr in this study but appeared to reduce the efficiency of energy metabolism. Given that spleen is a lymphoid organ contributing to immune defence (Press & Evensen 1999), the splenic enlargement may be a host response to cope with the infection. However, the potential uncontrollable differences in rearing conditions (cataract-bearing infected fish in unfiltered vs. healthy fish in filtered water) as such may also have influenced the difference between the infected and healthy fish.

Based on our novel findings, it is possible that the association between the energy metabolism of the fish host and the dynamics of the *Diplostomum* spp. infection is interactive (A. Voutilainen, J. Taskinen, H. Huuskonen in prep.) and, moreover, the pattern of association may depend on temperature (A. Voutilainen, H. Huuskonen, J. Taskinen in prep.). However, these findings are preliminary by their nature and they need to be retested before final conclusions can be made.

Fighting against *Diplostomum* spp. and cataracts

Praziquantel, also called Droncit®, developed by Bayer Corporation is a broadspectrum anticestode (Thomas and Gönner 1977) and antischistosome (Gönner and Andrews 1977) that has been shown to function against fish parasites such as *Diplostomum* spp. (Bylund and Sumari 1981, Szekely and Molnar 1991). In our *in vitro* tests, *Diplostomum* spp. cercariae were highly sensitive to praziquantel causing rapid deformation (swellings and ruptures in tegument) and impaired swimming ability of *Diplostomum* spp. (Voutilainen et al. 2009b), as has been found also by Björklund and Bylund (1987). We have also commenced experimental research in order to study whether vision impaired by parasite-induced cataract can be regained after praziquantel treatment.

3.1.2 Pathogen infection

In hatchery conditions, where diseases can spread like wildfire, fish are very susceptible to infectious diseases. Bacterial infections, indeed, are annual nuisance at fish farms. Atypical *Aeromonas salmonicida* infections (aAS) are among the most common bacterial diseases among farmed salmonid fishes in Finland (Rintamäki-Kinnunen and Valtonen 1991). Charr and grayling appear most susceptible to aAS infection and mortality during the outbreaks can exceed 60% (Pylkkö 2004). Interestingly, charr reared in indoor tanks have been reported to be very suscep-

tible to non-parasitic cataract as early as two to four months after hatching (Pylkkö et al. 1996) although in our own survey we did not find signs of cataracts in 0+ charr examined early summer (N. Peuhkuri, H. Kuukka-Anttila, I. Kolari, A. Lindén in prep.).

A recent study by Pylkkö et al. (2006) found no indication of concomitant bacterial exposure enhancing the severity of grayling eye rupture and nuclear extrusion induced by *Diplostomum* spp. eye fluke, but parasite invasion into grayling increased the proportion of fish carrying aAS in their heart tissue. It was concluded that penetrating diplostomids may enhance bacterial infections in fish (Pylkkö et al. 2006). However, the bacterium can inhabit the eye without a tissue penetrating parasite vector. Some earlier anecdotal evidence suggests a potential relationship between bacterial infection and cataracts such that cataracts might be secondary (P. Pylkkö pers comm.), but the role of bacterial inflammation as a cause of opaqueness in fish lens has not been examined earlier. Since preliminary ocular examination of charr brood stocks and fish prior to restocking had revealed ocular signs that might be attributed to infection, a study was performed in order to describe the ocular changes in farmed Arctic charr in Finland as well as to investigate the possible role of sub-clinical bacterial infection in the described ocular changes.

Based on ophthalmic investigation by slit-lamp microscopy and more detailed histopathological examination (Figure 7) of eye samples of cataract-bearing Arctic charr from three Finnish freshwater hatcheries, different types of ocular changes were detected depending much on the hatchery (Bjerkås et al. submitted). Cataracts of different stages were diagnosed in nearly 40% of the sampled 64 fish, and eye flukes in one of the hatcheries. In the other two hatcheries, no eye flukes were diagnosed but the signs of ocular changes were more obvious.

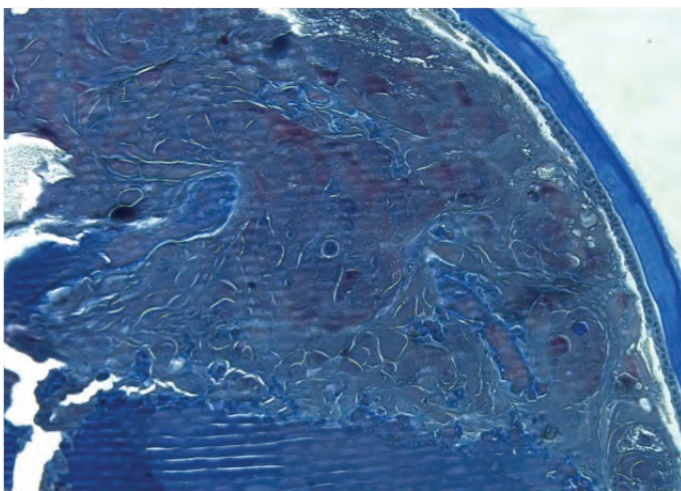


Figure 7 A stained lens of a charr with a severe cataract (photograph by E.-O. Koppang).

Bacteriological samples as well as analyses of immunohistochemistry revealed bacterial growth in fish from all farms, the majority of samples being *Aeromonas* spp. positive in two farms. In one farm, a variety of bacteria were found, possibly reflecting the route of entry through a ruptured cornea. Immunological responses (cells MHC II positive) were diagnosed in one farm.

As expected, the flukes caused secondary cataracts. However, the results also indicated that haematogenous delivery of bacteria like aAS may cause subclinical ocular infection with the possibility of further development of ocular changes to include keratitis, uveitis and secondary cataracts, as has been shown in other animal species (Hendrix 2007).

3.2 Genetics underlying cataracts

3.2.1 *Inheritance of cataract*

Anecdotal evidence (Kincaid unpublished, censu Kincaid & Calkins 1991) suggests that offspring of parents with cataract are likely to have higher incidence of cataract than progeny of healthy parents in lake trout. This implies at least to some level of inheritance in susceptibility to non-parasitic cataract. In our own preliminary study, some evidence of genetic differences was found in the susceptibility to eye fluke infection in 0+ fish of the hatchery stock of Arctic charr when being subject to natural parasite infections in hatchery conditions (R. Kortet, T. Lautala, J. Taskinen, H. Hirvonen unpublished; poster at the VIIth International Congress on the Biology of Fish, Canada), potentially resulting in concomitant genetic differences in parasite-induced cataract development. In addition, the expressions of cataract for a given parasite load (i.e., tolerance) might also be genetically determined such that a certain number of parasites would induce cataract of different severity in different individuals. We have studied the genetic basis of cataract development both experimentally and making use of breeding programs of salmonids in Finland and Sweden.

Breeding ornaments have been suggested to provide reliable information of an individual's genetic quality and heritable parasite resistance (Zahavi 1975, Hamilton and Zuk 1982, Folstad and Karter 1992) but unequivocal tests of the dependency of offspring pathogen resistance on sire ornamentation have to date been rare (immunocompetence: Kurtz & Sauer 1999; parasite load: Barber et al. 2001; pathogen-induced mortality: Wedekind et al. 2001). Our experiment with offspring of Arctic charr sires with bright and pale nuptial colouration from a controlled breeding design (eggs one female always fertilized with milt of one bright and one pale male) suggested that the genetic quality of the males is passed on to their offspring (H. Kuukka-Anttila, J. A. Vallunen, M. Janhunen, N. Peuhkuri, I. Kolari, J. Piironen, C. R. Primmer in prep.). Progeny of bright males showed less severe para-

site-induced cataracts, reflecting their better *Diplostomum* spp. eye fluke resistance, compared to progeny of pale males (Figure 8). Breeding ornamentation may thus serve as an honest signal of heritable quality in male charr. This phenomenon might prove useful to be taken into account when selective breeding programs of Arctic charr are implemented. Contrary to an assumption that individuals with better vision (lower cataract score) than their half-sibs would also surpass them in growth and body condition (Ersdal et al. 2000, Breck and Sveier 2001), we did not find any indication for such outcome. Our finding may thus be an indication of a trade-off in resource allocation between immunocompetence and growth (Soler et al. 2003, Brommer 2004, Tschirren and Richner 2006, Uller et al. 2007) such that fish better in resisting parasites pay for this by lower growth. Actually, Karvonen and Seppälä (2008) did not find growth to be affected by parasite-induced cataract in whitefish *Coregonus lavaretus* until the cataract coverage was 100% of the lens in both eyes.

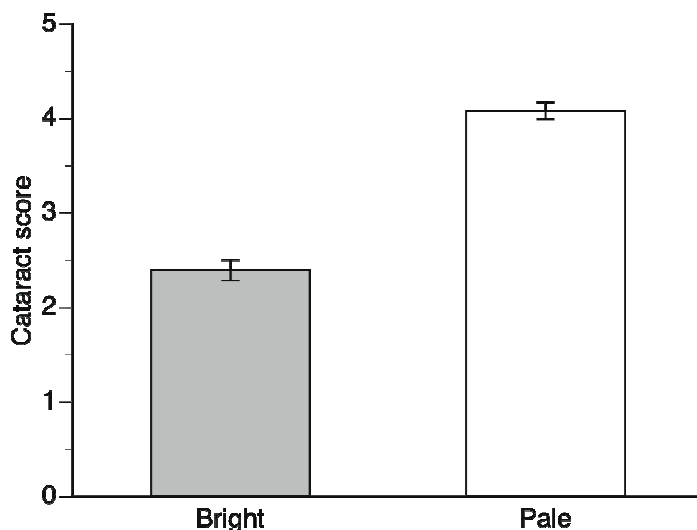


Figure 8 Cataracts (average score per fish $\pm$ SE) in offspring of bright and Arctic charr males (data from the 10 bright-sired and 10 pale-sired families are pooled).

To clarify the genetic basis of cataracts in the same Arctic charr population in more detail, i.e., whether certain families (genotypes) would be less susceptible to both parasite-induced and non-parasitic cataracts, a continuation to the rearing experiment with charr in filtered and non-filtered water was carried out, now controlling also the genetic background of the fish (N. Peuhkuri, I. Kolari, H. Kuukka-Anttila in prep.). 48 families were produced using a nested breeding design (one male always crossed with two females) with independent replicates allowing assessing how much of the phenotypic variation in cataracts is genetically and environmentally based. After the first growth season, approximately 40% of the fish in the non-filtered water had developed cataract in one or in both their eyes. These fish commonly were infected by *Diplostomum* spp. eye

fluke. In the filtered water, less than 1% of the fish had cataract. Although the cataracts were generally small, charr in non-filtered water developed larger cataracts (Figure 9). Our preliminary results suggest no indication of the genetic background influencing cataract development, neither for parasite-driven nor for non-parasitic cataract in one-summer-old charr (N. Peuhkuri, I. Kolari, H. Kuukka-Anttila unpublished).

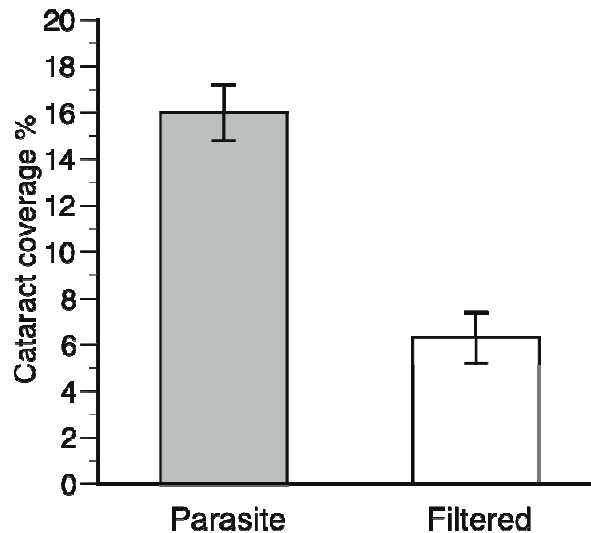


Figure 9 The coverage percentage of cataracts (mean $\pm$ SE) in Arctic charr reared in non-filtered (parasite) and filtered water (data pooled for the different families, $n = 27$ for non-filtered and $n = 28$ for filtered water).

It is possible that the genetic differences in parasite-induced cataract development were not yet observable given that the numbers of parasites in the infected lenses after the first growth season were low (range 1–3 eye flukes/eye). The experiment is currently running and data gathered later on will reveal the state of affairs. The likeliness of the genetic effects to come up at later stage is supported by our finding of differences in cataract severity in offspring of males with pale and bright nuptial colouration not occurring until the fish are older than one year (N. Peuhkuri, H Kuukka-Anttila, I. Kolari unpublished).

A breeding program of Arctic charr in Sweden was used to survey cataract susceptibility and its heritability in another charr population for comparative purposes. The program has been going on since 1984, offering excellent opportunities for family comparisons of the susceptibility to cataract. 510 fish out of the total of 1200 fish from 62 families were examined for the degree of cataract and possible *Diplostomum* spp. infection. Here, our preliminary results indicate family-level differences in the severity of cataract with no relationship between fish size and cataract development (H. Kuukka-Anttila, E. Brännäs, N. Peuhkuri, A. Kause unpublished). More detailed handling of the data will reveal the level of heritability in cataract formation.

We have estimated heritability of resistance to *Diplostomum* spp. eye fluke and thus to parasite-induced cataract also in rainbow trout originating from a breeding program in Finland in order to clarify the generality of the genetic basis for parasite resistance and the following cataract formation. We also estimated phenotypic and genetic correlations of resistance with fish body weight and age at maturity. A partial factorial mating design allowed for heritability measurements and investigating the genetic and phenotypic correlations. All the 969 investigated individuals had cataract in their eyes and our results suggest for moderate heritability in parasite-induced cataract ($h^2 = 0.35$, Kuukka et al. 2009). In line with our results from offspring of bright vs. pale male, the findings from rainbow trout indicate that selection could be applied to increase parasite resistance and reduce cataracts. In fact, selection against severe cataracts has been practiced in the Finnish breeding programme since 2003 (A. Kause, pers. comm.).

3.2.2 The importance of geographic origin in the relationship between salmonid hosts and their Diplostomum spp. parasites and cataract formation

The observed strain-specific differences in non-parasitic cataracts in lake trout and Atlantic salmon suggest that there might be genetically determined differences between populations in cataract formation (Kincaid & Elrod 1991, Ersdal et al. 2001). Although indication of species-specific differences in susceptibility to *Diplostomum* spp. invasion exists (Betterton 1974, Wootten 1974, Speed & Pauley 1984), studies conducted at population level of either the parasite or the host have been rare (Ballabeni and Ward 1993, Kalbe and Kurtz 2006) and totally lacking in aquaculture conditions.

To complete their life cycle, the *Diplostomum* spp. eye flukes have to be effective in both infecting the fish and producing cataract formation in the lens of the fish eye in order to make the fish susceptible to bird predation. Host-parasite co-evolution theories suggest that parasite infection develops to act most effectively on local populations (Hamilton 1980, Kaltz and Shykoff 1998). In other words, local adaptation of parasites should lead to higher infectivity of parasites in sympatric host populations compared to allopatric ones that are not geographically in contact with the parasite population in question. It has been suggested that parasites often win the host–parasite ‘arms race’ due to their shorter generation times, higher mutation rates and larger population sizes leading to greater evolutionary potential (Price 1980, Kaltz and Shykoff 1998, Lively and Dybdahl 2000, Gandon and Michalakis 2002, Dybdahl and Storfer 2003).

Our research on the infectivity of *Diplostomum* spp. in their farmed salmonid fish hosts with respect to the origin of the parasite and the host revealed differences in parasite infection depending on the geographical

distance between the host and the parasite population (Voutilainen et al. 2009a). After a controlled exposure with *Diplostomum* spp., higher infectivity of eye flukes in local parasite-host combinations compared to those separated by greater geographical distance was found in two anadromous and one landlocked Atlantic salmon hatchery populations. Prevalence of *Diplostomum* spp. infections was 100% in both local populations and 86% in the non-local population. Also the parasite abundance varied across the populations depending on the whether the salmon strain was originally local or non-local with the parasite population (Figure 10).

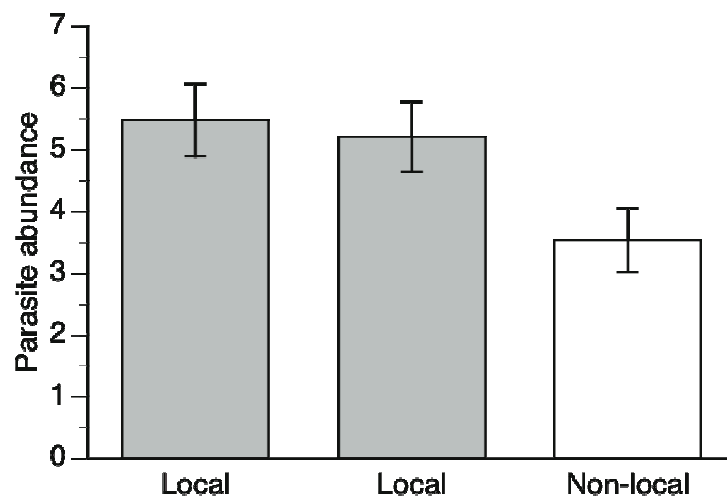


Figure 10 Abundance (mean $\pm$ SE) of *Diplostomum* spp. after an experimental exposure to parasites from a population local or non-local with Atlantic salmon populations. (Redrawn from Voutilainen et al. 2009a)

A similar outcome was apparent also with the population of Arctic charr exposed to local and non-local *Diplostomum* spp. cercariae. Prevalence of *Diplostomum* spp. infection was higher among fish exposed to the local parasites (87 and 80%) than among fish exposed to the non-local parasites (60%), and the abundance of the non-local *Diplostomum* spp. cercariae in Arctic charr tended to be lower compared to the local parasite populations (Voutilainen et al. 2009a).

Both parasite prevalence and intensity of parasite infection were thus dependent on whether the parasite was local or non-local to the studied salmonid strain such that the parasite appeared to be more efficient in infecting local strains. In this short-term study, the development of cataracts was not followed (Voutilainen et al. 2009a).

The importance of local adaptation in the host-parasite interactions and thereby in the costs of *Diplostomum* spp. exposure to the fish hosts became evident also in another experiment with three Atlantic salmon strains investigating metabolic rate and parasite-induced cataract (Sepänen et al. 2008). The fish were exposed to natural *Diplostomum* spp. infection with one of the strains being local to the parasite. The non-local

populations were different than those used in Voutilainen et al. (2009a) but the local strain was the same. The fish were screened for cataracts and cataracts were determined to be parasite-induced. Most cataract-bearing individuals were found in the salmon strain local to the parasite (cataract prevalence 88% vs. 72% and 58% in the non-local strains). Individuals from this strain also had higher cataract scores compared to those of the two other strains geographically more distant to the parasite (Figure 11). The parasite population at the hatchery where the experiment was conducted may be specialized in the local strain because this strain is geographically the nearest one and, in addition, most farmed at this particular hatchery.

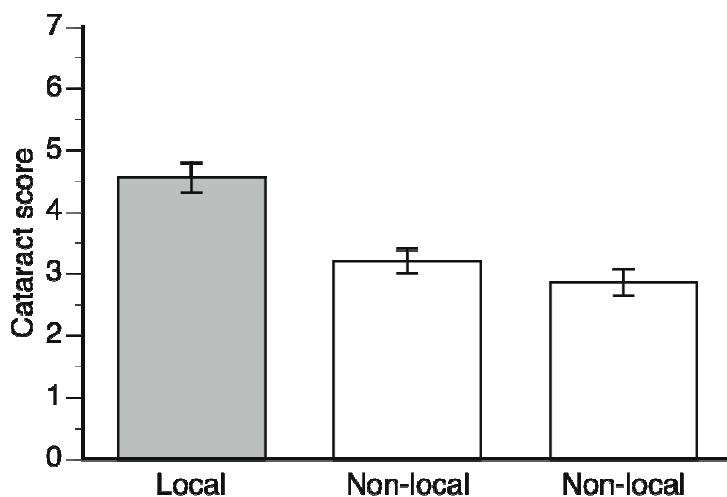


Figure 11 Cataract score (mean $\pm$ SE, $n = 50$) in three salmon strains local and non-local with *Diplostomum* spp. parasite. (Redrawn from Seppänen et al. 2008)

The abovementioned two experiments indicate that *Diplostomum* spp. parasites are able to overcome the defences of certain, local host genotypes and show adaptation to them. This emphasizes the importance of maintaining as much genetic diversity as possible in the hatchery strains, such that there would exist genotypes that the parasites have not yet succeeded to win in the ‘arms race’. This goal may be possible to achieve by mating designs efficient in preserving the genetic variation in the hatchery population (Fiumera et al. 2004, Dupont-Nivet et al. 2006).

We have also commenced a rearing experiment with offspring of three geographically distinct Finnish populations of Arctic charr and their hybrids produced by a controlled breeding setup. The fish are under rearing in common conditions in a hatchery. The populations are genetically distinct entities and also differ in their genetic variation as measured with microsatellite DNA (C. R. Primmer, pers. comm.). The fertilizations were conducted in 2005 and the fish have been sampled this far twice for their eyes. Preliminary results suggest some cataract development, in most cases accompanied with *Diplostomum* spp. eye fluke infection. However,

the *Diplostomum* spp. prevalence and the numbers in the eyes have been very low this far. The rearing will continue until the fish reach maturity and cataract development will regularly be followed during this period.

3.2.3 Cataract in relation to genetic variability

Genetic variability often diminishes in hatchery strains due to inbreeding, genetic drift and founder effects (Allendorf & Waples 1995). For example, variability (as measured with microsatellite-DNA) is very low in the hatchery population of the southernmost landlocked Arctic charr population in Finland, with only two alleles found for each analysed locus (Primmer et al. 1999). This hatchery strain also has high cataract incidence (Pylkkö et al. 1996, included also in our survey in Figure 2). When it comes to cataracts, especially those induced by parasites, polymorphism in MHC (major histocompatibility complex) genes may be even more important because MHC polymorphism has high significance in immune functions (Kurtz et al. 2004). Comparing the genetic variability in microsatellite-DNA and MHC provides understanding on the relative roles of genetic variability as such and the specific role of MHC in influencing the susceptibility to parasite-induced cataract.

Genetic polymorphism in microsatellite DNA and MHC was investigated in Arctic charr on grounds of the implication in our study for genetic basis for parasite-induced cataracts (H. Kuukka-Anttila, M. Janhunen, J. A. Vallunen, N. Peuhkuri, I. Kolari, J. Piironen, C. R. Primmer in prep.). Brown trout was originally considered to be included in the study because of its relatively high genetic polymorphism in the hatchery populations in Finland. However, there were problems in the DNA-analyses of this species and we thus had to skip trout from our research. We also sampled Lake Ladoga Arctic charr and analysed their MHC variation. This served as an important baseline data in order to ascertain if levels of MHC variation in the hatchery fish where cataracts occur are lower than those that occur in natural populations. Wild fish are practically impossible to get from Lake Saimaa charr and Lake Ladoga is the phylogenetically closest population.

For the genetic analyses, MHC DNA sequence variation analysis system was optimized for Nordic Arctic charr populations. Our results indicate only two MHC alleles in the hatchery population of landlocked Lake Saimaa Arctic charr (H. Kuukka-Anttila, M. Janhunen, J. A. Vallunen, N. Peuhkuri, I. Kolari, J. Piironen, C. R. Primmer in prep.). However, an equally low level of MHC DNA variability was also found in a wild population of Arctic charr from northernmost Finland (Kekäläinen et al. submitted), in contrast to Lake Ladoga charr, in which 12 MHC alleles were found (C. R. Primmer unpublished). Still, MHC heterozygous fish from the northern population had a lower load of *Diphyllbothrium dendriticum* (Cestoda) plerocercoid cysts in their body cavity and muscles

than either of the homozygotes (Kekäläinen et al. submitted). However, when the progeny of bright and pale Arctic charr males from the hatchery strain were checked for the dependency of the observed cataracts on their allelic composition of MHC or microsatellite-DNA diversity, no evidence of an effect of genetic variability on progeny cataract score was found even if there was a positive relationship between male nuptial colouration and microsatellite variation (H. Kuukka-Anttila, M. Janhunen, J. A. Val-
lunen, N. Peuhkuri, I. Kolari, J. Piironen, C. R. Primmer in prep.). This suggests that the red breeding colouration of charr males, by resulting in offspring with less severe cataracts, could be an expression of male vig-
our via their genetic heterozygosity (Brown 1997).

4. Individual performance

Behaviour is one of the most important traits by which organisms cope with their environment (Heath & Blouw 1998). If optimal behaviour in a certain environment is constrained by sensory deficiencies this may have significant bearing on individual performance and fitness compared to the normal-eyed cohort members both via impaired ability to acquire food and to avoid predation.

When stocking of hatchery-reared fish in the wild is considered, the negative effects of cataract may be most severe soon after stocking and when the fish need to learn to utilize live prey and to avoid predators they have not encountered in their captive environment (Kincaid & Elrod 1991). Information on performance of fish having cataracts versus healthy fish is crucial for our understanding of the effects of cataract on ecological interactions and thereby in the profitability of stocking.

4.1 Foraging ability

For visual feeders, such as salmonid fishes (Ali 1959), eye opacity may significantly limit prey detection (Savino et al. 1993) and the ability to compete for resources (Barber et al. 2000). Poor vision might also affect the diet composition if certain types of food were easier to detect and catch by the disabled individuals. For example, it could be hypothesized that feeding on moving prey would require more concentration than feeding on more stationary benthic prey.

In order to evaluate the competitive disadvantages of Arctic charr having cataracts, individual monitoring of foraging behaviour in groups of two-year-old Arctic charr was conducted. Differences in exploratory activity of healthy fish and fish with cataract (at least 70% of the lens area opaque when summed for both eyes) were investigated in a feeding habitat. The movements between feeding and hiding patches were monitored by PIT-tag systems that recorded individual fish during three months in each trial. The study indicated a pronounced difference in activity into the feeding patch, healthy fish spending significantly more time in the feeding patch as compared to cataract-bearing fish. This is likely to reflect the poorer competitive ability of fish having cataracts. (E. Brännäs, H. Kuukka-Anttila, N. Peuhkuri in prep.).

When comparing the ability of single healthy and cataract-bearing fish to feed on pellet food while presenting 10 fish pellets three times a day and counting the pellets immediately eaten and the rejected pellets after 30 minutes, the feeding trial showed no significant difference in the

amount of pellets eaten from the bottom after 30 minutes and a slight but not significant difference in the amount of pellets caught from the water column, indicating some tendency for the healthy fish to be better off in catching food from the water (E. Brännäs, H. Kuukka-Anttila, N. Peuhkuri in prep.). As Arctic charr readily eats pellets from the bottom of the tank and can do so in darkness no difference when feeding from the bottom was expectable. Given that charr in the two experiments presented above had bilateral cataracts (cataract coverage >70% in combined lenses) our results are in line with those of Savino et al. (1993) who noted bilateral cataracts to reduce foraging efficiency in lake trout. No effect on average capture rate of moving prey was found in fish with unilateral cataracts compared to healthy fish but variation in capture rate was higher (Savino et al. 1993), suggesting that feeding performance of fish with unilateral cataracts could also be impaired. It is expectable that in commercial aquaculture the feeding problems of cataract-bearing fish will be pronounced especially in net pens where the fish cannot feed from the bottom.

A foraging experiment with 0+ Arctic charr confirms that catching moving prey is more difficult for fish with cataracts compared to fish with healthy eyes. The parasite-induced cataract reduced the capability of charr young to forage planktonic food (Voutilainen et al. 2008). The fish with healthier eyes reacted to zooplankton faster, made more catching attempts and caught zooplankton with higher success compared to the cataract-bearing fish in the same group (Figure 12).

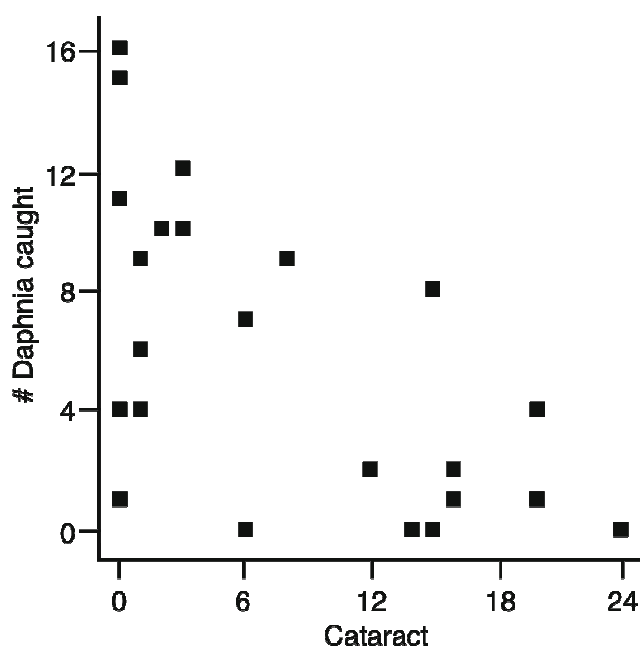


Figure 12 Relationship between the number of *Daphnia magna* caught in 5 min by Arctic charr and the overall cataract score [product of cataract score (1–4) and the thickness of cataract (1=translucent, 2=partially translucent, 3=opaque) pooled for both eyes, range from 0 to 24]. (Redrawn from Voutilainen et al. 2008).

Together the foraging experiments and the heritability of parasite-induced cataracts as found in rainbow trout (Kuukka et al. 2009) suggest that positive achievements of selecting healthy-eyed individuals would most probably include also higher growth because increased cataract was in the rainbow trout found to be related to reduced body mass, presumably owing to the severity of the found cataracts (Karvonen and Seppälä 2008) and the following reduction in foraging ability (E. Brännäs, H. Kuukka-Anttila, N. Peuhkuri in prep., Voutilainen et al. 2008). However, the degree of negative effect of cataract in fished fish is likely dependent of the species. For example, Arctic charr is a species that spends half its life in lakes covered with thick layers of snow and ice and the species is more adapted to forage in darkness than for instance salmon.

4.2 Avoidance of predation

Differences in the anti-predatory behaviour and other traits important in predator avoidance of the infected and healthy fish may predispose the infected fish to predation. *Diplostomum* spp. eye flukes have been shown to reduce fish escape responses and crypsis (Seppälä et al. 2004, 2005a), and to predispose them to artificial predators (Seppälä et al. 2004, 2005b). Recently, Seppälä et al. (2008) showed with rainbow trout that infection by *Diplostomum* spp. eye flukes led to reduced shoaling tendency as compared to non-infected fish indicating reduced anti-predator behaviour in the infected fish (Pitcher and Parrish 1993). According to Ersdal et al. (2001), blind fish also tend to swim near the surface and their actions are slower than those of healthy fish. As fish with impaired vision have to allocate more time for foraging to attain similar food intake rate as their healthy conspecifics (Barber et al. 2000), they may experience further costs in predator avoidance due to the trade-off between foraging and predator avoidance (Lima & Dill 1990).

We have experimentally tested at the actual risk of cataract-bearing and healthy fish of being predated by different fish predators. Our experiment where the predator, either burbot or pikeperch, was allowed to attack and feed on groups of 1+ grayling (half of the fish cataract-bearing and half of them healthy) implied to healthy fish falling prey less than cataract-bearing fish (I. Kolari, H. Kuukka-Anttila, N. Peuhkuri in prep.).

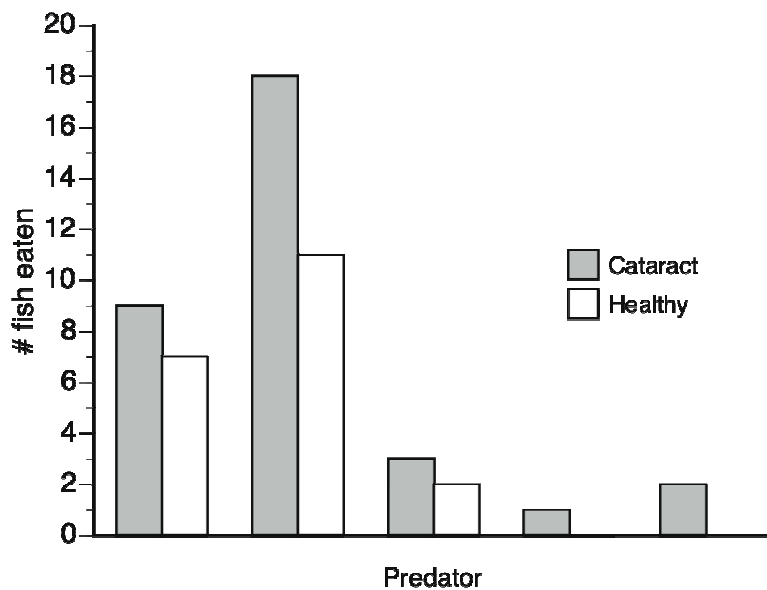


Figure 13 The total number of cataract-bearing and healthy juvenile grayling eaten by the fish predator ($n = 5$ burbot). The result was equivalent with pikeperch as predators.

It appears that cataract is costly to prey in terms of their predation risk. The result was similar even if the two predators used are exploiting different tactics when searching and catching prey. To be able to evaluate whether the differential predation risk of cataract-bearing and healthy fish is a consequence of behavioural differences among the prey further studies are needed. The behavioural experiment would show whether such increased predation risk may relate to more risk-prone behaviour as suggested by the foraging experiment with Arctic charr.

We have experimentally tested the behaviour (swimming activity, position, approach of the predator compartment) of cataract-bearing and healthy 1+ European grayling towards a fish predator (pike perch) as opposed to a control situation where the pikeperch was not present in the predator compartment. The grayling had visual or both visual and odour (chemical) contact with the predator or with the empty compartment. The video material is currently under processing.

4.5 Maturation

In fish, sexual maturation depends on several intrinsic and extrinsic factors, among them for instance nutritional status and growth rate (Alm 1959). If cataract reduces growth of the fish it is possible that it can have negative impact also on their maturation process

Rainbow trout females and males were found in our research to differ in the relationship between maturity age and cataracts (Kuukka et al. 2009). Female maturity was clearly postponed due to cataracts whereas no such relationship was found between cataract and maturity age in

males. The reduced body size and condition as found in cataract-bearing fish was probably reflected in the phenotypic association between a high cataract score and delayed age at maturity in females. Because rainbow trout males mature on average one year earlier than females it is possible that *Diplostomum* spp. infection had less time to influence male maturation process compared to female maturation. Because eggs are considered more costly to produce than sperm (Bateman 1948), it is also possible that the females with cataracts are not able to mature as early as healthy females.

Another possible relationship between maturation and cataracts relates to the trade-off between reproduction and immune function (Lochmiller and Deerenberg 2000). Immunosuppression in the maturing individuals may thus make them more susceptible to parasite infection and the following parasite-induced cataracts. However, we did not find support to this assumption when comparing precocious and normal salmon parr of similar age from three hatchery populations. Sexual maturation of salmon parr did not have effect on the susceptibility of fish to eye fluke infection and thus cataracts (J. Taskinen unpublished).

4.4 Performance in the wild

In the multigenerational genetic analysis of survival of 300.000 individually tagged rainbow trout from the Finnish breeding programme, increased cataract liability was significantly genetically related to increased mortality until two years of age (H. Vehviläinen, A. Kauser, H. Kuukka-Anttila, T. Paananen, H. Koskinen in prep.). However, in the preceding study with a single year-class, individual survival was not related to cataracts either genetically or phenotypically (Kuukka et al. 2009). Cataracts may thus not always cause death under the circumstances where predation is lacking and food is offered *ad libitum*. These results are consistent with the observations that genetic characteristics of rainbow trout survival vary extensively in space and time, likely due to multitude of mortality factors (Vehviläinen et al. 2008). However, our finding of the poorer capability of the cataract-bearing fish to forage (E. Brännäs unpublished, Voutilainen et al. 2008) and avoid predators (I. Kolari, H. Kuukka-Anttila, N. Peuhkuri in prep.) compared to their healthy conspecifics is likely to lead to poorer performance in nature where the conditions are harsher than in hatchery, both in terms of food availability and risk of predation.

Based on the recapture statistics collected by FGFRI the recovery of the anadromous Atlantic salmon group that was surveyed for cataracts has been very poor. During the first three years after stocking only seven fish out of the total of 1978 tagged fish have been reported caught by fishermen, whereas the normal recovery rate of anadromous Atlantic

salmon has during recent years been about 2–3% of the stocked fish (M. Naarminen, pers. comm.). Given that the recovery of the investigated fish has this far been so low, it is impossible to make far-reaching conclusions about the role of cataracts in the performance of the fish. Recovery data from stocked landlocked salmon (19 recoveries out of the 3990 stocked) and brown trout (6 recoveries out of the 3987 stocked) have also started to accumulate but they too are still so scarce that it is better not to jump to a conclusion at this stage.

In a pilot stocking experiment with 2-year-old Arctic charr ($n = 70$) having different cataract scores (only one healthy fish was available!) half of the stocked fish were recovered after one growing season (three months) in the lake. No differences in the survival of fish with different cataract scores were observed. The fish with different scores were recovered in approx. the same proportion as they had been stocked (I. Kolari, H. Kuukka-Anttila, N. Peuhkuri unpublished; Figure 14).

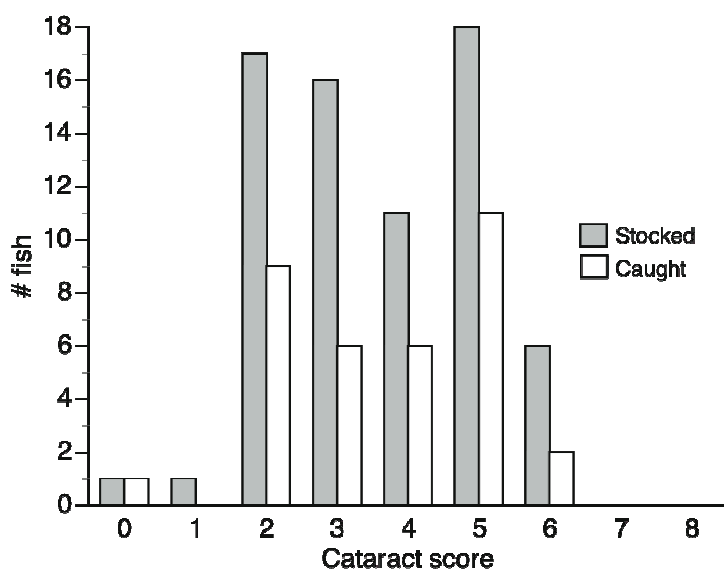


Figure 14 The frequencies of charr with different cataract scores per fish at the time of stocking ($n = 70$) and of charr caught three months post-stocking ($n = 35$).

A follow-up study with cataract-bearing (approx. 25% of the combined lens area opaque) and healthy 1-yr-old charr ($n = 212$ in both stocking groups) from the same hatchery strain confirmed the results of our pilot research. Roughly 20% of the stocked fish were recovered after 15 months in the lake, and approximately in the proportion to their stocking proportions. However, the preliminary results hint to survival differences in different-sized fish (I. Kolari, H. Kuukka-Anttila, N. Peuhkuri in prep.).

5. Conclusions and recommendations

Based on the results emerging from the present project under the auspices of Nordic Council of Ministers we have been able to show progress in several aspects considering the occurrence and causes and consequences of cataract in salmonid fishes.

The project found cataracts to be relatively common in a number of salmonid species reared in the hatchery in Finland and Sweden, and *Diplostomum* spp. infection was often the underlying factor in cataract development, in contrast to the findings from Norway where nutritional and environmental causes have more often been evoked as causes for cataract development. The likely role of bacterial infection in cataract formation was a novel finding and stresses the importance of preventive actions against infectious bacterial diseases in hatchery conditions.

The project has also enlightened the role of genetics in cataract formation and the potential for selection against cataract development when cataracts are caused by *Diplostomum* spp. parasites. When the purpose of fish rearing is food production, selection may help in preventing or limiting cataract formation in fish farming where planned selective breeding designs are applicable as a means to manage the stock. However, when the aim of hatchery propagation is to enhance endangered populations no directional selection whatsoever should be carried out but all possible genetic variation in the population should be preserved in order to protect the population from deleterious effects of the artificial environment. However, whenever possible, appropriate actions for preventing the occurrence of the *Diplostomum* spp. parasite in the hatchery, such as water filtering, creating outdoor rearing pools/raceways that do not harbour suitable habitat for the *Lymnaea* snails, using measures to get rid of gulls that act as vectors for the *Diplostomum* spp., etc., are of course the prime option to utilise. In addition, it would presumably prove useful to develop further possible physical and/or biological methods to decrease the parasite burden and bacterial infections in fish hatcheries.

The level of our knowledge of the potential consequences of cataract formation both for hatchery and wild fish has also increased as an outcome of the project and the long-term research commenced under the project on this matter will reveal more information in the future, ready to be taken into account in management actions.

The results of the project have been, and will be communicated in international scientific forums (journals, symposia) and in national aquaculture and fisheries journals. Communication of the results has been done

also directly to the representatives of aquaculture. Indeed, one of the main achievements of the LFITE-project has been the increase of the common knowledge of fish eye diseases among the farmers and fishery managers. The results have produced invaluable information directly applicable to designing and implementing management practices both for salmonid conservation and commercial aquaculture. As an example, the project has resulted in that in state-run stocking programs in Finland, investigating the eyes for cataracts will be included as a matter of routine in the health and quality checking of the fish to be stocked in the wild wherever applicable. The project recommends such procedure to be applied on regular basis in fish farming in general and in stocking programs in particular. Rigorous follow-up and close relationships with the farmers will make it possible to react to the problem when needed and hopefully, in the long run, to significantly diminish it.

References

- Ali, M. A. (1959) The ocular structure, retinomotor and photobehavioural responses of the juvenile Pacific salmon. *Can. J. Zool.* 37:965–996.
- Allendorf, F. W., Waples, R. S. (1996) Conservation and genetics of salmonid fishes. In *Conservation genetics: case histories from nature* (J. C. Avise & J. L. Hamrick eds), pp. 238–280, Chapman & Hall, New York.
- Alm, G. (1959) Connection between maturity, size and age in fishes. *Rep. Inst. Freshw. Res. (Drottningholm)*. 40:5–145.
- Ashton, N., Brown, N., Easty, D. (1969) Trematode cataract in fresh water fish. *J. Small Anim. Pract.* 10:471–478.
- Ballabeni, P., Ward, P.I. (1993) Local adaptation of the trematode *Diplostomum phoxini* to the European minnow *Phoxinus phoxinus*, its second intermediate host. *Funct. Ecol.* 7: 84–90.
- Barber, I., Hoare, D., Krause, J. (2000) Effects of parasites on fish behaviour: a review and evolutionary perspective. *Rev. Fish Biol. Fish.* 10:131–165.
- Barber, I., Arnott, S. A., Braithwaite, V. A., Andrew, J., Huntingford, F. A. (2001) Indirect fitness consequences of mate choice in sticklebacks: offspring of brighter males grow slowly but resist parasitic infections. *Proc. R. Soc. B* 268:71–76.
- Bateman, A. J. (1948) Intrasexual selection in *Drosophila*. *Heredity* 2:349–368.
- Betterson, C. (1974) Studies on the host specificity of the eyefluke, *Diplostomum spathaceum*, in brown and rainbow trout. *Parasitology* 69:11–29.
- Bjerkås, E., Bjørnstad, E. (1999) Is there a connection between rapid fluctuation in water temperature and cataract development in the Atlantic salmon (*Salmo salar* L.)? *Bull. Eur. Assoc. Fish Pathol.* 19:166–169.
- Bjerkås, E., Sveier, H. (2004) The influence of nutritional and environmental factors on osmoregulation and cataracts in Atlantic salmon (*Salmo salar* L.). *Aquaculture* 235:101–122.
- Bjerkås, E., Bjerkås, I., Moksness, E. (1998) An outbreak of cataract with lens rupture and nuclear extrusion in wolf-fish (*Anarhichas* spp.). *Vet. Ophthalmol.* 1:9–15.
- Bjerkås, E., Wall, A. E., Prapas, A. (2000) Screening of farmed sea bass (*Dicentrarchus labrax* L.) and sea bream (*Sparus aurata* L.) for cataract. *Bull. Eur. Ass. Fish Pathol.* 20:180–185.
- Bjerkås, E., Bjørnstad, E., Breck, O., Waagbø, R. (2001). Water temperature regimes affect cataract development in smolting Atlantic salmon, *Salmo salar* L. *J. Fish Dis.* 24:281–291.
- Bjerkås, E., Holst, J. C., Bjerkås, I., Ringvold, A. (2003). Osmotic cataracts causes reduced vision in wild Atlantic salmon postsmolts. *Dis.Aquat. Org.* 55:151–159.
- Bjerkås, E., Kuukka, H., Sørum, H., Koppang, E. O. *Aeromonas* spp. as possible causes of endophthalmitis and cataract in Arctic charr (*Salvelinus alpinus* L.). Submitted manuscript.
- Bjerkås, E., Waagbø, R., Sveier, H., Breck, O., Bjerkås, I., Bjørnstad, E., Maage, A. (1996) Cataract development in Atlantic salmon (*Salmo salar* L.) in fresh water. *Acta vet. scand.* 37:351–360.
- Björklund H., Bylund G. (1987) Absorption, distribution and excretion of the anthelmintic praziquantel (Droncit) in rainbow trout (*Salmo gairdneri* R.). *Parasitol. Res.* 73:240–244.
- Breck, O., Sveier, H. (2001) Growth and cataract development in two groups of Atlantic salmon (*Salmo salar* L.) post smolt transferred to sea with a four week interval. *Bull. Eur. Assoc. Fish Pathol.* 21:91–103.
- Breck, O., Bjerkås, E., Campbell, P., Rhodes, J. D., Sanderson, J., Waagbø R (2005) Histidine nutrition and genotype affect cataract development in Atlantic salmon, *Salmo salar* L. *J. Fish Dis.* 28:357–371.
- Brommer, J. E. (2004) Immunocompetence and its costs during development: an experimental study in blue tit nestlings. *Proc. R. Soc. B* 271(Suppl. 3):S110–S113.

- Brown, J. L. (1997) A theory of mate choice based on heterozygosity. *Beh. Ecol.* 8:60–65.
- Bruno, D. W., Raynard, R. S. (1994) The effect of water temperature on eye opacity in Atlantic salmon, *Salmo salar* L. *Bull. Eur. Assoc. Fish Pathol.* 14:86–88.
- Bylund G., Sumari O. (1981) Laboratory tests with Droncit against diplostomiasis in rainbow trout, *Salmo gairdneri* Richardson. *J. Fish Dis.* 4:259–264.
- Chappell, L. H. (1995) The biology of diplostomatid eyeflukes of fishes. *J. Helminthol.* 69:97–101.
- Chappel, L. H., Hardie, L. J., Secombes, C. J. (1994) Diplostomiasis: the disease and host-parasite interactions. In *Parasitic Diseases of Fish* (A. W. Pike & J. W. Lewis, eds), pp. 59–86. Samara Publishing Limited, Dyfed.
- Cullen, A. P., Monteith-McMaster, C. A., Sivak, J. G. (1994) Lenticular changes in rainbow trout following chronic exposure to UV radiation. *Curr. Eye Res.* 13:731–737.
- Deng, D.-F., Wilson, R. P. (2003) Dietary riboflavin requirement of juvenile sunshine bass (*Morone chrysops* × *Morone saxatilis*)
- Dupont-Nivet, M., Vandeputte, M., Haffray, P., Chevassus, B. (2006) Effect of different mating designs on inbreeding, genetic variance and response to selection when applying individual selection in fish breeding programs. *Aquaculture* 252:161–170.
- Dybdahl, M. F., Storfer, A. (2003) Parasite local adaptation: Red Queen versus Suicide King. *Trends Ecol. Evol.* 18:523–530.
- Einum, S., Fleming, I. A. (1997) Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *J. Fish Biol.* 50:634–651.
- Einum, S., Fleming, I. A. (2001) Implications of stocking: ecological interactions between wild and released salmonids. *Nordic J. Freshw. Res.* 75:56–70.
- Ersdal, C., Midtlyng, P. J., Jarp, J. (2001) An epidemiological study of cataracts in seawater farmed Atlantic salmon *Salmo salar*. *Dis. Aquat. Org.* 45:229–236.
- Fiumera, A. C., Porter, B. A., Looney, G., Asmussen, M. A., Avise, J. C. (2004) Maximizing offspring production while maintaining genetic diversity in supplemental breeding programs of highly fecund managed species. *Cons. Biol.* 18:94–101.
- Fleming, I. A., Hindar, K., Mjølnerod, I. B., Jonsson, B., Balstad, T., Lamberg, A. (2000) Lifetime success and interactions of farm salmon invading a native population. *Proc. Roy. Soc. Lond. B* 267:1517–1523.
- Folstad I., Karter, A. J. (1992) Parasites, bright males and the immunocompetence handicap. *Am. Nat.* 139:603–622.
- Fraser, P. J., Duncan, G., Tomlinson, J. (1990) Nuvar and cataracts in Atlantic salmon (*Salmo salar*). *Exp. Eye Res.* 50: 443–447.
- Gandon, S., Michalakis, Y. (2002) Local adaptation, evolutionary potential and host-parasite coevolution: interactions between migration, mutation, population size and generation time. *J. Evol. Biol.* 15:451–462.
- Gönnert R., Andrews P. (1977) Praziquantel, a new broad-spectrum antischistosomal agent. *Z. Parasitenkunde* 52:129–159.
- Hamilton, W. D. (1980) Sex versus non-sex versus parasite. *Oikos* 35:282–290.
- Hamilton W. D., Zuk, M. (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387.
- Hargis, W. G. (1991) Disorders in the eye in finfish. *Annu. Rev. Fish Dis.* 1:95–117.
- Heath, D. D., Blouw, D. M. (1998) Are maternal effects in fish adaptive or mere physiological size-effects? In *Maternal effects as adaptations* (T. A. Mousseau & C. W. Fox, eds), pp 178–201, Oxford Univ Press, New York.
- Hendrix, D. V. H. (2007) Diseases and surgery of the canine anterior uvea. In *Veterinary ophthalmology 4th Edition* (K. N., Gelatt ed.), pp 812–858. Blackwell Publishing Asia, Victoria, Australia.
- Hughes, S. G. (1985) Nutritional eye diseases in salmonids: a review. *Prog. Fish-Cult.* 51:189–193.
- Huntingford, F. A. (2004) Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *J. Fish Biol.* 65(Suppl A):122–142
- Höglund, J. (1991) Ultrastructural observations and radiometric assay on cercarial penetration and migration of the digenean *Diplostomum spathaceum* in the rainbow trout *Oncorhynchus mykiss*. *Parasitol. Res.* 77:283–289.
- Höglund, J., Thuvander, A. (1990) Indications of non-specific protective mechanisms in rainbow trout *Oncorhynchus mykiss* with diplostomosis. *Dis. Aquat. Org.* 8:91–97.
- Iwata, M., Komatsu, S., Collie, N. L., Nisioka, R. S., Bern, H. A. (1987) Ocular cataract and seawater adaptation in Salmonids. *Aquaculture* 66:315–327.
- Joblin, M. (1994) *Fish Bioenergetics*. Chapman and Hall, London.
- Kalbe, M., Kurtz, J. (2006) Local differences in immunocompetence reflect resistance of sticklebacks against the eye fluke *Diplosto-*

- mum pseudospathaceum*. Parasitology 132:105–116.
- Kaltz, O., Shykoff, J.A. (1998) Local adaptation in host-parasite systems. Heredity 81: 361–370.
- Karvonen, A., Seppälä, O. (2008) Effect of eye fluke infection on the growth of whitefish (*Coregonus lavaretus*) – an experimental approach. Aquaculture 279:6–10.
- Karvonen, A., Paukku, S., Valtonen, E. T., Hudson, P. J. (2003) Transmission, infectivity and survival of *Diplostomum spathaceum* cercariae. Parasitology 127:217–224.
- Karvonen, A., Seppälä, O., Valtonen, E. T. (2004a) Eye fluke-induced cataract formation in fish: quantitative analysis using an ophthalmological microscope. Parasitology 129:473–478.
- Karvonen, A., Hudson, P. J., Seppälä, O., Valtonen, E. T. (2004b) Transmission dynamics of a trematode parasite: exposure, acquired resistance and parasite aggregation. Parasitol. Res. 92:183–188.
- Karvonen, A., Seppälä, O., Valtonen, E. T. (2004c) Parasite resistance and avoidance behaviour in preventing eye fluke infections in fish. Parasitology 129:159–164.
- Kekäläinen, J., Vallunen, J. A., Primmer, C. R., Rättä, J., Taskinen, J. Major histocompatibility complex overdominance in a wild salmonid population. Submitted manuscript.
- Kihlslinger, R. L., Nevitt, G. A. (2006) Early rearing environment impacts cerebellar growth in juvenile salmon. J. Exp. Biol. 209:504–509.
- Kincaid, H. L., Elrod, J. H. (1991) Growth and survival of stocked lake trout with nuclear cataracts in Lake Ontario. North Am. J. Fish. Manage. 11:429–434.
- Kincaid, H. L., Calkins, G. T. (1991) Rapid classification of nuclear cataracts in lake trout. Prog. Fish Cult. 53:120–124.
- Kurtz, J., Sauer, K. P. (1999) The immunocompetence handicap hypothesis: testing the genetic predictions. Proc. R. Soc. Lond. B 266: 2515–2522.
- Kurtz, J., Kalbe, M., Aeschlimann, P. B., Häberli, M. A., Wegner, K. M., Reusch, T. B. H., Milinski, M. (2004) Major histocompatibility complex diversity influences parasite resistance and innate immunity in sticklebacks. Proc. R. Soc. Lond. B 271: 197–204.
- Kuukka, H., Peuhkuri, N., Kolari, I., Paananen, T., Kaase, A. (2009) Quantitative genetic architecture of parasite-induced cataract in rainbow trout, *Oncorhynchus mykiss*. Heredity, provisionally accepted.
- Laitinen, M., Siddall, R., Valtonen, E.T. (1996) Bioelectronic monitoring of parasite-induced stress in brown trout and roach. J. Fish Biology 48:228–241.
- Lima, S. L., Dill, L. M. (1990) Behavioral decision made under the risk of predation – a review and prospectus. Can. J. Zool. 68:619–640.
- Lively, C. M., Dybdahl, M. F. (2000) Parasite adaptation to locally common host genotypes. Nature 405: 679–681.
- Lochmiller, R. L., Deerenberg, C. (2000) Trade-offs in evolutionary biology: Just what is the cost of immunity. Oikos 88:87–98.
- Lyholt, H. C. K., Buchmann, K. (1996) *Diplostomum spathaceum*: effects of temperature and light on cercarial shedding and infection of rainbow trout. Dis. Aquat. Org. 25:169–173.
- Marcogliese, D. J., Compagna, S., Bergeron, E., McLaughlin, J. D. (2001) Population biology of eyeflukes in fish from a large fluvial ecosystem: the importance of gulls and habitat characteristics. Can. J. Zool. 79:1102–1113.
- McKeown, C. A., Irwin, S. W. B. (1997) Accumulation of *Diplostomum* spp. (Digenea: Diplostomatidae) metacercariae in the Eyes of 0+ and 1+ roach (*Rutilus rutilus*). Int. J. Parasitol. 27:377–380.
- McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., Cross, T., Ferguson, A. (1997) Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES J. Mar. Sci. 54:998–1008.
- Menzies, F. D., Crockford, T., Breck, O., Midtlyng, P. J. (2002) Estimation of direct costs associated with cataracts in farmed Atlantic salmon (*Salmo salar*) Bull. Eur. Assoc. Fish Pathol. 22:27–32.
- Midtlyng, P. J., Ahrend, M., Bjerkås, E., Waagbø, R., Wall, T. (1999) Current research on cataracts in fish. Bull. Eur. Ass. Fish Pathol. 19:299–301.
- Pitcher, T., Parrish, J. K. (1993) Functions of shoaling behaviour in teleosts. In Behaviour of teleost fishes 2nd edn (T. J. Pitcher, ed.), pp. 363–439. Chapman & Hall, London.
- Press, C. McL., Evensen, Ø. (1999) The morphology of the immune system in teleost fishes. Fish Shellfish Immunol. 9:309–318.

- Price, P. W. (1980) Evolutionary Biology of Parasites. Princeton University Press, Princeton, NJ.
- Price, E. O. (1999) Behavioral development in animals undergoing domestication. *Appl. Anim. Behav. Sci.* 65:245–271.
- Priede, I. G. (1985) Metabolic scope in fishes. In *Fish Energetics* (P. Tytler & P. Calow, eds), pp. 33–64, Croom Helm, London.
- Primmer, C. R., Aho, T., Piironen, J., Estoup, A., Cornuet, J. M., Ranta, E. (1999) Microsatellite analysis of hatchery stocks and natural populations of Arctic charr, *Salvelinus alpinus*, from the Nordic region: implications for conservation. *Hereditas* 130:277–289.
- Pylkkö, P. (2004) Atypical *Aeromonas salmonicida* infection as a threat to farming of Arctic charr (*Salvelinus alpinus* L.) and European grayling (*Thymallus thymallus* L.) and putative means to prevent the infection PhD-thesis. Jyväskylä Studies in Biological and Environmental Science. Jyväskylä University Printing House, Jyväskylä.
- Pylkkö, P., Pohjanvirta, T., Pursiainen, M. (1996) Nieriän (*Salvelinus alpinus*) silmäsamentumat. RKTL Kalatutkimuksia 109 (in Finnish).
- Pylkkö, P., Suomalainen, L.-R., Tirola, M., Valtonen E. T. (2006) Evidence of enhanced bacterial invasion during *Diplostomum spathaceum* infection in European grayling, *Thymallus thymallus* (L.). *J. Fish Dis.* 29:79–86.
- Riley, W. D., Ives, M. J., Pawson, M. G., Maxwell, D. L. (2006). Seasonal variation in habitat use by salmon, *Salmo salar*, trout, *Salmo trutta* and grayling, *Thymallus thymallus*, in a chalk stream. *Fish. Man. Ecol.* 13:221–236.
- Rintamäki-Kinnunen, P. & Valtonen, E. T. (1997). Epizootiology of protozoans in farmed salmonids at northern latitudes. *Int. J. Parasitol.* 27:89–99.
- Sangster, C. R., Dove, A. D. M., Bowser, P. R. (2004) *Diplostomum* in pond-reared walleye *Stizostedion vitreum* - implications of a management strategy for control. *Aquaculture* 236:95–102.
- Savino, J. F., Henry, M. G., Kincaid, H. L. (1993) Factors affecting feeding-behaviour and survival of juvenile lake trout in the Great-Lakes. *Trans. Am. Fish. Soc.* 122:366–377.
- Seppälä, O., Karvonen, A., Valtonen, E. T. (2004) Parasite-induced change in host behaviour and susceptibility to predation in an eye fluke-fish interaction. *Anim. Behav.* 68:257–263.
- Seppälä, O., Karvonen, A., Valtonen, E. T. (2005a) Impaired crypsis of fish infected with a trophically transmitted parasite. *Anim. Behav.* 70:895–900.
- Seppälä, O., Karvonen, A., Valtonen, E. T. (2005b). Manipulation of fish host by eye flukes in relation to cataract formation and parasite infectivity. *Anim. Behav.* 70:889–894.
- Seppälä, O., Karvonen, A., Valtonen, E. T. (2008) Shoaling behaviour of fish under parasitism and predation risk. *Anim. Behav.* 75:145–150.
- Seppänen, E., Kuukka, H., Huuskonen, H., Piironen, J. (2008) Relationship between standard metabolic rate and parasite-induced cataract of juveniles in Atlantic salmon stocks. *J. Fish Biol.* 72:1659–1674.
- Seppänen, E., Kuukka, H., Voutilainen, A., Huuskonen, H., Peuhkuri, N. (2009) Metabolic depression and spleen and liver enlargement in juvenile Arctic charr exposed to chronic parasite infection. *J. Fish Biol.*, in press.
- Shariff, M., Richards, R. H., Sommerville, C. (1980) The histopathology of acute and chronic infections of rainbow trout *Salmo gairdneri* Richardson with eye flukes, *Diplostomum* spp. *J. Fish Dis.* 3:455–465.
- Shingawa, K., Urabe, M., Nagoshi, M. (2001) Effects of trematode infection on metabolism and activity in a freshwater snail, *Semisulcospira libertina*. *Dis. Aquat. Org.* 45:141–144.
- Soler, J. J., de Neve, L., Perez-Contreras, T., Soler, M., Sorci, G. (2003) Trade-off between immunocompetence and growth in magpies: an experimental study. *Proc. R. Soc. B* 270: 241–248.
- Speed, P., Pauley, G. B. (1984) The susceptibility of four salmonid species to the eyefluke, *Diplostomum spathaceum*. *Northw. Sci.* 58:312–316.
- Stables, J. N., Chappell, L. H (1986) The epidemiology of diplostomiasis in farmed rainbow trout from north-east Scotland. *Parasitology* 92:699–710.
- Szekely C., Molnar K. (1991) Praziquantel (Droncit) is effective against diplostomosis of grasscarp *Ctenopharyngodon idella* and silver carp *Hypophthalmichthys molitrix*. *Dis. Aquat. Org.* 11:147–150.
- Thomas H., Gönner R. (1977) The efficacy of praziquantel against cestodes in animals. *Z. Parasitenkunde* 52:117–127.
- Tiira, K., Piironen, J., Primmer, C. R. (2006) Evidence for reduced variation in severely

- deformed juvenile salmonids. *Can. J. Fish. Aquat. Sci.* 63:2700–2707.
- Tschirren, B., Richner, H. (2006) Parasites shape the optimal investment in immunity. *Proc. R. Soc. B* 273:1773–1777.
- Uller, T., Isaksson, C., Olsson, M. (2007) Immune challenge reduces reproductive output and growth in a lizard. *Funct. Ecol.* 20:873–879.
- Valtonen, E. T., Gibson, D. I. (1997) Aspects of the biology of diplostomid metacercariae (Digenea) populations occurring in fishes in different localities of northern Finland. *Ann. Zool. Fennici* 34:47–59.
- Valtonen, E. T., Holmes, J. C., Koskivaara, M. (1997) Eutrophication, pollution and fragmentation: effects on parasite communities in roach, *Rutilus rutilus*, and perch, *Perca fluviatilis*, in four lakes in central Finland. *Can. J. Fish. Aquat. Sci.* 54:572–585.
- Vehviläinen H, Kauser A, Quinton C, Koskinen H, Paananen T. (2008) Survival of the currently fittest – Genetics of rainbow trout survival across time and space. *Genetics* 180:507–516.
- Voutilainen, A., Taskinen, J. (2009) Infectivity of *Diplostomum* spp. in Arctic charr: aspects of exposure duration and cercariae morphology. *J. Parasitol.*, in press.
- Voutilainen, A., Figueiredo, K., Huuskonen, H. (2008) Effects of the eye fluke *Diplostomum spathaceum* on the energetics and feeding of Arctic charr *Salvelinus alpinus*. *J. Fish Biol.* 73:2228–2237.
- Voutilainen, A., Valdez, H., Karvonen, A., Kortet, R., Kuukka, H., Peuhkuri, N., Piironen, J., Taskinen, J. (2009a) Infectivity of trematode eye flukes in farmed salmonid fish – effects of parasite and host origins. *Aquaculture*, provisionally accepted.
- Voutilainen, A., Saarinen, M., Suonpää, A., Taskinen, J. (2009b) In vitro efficacy of praziquantel against the cercariae of *Diplostomum* sp., *Rhipidocotyle fennica* and *R. campanula*. *J. Fish Dis.*, in press.
- Waagbø, R., Bjerkås, E., Hamre, K., Berge, R., Wathne, E., Lie, Ø., Torstensen, B. (2003) Cataract formation in Atlantic salmon, *Salmo salar* L. smolts relative to dietary pro- and antioxidants and lipid level. *J. Fish Dis.* 26:213–229.
- Waagbø, R., Hosfeld, C. D., Fivelstad, S., Olsvik, P. A., Breck, O. (2008) The impact of different water gas levels on cataract formation, muscle and lens free amino acids, and lens antioxidant enzymes and heat shock protein mRNA abundance in smolting Atlantic salmon, *Salmo salar* L. *Comp. Biochem. Physiol.* A149:396–404.
- Wall, A. E. (1998) Cataracts in farmed Atlantic salmon (*Salmo salar*) in Ireland, Norway and Scotland from 1995 to 1997. *Vet. Rec.* 142:626–631.
- Wall, T., Bjerkås, E. (1999) A simplified method of scoring cataracts in fish. *Bull. Eur. Ass. Fish Pathol.* 19:162–164.
- Wedekind, C., Müller, R. & Spicher, H. (2001) Potential genetic benefits of mate selection in whitefish. *J. Evol. Biol.* 14: 980–986.
- Whyte, S. K., Allan, J. C., Secombes, C. J., Chappel, L. H. (1987). Cercariae and diplostomules of *Diplostomum spathaceum* (Digenea) elicit an immune response in rainbow trout, *Salmo gairdneri* Richardson. *J. Fish Biol. (Suppl. A)* 31:185–190.
- Wootten, R. (1974) Observations on strigeid metacercariae in the eyes of fish from Hanningfield Reservoir, Essex, England. *J. Helminthol.* 48:73–83.
- Zahavi A. (1975) Mate selection – A selection for a handicap. *J. theor. Biol.* 53:205–214.

Sammandrag

Laxfiskar odlas i de Nordiska länderna som matfisk för slakt och för att restaurera naturliga bestånd. Utsättning av odlad fisk görs också för att förbättra både det kommersiella såväl som fritidsfisket. Exempelvis utsättning av röding för isfiske och för utsättning av lax och öring smolt för att kompensera för uppdämda älvar.

Initiativet för detta Nordiska samarbetsprojekt togs efter att ett ökat frekvens av katarakt diagnostiserades hos odlade laxfiskar under senare år. Katarakt är ett patologiskt tillstånd i ögat där den normalt genomskinliga linsen grumlas i olika grad. Tillståndet utgör ett tydligt problem i moderna fiskodlingar då effekten blir en försämrad syn eller fiskarna blir helt blinda. I Norge har laxodlingsindustrin drabbats av stora ekonomiska förluster på grund av försämrad tillväxt och ökad dödlighet i besättningarna på grund av problem med katarakt. Dessutom försämrar troligen katarakt resultatet av utsättningsprogram av lax eller öring. Katarakt är dessutom ett etiskt och välfärdsproblem hos fisken.

Norge har, av de nordiska länderna, haft en ledande roll inom forskningen på orsakerna bakom katarakt då detta är av stor ekonomisk betydelse för den stora laxodlingsindustrin. Informationen om vilka faktorer som ligger bakom utvecklingen av katarakt hos fisk har ackumulerats under senare år med stora kunskapsluckor om orsaker och konsekvenser saknas fortfarande. Dessutom saknas kvantitativa data om förekomsten av katarakt i Sverige och Finland. Genom ett samarbete mellan de Nordiska länderna Finland, Sverige och Norge, avsåg vi att i största möjliga mån fylla i kunskapsluckorna om katarakt.

Den tillgängliga informationen om förekomsten av katarakt de Nordiska länder som deltog i detta projekt uppdaterades och nya data samlades in från fisk i odlingar i Finland och Sverige. Vildfångad fisk ingick också i studien. Studien visade att katarakt var ganska vanlig i alla sex laxartade fiskar som undersöktes men den exakta förekomsten och graden av påverkan (hur stor del av hornhinnan som var täckt) var mycket varierande och kan sättas i samband med exponeringen av *Diplostomum* spp. parasiten. Dessa resultat motsatte de Norska studierna där näringsbrist och faktorer i miljön anses vara den största orsaken bakom utvecklingen av katarakt. Detta projekt gav också ny information om förekomsten av katarakt hos vilda populationer.

Forskningen om kataraktens orsaker koncentrerades till proximala biotiska faktorer, parasiter och patogen smitta samt ärvbarhet och under projektets gång har förståelsen för den potentiellt signifikanta rollen som dessa faktorer spelar. Baserat på korta experimentella studier har nytt ljus kastats på sambandet mellan fiskars tillväxt och förekomsten av katarakt.

Ämnesomsättning hos individuella fiskar och *Diplostomum* spp. infektion och parasit-inducerade katarakt var beroende av varandra. Katarakt påverkade dessutom både födobeteende och predationsrisken i kontrollerade experimentella förhållande. Dessutom verkade katarakt påverka fiskarnas odlingscykel genom att könsmognadsprocessen fördröjs hos honor. Projektet inkluderade även långsiktig forskning om förekomsten av katarakt för att klargöra förhållandet av ovannämnda faktorer ytterligare.

Förutsatt att *Diplostomum* spp. parasiter har en viktig roll rör förekomsten av katarakt i sötvattensodlingar (åtminstone i Finland and Sverige), är rekommendationen att minimera parasitens förmåga att infektera fisken genom en rad åtgärder. Speciellt ska bakteriella infektioner undvikas då detta verkar underlätta parasitens angrepp på ögat. I avelsprogram bör kataraktförekomst och de tillväxt- och överlevnadsproblem som bli effekten ingå i selektionskriterierna. Detta är speciellt viktigt i fiskodling avsett för utsättningar där bevarande av naturliga populationer är målet. Projektet rekommenderar också att undersökningar görs som standard på fiskodlingar speciellt för utsättningar. Detta underlättar om specifika åtgärder behöver tas.

Preface

This report is based on a joint Nordic research project “Looking fish in the eye – cataract as a problem in fish farming” (LFITE), which received funding from the Nordic Council of Ministers (the Nordic Working Group of Fishery Research, NAF) 2005–2007. During past years, increasing numbers of farmed salmonids have been observed to suffer from cataracts that can lead to impaired vision, and ultimately, to total blindness of the fish. Therefore, the project’s aims were to

- Update information on the prevalence of cataract in hatchery (and wild) populations of salmonid fishes in the Nordic countries.
- Elucidate factors important in influencing cataract development.
- Cast new light on consequences of cataract to performance of the fish in the hatchery and to stocked fish in the wild.

The project was carried out by scientists from Finland, Sweden and Norway.

The report summarizes what is known of cataract prevalence in salmonids in the participating countries based on literature and new data gathered from hatchery and wild-caught fish under the LFITE-project. This section is followed by a presentation of case studies conducted during the project with special attention to environmental (biotic) and genetic factors potentially important in cataract formation. Investigation into the influence of cataract on individual performance is also covered. Finally, conclusions and recommendations regarding possible lines of future actions are made.

Summary

Salmonid fishes are nowadays subject to extensive aquaculture in the Nordic countries with the aim to produce food for human consumption and, on the other hand, to enhance endangered populations by stocking of captive-propagated fish. Stocking is also conducted to underpin fisheries.

The initiation of this joint Nordic project was an outcome of the observation that increasing frequencies of cataracts have been diagnosed in farmed salmonids during past years. Cataract is a pathological condition of the eyes where the normally transparent eye lens turns opaque to a varying degree. Cataract has proven a pronounced problem in modern fish farming because it leads to impaired eyesight and even total blindness of the fish. In Norway, the Atlantic salmon industry has suffered from monetary losses owing to reduced growth and increased mortality of the fish due to cataracts. In addition to economics, concern has also arisen over the potential role of this eye disease in the failure of stocking programs. The occurrence of cataracts in farmed fish is also an ethical issue of animal welfare.

Of the Nordic countries, Norway has been the leading quarter in research on the causes of cataracts owing to the need to solve this problem that has been noticed to prevail in the economically significant Atlantic salmon farming. Therefore, information of factors underlying cataract development in salmon has started to accumulate during past years. However, there still are gaps in our knowledge on the causes of cataract as well as on its consequences. Furthermore, quantitative information on the severity of the problem in the other Nordic countries than Norway is largely lacking. Through co-operation between the Nordic countries Finland, Sweden and Norway it was possible to make progress in filling these gaps in our knowledge.

The available information on cataract occurrence in salmonids in the participating Nordic countries was updated with new data gathered during the project on the prevalence of cataract in hatchery populations of salmonid fishes in Finland and Sweden. Wild-caught fish were also included in the research. Cataracts appeared relatively common in all the six salmonid species included in the surveys but the exact prevalence and severity (coverage of eye lens) were variable being most notably related to the exposure to *Diplostomum* spp. parasite. This result is clearly a contrast to those of Norwegian studies in which nutritional imbalance and environmental (abiotic) factors have generally been established as primary explanatory causes for cataract development. New information on the occurrence of cataracts in wild fish was also gained during the project.

The research on the causes of cataracts concentrated on proximate biotic factors, parasite and pathogen infestation, as well as on the role of

genetic predisposition, and progress was achieved in the course of the project in the understanding of the potentially significant role of these factors in cataract development. Based on short-term experimental work, new light was shed also on the relationship between fish performance and the occurrence of cataract. Individual energy metabolism and *Diplostomum* spp. infection and consequently parasite-induced cataracts were found to be interrelated, and cataracts were furthermore found to clearly influence both foraging and risk of predation in controlled experimental conditions. In addition, cataracts appeared to influence also the breeding biology of the fish by slowing down the female maturation process. Long-term research was also commenced on cataract occurrence and individual performance to clarify the dependency between these two phenomena more thoroughly.

Given that *Diplostomum* spp. parasites appear to play such an important role in cataract development in freshwater fish hatcheries (at least in Finland and Sweden), it is highly recommended that expedient means available for preventing or minimising the incidence of the parasite in the hatchery conditions are brought into play widely by the fish farmers. Attention should also be paid to efficient actions preventing infectious bacterial diseases that may predispose the fish to cataracts. In breeding programs and commercial aquaculture, selection against cataracts may be considered as an applicable measure to diminish cataract prevalence and severity and the growth and survival problems associated with them. When hatchery propagation and rearing is carried out for conservation purposes selection should be used on no account. The project also recommends that examination of cataracts should be included as a standard practice in fish farming, and stocking programs particularly. This will help in discerning when there is a need to take requisite actions.