GREAT LAKES FISHERY COMMISSION

2003 Project Completion Report[1]

Assessing ecological fitness of fish populations of the world's large water bodies

by:

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BOARD OF TECHNICAL EXPERTS

RESEARCH TASK FINAL REPORT

Project Title: Assessing ecological fitness of fish populations of the world's large water bodies

Principal Investigators: R. Hecky and D. Stewart

Project Initiation Date: 10 June 1999

Project Completion Date: June 2003 (extended to July 31, 2003)

Project Objectives: The overall goal of the project is to improve the ability of fisheries managers to assess fitness of fish communities to determine best practices to improve fitness of desirable species while maintaining ecosystem integrity. Specific objectives are:

1. Identify current approaches for assessing and managing the fitness of fish populations inhabiting diverse, large water bodies.
2. Provide a foundation for an international network concerning fitness assessment.
3. Organize annual symposium at IAGLR for information presentation.
4. Distill and synthesize annual symposium results to highlight management approaches
5. for improving fitness of target species and communicate these to the commission.
6. Provide opportunities for visiting scientists to further collaborate with the North American Great Lakes research community.
7. Synthesize information for journal publication.

Project Deliverables:

1. Host three successive annual symposia at IAGLR.
2. Provide progress reports and summaries of identified "best practices" for assessing and managing from a "fitness" perspective
3. Produce final report documenting insights from the symposia and collaborations.

Period Covered in This Report: June 1999-June 2003

Progress Towards Objectives/Deliverables:

All deliverables were met. The three sessions were successfully held and included scientists addressing large lakes and coastal waters around the world. In total 23 scientists received total (15) or partial support (8) for attendance. In most cases for the sponsored attendees, this was their first IAGLR meeting and their first opportunity to interact with fisheries scientists and issues on the Laurentian Great Lakes. All agreed there were remarkable similarities in the stresses on fish populations especially in terms of exploitation but divergence on some of the environmental issues e.g. African lakes concerned with impacts of increasing eutrophication while Laurentian lakes are recovered and concern is on oligotrophication and exotic species. Summaries of the sessions in 2001 and 2002 have already been provided in previous progress reports (and are given in appendix B and C) although the summaries are not focussed on the "fitness" theme (see discussion of objectives below). The synopsis of this year's session is included as Appendix D. In the appendix A to this report are the abstracts/announcements for each of the special sessions. The summaries highlight the subject matter of the presentations offered and emphasize any substantive conclusions.

The objectives of the project were inconsistently achieved and are reviewed here: Identify current approaches for assessing and managing the fitness of fish populations inhabiting diverse, large water bodies.

- *Identify current approaches for assessing and managing the fitness of fish populations inhabiting diverse, large water bodies*. This objective was poorly met although the issue of fitness was the topic of several presentations in each session. It proved difficult to find international speakers from different parts of the world who could address fitness in a quantitative manner. So the decision was made and vetted through BOTE to deemphasize the fitness focus in order to maintain broad international participation and perspective. The difficulty with "fitness" as a topic is best illustrated by the response of an African scientist during the first session as to what is fitness. To him it was a fish that could sustain the fishing pressure of current exploitation rates, a very practical approach but best addressed as viability of the population. In Africa the greatest issue in the fisheries is trying to control effort or maintain total fish production in the face of burgeoning and hungry human populations. Concern about species extinction, let alone genetic shifts in populations, are hardly an issue yet, despite these African lakes having the highest ichthyodiversity in the world. Consequently the focus of the sessions shifted away from fitness towards viability of fish populations and global factors that can affect viability and fitness.
- *Provide a foundation for an international network concerning fitness assessment.* There was a strong sense of community based upon the concept of sustainability of fisheries and viability of desirable fishes. Good linkages with some of the African research institutions in particular were forged among the international scientists. The GLFC has the potential to provide significant guidance to fledging international management organizations such as the Lake Victoria Fisheries Organization (LVFO). As most successful networks are, at their core, founded on personal relationships among practicing professionals, it can be said that a good foundation has been laid for continued cooperation and interaction. It cannot be said that the sessions culminated in a network for assessing fitness. Though desirable, such a network is still in the distant future.
- *Organize annual symposium at IAGLR for information presentation.* This objective was very successfully accomplished with outstanding scientists and excellent presentations.
- *Distill and synthesize annual symposium results to highlight management approaches for improving fitness of target species and communicate these to the commission.* For each session, summaries were made of the presentations and included in the BOTE progress reports. Because the sessions generalized the fitness topic and became more focussed on sustainability of fisheries, this objective as originally formulated could not be met.
- *Provide opportunities for visiting scientists to further collaborate with the North American Great Lakes research community.* This objective was accomplished not only through sharing of information and data at the meetings; but, in at least three cases, collaborative research initiatives were initiated. However, the participation of North American scientists working on the Laurentian lakes in the sessions was less than anticipated, and this restricted the opportunities for collaboration.

- *Synthesize information for journal publication.* Agreement was reached among most of the participants in the 2002 session on Vision, Visibility and Viability to prepare a review/perspective article for primary publication, most likely *Canadian Journal of Fisheries and Aquatic Sciences* with R. Hecky to take the lead. There was also agreement reached at the 2003 session for the participants to submit articles for publication in *Journal of Great Lakes Research* or another suitable journal as a special section of viability of fish populations (D. Stewart to coordinate).

Lessons learned by the co-organizers:

There was a presumption that North American scientists would willingly participate in these fisheries oriented sessions at IAGLR. In fact this was not the case. Participation by "non-sponsored" scientists from the North American lakes (i.e. excluding the co-organizers who participated in each session) was quite limited. The sessions were well attended and did attract participation by North American scientists working on international great lakes to nearly the same extent that it attracted North American scientists working on North American Great Lakes. As a result, opportunities to form collaborative ventures between Laurentian Great Lake scientists and international scientists were more limited than expected. In part this may be the result of North American fisheries scientists preferring other meeting venues to IAGLR, or it may simply be that the session topics were not as attractive as they might have been. If it were to be done again, it might be preferable to "pair" lakes, e.g. Lake Erie and Lake Victoria or Lake Superior and Lake Baikal, and invite both North American and international scientists working on those lakes to participate to increase the possibilities for collaborative analysis and research. An example of this approach is a proposed Special Session at next year's 2004 IAGLR by GLOW (Great Lakes of the World; this will be the fourth International GLOW symposium) on "Great Lake Canaries: The Shallow Great Lakes will invite speakers on Lakes Erie, Winnipeg and Victoria" to share perspectives on environmental and fisheries issues in these productive shallow lakes that have large fisheries and are the first to respond to environmental disruptions. This session is co-organized by M. Munawar and R.E. Hecky, and GLFC might want to consider co-sponsoring the session as a continuation of this international task. The previous GLOW symposia have each led to book publications, and that is the intention for the 2004 symposium/session.

Participation was sponsored for Russian scientists in the last two sessions (Lake Baikal and Lake Ladoga) but their ability to interact with other scientists was restricted by their very limited knowledge of English. Future invitations should be linked either to a specific request to Russian scientists with good English skills (all our correspondence was in English but verbal performance was different!) or recognize the need for the provision of an interpreter.

International participation is expensive for the participants; and, certainly from Africa, their ability to participate (without sponsorship) will be limited for the near future. GLFC might consider a "twinning" relationship with LVFO in which LVFO might nominate an outstanding African scientist working on Lake Victoria to attend the annual IAGLR meeting to strengthen cooperation between the organizations and insure information and technology transfer between the lakes. We did manage to attract European scientists who were willing to self-fund, but the capacity for Russian scientists is nearly as limited as the African scientists. It would be worth exploring if this is as great a problem at other international meetings which are more focused on fisheries than IAGLR, i.e. the individual scientist's capacity to generate national funding for meeting attendance may be easier for large international fisheries meetings.

Publications from this task are expected, but there will be issues of costs for the participating scientists and even of editorial time for those putting together the publications. These costs issues (JGLR is expensive especially by African but even European standards) could erode enthusiasm for adhering to planned publication commitments. With the termination of the international task, this issue will be aggravated. BOTE may want to consider continuing support to the task to insure that planned publications are realized.

Anticipated Progress Next Reporting Period: This project is completed unless renewed/extended.

Manuscripts Submitted/Published: None yet; but commitment made for papers from 2003 session on "Viability of Fish Populations" and for a review article on "Vision, Visibility and Viability of Fish Populations" as outlined above.

Signature of Principal Investigator(s): Don Stewart and Robert Hecky

Date: 31 July 2003

Appendix A. Descriptions of special sessions from IAGLR website

Special Session Abstract for IAGLR 2001

Fitness of fish communities in large lakes of the world (I)

This first of three symposia sponsored by the GLFC to be held at forthcoming annual IAGLR meetings to address the topic of fitness will examine depth and area and their co-related environmental variables such as temperature, light, nutrients, oxygen *et al*. as habitat features which generate potential niche space (*sensu* Hutchinson) for founding fish species and their supporting food webs to occupy. Great lakes generally differ from smaller lakes in their greater depth and area compared to other lakes and especially compared to rivers which often supply the founding stocks. The life history, behavioral and physiological characteristics of the founding fish stocks may limit their ability or the ability of the species constituting their forage base to occupy or compete in the offshore and deeper regions of great lakes. The perception of how the extant species exploit such regions of lakes has been revolutionized by the application of hydroacoustic techniques in stock assessments which are now available for many deep and ancient lakes in North America, Africa, Europe and Asia. Equally incisive have been recent studies demonstrating the importance of visual characteristics of environments to behavior, mate selection and predation. Many questions can be posed to such studies? Do species with different evolutionary and ecological histories exploit depth and the offshore pelagic in similar ways in different lakes? Has there been convergence in adaptive traits of open water and deep water species around the world or are there limits in biology and time to the adaptation possible by founding stocks? If there are limits, does this make pelagic and deep water communities vulnerable to exotic invasion, trophically inefficient or at risk of extinction by environmental disturbance? Scientists working on large water bodies around the world are invited to share their knowledge and hypotheses concerning adaptation and evolution in great lakes fish stocks and food webs.

Vision, Visibility and Viability in Fish Populations

Fishes rely on their vision to interpret and exploit their environment. Vision is fundamental to habitat selection, schooling, predator-prey interactions, predator avoidance, and mate selection. Therefore, the success of fish populations is directly influenced by their inherent ability to receive and process optical information from their environment. Around the world, lakes are under a variety of stresses that can alter visibility for fishes and thereby alter fitness of populations. In the Laurentian Great Lakes optical clarity in many areas has improved over the last few decades as algal populations decline because of P control and the filtering activity of exotic mussels. In other lakes of the world including the African lakes and Lake Baikal with historically exceptional water clarity, turbidity is increasing due to eutrophication and increased sediment loading. These changes in optical characteristics will have consequences for the viability of fish populations adapted to specific visual regimes and optical habitats. This special session, sponsored by the Great Lakes Fishery Commission, will bring together experts on fish vision, environmental determinants of visibility and those studying consequences on fish populations due to changing visibility. The goal of the session will be to determine the significance of optical changes in global great lakes to the viability of their fish populations and species diversity.

Special Session Abstract for IAGLR 2003

Viability of Exploited Fish Populations in Great Lakes of the World

Our goal is to bring together fish biologists who are studying sustainability of fish populations that occur in diverse large-lake ecosystems of the world. The dominant fishes in various areas of the world have dramatically different life-history characteristics that will influence harvest potential [e.g., mouth-brooding cichlids in Africa, sculpins in Lake Baikal, salmonines, percids, invasive species like alewife, smelt, gobies, etc.]. A population is considered viable if it is able to sustain itself in the face of human intervention and ecosystem variability. We encourage presentations that are quantitative and comparative analyses among different species, but single-species analyses are equally welcome.

Appendix B

Fitness of Fish Populations in Large Lakes of the World
by Piet Verburg, University of Waterloo

Factors such as environmental pressure, climate change and species introductions affect the evolutionary fitness of fish species in Large Lakes around the world. Fitness is initially determined by the adaptive and reproductive success of ancestors under past conditions. Fitness of fish populations is a concept of interest to the management of fish populations in lakes and past and extrapolated prospective change in fitness merits examination. Fish in lakes generally originate from species in large river systems, which are much less ephemeral on geological time scales than lakes. However, Great Lakes supply a vastly different environment and ecological conditions for fish species to adapt to and exploit, compared with the riverine habitats of their ancestors. Though there are trophic similarities between pelagic fish communities in large tropical and large northern lakes, they evolved from different taxa and have developed different biological properties in response to their environment. Those in northern lakes typically have seasonally varying growth rates, relatively high fecundity, and varying age and size at maturity. In the warm tropical lakes seasonality is near absent, fecundity lower, but reproduction continuous, and age and size at maturity is relatively constant.

Upon formation of the lakes, adaptation of founding fish species to their new lacustrine environment is subject to natural selection. Having to evolve and adapt in a geologically short time and being restricted to taxa available in the catchment before the formation of the lake, the relative fitness of lacustrine species may often be suboptimal even under low environmental stress. Now, with modern environmental conditions changing rapidly in many lake systems, the natural selection process is affected, and native fish species may become less well adapted to their lacustrine environment. This relatively low fitness of native stocks may lead to major shifts in the faunal composition of large lakes as environmental and faunal conditions change. Introduced species can compete for resources and habitat and alter fitness of native species. Zebra mussels for instance in the North American Great Lakes direct energy flow from the pelagic to the littoral, with complex consequences for the native fish species.

The East African Great Lakes are each isolated systems, each containing generally hundreds of endemic fish species. Especially cichlids adapted well to the lacustrine habitat in East Africa, but species flocks also originated in other fish families. Evolution and radiation in fish species was explosive in these lakes, with many specialists filling the new trophic possibilities. The relatively young Laurentian Great Lakes are interconnected by navigable waterways. The number of endemics in the East African Great Lakes is often over 80 %, while in the Laurentian Great Lakes, with a lower total number of fish species (159), endemicity is only 3 %. Species introductions have been relatively numerous in the Laurentian Great Lakes, with 23 exotic fish species, compared with the African lakes. Like the African Great lakes, also the old and isolated lake Baikal in Siberia, where the sculpins radiated into a species flock, has a high degree of endemicity (60 %) and 6 introduced fish species. Though introduced species numbers are low in the African lakes, the introduction of the Nile perch in Lake Victoria has had a dramatic influence. The Nile perch became very abundant in little more than a decade and decimated native fish species. Several hundred fish species were lost. Also eutrophication in Lake Victoria has contributed to loss of fish species through reduced light penetration causing loss of chromatic volume, reduced benthic algal depth distribution, and deep water hypoxia. Foodwebs in Lake Victoria were dramatically altered in as little time as a decade. In the temperate lakes pollution is more of a concern. In Lake Erie, the presence of sediments contamined with PCB’s and other compounds, is linked with high rates of abnormalities in fish, up to 75%.

In the relatively undisturbed Lake Tanganyika, the main environmental changes over the past century are the result of high fishing pressure since the early sixties on the few pelagic species and the effects of climate warming. The primary production in the offshore foodweb is maintained by seasonal and local inputs of phosporus, nitrogen and silica by upwelling and recycling in this deep meromictic lake. Annual differences in upwelling, and a general decrease of upwelling intensity and mixing due to climate warming, have a major effect on the production and may force changes in the foodweb and in the fisheries. The major pelagic planktivores in the relative simple offshore foodweb of Lake Tanganyika are clupeids, while those in Lakes Victoria and Malawi are cyprinids. Clupeids are of marine and pelagic origin, and have sometimes been considered more efficient by adaptation to the offshore environment of Large Lakes than cyprinids which as a group are predominantly riverine. A comparison of the fitness of these groups by study of growth parameters revealed no substantial differences in their performances. Therefore, there would be no potential benefit from a proposed introduction of clupeids to Lakes Victoria or Malawi.

Fitness predicts success for progeny in an environment similar to that in which their ancestors were successful. In changed environments there is a need to monitor the ecological fitness of key fish populations. Climate warming will decrease the fitness in Pacific salmon. Migration and reproduction are affected by high temperatures, increasing energy use during migration and spawning and slowing growth rates. The salmon are affected in each stage of their life history by increased water temperatures, resulting in smaller fry, greater predation risk, a development out of phase with the spring plankton bloom and decreased energy reserves during migration. With an expected temperature increase of 3 °C this century, the expected weight loss in Pacific salmon is c. 10%. Extirpation at their southern range is expected, with repercussions for the riverine food webs dependent on the salmon.

Concerns for salmon and trout stocks in the Baltic (which in view of its low salinity can be considered a lake) are of a completely different nature. Between 90 and 75% of all salmon in the Baltic are of hatchery origin. The hatchery fish have a less well adapted antipredator behavior, lower variance, lower survival rates, and generally a lower fitness, than fish of wild origin. The abundance of hatchery reared brook trout in tributaries to Lake Superior may also pose a problem for the coaster brook trout population, which are indigenous to the lake but spawn upriver.

With the introduction of many non-native fish species in the North American Great Lakes, the predation pressure for invertivores has shifted from immature to more mature age classes. This has caused an onset of reproduction several years earlier in the native invertivore fish. Also hatchery reared lake trout, a piscivore, reproduce several years earlier than wild lake trout. The trade off between reproduction and growth in the upper levels of the food webs of the Great Lakes has important implications for the fitness of the populations and fishery management.

An especially poignant case of loss of fitness by change of fitness determinants is illustrated by the developments in Lake Victoria. Eutrophication occurred over the last few decades in Lake Victoria through increases of nutrient loads by human impacts. Transparency decreased to such levels that numerous fish species nearly all from the family Cichlidae, which depend on vision for mate recognition, are threatened in their existence. The decreased transparancy by particulate and dissolved matter not only lowers ambient light levels but also narrows the bandwidth of the visible spectrum of light wave lengths by wave length specific absorption. Red and blue are the main colors for males in many cichlids species. Wave lengths of blue and red light, at both ends of the visible spectrum, are both more scattered or absorbed by organic matter than light with colors of intermediate wavelengths. Red and blue colors are therefore often not or less discernable to their potential mates. In Lake Victoria where fish species have evolved only since 12 ka BP, and where female mate recognition and sexual selection have been a main driving force of evolution, many species have not yet evolved physiological reproductive barriers. Sexual selection is slowed down, or in the worst case, incipient sympatric species tend to merge and disappear. The decrease of the visual field of fish may also lead to a decrease in prey encounter rate and affect species coexistence and survival by dietary changes, generally towards less specialization and dietary overlap.

In general the increased eutrophication in Lake Victoria will lead to a further loss of diversity by several mechanisms, in this already severely impacted lake. Lake Victoria has the largest total fish catch of all lakes in the world. With eutrophication, large shifts in nutrient cycles occurred, with phosphorus increasing, while silica fell to much low levels. This precipitated a large shift in phytoplankton taxa, from diatoms to predominantly bluegreen algae. Important shifts in the composition of zooplankton and benthic invertebrates followed. The environmental developments favored generalist species and impacted especially the numerous cichlid species, most of which are highly specialized trophically and behaviorly. The pelagic planktivore cyprinids were relatively unaffected. However the introduced Nile perch started feeding on cyprinids after the collapse of cichlids. Monitoring of these developments is of paramount importance to a proper management of the fish stocks and will provide insight into dynamic lake ecosystems functioning under stress. High stability tends to promote narrowing of specializations of fish species and a high fitness. In a dynamic, changing environment fitness decreases and more diverse diets are more of advantage. Only those species with the genetic capability to adjust to changing variability will survive. Adaptability may be related to life history traits or to physiological characteristics. Limited as they may be in their adaptative possibilities, freshwater pelagic and deep water species may be vulnerable to exotic invasions in disturbed environments. The concept of fitness can be of pragmatic use in fisheries management monitoring population dynamics of key species.

Appendix C.

Vision, visibility and viability of fish populations

In the last 50 years there have been substantial changes in the transparency of many large lakes around the world. Fish species are affected by such changes either indirectly through the food chain or directly depending on their feeding and other behavioral strategies. In this session of the 45th Conference on Great lakes Research, fifteen speakers discussed visibility in freshwaters and the physiology and importance of vision in fish.

The transparency of aquatic ecosystems is a master variable affecting their physical properties (hydrodynamics), chemistry (photochemistry), and biology (trophic dynamics). It is a sensitive and dynamic property determined by natural processes in watersheds and lakes adding dissolved color and suspended particles, but it is also affected by anthropogenic activities: eutrophication, acidification, coastal and bottom erosion, watershed disturbance, climate change, and species introductions. Fish, as highly visual animals, will be affected by transparency changes at all time and space scales. Our current understanding is too limited to appreciate the possible affects of transparency in determining fitness and success of fish populations, and it is urgently needed to greatly improve our characterization and understanding of “visual” habitat in order to make predictions about future states of large water bodies..

Many of the changes in transparency of large lakes were associated with either eutrophication or recovery from eutrophication. Imposed limits on phosphorus loads to lakes have resulted in increased transparency in North American lakes. Exotic species can also have large and various impacts on visibility. The high filtration rates of *Dreissena* in North America have accelerated the return to an oligotrophic state in terms of clarity in the water column of Lake Erie. On the other hand, the exotic Nile perch in Lake Victoria annihilated zooplanktivore cichlid species, which may have reduced graxing pressure on algal biomass accumulation. In Lake Victoria, eutrophication worked in tandem with increased sediment loads and the effects of the Nile perch to increase turbidity. The increase in turbidity likely worked in favor of the Nile Perch as an ambush predator adapted to preying under low light conditions.

The pelagic environment is without any structural hiding sites. The encounter rates between prey and predators is affected by changes in the visual range. Increased light absorption can change dominance from visual to nonvisual foragers. Fishes can perceive their world in different species specific ways. Changes in transparency affects only the sense that depends on visibility, vision. The optical properties of the fish eye are different from those of the eyes of terrestrial animals. Of the fish eye, the part most different from that of humans is the spherical lens. While the lens of the terrestrial eye becomes more elliptical with age, the fish lens remains spherical throughout its lifespan. The lens is the only refractive element of the fish eye; and therefore, determines its optical quality. The pupil does not change in size, does not react by accommodation to light levels and the eye operates always at low f-stop levels. The focal length is determined by the diameter of the lens and is generally equal to 2.5 times the radius. This focal length does not change as refractory power diminishes from the side to the centre of the lens. The focal length may only vary with wavelength (chromatic aberration) or, only in case of a spherical aberration, with the position of the incident light ray on the lens. The variation in refraction by the lens due to lens development with age is the only means of controlling such spherical fish lens aberrations. The optical quality of fish lenses varies between species and within species and this variation can be correlated with visual need, habitat and ecological success of the species.

The benefit of fish vision depends on the transmission of light through the water column. In clear water of low color and turbidity, light of short and especially long wavelengths within the visible spectrum (400-700 nm) are attenuated fastest with depth, until only blue light (approximately 480 nm) remains. Transmission of light in natural waters is not only dependent on its wavelength. With high amounts of organic matter in the water absorption is more rapid at all wavelengths but the absorption shifts more towards the shorter wavelengths. The spectral distribution of the light shifts from blue to green (550 nm) and eventually to red (630 nm) with increasing dissolved organic matter content.

Most fish species are visual predators, and dependent on light to detect prey. The risk of mortality by predation decreases at lower ambient light conditions, as found either deeper in the water column or by an increase in turbidity. Vertical positioning can change schedules of growth and mortality. Vertical gradients generate a classical trade-off between growth and mortality. Behavioral strategies of fish larvae and zooplankton maximize their fitness, by compromising between optimal depth for growth and visual range that determines risk of predation. Turbulence determines the rate at which zooplankton enters the visual range of larval fish. The range of vision as determined by turbidity or depth therefore governs the influence of turbulence on feeding rates in larval fish. Feeding rates of fish larvae increase both with light levels and turbulence. Mortality of zooplankton and fish larvae increases with predation pressure but decreases when transparency is lower. Small pelagic fish find less food but meet fewer predators at increasing turbidity, which decreases growth rates while increasing their survival. In fact recruitment success increases with piscivory when turbidity is high. At low predation levels turbidity reduces the recruitment success. Light and the optical properties of the water column influences strongly the structure of pelagic food webs. Larger zooplankton stays deeper in the water column as their size makes them too vulnerable in the well illuminated shallower water layers. They are more visible to predators as large objects reflect relatively much of the light passing through the water column. Small prey has a lower risk of predation in the upper water layers.

Visual predation is generally much more effective than tactile predation unless vision is limited by light conditions. Among fish species, visual feeders are more efficient than tactile feeders when light is adequate. The abundance of visual predators, i.e. fish, is inversely related to light extinction when light is limiting for feeding. Planktivorous fish abundance was inversely related to light extinction in Norwegian fjords and for a 32-year Black Sea time-series. Light and optical properties of the water column represent an effective control on the abundance of visual and tactile predators and thereby on marine food web structure. At relatively high light extinctions with depth (i.e. low transparency) non-visual predators such as jellyfish can be favored in the role of main predator of small prey, both in freshwaters and marine systems. However, the tactile feeding jellyfish are much less efficient predators than fish, and zooplankton is both more abundant and larger in size in Norwegian fjords where jellyfish are a common predator. Among twelve sampled fjords on the Norwegian west coast those with higher visibility have higher fish biomass, while jellyfish are abundant in those with reduced visibility. The same was found for planktivorous fish in the Black Sea. The annual mean biomass of Black Sea sprat and anchovy was, for a time series of 32 years, significantly higher in years with high transparency as inferred from annually and spatially integrated Secchi disc measurements. In the Black Sea a decrease in transparency coincided with a dramatic shift from fish to gelatinous predators while the fishery harvest declined.

Similarly in Lake Tanganyika a small hydrozoan medusa occurs, one of the world's few freshwater jellyfish. It can occur at times in high numbers per m^3 and, as with jellyfish in the Norwegian fjords and the Black Sea, its abundance is significantly and negatively correlated with Secchi disc depth. Nevertheless Lake Tanganyika is in general a highly transparent lake with maximum Secchi disc depths over 20 m. Jellyfish often constitute a dead end of the food chain, as few organisms can feed on them. When food items on the menu of planktivorous fish are appropriated by jellyfish, the food chain is short circuited and less energy and biomass is channeled to the higher trophic levels.

The colorful fishes of Lake Malawi and coral reefs bear visible witness to the role that vision can play in the ecology of fishes. They suggest a very rich visual ecology and a habitat conducive to the utilization of light as a basis for ecological interactions.

Water has low transmission of visible light and is highly selective for different wavelengths. Especially red light is attenuated quickly, even by clear water, while dissolved materials arising from degradation of organic matter absorb strongly in the blue spectrum. Particles can scatter as well as absorb light. The effects of absorption by water, dissolved coloring matter, particles as well as the effects of scattering are combined in the vertical attenuation coefficient $K_t = K_w+K_d+K_p+K_s$, where K_t is measured as the vertical loss of irradiance I with depth z, $Kz =-\ln (I_z/I_0)$. The penetration of image forming light or the attenuation of contrast between an object and its background can be estimated by the Secchi disk depth observation which is also related to K_t because light availability eventually would limit Secchi even in particle free water. Scattering by particles affects image forming light, i.e. the attenuation of contrast between an object and its background represented by the Secchi disc depth, more than the attenuation of light; but both are important to the visual field of fishes. Scattering efficiency rises rapidly with particle size up to particles over 1 micrometer above which efficiency is independent of size. Most scattering is in the forward direction so the effect of scattering on light penetration is to increase path length to any depth and to disorganize coherent light beams. Consequently scattering has a more direct and significant affect on visibility than penetration of light per se, and it is relatively non-selective spectrally. In Southern Indian Lake in northern Manitoba shorelines were eroded by flooding in 1974-1978 which greatly increased sediment loads into the lake. The contribution by scattering by suspended materials to the attenuation coefficient increased substantially and the Secchi disc depth was affected more than euphotic zone depth. Before flooding Secchi disc depth was 40% of the euphotic zone depth and after flooding it was only 30% of the euphotic zone depth, while the absorption by chlorophyll did not change. Reduced visibility and outmigration resulted in shifts in whitefish (*Coregonus clupeaformis*) populations as inferred from fishing effort data from the fishery after flooding. After flooding, daytime light intensities in the deeper areas of Southern Indian Lake were below those required for schooling and feeding for most fishes.

In aquatic systems, spectral attenuation and scattering rapidly alter visibility with depth and distance. Species and communities dependent on good visibility for their success may be at risk if conditions of visibility change. Because of accessory pigments, algae can use nearly the whole visible spectrum of light. However, spectral attenuation will rapidly affect the discrimination of colors by fishes and scattering of light by particles cannot be compensated for by visual systems. A consequence is that depth of photosynthesis (trophogenic habitat volume) can be decoupled from visual habitat volume if particle concentrations increase.

Increased light attenuation and reduced Secchi disc transparency in Southern Indian Lake (Manitoba) resulted in *Mysis relicta* entering the water column during daylight which resulted in increase catches of *Mysis* in zooplankton hauls. And in Lake Victoria eutrophication has contributed to loss of fish species through reduced light penetration causing loss of chromatic volume, and reduced benthic algal depth distribution and altering foodwebs as well as causing deep water hypoxia. The number of haplochromine species in littoral habitats in Lake Victoria is related to the spectral transmissivity of the water. Clear waters had more species.

Eutrophication reduces the availability of trophogenic bottom area. Globally there is a strong relationship between total phosphorus and chlorophyll and thereby light extinction by chlorophyll. In offshoe waters with low coloring matter and no sources of eroded mineral sediments , chlorophyll dominates light extinction. Malawi and Victoria are such clear water systems. The relations among extinction of light, chloroplyll and phosphorus can be used to illustrate the effect of eutrophication on the availability of trophogenic bottom area (>1% of surface light) for the morphometry of Lake Malawi. The bottom area is approximately linearly related to depth in Malawi but the illiminated benthic habitat decreases logarithmically with phosphorus loading. The cautionary lesson is that the greatest relative loss of trophogenic bottom habitat will occur during the initial stages of eutrophication. Secchi disc depth is also a function of the concentration of chlorophyll and near bottom visual habitat will be similarly affected but to a greater degree because of increasing light scattering. In the African Great Lakes protecting endemic biodiversity especially for littoral fishes which constitute much of that biodiversity will require maintaining clear water conditions. Increasing light attenuation will be primarily due to increased concentrations of suspended matter, in part by high sediment loads carried by rivers and run off due to land use practises which augment erosion, and especially chlorophyll from eutrophication. The habitat of littoral fishes will suffer from loss of bottom area which supports net primary productivity but loss of visual habitat due to spectral attenuation and light scattering will be even greater. The greatest proportional loss of illuminated bottom area and visual habitat will occur with first changes in nutrient concentrations. Watershed and habitat protection will be the most cost-efficient strategy to maintain biodiversity in these epicenters of freshwater biodiversity.

A conceptual model of effects of variation in optical properties of water on fish diversity involves the interference of organic matter with light transmission, scattering of light by particulate non-living matter, and light absorption by dissolved substances and algae and cyanobacteria. The effect of variation in the amount of dissolved and dispersed matter is twofold. Turbidity and light extinction vary, affecting the visual range of fishes. Secondly the spectral composition of down-welling and side-welling (space) light vary because scatter and absorption are wavelength-specific, affecting color vision of fish. Light transmission properties of water affect, through visual range and colour, e.g. foraging, predator avoidance, communication. Foraging is affected by a reduction in visual range, prey encounter rates and predator specialisation which ultimately reduces species diversity. For visual predators the encounter rates with prey are proportional to the volume of the predator's visual field. Encounter rates determine prey selectivity of a predator. Foraging behavior evolves in a way dependent on its sensitivity to the marginal value: the gain in energy that just balances the cost of obtaining that energy. The time and energy needed to catch a particular prey item must be balanced by the energy gain. The marginal value theorem in foraging theory can be used to evaluate chances of specific prey capture. The probability p_2 of consuming a prey item other than of the preferred kind (type 2 prey) depends on the search time required to find an item of the preferred kind. The search time decides whether a prey item is on the diet of a predator or not. In its general form the marginal value theorem predicts prey selection among n types of prey. Because water transparency affects the search time, it affects the breadth of the prey spectrum of a visual predator. Predators, specialized on one type of prey in clear water should include increasingly less preferred prey as their visual field shrinks. Implications for niche partitioning and species coexistence are inevitable. Good visibility will lead to ecological differentiation of functionally different predator species because high prey encounter rates translate into short search times, and high energy returns, allowing each to specialize on a narrow spectrum of preferred prey, e.g. prey fish of narrow size ranges. Everything else being equal, declining transparency predictably leads to convergence in prey spectra. Increased competition will then lead to competitive exclusion when populations are resource-limited. The relationship between visual range and visual encounter rate with prey depends on prey size. Small prey cannot be ignored anymore under reduced visibility. Behavioral changes in prey, such as as a change in the predator detection ability, may affect the relationship. Therefore, with convergence in prey spectra, competition may increase asymmetrically and competitive exclusion of species will follow. Vulnerability to competitive exclusion may depend among other factors on typical prey detection distance. Specialists on prey detectable only at short distance (e.g. benthos, plankton) should be less affected, and might add competitive pressure on others that are forced to share prey with them because their own energetically preferred but long distance-detected prey is no longer encountered at sufficient rates. It is predictable that eutrophic waters favour generalists and small prey consumers, and do not support specialized higher level visual predators. Lake Victoria can function as a model system where an increased eutrophication coincided with a dramatic simplification in the fish community and loss of most piscivorous species. Until about 20 years ago >100 piscivorous cichlid species partitioned the prey spectrum largely along two axes: prey size and water depth. Within 20 years all but about 10 very small species disappeared, and 1 big but generalized predator (the introduced Nile perch) boomed. The variation in extinction curve slopes among cichlid genera is consistent with the hypothesis that impaired vision is one of the determinants of extinction risk. Predators on larger, more evasive and deeper living prey were lost faster than others. Of algae feeders and those that prey on soft bottom insects only 40 % of those present around 1980 became extinct while of the piscivores less than 20 % remained by the early 1990ties and none of those that fed on deep zooplankton. In this time Secchi disk depth redcued from 2-3 m down to 1.2-1.6 m.

Variation in the spectral diversity of ambient light affects color vision of fish. Fish often have trichromatic vision with single cones containing often either a blue- or a UV-sensitive pigment and double cones holding often a green/yellow and an orange/red sensitive pigment in separate cells. Trichromatic vision in shallow water aids in the detection of both light and dark objects. A trichromat is able to detect prey when a broad band width of the light spectrum allows discrimination of dark objects as silhouettes and bright objects by contrast. The ability to discriminate is impaired if the band width of the light spectrum gets narrower. Under low transparency, the wave length spectrum necessary to offset objects from the background is lost. Wave lengths can simply only be reflected from objects if those wave lengths are present in the available light. Hue discrimination is possible in polychromatic environments but is impaired in monochromatic environments. An impaired signal discrimination ability compromises the opportunity for dietary specialisation. A loss of specialisation and increased interspecific competition ensues.

Foraging theory can be applied to the origin of ecological diversity. Ecological theory of speciation predicts that intraspecific competition (frequency and density dependent selection) exerts selection for ecological diversification, e.g. divergence of preferred prey sizes. However a response to such selection can occur only where prey encounter rates allow alternative specialisations. Complexes of trophic morphs or species in post-glacial lakes are almost all in clear lakes. Examples are arctic charr (up to 4 morphs), threespine stickleback (2 morphs), lake trout (2 morphs) and sunfish (2 morphs). The loss of ecological and morphological disparity between sympatric sticklebacks in Enos lake (UK) between 1984 and 2000 was associated with environmental changes and increased turbidity.

Light intensity and the range of the spectrum are important in intraspecific communication. Where fish communicate by exchange of visual signals, e.g. in courtship, changes in water transparency and the color of light both have effects on communication via constraints to signal detection and discrimination that are analogous to the constraints on foraging to prey detection and discrimination. Turbidity affects encounter rate with, and quality (color and contrast) of signals. As in foraging theory, only the encounter rate with the preferred signal matters to determine the likelihood of responding to a less preferred signal. Female preferences for particular male mates are reduced or disappear altogether when the light wave spectrum is narrow and the proportion of hybrids increase with turbidity. The number of cichlid species that can be sexually isolated in sympatry is a function of the width of the light spectrum (which is strongly correlated with water transparency). Eutrophication has a negative effect on the diversity of sympatric prezygotically isolated species.

The effects of variation in optical properties of water can significantly influence the ecology of fish. Although different fish species are affected to different extents, a general prediction, that can largely be derived from the marginal value theorem, is that increased turbidity, entailing decreasing visual range, visual resolution, and visual dimensionality, leads to loss of functional and species diversity by mechanisms that are independent of, but may interact with food-web changes. Experimental and correlational studies are needed to further test these predictions.

Ecological and genetic differentiation among haplochromine cichlids in Lake Victoria changes along a transect where transparency varies from 0.5 to 2.5 m secchi disk depth. Species are more similar and species diversity lower at lower transparancy. Closely related species tend to lack postmating barriers to hybridization. Evolutionary theory predicts that low viability or ecological disadvantage of hybrids often hinders propagation of hybrid strains. Lake Victoria haplochromine cichlids do not conform to this theory: they produce fully fertile hybrids under laboratory and natural conditions, yet they constitute one of the most diverse faunas with more than 500 endemic species. This underlines the importance of mate recognition for these species, which in turn fully depends on the intensity of light in their habitat and the width of the spectrum of available wavelengths. Female mate choice is responsible for reproductive isolation among the haplochromine species. Visibility in the water affects visual mate choice. Male color variation is better visible in bright and broad spectral light. With the water quality of eutrophic Lake Victoria blue light does not penetrate far in the water column as it is attenuated faster than light in the red part of the visible spectrum. Thus blue males are more conspicuous in shallow water, and indeed blue species are relatively more common in shallow than red species. Between two closely related cichlid species in Lake Victoria, one of blueish color (*Pundamilia pundamilia)* and the other containing more red (*P. nyererei*), no intermediates are observed at clear water sites. Their colour differences are extreme and the species are ecologically different. Gene flow was found to be limited even between colour morphs of the same species and ecological niches are distinct. The blue species lives relatively shallow and feeds on benthos while the red species lives deeper and feeds on zooplankton. With eutrophication the transparency of Lake Victoria dropped from 2-3m to an average 1-2 m in the past 20 years. Intermediates between the 2 species of cichlid are now commonly found in the more turbid sites. The depth ranges of the red and the blue species in turbid overlap almost fully, unlike in clear water, as red colored species shift their habitat to shallower water. Also their diet overlaps in turbid water, with the red species feeding more on benthos than in clear water areas, suggesting niche contraction. Stomach contents analysis provided evidence of the convergence of the diets of the two species. Data on the ratios of stable isotopes of carbon and nitrogen, ^{13}C and ^{15}N, which in fish form reliable and more conclusive tracers of food sources over a longer term than stomach analysis of daily meals can supply, confirmed this. Genetic and ecological differentiation breaks down in turbid water with a loss of reproductive isolation and hybrids appear. The high species diversity in Lake Victoria developed in a very short time, in the past 14,600 years by a very rapid evolution of closely related extreme specialists with a fine ecological niche differentiation. In recent decades much of this high diversity has been lost. Fish species diversity, first decimated by the introduction of the Nile perch, will further decrease as transparency in the lake deteriorates. This was a catastrophic lesson learned in Victora and is clearly applicable to the management of the other highly transparent and biodiverse African Great Lakes

Fish have both rod photoreceptors and cones in their retina. Rods function best under low light such as at night (scotopic vision) while the pigments in cone receptors are useful in daylight (photopic vision). The retina of two species of the genus *Comephorus* in the Siberian Lake Baikal, related to the North American sculpins, contains only rod photoreceptors, no cones. They inhabit deep and dark pelagic water (from 150 to 1500 m deep) and feed on diurnally vertically migrating zooplankton. Rod photoreceptors are generally used for night vision (scotopic vision) as opposed to cones which function better at high light levels. The low ambient light levels makes the possession of cones of little use to these species and they have lost them during the long isolation in this ancient lake. These deep water fish species in Lake Baikal have adapted to eternally low light levels where rods function better than cones, by a well developed scotopic vision.

The spectral locations of a fish's visual pigments in the cones is potentially critical to its survival. Visual acuity is generally higher in diurnal fishes than in crepuscular and nocturnal species. Visual acuity improves as a fish grows, particularly in the juvenile phase, as the density of cone photoreceptors increases with growth. Larger individuals therefore can detect objects at greater distances, which increases the search volume for adults compared with juveniles and larvae which often feed on smaller items such as plankton. On the other hand, the broad range of visual pigments available to larval fishes is narrowed during growth. Most fish larvae have a photosensitivity with a wide spectral range, which often includes UV-A light (320-400 nm). Experiment has shown that larvae with pigments which have absorbance maxima at short wave length (such as UV) can in fact feed on zooplankton when exposed solely under short wave length illumination. Foraging by larvae is often more efficient when UV light is available to them. A broad spectral sensitivity with multiple visual pigments in many larval fishes improves the detection of the small, transparent and low contrast targets represented by zooplankton. UV-A light (320-400 nm) is abundant in clear water but it is attenuated faster with depth than light in the spectrum visible to humans (400-700 nm), especially when transparency is low. During their development many fish show a shift in absorbance peaks from (ultra)violet to blue wave lengths as the short wave length visual pigments disappear. This coincides with shifts in diets from zooplankton to larger foods and changes in habitat. UV-A vision has also been demonstrated in adult cichlids in Lake Malawi where water clarity is very high. In the highly transparent water of Lake Malawi fish species can retain their ability to sense UV-A throughout their life span. The main component of the visual pigments is a protein, opsin. The same five genes for the five different cone opsin pigments are present in different species. There is however a marked difference in the expression of these opsin genes between adults of fish species, related to their habitat and life style. The adults of those fish species that live relatively shallow on rocky shores, the mbuna, have a pigment with a peak aborbance of about 370 nm, while those fish which live in sandy habitats do not. It is especially the mbuna in which visual communication between generally drab colored females and brightly colored males plays a key role in mate recognization and mate choice. Other fish species apparently lose their ability to express the opsin gene for UV-A during their development. Changes not in gene sequences but in gene expression may have contributed to the rapid speciation of these cichlids.

Detection of UV light provides not the only cue which is available to fish but not to humans. The polarization of light is also used by some species, for instance by salmons in their navigation. Many fish species can perceive ultraviolet optical stimuli with specialized cone photoreceptors, in addition to those which are sensitive to visible light. UV vision enables fish to detect plane-polarized light. Salmonids use UV polarization vision cues in spatial orientation and their navigation. Many vertebrates have a four cone system with visual pigments. The UV-sensitive cone is most sensitive to ~380 nm. The sensitivity of the red, green and UV sensitive cones depends on the orientation of incoming light. Horizontal and vertical polarized UV light is reflected by the red and green sensitive cones onto the UV cones. Polarization vision with UV cone photoreceptors is present in juveniles and adults but not in smolts and can be induced by thyroxine or by the onset of sexual maturity in adults. Salmonids have the capability of remodeling their visual capabilities as they move into differing visual environments throughout their migratory journeys. Differences in temporal expression of visual pigment genes can potentially lead to speciation. Experiments showed that polarization vision guides spatial orientation in salmonids. UV polarization vision plays an important role in guiding their navigational behavior and allows them to return to their location of hatching while magnetosensitivity and olfaction are also key modalities.

Variable turbidity affects predator-prey interactions. Fish have some control over their chances of mortality, for instance by limiting the rate of encounters with predators. With an increase in turbidity the visual range of fish decreases. Under the assumption that vision is the primary sense for detecting and responding to predators, the role of behavior in predator-prey interactions and prey selection decreases. As a result size-related mortality becomes more random as size-related antipredator tactics become useless in turbid water. However the loss of visual range may be compensated for by the use of other senses. The lateral line, which registers very fine pressure changes, is one of the other senses available to fish in detecting their environment but little is known of its relative importance. For instance alewife catch mysids at night by the use of their lateral line. There is however a large variation between fish species in the development of the lateral line system over the body of the fish. Fish species which are used to low light levels generally have a better developed lateral line system. With a reduced visibility a shift may occur in the fish species community composition towards species with a higher degree of development and sensitivity of the lateral line system. Some fish certainly do better under low light conditions. In the Bay of Quinte, Lake Ontario, a decline in walleye stocks, a fish popular with anglers which prefers fairly cool water and low light levels, followed the reduction in phosphorus loading since the 1970’s and the introduction of zebra mussels in the late 1990’s. Habitat availability for walleye has decreased, mainly driven by improved water clarity. The Bay of Quinte is now no longer an ideal walleye ecosystem.

Walleye has met with a similar fate in other North American lakes. Lake Oneida (NY) with reduced phosphorus loads since the 1970’s changed from an eutrophic lake to an oligotrophic lake around 1990. Transparency then reached over 3 m, above the range where walleye are comfortable, and the fitness of walleye in Lake Oneida decreased. Weekly walleye growth data collected since the 1970’s indicate that yearling growth rates, mean size and total biomass of walleye are now lower than in the 1970’s. Size-selective fishery and predation could however be operating to drive this trend which could confuse the determination of the growth rates. It often is a difficult task to evaluate the effects of each environmental change on the fitness of a given fish species. When environments have substantial changes (e.g., nutrient reduction, zebra mussel invasion), their impacts on fish growth often confound each other in a trajectory of body length over ages. Often different processes affect early and later growth. Mortality of fish depends on their size and therefore on growth rates, as large fish are more successful in avoiding predators. Poor growth leads to disease and winter mortality and population declines.

In a database of hundreds of lakes in Ontario prominence of walleye in a lake’s fish community is well predicted by Secchi disc transparancy. The supply of walleye habitat depends on its water clarity, bathymetry and thermal stratification. Walleye presence peaks when the Secchi disc depth is no more than 2 m, while for smallmouth bass and especially lake trout far higher transparencies are optimal. The optical habitat area where walleye can live in a lake is reduced when underwater light levels increase, as it does between sunrise and sunset but which is also a long term trend in many of the Ontario lakes over the past decades. The proportion of the basin area in the west basin of Lake Erie which is both thermally and optically appropriate for walleye reduced from 15 % to 5 % between 1985 and 1995, with the advent of the zebra mussels. When light levels increase walleye have to move to deeper water, which is not available in many of the smaller and shallower lakes in Ontario, where zebra mussels are now ubiquitous. Also shallow thermoclines, with water too cold for walleye below the thermocline, reduce the habitat available to walleye.

A general conclusion is that vision is a highly developed and highly adaptive sense in many fishes. Fishes rely on their vision among other senses to interpret and exploit their environment especially for close interactions. Vision, together with other senses, is fundamental to habitat selection, schooling, predator-prey interactions, predator avoidance, and mate selection. Therefore, the success of fish populations is directly influenced by their inherent ability to receive and process optical information from their environment. Around the world, lakes are under a variety of stresses that can alter visibility for fishes and thereby alter fitness of populations. In the Laurentian Great Lakes optical clarity in many areas has improved over the last few decades as algal populations decline because of phosphorus control and the filtering activity of exotic mussels. In other lakes of the world including the African lakes and Lake Baikal with historically exceptional water clarity, turbidity is increasing due to eutrophication and increased sediment loading. These changes in optical characteristics will have serious and possibly predictable consequences for the viability of fish populations adapted to specific visual regimes and optical habitats.