Environmental Biology of Fishes **64:** 9–14, 2002.

Developments in the ecology, evolution, and behaviour of the charrs, genus *Salvelinus*: relevance for their management and conservation

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Salvelinus species are one of the most thoroughly studied groups of fishes. Many reasons explain this intense interest in charr biology. First, charrs have a Holarctic distribution encompassing many Asian, North American, and European countries and occupy a diversity of aquatic environments, including both marine and freshwater habitats. For instance, the presence of anadromous, stream-resident, and lacustrine life histories within and among species provides a rich template for ecological and physiological study and experimentation. Second, most of the current distribution of charr includes areas that were directly influenced by climate and topographic change associated with the many Pleistocene glaciations. This means that there has been tremendous opportunity for repeated episodes of isolation, divergence in distinct refugia (and different selective environments), and recontact between divergent lineages. Undoubtably, these conditions have promoted much of the tremendous morphological, ecological, and genetic variability and plasticity within species of the genus and make charr very good models to study evolutionary processes 'in action'. Third, many charr species exhibit demographic characteristics such as slow growth, late maturity, and life in extreme environments, that perhaps make them more susceptible to extinction from habitat changes and overexploitation, particularly because they often occupy depauperate aquatic habitats. This vulnerability makes understanding their biology of great relevance to biodiversity and conservation. Finally, charr are of great cultural, commercial, and recreational significance to many communities, and their intimate linkage with human societies has therefore undoubtedly stimulated much interest in this enigmatic genus.

During the last two decades, a series of events and publications have contributed markedly to the advancement of knowledge on *Salvelinus* species. In 1980, a first important monograph 'Charrs: Salmonid fishes of the genus *Salvelinus*' was edited by Eugene Balon. This monograph (Balon 1980) contains reviews of the main species as well as original studies on taxonomy, biogeography, phylogeny, morphology, ontogeny, ethology, physiology, and ecology of charr over their geographical distribution. Soon after, and stimulated by Balon's (1980) monograph, the first International Charr Symposium was held in Winnipeg (Canada) from 4 to 8 May 1981. This symposium was devoted mainly to Arctic charr, *Salvelinus alpinus*, and lead to the publication of the proceedings 'Biology of the Arctic charr' edited by Johnson & Burns (1984). The second International Charr Symposium was held in Sapporo (Japan) from 3 to 9 October 1988. The organizers extended their symposium to Masu salmon, *Oncorhynchus masou masou*, because of the similarities in life histories of Masu salmon and charrs and because the salmon's distribution is confined to the northern far East. The proceedings of this symposium were published in a special issue of Physiology and Ecology Japan, edited by Kawanabe et al. (1989). The third International Charr Symposium was held in Trondheim (Norway) from 3 to 18 June 1994, and a collection of papers presented at this symposium was published in a special issue of Nordic Journal of Freshwater Research, edited by Klemetsen et al. (1995).

The fourth International Charr Symposium was held in Trois-Rivières (Canada) from 25 June to 1 July 2000. This special volume of Environmental Biology of Fishes is devoted to a selection of papers presented at this symposium. A total of 123 presentations (72 talks and 51 posters) were given at the symposium, which attracted more than 160 scientists from 12 different countries (Canada, England, France, Finland, Iceland, Japan, Norway, Russia, Scotland, Sweden, USA). To pursue the tradition of the charr symposia, concurrent sessions were avoided in order to bring together all participants and allow them to attend every presentation. The opening keynote lecture was presented by Geoffrey Power and invited speakers opened most of the topical sessions. A poster session was held in the main mall of the Conference Center, and posters were kept in the mall for the duration of the Symposium, giving them additional visibility. The Symposium was followed by a scientific excursion to James Bay, northern Québec, which attracted 45 participants.

The organisation of the fourth International Charr Symposium as well as the production of this special issue would have not been possible without the enthusiasm, involvement, and commitment of many persons and organisations. We first express our special acknowledgements to the students who played a major role in the symposium organisation and logistics, Julie Adams, Mélanie Caron, Angélique Dupuch, Danielle Héroux, Guillaume Lapierre, Raphaël Proulx, Martin-Hugues St-Laurent, and Isabelle St-Onge from the Université du Québec à Trois-Rivières. We are also grateful to the symposium sponsors, Brook Trout Foundation, Centre for Research and Education, Fondation de la faune du Québec, Hydro Québec, Ministère de la Recherche, de la Science et de la Technologie (Québec Government), Société de la faune et des parcs du Québec (Québec Government), and Université du Québec à Trois-Rivières. We thank Office du Tourisme et des Congrès de Trois-Rivières and Université du Québec à Trois-Rivières for their invaluable logistic support. We thank Eugene Balon and David Noakes, who supported the project of a special volume on *Salvelinus* species, and the numerous referees, listed at the end of this journal's volume, for their careful reviews of the papers submitted for publication. We are very grateful to Laure Devine and Raphaël Proulx for their meticulous work with editing and processing of papers published in this volume. Eugene Balon was also particularly helpful with the final editorial process. Finally, we want to express our gratitude to the invited speakers and to all participants at the Symposium as well as to authors of this special volume for their significant scientific contributions.

Contents and organisation

This special volume contains 31 papers that were accepted following the review process. All papers submitted for publication were reviewed by two referees and evaluated following the usual rules of the Journal. The papers are assembled into seven parts as follows: Keynote presentation, Ecological interactions and behaviour, Trophic polymorphism, Movement and migration, Ecophysiology and evolutionary genetics, Ecological parasitology, and Environmental stress and conservation. We maintained the use of the vernacular name 'charr' to denominate *Salvelinus* species for consistency with the phylogeny of the genus and to follow the common usage that emerged since the publication of 'Charrs: salmonid fishes of the genus *Salvelinus*' (Balon 1980) and the charr symposium series (see Morton 1980).

Illustrations of *Salvelinus* species and forms made by Paul Vecsei are also included in this volume. Paul Vecsei holds degrees in geography (Concordia) and zoology (Guelph) (Vecsei 2000), and is currently enrolled in doctoral studies in fisheries (Athens, Georgia). A number of his drawings of various fish species have been published previously in Environmental Biology of Fishes (Vecsei 1997, Vecsei & Heaton 2001) and elsewhere. His most recent publication is dedicated to the sturgeons, the current ichthyological infatuation of his (Vecsei & Charette 2001). For a number of years he focused similar attention on charrs. Specimens for all the Great Bear Lake charr drawings were supplied by C. Blackie and D. Weese.

The first paper (Power 2002), by the keynote speaker of the Symposium, describes conditions experienced by charrs of eastern North America during recent phases of their evolution, and discusses the imprints this history may have left on life cycles and ecological characteristics displayed today. The paper has implications on the way we view the genus and for decisions that might be taken regarding its future conservation.

In the first paper of Part 1, Klemetsen et al. (2002) report the results on a long-term study (1980–1999) investigating the ecology of Arctic charr, brown trout, *Salmo trutta*, three-spined stickleback, *Gasterosteus aculeatus*, and various species of planktonic and benthic crustaceans before and after the intensive fishing of Arctic charr from 1984 to 1989. Dempson et al. (2002) examine the diet of anadromous Arctic charr from northern Labrador in relation to apparent widespread environmental and ecological changes that have occurred in the northwest Atlantic Ocean during the 1990's. Winfield et al. (2002) examine horizontal differences in the diet of Arctic charr along the long axis of Loch Ness in relation to spatial variation in the availability of prey populations. Power et al. (2002) describe growth and diet of Arctic charr and brook charr, *Salvelinus fontinalis*, in three lakes from a watershed situated on the north shore of the St. Lawrence Gulf, and assess variation among Arctic charr stocks within a limited geographical area at the southern fringe of their distribution. They also explore how stable isotopes can be used for determining potential niche separation and dietary niche shifts in closely related species. Koseki et al. (2002) studied precocious male parr of the Miyabe charr, *Salvelinus malma miyabei*, under experimental and natural conditions and address the hypothesis that refuges such as debris and shallow areas provide shelter from aggressive attacks and allow precocious salmonid males to hold positions closer to the mating pair and sneak more easily at spawning.

In a thorough review on trophic polymorphism of Arctic charr complex in Transbaikalia (Russia) that starts Part 2, Alekseyev et al. (2002) summarize the research done on 16 lakes and provide new information on five other lakes. Their main objectives are to assess the diversity of charr in this region of the world and to evaluate the role of trophic polymorphism and its speciation modes in the evolution of forms, based on morphology and feeding of dwarf, small, and large individuals in the Transbaikalian study lakes. In a study of Gander Lake, the third largest lake in Newfoundland, O'Connel & Dempson (2002) investigate aspects of the biology, and spatial and temporal distributions of two morphs of Arctic charr, based on colour (dark and pale) and meristic characteristics, and compare their results with findings reported for elsewhere in Newfoundland and Labrador, North America, and Europe. Although morphological differences among forms have often been observed, little is known about the adaptive value of these differences in terms of the relative performance of individuals. In the last paper of this part, Proulx & Magnan (2002) compare the physiological performance of littoral and pelagic brook charr for individuals of both forms that were restricted to feeding on zooplankton in the pelagic zone.

In the first paper of Part 3, Gowan & Fausch (2002) tests the hypotheses that foraging stream salmonids move during summer because they monitor habitat conditions at a reach scale, and that dominant fish move when conditions in their present foraging location become suboptimal relative to conditions at other locations in the reach. The authors quantify variation in foraging habitat quality for brook charr between late spring and early fall in a stream reach, predict fish distributions within the reach based on optimal foraging principles, and examine individual responses following experimental manipulation of access to foraging sites. Bélanger & Rodríguez (2002) present an approach based on the assumption that measures of local movement, such as habitat-specific immigration and loss rates, provide useful indicators of habitat quality. A dynamic turnover model was used in conjunction with capture-mark-recapture techniques to estimate movement parameters for brook charr and Atlantic salmon, *Salmo salar*, in different stream habitats during the summer. The abundance of migrant Arctic charr in the Dieset River, northwestern Spitsbergen (Norway), was correlated with river flow, rainfall, and air temperature during the migratory period (Svenning & Gullestad 2002); the authors investigate how annual climate variability restricts the ability of the charr population to migrate to sea and then ascend the home river. Finally, Baril & Magnan (2002) investigate seasonal timing and diel activity patterns in a lacustrine brook charr population during spawning migration to a lake outlet, as well as the homing of reproducing individuals. Their results indicate that lacustrine brook charr show similarities to other anadromous and lake-spawning salmonid populations when migrating to spawning grounds.

Whether or not differences between high- and sub-Arctic environments are accompanied by differences in the regulation and expression of the development, and subsequent loss of seawater tolerance in anadromous Arctic charr inhabiting these environments remains unclear. In the first paper of Part 4, Jørgensen & Arnesen (2002) investigate this hypothesis by comparing these processes experimentally in Arctic charr derived from two anadromous populations originating from Svalbard (79°N) and North Norway (70°N). Although the thermal physiology of Arctic charr has rarely been studied in relation to the growth rate-temperature curve, Arctic charr has a low optimum temperature for growth and is therefore often raised at temperatures close to or above this optimum; Lyytikäinen et al. (2002) examine the relationship between temperature and growth and acute stress responses in Arctic charr, and compare the acute stress reactions of fish subjected to diel temperature fluctuations with those of fish held at constant temperature. At least two phenotypes of lake charr, *Salvelinus namaycush*, coexist in Lake Superior: a lean morph frequents the shallow inshore waters (<50 m) and a fat morph (siscowet) occupies the deeper offshore waters (50–250 m); Henderson & Anderson (2002) determine if the elevated lipid concentration in siscowets reduces the costs of swimming in deep water. They model the effect of body-lipids composition on the costs of swimming, and compare model results with empirical evidence obtained from Cesium 137-based estimates of food consumption, gross energy conversion, and swimming costs. Unlike chinook salmon, *Oncorhynchus* *tshawytscha*, and rainbow trout, *O. mykiss*, sex-linked loci have not been identified in lake charr; Stein et al. (2002) describe the preparation of a DNA library from the short arm of the lake charr Y chromosome and the isolation and genetic analysis of a microsatellite locus from this library. Westrich et al. (2002) present a phylogenetic analysis of the genus *Salvelinus* based on data from the sequences of the duplicate GHC and GHD introns. Fluorescence in situ hybridization (FISH) is increasingly being applied to the study of chromosome structure and evolution in fishes; Phillips et al. (2002) report the localization of the 5S rDNA sequences and the three different families of centromeric sequences on the chromosomes of all five North American *Salvelinus* species using dual-color FISH, and examine the arm homology of the sex chromosome pair of *S. namaycush* with Yp and Yq probes for these same five species. Finally, Boula et al. (2002) compare anadromous and river-resident brook charr forms from the Laval River (Québec, Canada) using physiological variables involved in the smolting process. They determine whether the physiological and endocrine differences observed between anadromous and resident fish can be explained by reproductive isolation using both neutral genetic markers and a transplant experiment under laboratory conditions.

The pseudophyllidean tapeworms, *Eubothrium crassum* and *E. salvelini*, are widely distributed parasites of salmonid fishes like brown trout and Arctic charr. Even though the validity of both species has not been disputed, difficulties in their differentiation still exist. The first paper of Part 5, by Hanzelová et al. (2002), describes the morphogenesis of *E. crassum* and *E. salvelini*, and compares morphological characteristics of these parasites in an intermediate copepod host. Knudsen et al. (2002) provide indirect evidence of parasite-induced host mortality (PIHM) using the common traditional methods and present a new approach, where adjustments are made for fluctuating parasite recruitment to the target host population.

The last Part 6 presents a series of papers dealing with the usefulness of rigorous scientific research to management and conservation. Tagging methods are important tools in the research and management of salmonids. The first paper, Rikardsen et al. (2002), examines the effectiveness of the Floy FTF-69 and the new soft VIalpha tags on Arctic charr under hatchery conditions, and compare results for tagged fish and untagged controls. The Carlin tag is also widely used, especially in anadromous salmonids. However, this tagging method may interfere with fish behaviour and increase post-smolt mortality. Strand et al. (2002) test whether Carlin tags affect the growth and survival of hatchery-reared Arctic charr relative to control groups marked with colour tags. Although there are many studies of exploited lake charr populations, there are few studies of the abundance, natural survival rates, and recruitment variability of lake charr in unexploited populations; Mills et al. (2002a) examine the long-term variation of these descriptors in nine lake charr populations, seven from unexploited lakes, one from an exploited lake, and another from an experimentally-acidified lake. Mills et al. (2002b) compare the changes in lake charr biomass and production in a small northwestern Ontario lake (Canada), during progressive acidification and pH recovery in an unaffected lake. Water management in reservoirs, where water levels are lowered during the winter, may expose eggs deposited around shallow shorelines during the fall. Artificial spawning areas below drawdown depth may alleviate the negative effects of drawdown on spawning success. Benoît & Legault (2002) evaluate the feasability of inducing lake charr reproduction below the range of fluctuating water levels by the sequential construction of artificial reefs and limitation of access to natural spawning habitat. Arctic charr tend to form stunted populations of low value for human consumption or sports fisheries; Jansen et al. (2002) present long-term data on Arctic charr catch statistics from an intensive fishing program aimed at reducing stock density and increasing growth and harvestable sizes in a natural alpine lake in Norway. They also present data of shorter-term studies on growth, size-, and age-distributions, as well as size-related habitat and resource utilisation of Arctic charr and brown trout from this lake. Large-bodied migratory forms of bull charr, *Salvelinus confluentus*, were historically abundant in northwestern North America, but in some regions many remaining populations of this now-threatened species presently persist as small-bodied residents isolated in headwater streams; Nelson et al. (2002) examine whether the migratory form has been lost from headwater populations of bull charr and investigate whether it can be reestablished with improved habitat management. From a fishery management as well as an evolutionary perspective, it is important to determine if factors influencing redd site selection, which have evolved in natural environments, are maintained in artificial habitats. Bernier-Bourgault & Magnan (2002) investigate the physical and chemical factors contributing to redd site selection as well as the hatching and emergence success of brook charr within an artificially enhanced site and compare their results to those obtained in the natural environment. Finally, Gunn (2002) reports the results of an unplanned study into the effects of the 1998 El Niño event on a lake charr population in the Boreal Shield of Canada. The findings evolved from a study of the survival and growth of hatchery stocked lake charr in lakes recovering from acidification. The occurrence of the 1998 El Niño event led to the surprising occurrence of lethal conditions in one of the study lakes.

Conclusion

The research presented in this special volume builds on preceding work and presents new developments in a variety of fields. These studies certainly cannot cover all recent developments in the ecology, behaviour, and evolution of *Salvelinus* species, but we hope that collecting these original studies into a special volume will bring attention to some of the current research on this important genus as well as stimulate further work on *Salvelinus* species.

It is always hard to predict the next focus of research in a field as diverse as biology. Two areas, however, are likely to receive increased attention using charr as model species. The first involves the continuing revolution in molecular biology and its relevance to studies of adaptation and speciation in charr. Genome mapping projects in salmonids are increasing and the rich database on ecological and morphological variability in charrs make them a natural for studying the genetic basis of adaptation and speciation. Second, climate change is predicted to have its greatest consequences in northern latitudes. Because charrs are predominantly north temperate and Arctic in distribution, climate change scenarios will have pronounced effects on the distribution, productivity, and persistence of charr populations. The study of charrs should make important contributions to these two areas of interest in biology. In addition, the origin and persistence of much of the ecological and genetic variability in charr still requires mechanistic explanation. The role of studies of charr in resolving new and persistent areas of uncertainty in biology means that there will be a continuing need for regular gatherings to present and synthesize new findings and stimulate future work on this fascinating group of fishes.

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