

GREAT LAKES FISHERY COMMISSION

2017 End-of-Project Completion Report¹

COMPARATIVE GENETIC AND PHENOTYPIC ANALYSIS OF LAKE TROUT MORPHS IN REPRESENTATIVE NORTH AMERICAN LAKES: GENETIC ASPECTS OF PHENOTYPIC VARIATION IN LAKE SUPERIOR LAKE TROUT MORPHS

2005_BEN_44001 and 2008_BEN_44004

by:

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August 2017

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ABSTRACT:

The main goal of the funded project was to assess genetic and phenotypic variation of lake trout *Salvelinus namaycush* within and among large lakes across North America. Lake trout develop morphologically differentiated ecotypes (morphs) and persist in boreal lakes under a spectrum of human induced habitat alteration. Consequently, the genetic and morphological diversity of trout populations have been differentially eroded across their range, particularly in the Laurentian Great Lakes. Although lake trout numbers in Lake Superior have been recovered through stocking efforts, there was morphological evidence to suggest that the slow process of diversifying selection has been stalled, or reversed, by human disturbance. Ultimately, this research was intended to inform rehabilitation projects of the Great Lakes Fisheries Commission (GLFC) in the Laurentian Great Lakes that aim to restore phenotypic diversity. The main goal was approached using a series of research questions: 1) What is the relationship between genetic and morphological distinctiveness among morphs in lesser studied populations, e.g., Rush Lake, redfin morph in Lake Superior? (Objective 1); Are morphs in Great Bear Lake, Great Slave Lake, Lake Mistassini, Lake Superior, and Rush Lake the result of sympatric divergence? (Objective 2); Is there genetic evidence for 'reverse speciation' in Lake Superior? (Objective 3); What are the axes of genetic divergence, and do they exist in parallel within and among lakes? (Objective 4). Samples collected during 2002 to 2013 were genotyped using 10-20 microsatellite loci, and major histocompatibility complex and mitochondrial RFLP markers. Morphology and life history data sets were contributed in collaboration by colleagues. In a comprehensive ecological monologue on Rush Lake, we showed that the two distinct morphs comprised a single genetic population with evidence for weak restriction of gene flow. Redfin morphs, according to microsatellite loci were not a distinct group, and genetic diversity exists along a continuum across morphs. In each lake, different morphs originated from the same mitochondrial lineage, thus morphs likely evolved in sympatry. We showed that historical colonization may have occurred in parallel from shallow to deep water, indicating an ancestral lean morph. In Lake Superior, we documented an ongoing loss of genetic diversity during 1948-1990 and 1990-2013, in conjunction with increased genetic overlap among morphs supporting the reverse speciation hypothesis. However, active ecological gradients, e.g., water depth, were shown to exist. Taken together, our findings show that lake trout developed divergent morphs in sympatry along multiple ecological axes that promoted adaptive diversification. These processes were shown to occur in parallel within and among lakes. Moreover, where genetic diversity has been lost due to human disturbance, multiple axes of ecological gradients do persist that may help preserve morph diversity given protection of habitat and prey assemblages. This work contributes to the evolving framework for understanding the evolutionary potential of lake trout for managers and conservation programs seeking to re-establish declining or extirpated populations.

RESEARCH HIGHLIGHTS:

- The overarching theme of this project was to determine the level of genetic differentiation among lake trout morphs and populations, so hypotheses could be tested on the origins of divergent lake trout morphs in large deep North American lakes. The genetic population structure and origins were seen as important to Great Lakes Fishery Commission, because they may reveal mechanisms that maintain genetic diversity in natural populations, which can inform species re-establishment plans. In this study, lake trout were found to be genetically distinct among lakes. Within each lake, different morphs appear to have originated from a common (founding) shallow water ancestor. Together, these results supported a parallel sympatric divergence hypothesis. Unexpectedly, the huge morphological differences among morphs did not correlate strongly with genetic differences, which lead us to consider genetic correlations with habitat, rather than correlations with body shape. Thus, investigation on the physical habitat-genetic link that maintains lake trout diversity ensued.
- Lake trout, extirpated from most of the Laurentian Great Lakes, can be found only in Lake Superior and the Georgian Bay region of Lake Huron Lake today. In this study, the state of lake trout genetic diversity in Lake Superior was investigated to contribute to a long-term genetic dataset based on that lake. We compared genetic data sets collected during the historical fishery collapse (*c.* 1959), post-collapse recovery (*c.* 1995-1999), and contemporary (*c.* 2004-2013) periods, and found continued losses in genetic diversity over time. Genetic differences among morphs also were found to shrink over time. These results were alarming because they indicated a possible increase in hybridization among morphs, which may threaten their genetic diversity in the long-term. A key implication of these results for management of Great Lakes freshwater fisheries was that long-term genetic effects of harvest, sea lamprey predation, and stocking have not been ameliorated.
- Using genetic-based evidence, this study showed that water depth is an important ecological factor that promotes and maintains lake trout diversity. We found that despite weak genetic differentiation among morphs, there were strong genetic differences among lake trout inhabiting different water depths. Morphological and life history traits were found to vary along a water depth gradient, and this was correlated with genotypic patterns. This phenomenon was upheld in replicate at multiple spatial scales, within a sampling region (e.g., Isle Royale, Lake Superior), multiple sampling regions within a lake (e.g., Lake Superior), and within lakes across North America. This work provides a framework for understanding the evolutionary potential of lake trout for managers and conservation programs seeking to re-establish declining or extirpated populations.
- Immunogenetic diversity of lake trout was examined to ascertain whether immune genes would be useful for current and future lake trout habitat-genetic studies. Immune genes are often closely tied to habitat, because pathogen diversity varies greatly among local environments. We showed that major histocompatibility complex (MHC Class II β exon 2) gene diversity better reflected habitat (water depth) differences than microsatellite markers. The MHC data re-enforced findings based on microsatellite markers that differentiation among Lake Superior morphs has decreased greatly since the 1990s. Additionally, we were successful in genotyping MHC from archival scale samples dating back to 1948, and thus show that use of archival fin clips is another plausible tool for genetics studies that aim to investigate historical genetic patterns in lake trout.

SUMMARY STATEMENT:

The overarching theme of this project was to test for parallel sympatric divergence of lake trout morphs within lakes across North America and to assess genetic and phenotypic variation. The research objectives changed overtime, albeit not largely, due to changes in personnel when the original PhD student Craig Blackie left the project. As a result, the Lake Superior research questions became a main focus, rather than Great Bear Lake, yet all lakes were included in the study as per the original plan. The Great Bear Lake part of the study was conducted by Louise Chavarie, a postdoc of Charles Krueger at Michigan State University. The personnel changes were naturally followed by development of new ideas as data analysis and discussions progressed.

The following list of objectives is from the original proposal written in 2005:

- 1) Quantify morphological, genetic and growth variation among morphotypes of lake trout from Great Bear Lake and compare to Lake Superior morphotypes,
- 2) Quantify gene flow among morphotypes within and between geographical regions of GBL and compare to patterns seen in Lake Superior,
- 3) Determine whether morphotypes in Great Bear Lake, Great Slave Lakes, Lake Mistassini, Lake Superior, and Rush Lake are the result of parallel patterns of sympatric divergence, or whether they have origins in different glacial refugia,
- 4) Test for evidence of natural selection acting to promote phenotypic diversity in lake trout.

By 2014, the objectives of the project based at Dalhousie University were re-written as follows (*numbers in square brackets refer to manuscripts listed in the Deliverables Section*):

- 1) Characterize the population genetics of some lesser studied populations, e.g., Rush Lake ON [2], and investigate the relationship between genetic and morphological distinctiveness among morphs at Isle Royale, Lake Superior [1,3]
- 2) Determine whether morphs in Great Bear Lake, Great Slave Lakes, Lake Mistassini and Lake Superior are the result of parallel patterns of sympatric divergence, or whether they have origins in different glacial refugia [10,11]
- 3) Reverse speciation of lake trout in Lake Superior: the homogenizing effects of environmental disturbance [4,5]
- 4) Quantify morphological, genetic and growth variation within and between morphs and geographical regions of Great Bear Lake and compare to patterns seen in Lake Superior morphs [6,7,8,9]

Because the results of Objective #2 have not yet been published, a brief summary of those results and their significance are included in Anticipated Manuscripts (#10 and #11) below. Using genetic (microsatellite markers, mitochondrial DNA, and immune genes), morphological, and life history data, we show that large, deep lakes were characterized by processes of incipient speciation of lake trout from an ancestral lean morph. These processes occurred in replicate (parallel) within and among the North American lakes studied. These findings help clarify the mechanisms on the origins of lake trout morphological and genetic diversity. The Great Lakes Fishery Commission was interested in this because local adaptation and maintenance of intraspecific genetic diversity are important to a species' persistence in the face of rapidly changing environmental conditions.

DELIVERABLES:

Peer Reviewed Scientific Publications (newest to oldest)

Published manuscripts

1. **Baillie SM**, Hemstock RR, Muir AM, Krueger CC, **Bentzen P** (2017) Small-scale intraspecific patterns of adaptive immunogenetic polymorphisms and neutral variation in Lake Superior lake trout. *Immunogenetics*, DOI: 10.1007/s00251-017-0996-4
2. Chavarie L, Muir AM, Zimmerman MS, **Baillie SM**, Hansen MJ, Nate NA, Yule DL, Middel T, **Bentzen P**, Krueger CC (2016) Challenge to the model for lake trout evolution: Co-existence of shallow- and deep-water morphs in a small postglacial lake. *Biological Journal of the Linnaean Society B*, DOI: 10.1111/bij.12913
3. **Baillie SM**, Muir AM, Krueger CC, **Bentzen P** (2016) Genetic and phenotypic variation along an ecological gradient in lake trout *Salvelinus namaycush*. *BMC Evolutionary Biology*, DOI: 10.1186/s12862-016-0788-8
4. **Baillie SM**, Muir AM, Krueger CC, Scribner K, **Bentzen P** (2016) Loss of genetic diversity and reduction of genetic distance among lake trout *Salvelinus namaycush* ecomorphs, Lake Superior 1959 to 2013. *Journal of Great Lakes Research*, DOI: 10.1016/j.jglr.2016.02.001
5. **Baillie SM**, **Blackie CT**, Gerardi L, **Bentzen P** (2015) Deciphering hatchery stock influences on wild populations of Vermont lake trout *Salvelinus namaycush*. *Transactions of the American Fisheries Society*, 144, 124-139
6. **Blackie CT**, Vecsei P, Cott PA (2012) Contrasting phenotypic variation among river and lake caught cisco from Great Slave Lake: Evidence for dwarf and large morphs. *Journal of Great Lakes Research*, DOI: 10.1016/j.jglr.2012.09.018
7. Muir AM, **Blackie CT**, Marsden JT, Krueger CC (2012) Lake trout *Salvelinus namaycush* spawning behaviour: new field observations and a review of current knowledge. *Reviews in Fish Biology and Fisheries*, DOI: 10.1007/s11160-012-9258-6

Manuscripts in prep (including abstracts)

8. **Baillie SM**, Perrault-Payette A, Bronte C, Hansen MJ, Muir AM, Krueger CC, **Bentzen P** (*draft completed but touch up is delayed; new draft date 5th September 2017*) Parallelism along a water depth gradient despite genetic divergence among restored populations of lake trout across Lake Superior. To be submitted to *Ecological Applications*

In post-glacial lake ecosystems, low species density creates adaptive opportunities to better exploit diverse trophic resources and habitats, which leads to divergence, development of ecotypes within, and new species. Numerous ecotypes of lake trout *Salvelinus namaycush* have developed within and among large lakes across North America. However, in Lake Superior, lake trout numbers were reduced through heavy fishing pressure and predation by exotic sea lamprey, which may have induced a loss of genetic diversity and morphological distinctness among ecotypes. Although lake trout numbers have been restored, there is concern about whether ecotype development has the capacity for future divergence. Genetic and phenotypic traits organized along replicate ecological gradients can provide important insights into diversification processes and species' resilience. Therefore, we tested a hypothesis of parallel adaptive variation in lake trout and considered variation as a cline rather than among discrete ecotypes. Analyses of microsatellite DNA revealed that genetic divergence

increased with water depth and historical colonization may have occurred in parallel from shallow to deep water at several presumed spawning shoals across Lake Superior. We found significant correlations between genotype and all morphological and life history traits. At each shoal, and even within ecotypes, locomotive and life history-related traits varied clinally with water depth. However, cranio-skeletal trait variation related to feeding was explained better by ecotype than by water depth. Divergent natural selection likely shaped these clines, as divergence of several life history, and locomotive- and feeding-related, traits exceeded neutral expectations set by F_{ST} of microsatellite markers. Taken together, our results indicate multiple instances of parallel phenotypic evolution within one large lake, and an immense capacity for polymorphism in this species along multiple niche axes. Our results demonstrate that a persistent adaptive gradient maintains intraspecific biodiversity in Lake Superior. This work provides a framework for understanding the evolutionary potential of lake trout for managers and conservation programs seeking to re-establish declining or extirpated populations.

9. Chavarie L, Howland KL, Harris LN, Hansen MJ, Gallagher C, **Baillie SM**, Malley B, Tonn WM, Muir AM, Krueger CC (*draft completed and in review by coauthors*) Multiple axes of divergence from top to bottom: do Lake Trout diversify along a depth gradient in Great Bear Lake, NT? To be submitted to *Ecological Applications*

Due to the strong association of Lake Trout intraspecific diversity with depth partitioning combined with the fact that Great Bear Lake is one of the largest and deepest freshwater systems in North America, Lake Trout intraspecific diversity organized along a depth axis would be expected within this system. Thus, we investigated whether a deep-water morph co-existed with the four shallow-water morphs of Lake Trout previously described within the system. We compared morphology, neutral genetic, isotopic niche, and life-history, in Lake Trout across differing depths (0-150 m). Due to the propensity of Lake Trout with high levels of morphological diversity to occupy multiple habitat niches, a novel method including a multivariate grouping using a suite of ecological variables was added to two independent traditional grouping methods, classifying individuals by depth and by morphology. Depth alone was not a major explanatory variable of Lake Trout diversity in Great Bear Lake, rather, an ecological continuum existed with some evidence for adaptation to local conditions to deep-water habitat. Overall, phenotypic divergence in linear measurements (e.g., fin lengths), showed some low level of genetic differentiation, higher lipid content (C:N ratio) linked to higher buoyancy, an increase of higher trophic level that suggested an increase of piscivory (including cannibalism) with the use of deep- vs. to shallow-water habitat. Why phenotypic divergence between shallow- and deep-water Lake Trout is lower than expected is unknown, especially when the potential for phenotypic variation seems high in Great Bear Lake and in Lake Trout, and when depth partitioning seems to be an important driver for Lake Trout intraspecific diversity elsewhere. The great deal of ambiguity surrounding the mechanism(s) driving divergence in Lake Trout of Great Bear Lake should be seen as part of the highly variable nature of divergent selection itself, and will result in a better understanding of the transition (if any) from early to advanced stages of divergence.

Anticipated manuscripts

10. **Baillie SM**, McCracken G, Muir AM, Krueger CC, **Bentzen P** (*draft date Fall/Winter 2017*). MHC supertype and allelic structure and divergence in lake trout ecotype pairs across populations in North America. *Immunogenetics*

The major histocompatibility complex (MHC) is thought to be under strong selection pressure because of its integral role in pathogen recognition, as well as mate choice. Previous research on MHC has shown that lake trout ecotypes, lean and siscowet, are divergent at MHC loci. This indicates patterns of MHC genetic variation reflect different selection pressures between ecotypes. Here, we examine MHC supertype (allele groups with similar epitope recognition) and allelic variation at the MHC class II-B1 exons in lake trout across North America.

11. **Baillie SM**, Chavarie L, Muir AM, Zimmerman MJ, Hansen MJ, Bronte CR, **Bentzen P**, Krueger CC (*draft date Winter/Spring 2018*). Multiple instances of parallel sympatric divergence of lake trout ecotypes across North America. *Journal of Biogeography*

Studies that target newly diverging populations are key to understanding the importance of plasticity-related genes that mediate an organism's environmental responsiveness. Lake trout *Salvelinus namaycush* across North America represent young populations in the early stages of divergence and exhibit multiple morphologies of shallow and deep-water ecotypes. The phenotypic distinctiveness of ecotype morphologies suggest that morphological differences are under some form of genetic control and have evolved some degree of reproductive isolation. In this study, we test the hypotheses that lake trout ecotypes are reproductively isolated and arose via parallel ecological sympatric speciation. We sampled tissue from ecotypes within four large lakes, Great Bear Lake, Great Slave Lake, Lake Mistassini and Lake Superior, and one small lake, Rush Lake. Results from mitochondrial and microsatellite DNA analyses, suggest that ecotypes arose independently in lakes after colonization and that morphologically and ecologically differentiated lake trout ecotypes within lakes are largely indistinguishable genetically using neutral markers. This may be a consequence of phenotypic differences being linked to divergence at (non-neutral) genes or genomic regions associated with trophic morphology and life history, or that epigenetic processes dominate trophic phenotype at this stage in lake trout evolution. MHC gene data as well as Bayesian approximate analyses will be incorporated into this paper to investigate the time since divergence of ecotypes within each lake, and test the hypothesis that Great Slave Lake (with the most genetically distinct ecotypes) is the oldest population based on glacial recession dates.

Pilot Study Report (including abstract)

12. **Baillie SM**, Rutledge L, Vinson M, Muir AM, Krueger CC, **Bentzen P** (2015) Preliminary report on pilot study: DNA quantity and MHC sequencing in archival salmonid scale samples (c. 1948 – 1998). Great Lakes Fisheries Commission.

In preparation for a genome-wide SNP haplotype study, using restriction-site associated DNA sequencing (RADseq), to test hypotheses on loss of adaptive genetic diversity and reverse speciation of Lake Superior lake trout ecotypes, we executed a pilot test on archival lake trout scale samples. This test compared DNA quality and quantity, as well as Sanger sequencing to rule out the possibility of sample contamination. The samples were extracted and analysed in duplicate at two Canadian genomics facilities, the Marine Gene Probe Lab Dalhousie University and the Ancient DNA Lab Trent University. The lake trout scale samples (N = 40) collected during 1948 to 1998 were chosen for this pilot study to represent six contiguous decades. We found that DNA quantity decreased with age of sample. However, we were able to sequence samples in all year classes, including the 1940s, and 78% of the archived historical samples yielded sufficient DNA for RADseq studies.

Book chapters

Bernatchez L, Wellband K, **Baillie SM**, **Bentzen P**, Wilson C, Scribner K (*draft date 31st December 2017*) Chapter 5: Genetic Diversity in Lake Trout *Salvelinus namaycush*: Biology, Ecology, Distribution, and Management. Springer Fish & Fisheries Series; Ed.: D. Noakes.

The purpose of this book is to provide a compilation and synthesis of modern information on lake trout *Salvelinus namaycush*.

Conference and Invited Presentations

- Muir AM, Baillie SM, Zimmerman MS, Hansen MJ, Middel T, Krueger CC, Bentzen P (Jan 2014) Rapid evolution in a slow-living species. Oral presentation of Rush Lake data at the **Canadian Conference for**

Fisheries Research (CCFFR), Yellowknife, Northwest Territories

- Baillie SM (May 2014) Rapid evolution in a slow-living species. **Canadian Society for Ecology and Evolution (CSEE)**, Montreal, Quebec
- Baillie SM, Muir AM, Krueger CC, Scribner K, Bentzen P (Mar 2015) Loss of genetic diversity and collapse of lake trout *Salvelinus namaycush* ectomorphs, Lake Superior 1948 to 2013. **Great Lakes Fishery Committee Meeting**, Ann Arbor, Michigan
- Baillie SM, Zimmerman MS, Muir AM, Hansen MJ, Middel T, Krueger CC, Bentzen P (2014, 2015, 2016) Rapid evolution in a slow-living species. Several oral presentations for the Acadia University, St Mary's U, Dalhousie U, **Biology seminar series**, Nova Scotia
- Baillie SM, Muir AM, Krueger CC, Bentzen P (July 2016) Genetic and phenotypic variation along an ecological gradient in lake trout *Salvelinus namaycush*. Annual **Fisheries Society of the British Isles Symposium (FSBI)**, Bangor, UK

HQP training

- Honours Student Riley Hemstock*, BSc Honours Project (Dalhousie University) 2015-2016. A comparison of Major Histocompatibility Complex (MHC) genes in shallow- and deep-water lake trout (*Salvelinus namaycush*) ecotypes
- Postdoc Shauna Baillie January 2016 Workshop on Genomics, Cesky Krumlov, Czech Republic

A 180-hour bioinformatics course that extensively covered fundamental techniques required of all studies utilizing modern sequence data. This included management and modification of modern sequence data files, using the Unix command-line and editors to manipulate large data files, genome assembly and best practices for sequence data generation, management, and analysis. The second-half of the Workshop was devoted to data analyses from within specific sub-disciplines of genomic sciences, RADseq, RNAseq, SMRT cell sequencing.

- Postdoc Shauna Baillie June 2013 Workshop on Informatics on High Throughput Sequencing Data, Bioinformatics Canada, Toronto

Genetic data sets and changes

- Microsatellite and RFLP DNA dataset quality assessment – Feb 2013
- Completed re-scoring of existing microsatellite and RFLP datasets for Lake Superior and Rush Lake - Mar 2013
- RFLP mitochondrial DNA (mtDNA) typing - May 2013
- Addition of Kim Scribner's Lake Superior lake trout microsatellite datasets from 1959 and 1999 - Oct 2013
- 'Filling in the gaps' of existing Lake Superior dataset. Added 10 new loci to existing Lake Superior dataset - Dec 2013
- Using the additional loci, Lake Superior microsatellite DNA plates 13-20, 32-35 were genotyped for comparison with 1950s and 1990s historical lake trout microsatellite DNA data - Mar 2014

- Extracted three more 96-well DNA plates of adults from Big Reef, Klondike Reef, and Grand Marais along with newly collected samples (Nov 2013) from Superior Shoal and Stannard Rock; genotyped at all 20 loci - Jan/Feb 2014
- Re-extracted three 96-well DNA plates of adults from Isle Royale to increase sample size and statistical power - Feb 2014
- MHC sequencing dataset and scoring sheets – 2015-2017
- Conducted pilot study on MHC sequencing from lake trout scale samples collected during the 1950s to 2000s - 2015

APPENDIX:

APPENDIX 1. A1 Baillie et al 2017 Immunogenet Small-scale patterns of adaptive immunogenetic polymorphisms and neutral variation in Lake Superior lake trout.pdf

APPENDIX 2. A2 Chavarie et al 2017 Biol J Linn Soc Challenge to the model for lake trout evolution.pdf

APPENDIX 3. A3 Baillie et al 2016 BMC Evol Biol Genetic and phenotypic variation along an ecological gradient in lake trout.pdf

APPENDIX 4. A4 Baillie et al 2016 J Great Lakes Res Loss of genetic diversity and reduction of genetic distance among lake trout ecomorphs.pdf

APPENDIX 5. A5 Baillie et al 2015 Trans Am Fish Soc Deciphering hatchery stock influences on wild populations of Vermont lake trout.pdf

APPENDIX 6. A6 Blackie et al 2012 J Great Lakes Res Contrasting phenotypic variation among river and lake caught cisco from Great Slave Lake.pdf

APPENDIX 7. A7 Muir et al 2012 Rev Fish Biol Fisheries Lake trout *Salvelinus namaycush* spawning behavior.pdf

APPENDIX 8. A8 Baillie et al 2017 Ecol Appl Parallelism along a water depth gradient among restored populations of lake trout.pdf

APPENDIX 9. A9 ABSTRACT Chavarie et al 2017 Ecol Appl Multiple axes of divergence in Lake Trout Great Bear Lake.pdf

APPENDIX 10. A10 ABSTRACT Baillie et al 2017 Immunogenet MHC supertype and allelic structure and divergence in lake trout ecotypes across NA.pdf

APPENDIX 11. A11 ABSTRACT Baillie et al 2017 J Biogeogr Multiple instances of parallel sympatric divergence of lake trout NA.pdf

APPENDIX 12. A12 Baillie et al 2015 Report on pilot study - DNA quantity and MHC sequencing in archival salmonid scale samples.pdf