GREAT LAKES FISHERY TRUST

FINAL REPORT

PROJECT ABSTRACT

Title: Using Genomic Tools to Investigate Adaptive Diversity in Great Lakes Cisco

Abstract Body: Cisco are an important component of the Great Lakes food web which facilitate transfer of energy between trophic levels, ensuring that ecosystem function is maintained. Historically, up to seven species of deepwater cisco and the congeneric lake herring were present in the Great Lakes, and these species supported large fisheries and facilitated energy coupling between trophic levels. However, changes in the Great Lakes ecosystem, including overfishing, habitat loss, and the introduction of invasive species, have led to decreases in cisco abundance as well as lake-wide and basin-wide extirpations of certain species. Luckily, recent changes in the Great Lakes ecosystem, including reduced abundances of invasive forage fish, may represent an opportunity for cisco to recolonize the niches that have been vacated. Scientists and managers from across the basin have recently emphasized cisco conservation and restoration, but one major knowledge gap that must be addressed to inform these efforts is cisco taxonomy. The goal of this project is to use genomic tools to clarify cisco population structure and taxonomy in the Great Lakes. We genotyped over 30 populations of cisco at thousands of genetic markers using restriction site-associated DNA (RAD) sequencing. We then conducted population genetic analyses to investigate genetic structure among lakes and forms. Finally, we examined adaptive variation across the cisco genome by leveraging a recently created cisco linkage map. We found that the main forms of cisco (*artedi*, *hoyi*, *kiyi*) are highly differentiated from each other wherever they are found. Additionally, we found that *artedi* are highly and consistently differentiated from deepwater forms across lakes, suggesting that the split between these two groups may have preceded the colonization of the Great Lakes. Within forms, *artedi* were consistently differentiated across lakes and sometimes within lakes, especially in northern Lake Huron. Other forms were more similar across lakes. In particular, *hoyi* from lakes Michigan and Huron displayed low genetic divergence. This finding suggests that the hypothesis that deepwater cisco in Lake Huron are a hybrid swarm is likely incorrect. Finally, adaptive divergence seems to be occurring throughout the genome with no particular “hotspots” of high differentiation. This finding provides further evidence that the forms have likely been mostly reproductively isolated for many generations. In general, our findings challenge the existing hypothesis that cisco are more similar within than among lakes and suggest that some or all cisco forms potentially evolved prior to colonization of the Great Lakes. Findings from this study are currently being integrated into a conservation planning. Specifically, Wes Larson is co-leading a team with Dr. Andrew Muir from the Great Lakes Fishery Commission to address box 1 of the CLC conservation objectives for cisco “resolve coregonine taxonomy using genetics and ecology.” This direct collaboration between scientists and management agencies will ensure that the findings from our study will be effectively integrated into conservation and restoration frameworks for cisco.

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Project Number: 2017.1700

Grantee Organization: US Geological Survey, Wisconsin Cooperative Fishery Research Unit, College of Natural Resources, University of Wisconsin-Stevens Point, 800 Reserve St., Stevens Point, WI 54481

Project Team: Wesley Larson, Wisconsin Cooperative Fishery Research Unit, College of Natural Resources, University of Wisconsin-Stevens Point; **Wendylee Stott**, Great Lakes Science Center, Department of Fisheries and Wildlife, Michigan State University; **Julie Turgeon**, University of Laval; **Kevin Donner**, Little Traverse Bay Band of Odawa Indians; **Jory Jonas**, Michigan Department of Natural Resources.

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Grant Amount: $105,000.00 (requested); $105,000.00 (spent)

Start and End Dates: January 1, 2018 – December 31, 2019

Key Search Words: coregonines, cisco, genomics, RAD sequencing, population genetics, adaptive divergence

Background/Overview

1. *Brief Project Summary:* Historically, cisco was the major forage fish component in the Great Lakes food chain and supported extensive commercial fisheries in multiple Great Lakes. However, anthropogenic impacts have led to massive declines in cisco abundance as well as local and global extirpations of multiple cisco species. We will use genomics to investigate the genetic basis of adaptation in cisco. This research will provide important data that can be used to preserve cisco diversity and inform restoration.

2. *Changes to Scope of Work:* No significant changes to the scope of work were made.

Outcomes

3. *To what extent and how (if at all) did this research project advance scientific knowledge of the issue?*

   This project significantly advanced the state of knowledge on cisco taxonomy in the Great Lakes. Before this project, the current hypothesis based on existing genetic data (allozymes, mtDNA, microsatellites) was that cisco were more similar within than among lakes. However, our genomic data shed new light on this view and suggest that the forms have likely been mostly reproductively isolated for many generations, potentially before the Great Lakes were recolonized. This finding has major implications for management of cisco as it indicates that differences among forms are likely to be highly heritable rather than due to phenotypic plasticity. In other words, stocking cisco in a certain environment and expecting them to quickly shift their phenotype to match that environment is likely not feasible. These findings will be important for drafting conservation and management plans as it is unlikely that forms will re-evolve on non-evolutionary timescales, therefore the diversity of currently existing forms should be preserved if possible.

4. *To what extent and how (if at all) did this project contribute to the education and advancement of graduate or undergraduate students focused on Great Lakes fishery issues?*

   No graduate student was dedicated to this research project but this project comprised a large part of postdoc Amanda Ackiss' research. Amanda has focused on cisco for approximately a year and half and was recently hired for a pathways position to research cisco genomics at the Great Lakes Science Center in Ann Arbor. This project was therefore instrumental in training a scientist who will likely lead the cisco genetics line of research in the Great Lakes over the next decade.

5. *To what extent and how (if at all) did this work help you or others on your team build new relationships with others in the research or management communities?*

   This project was instrumental for developing relationships between UW-Stevens Point, Michigan DNR, the Great Lakes Science Center, the Ontario Ministry of Natural Resources and Forestry (OMNRF), and tribal management agencies including the Little Traverse Bay Band of Odawa Indians. During the sample acquisition phase, we built relationships with various entities across the Great Lakes including OMNRF and the USGS Science Center in Ashland, WI. In particular, we were able to take a cruise aboard the RV Kiyi where we helped sample cisco and also strengthened our relationship with scientists at that center. Additionally, Amanda has discussed the results at multiple Lake Committee meetings (see below), which has presented an excellent opportunity to network with many scientists across the Great Lakes and has helped us build a large group of collaborators.

6. *To what extent and how (if at all) do the findings have action implications for fishery managers? If the research has direct management implications, do you have any knowledge of use of the findings by managers? If the research does not have direct management implications at this stage, to what extent did the research advance the process of identifying management responses to critical issues?*

   These findings have significant and immediate implications for fishery managers. In particular, the findings shed important new light on cisco taxonomy in the Great Lakes region. There have been many ongoing discussions by research and management agencies regarding the best way to restore cisco in the Great Lakes, and many of these discussions rely heavily on cisco taxonomy. For example, managers need to identify appropriate sources for stocking and assess the risk of stocking fish from a certain population or form on local cisco. At this point, we have no knowledge of this research being directly used by managers. However, this research is central to accomplishing the objective of box 1 of the CLC conservation objectives for cisco "resolve coregonine taxonomy using genetics and ecology." Once a new description of cisco taxonomy is agreed upon by CLC members, this information will be directly used to draft restoration strategies that could include action items such as stocking or developing protected areas.

7. *Considering the above or other factors not listed, what do you consider to be the most important benefits or outcomes of the project?*

   We believe the most important outcome from this study is the finding that cisco forms are highly and consistently differentiated from each other. This has significant management implications and will be central to developing conservation and restoration strategies for this important species.

Related Efforts

8. *Was this project a standalone effort, or was there a broader effort beyond the part funded by the GLFT? Have other funders been involved, either during the time of your GLFT grant or subsequently?*

   This project was part of a much larger effort to conduct genomic research on Great Lakes cisco. Other projects in this line of research include developing a genetic linkage map for cisco (funded by USGS GLSC through GLRI) and constructing a high-throughput GTseq marker panel to enable rapid analysis of cisco. This project directly was funded by the GLFWRA and directly leveraged data from the current GLFT project.

9. *Has there been any spinoff work or follow-up work related to this project? Did this work inspire subsequent, related research involving you or others?*

   Multiple spinoff project have been developed from these project. These include analyzing historic scale samples to investigate past cisco diversity (funded by GLSC through GLRI), a paired morphometric and genetic analysis of cisco in Lake Superior (funded by GLSC through GLRI), and pairing larval data with species identifications to estimate form-specific recruitment in Lake Superior (funded by GLSC through GLRI). In the broader sense, this project was the start of a genomic revolution for cisco and has inspired a line of research that will likely continue for the foreseeable future.

Communication/Publication of Findings

10. *List publications, presentations, websites, and other forms of formal dissemination of the project deliverables, tools, or results, including those that are planned or in process.*

    Ackiss, A., Larson, W., Stott, Wendylee. 2020. Genotyping-by-sequencing illuminates high levels of divergence among sympatric forms of coregonines in the Laurentian Great Lakes. *Evolutionary Applications.* Online early.

Ackiss, A., and Larson, W. January 2020. Using Genomics Tools to Investigate Adaptive Diversity in Great Lakes Cisco. Lake Superior Technical Committee Meeting. Marquette, MI.

Ackiss, A., Donner, K., Jonas, J., Stott, W., Larson, W. September 2019. Using Genomics Tools to Investigate Adaptive Diversity in Great Lakes Cisco. Annual Meeting of the American Fisheries Society. Reno, Nevada.

Ackiss, A., and Larson, W. August 2019. Using Genomics Tools to Investigate Adaptive Diversity in Great Lakes Cisco. Lake Michigan Technical Committee Meeting. Green Bay, WI.

Ackiss, A., Donner, K., Jonas, J., Stott, W., Larson, W. June 2019. Using Genomics Tools to Investigate Adaptive Diversity in Great Lakes Cisco. International Association of Great Lakes Research. Brockport, New York.

11. *Please characterize your efforts to share the findings of this research with state, federal, Tribal, and interjurisdictional (e.g., Great Lakes Fishery Commission) agencies charged with management responsibilities for the Great Lakes fishery. If other audiences were priority for this research, please characterize your outreach efforts to those audiences as well. (Please note: You may wish to consult midterm reports in which specific audiences for the findings, and means of outreach to these audiences, were identified.)*

    We have presented this research at regional meetings (IAGLR), national meetings (AFS annual meeting) and, in our opinion most importantly, at Lake Committee meetings. The Lake Committee meetings have been vital for getting these results out on the landscape and in the hands of managers who need them. Additionally, Amanda will be presenting the results again at the Upper Lakes Meeting in Sault St. Marie in a couple months. Additionally, Amanda drafted a manuscript describing our findings in a small part of our research area (the Apostle Islands) which was recently accepted in Evolutionary Applications, a well-respected and high impact (IF=5) journal. We chose to focus on the Apostle Islands first as they represent a hotspot for extant cisco diversity with all three major forms present. Additionally, focusing on this small geographic area allowed us to remove the confounding factor of spatial structure from our analysis. Regarding a manuscript describing cisco taxonomy across the Great Lakes, Amanda recently sequenced ~20 more populations to further add to the already large dataset. She plans to conduct thorough analysis of the Great Lakes data over the next six months with the goal of drafting a large manuscript by the end of the year. Importantly, the major findings from this work have already been shared with managers through presentations and are currently being integrated into conservation and restoration planning.

12. We have attached the following manuscript and presentation.

a. Ackiss, A., Larson, W., Stott, Wendylee. 2020. Genotyping-by-sequencing illuminates high levels of divergence among sympatric forms of coregonines in the Laurentian Great Lakes. *Evolutionary Applications.* Online early. (pdf titled: Ackiss_et_al-2020-Evolutionary_Applications.pdf).

b. Ackiss, A., and Larson, W. January 2020. Using Genomics Tools to Investigate Adaptive Diversity in Great Lakes Cisco. Lake Superior Technical Committee Meeting. Marquette, MI. (pdf titled: GL_cisco_LSTC_8Jan2010_ASA.pdf) No restriction.

Discussion (please see attached Evolutionary Applications manuscript for more details)

Our most important finding was that the main three cisco forms (*hoyi, kiyi, artedi)* are highly genetically differentiated from each other wherever they were encountered. This finding contrasts previous work conducted by Julie Turgeon who primarily investigated genetic structure of cisco in Canadian lakes using mtDNA and microsatellites and found that all forms within a given lake were more genetically similar to each other than they were to forms from other lakes. In other words, cisco were structured by lake first then sometimes but not always by form. Our findings suggest that this pattern is not the case in the Great Lakes. One particularly strong example that contradicts the pattern observed by Turgeon is *hoyi* in lakes Huron and Michigan, which are essentially genetically indistinguishable. Our results suggest that Great Lakes cisco may be atypical compared to previously studied populations in Canada because cisco forms in the Great Lakes appear to have been isolated for many generations and may have evolved prior to recolonization of the Great Lakes. The major implication of this finding is that cisco forms in the Great Lakes are likely highly heritable, that is, these forms do not appear to be the result of phenotypic plasticity. This means that once a form is lost, the unique genes that code for this form will likely not re-evolve for thousands of years. Additionally, cisco forms will likely retain similar functions and phenotypes if they are translocated or stocked in other areas. It is therefore imperative to conserve existing cisco diversity to ensure that the unique attributes of these forms are not lost.

One limitation of our study is that it did not include extinct forms and only included a few individuals from rare forms such as zenithicus and nigripinnis. We believe integrating these rare and extinct forms into future studies is important to determine (1) whether they represent genetically distinct forms and (2) how these forms relate to extant forms. With any restoration project, it is important to determine the baseline for restoration, and understanding the unique genetic attributes of these forms will be important for developing restoration strategies. An additional line of research that we believe will be important to pursue is the fitness of F1 and advanced generation hybrids. We found some evidence that cisco forms hybridize, but it is unclear whether they produce offspring past the first generation. Understanding the fitness consequences and genetic risks of hybridization will be important for assessing the risks of stocking certain forms near others in the future.