

Fourth Reintroduction of Native Fishes Workshop

Great Lakes Fishery Commission

Weber's Inn, Ann Arbor, MI December 12-14, 2012

WORKSHOP REPORT



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DISCLAIMER

The information presented herein is preliminary and the research summaries presented in Appendices I & II are simply the notes of the compilers of this report; therefore, the information herein should be considered preliminary and should not be cited (See Appendix III for participant contact information). In addition, this report represents a compilation of the material presented and discussed at the Fourth Reintroduction of Native Fishes Workshop; therefore, it does not reflect the views or policies of the writers, the Great Lakes Fishery Commission, or any other agency.

WORKSHOP OVERVIEW

The fourth Reintroduction of Native Fishes Workshop was held 12-14 December 2012 in Ann Arbor, MI. The purpose of the workshop was to provide a forum to discuss research relevant to lake trout, cisco, and sculpin biology and re-establishment in the Great Lakes in support of the Great Lakes Fishery Commission (GLFC) Board of Technical Experts' Re-establishment of Native Deepwater Fishes research theme (Zimmerman and Krueger 2009). The objectives of the workshop were as follows: 1) consider progress on research topics within the context of the current theme area; 2) assess the current hypotheses and identify new hypotheses that included management and applied hypotheses; and 3) consider how research results and tests of the theme hypotheses are informing management.

Sixty-five attendees representing nine state, provincial, federal, and tribal governments, 10 academic institutions, two private consultants, two non-governmental organizations, and stakeholders (i.e., recreational anglers) participated in the workshop. The agenda featured one invited talk on the status of and changes in Great Lakes lower food webs and one on the potential impacts of those changes to native fish re-establishment. The remainder of the agenda was filled by 11 cisco presentations and 16 lake trout presentations. The morning of 14 December featured two separate facilitated discussions on the evaluation of existing and development of new hypotheses centered on cisco and lake trout re-establishment. Eight posters were also presented during the evening socials.

The 27 workshop presentations and eight posters provided updates on progress towards answering the six existing cisco theme hypotheses (Table 1) and the seven lake trout theme hypotheses (Table 2). The current state of knowledge has been advanced considerably since the last Reintroduction of Native Fishes workshop (2006) and workshop participants believed that a symposium, such as the 1994 International Conference on Restoration of Lake Trout in the Laurentian Great Lakes (RESTORE; Journal of Great Lakes Research (Supplement 1), which would include the entire deepwater food web, was warranted.

Three highlights emerged from the cisco discussion: (1) progress on hypotheses five and six (see Table 1 for hypotheses) partially answers the questions raised under these hypotheses; (2) major gaps occur in our understanding of current and historical cisco life history and recruitment dynamics; and (3) three new hypotheses were developed: (a) ***Cisco morphs fulfill unique ecological functions***—new quantitative methods (i.e., fatty acids and stable isotopes) applied to populations inside and outside of the Great Lakes could help understand ecological function of cisco morphs in the Great Lakes food web, competitive interactions with non-native planktivores, and resiliency of the ecosystem to future invasions and perturbations; (b) ***Ciscoes will adapt to or tolerate climate change***—the Great Lakes environment will continue to change over the next century (e.g., thermal habitat, ice cover, storm events); what are the potential effects of these changes on species with life stages that overwinter nearshore? and (c) ***Cisco monitoring and assessment will provide information on the efficacy of the reintroduction program***—how can we use what is known about cisco sampling on Lake Superior and elsewhere (e.g., Europe) to develop a monitoring program that will detect stocked and wild recruits allowing the evaluation of restoration efforts? How can animals from different stocking events be identified?

Three highlights emerged from the lake trout discussion: 1) progress on hypotheses one, two, and six (see Table 2 for hypotheses) is sufficient to at least partially answer the questions raised under these hypotheses; 2) ongoing theme-funded projects will provide answers to several more questions raised under the remaining four hypotheses; and 3) new technologies (e.g., stable isotopes and pop-up tags) are powerful tools that will allow us to answer many of the outstanding questions regarding behavior and habitat use and partitioning and we expect new proposals using these methods will be submitted during 2013-2014.

Table 1. Re-establishment of Native Deepwater Fishes research theme hypotheses for ciscoes, current state of knowledge, and future work needed to address the hypothesis.

	Hypothesis	State of knowledge	Future considerations
1	Bloater in lakes Michigan and Huron introgressed when deepwater cisco populations collapsed.	The degree to which <i>C. artedi</i> and <i>C. hoyi</i> have introgressed is unknown.	The group agreed that the subgenus <i>Leucichthys</i> requires taxonomic revision.
2	Population regulation of deepwater ciscoes is intrinsic and density-dependent.	Population regulation mechanisms are unknown and variation among species or lakes is poorly understood, but climate and predation likely play a role.	Evidence for intrinsic regulation has been seen in <i>C. hoyi</i> and <i>C. artedi</i> , but when large ecosystem shifts occur, extrinsic factors could become important. Current recruitment patterns and age structure of <i>C. artedi</i> in Lake Superior are unlikely to explain historical harvests.
3	Cisco population structure is influenced by passive larval dispersal and active adult homing.	Our understanding of cisco population structure and the roles of dispersal and homing in defining that structure is insufficient.	More work is required to understand the role of dispersal and homing in cisco population structure. Pairing this work with the Physical Process theme could help address this hypothesis.
4	Exotic planktivores (rainbow smelt, alewife) have different effects on each pelagic cisco species.	The effects of exotic planktivores on ciscoes in the Laurentian Great Lakes are not well known.	Exotic planktivores may play an important role in cisco population regulation. A food web dynamics approach to studying interactions, possibly in inland lakes, could provide valuable insights.
5	Pelagic ciscoes are undergoing parallel processes of differentiation in large, deep lakes.	Pelagic and deepwater ciscoes are undergoing parallel sympatric differentiation in both large, deep lakes and small, inland lakes.	Common-garden experiments that raise morphs in similar environments could resolve the genetic component of variation among cisco morphs. Efforts to understand spawning behavior are required.
6	Hatchery propagation is a feasible option for reintroducing pelagic ciscoes.	Hatchery propagation is feasible for reintroducing pelagic ciscoes, but it is unknown if it is feasible for reintroducing deepwater ciscoes.	Methods for egg collection, culture, and rearing need to be refined and appropriate brood sources and stocking strategies need to be identified. Incorporating experimental culture into a research agenda that includes common-garden experiments could help to address many of the theme hypotheses, particularly H1 & H5.

Table 2. Re-establishment of Native Deepwater Fishes research theme hypotheses for lake trout, current state of knowledge, and future work needed to address the hypothesis.

	Hypothesis	State of knowledge	Future considerations
1	Diversity in diet and physical habitat use is greater in siscowet than in the other morphs; siscowet are more resilient to perturbations.	In general, we know how diet and depth preferences differ between lean and siscowet lake trout, but we know nothing about ontogenetic shifts in siscowet, little about humper diet, and nothing about changes in response to perturbations, such as prey availability.	Tools, such as pop-up tags and stable isotopes, offer approaches that will help address the question of diet and habitat use among morphs.
2	The humper morph will be less vulnerable to sea lamprey predation than the other morphs.	Klondike humper lake trout do not survive better than lean lake trout in Lake Erie; sea lamprey parasitism affects bioenergetics and immune function differently for leans and siscowets; life history mediates responses to sea lamprey predation with siscowets being less sensitive than leans.	Research to better understand sub-lethal effects of sea lamprey parasitism among morphs and siscowet vulnerability to lamprey predation is needed; how can these effects be incorporated into population models?
3	Lake trout and alewives coexist under specific conditions.	The effects of predation, competition, and early mortality syndrome (EMS) on lake trout recruitment require greater resolution, but it is clear the two species are not co-adapted and negatively affect each other.	One ongoing project will further our knowledge of thiamine issues and EMS, but inter-basin studies to determine the conditions under which alewife and lake trout coexist (i.e., Finger Lakes) are required.
4	Metapopulation structure of wild lake trout reflects dispersal and natal homing of adults.	Little is known about siscowet and humper reproduction, other than time of spawning and maturation. A recent project did not identify any deepwater siscowet spawning aggregations or habitat use. Common garden experiments show morphological variation has a genetic component.	Field studies are required to assess spawning habits and behavior of deepwater lake trout. Reproductive isolation and gene flow among morphs is unknown.
5	Lake trout spawning requires visual, sound, and olfactory cues.	We do not know if or how lake trout use visual, sound, and olfactory cues during spawning.	Three ongoing projects should provide insights into this hypothesis over the next few years.
6	Large, deep lakes are characterized by parallel speciation of lake trout.	Large, deep lakes are probably characterized by parallel processes of speciation with sympatric deep and shallow water lake trout morphs occurring in several lakes, including the northern Great Lakes and smaller inland lakes.	Two ongoing projects are expected to provide data to address H6 over the next few years.
7	Deepwater lake trout can be propagated and reintroduced from a hatchery environment.	Deepwater morphs are now propagated and reintroduced from federal hatcheries, but little is known about effects of culture on life history characteristics.	Incorporating experimental culture into a research agenda that includes common-garden experiments could help to address many of the theme hypotheses, particularly H1, H2, & H6.

AGENDA - Fourth Reintroduction of Native Fishes Workshop



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Wednesday, December 12, 2012

12:00 PM LUNCH - CENTURY ROOM

TIME	PRESENTER	TITLE
EAST & WEST BALLROOM		
1:00 PM	A. Muir	Introduction to the research theme: Reintroduction of Native Fishes in the Great Lakes
LOWER FOOD WEB		
1:20 PM	R. Barbiero	Status and changes in the lower food web across the Laurentian Great Lakes
1:50 PM	B. Bunnell	Potential impacts of changes in the lower food web on native fish reestablishment
SCULPINS		
2:20 PM	B. Bunnell	Sculpin predation on bloater eggs—is it sufficient to drive bloater recruitment variability?
COREGONINES		
2:40 PM	T. Pratt	Patterns of morphological and genetic diversity among ciscoes in deepwater lakes
3:00 PM	REFRESHMENT BREAK	
3:20 PM	K. Howland	Phenotypic diversity of cisco in Great Bear Lake, NT: variation in morphology, diet and demographics
3:40 PM	W. Stott	Morphometric and genetic analysis of cisco (<i>Coregonus artedii</i>) from the Great Lakes
4:00 PM	C. Madenjian	Spawning habitat unsuitability: an impediment to cisco rehabilitation in Lake Michigan?
4:20 PM	D. Hanson	Experience and recommendations for bloater egg takes
4:40 PM	J. Johnson	Pilot cisco egg take and culture study, Lake Huron, 2006-2011
6:00 PM	POSTER SOCIAL - CENTURY ROOM	

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Thursday, December 13, 2012

7:00 AM		CONTINENTAL BREAKFAST - EAST & WEST BALLROOM
TIME	PRESENTER	TITLE
		COREGONINES - EAST & WEST BALLROOM
8:00 AM	K. Loftus	Ontario's experience developing husbandry practices for <i>Coregonus hoyi</i> —lessons
8:20 AM	J. Dettmers	Coregonine culture and assessment in Finland—possible insights for North America
8:40 AM	B. Schroeder	Understanding and engaging stakeholders in coregonine reintroductions
9:00 AM	J. Markham	The future of cisco restoration in Lake Erie
9:20 AM	R. Eshenroder	Implications of the metapopulation concept for cisco reintroduction
10:00 AM		REFRESHMENT BREAK
		LAKE TROUT
10:20 AM	L. Chavarie	Understanding sympatric diversification in lake trout: exceptional shallow-water diversity in Great Bear Lake,NT
10:40 AM	A. Muir	Lake trout diversity at Isle Royale, Lake Superior
11:00 AM	S. Sitar	Differences between lean and siscowet lake trout: what we have learned from sampling wild fish in Lake Superior
11:20 AM	C. Stafford	Introduced lake trout exhibit life history and morphological divergence
12:00 PM		LUNCH - CENTURY ROOM
1:00 PM	J. Jonas	Results from preliminary population assessments of Elk Lake lake trout, an apparent remnant Lake Michigan form and deepwater spawner
1:20 PM	C. Murphy	The influence of life history on response to stressors: the sublethal impact of sea lamprey parasitism on siscowet and lean lake trout
1:40 PM	R. Goetz	Differences between lean and siscowet lake trout: what we have learned from six years of rearing in captivity and what we still don't know
2:00 PM	M. Hansen	Life history variation among lake trout morphotypes in North American lakes
2:20 PM	J. He	Life history plasticity in changing environments, ecosystem stability in changing environments, and lake trout rehabilitation in Lake Huron
2:40 PM	H. Swanson	Differences in egg size and lipid content between life history types of lake trout in the Canadian Arctic
3:00 PM		REFRESHMENT BREAK
3:20 PM	Y. Morbey	Skipped spawning in lake trout and implications for rehabilitation targets
3:40 PM	A. Evans	An overview of thiamine deficiency with regard to lake trout restoration
4:00 PM	M. Rogers	Klondike strain lake trout in Lake Erie (lake trout status included)
4:20 PM	E. Marsden	Artificial reefs in Thunder Bay, Lake Huron - restoration and research platform
4:40 PM	T. Binder	Reproductive behavior of wild and hatchery lake trout in the Drummond Island Refuge, Lake Huron
5:00 PM	S. Riley	Is lake trout spawning habitat associated with glacial bedforms?
6:00 PM		POSTER SOCIAL - CENTURY ROOM

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Friday, December 14, 2012

7:00 AM	CONTINENTAL BREAKFAST - EAST & WEST BALLROOM	
TIME	PRESENTER	TITLE
EAST & WEST BALLROOM		
8:00 AM	J. Dettmers & C. Bronte	Discussion kickoff
8:20 AM	J. Dettmers & C. Bronte	Strategies and future research needs for the cisco re-establishment program
10:00 AM	REFRESHMENT BREAK	
10:10 AM	C. Krueger	Discussion kickoff - Strategy for reintroduction of lake trout
10:30 AM	C. Bronte & A. Muir	Strategies and future research needs for the lake trout re-establishment program
12:10 PM	M. Hansen	A summary of future research required under the theme
12:30 PM	WORKSHOP ADJOURNED	

WORKSHOP PROCEEDINGS

Workshop overview—The fourth reintroduction of native fishes workshop was held 12-14 December 2012 at Weber's Inn, Ann Arbor, MI. The purpose of the workshop was to provide a forum to discuss research relevant to lake trout, cisco, and sculpin biology and re-establishment in the Great Lakes in support of the Great Lakes Fishery Commission (GLFC) Board of Technical Experts' Re-establishment of Native Deepwater Fishes research theme (Zimmerman and Krueger 2009). The objectives of the workshop were as follows: 1) consider progress on research topics within the context of the current theme area; 2) assess the current hypotheses and identify new hypotheses, including management and applied hypotheses; and 3) consider how research results and tests of the theme hypotheses are informing management. The workshop scope was limited to the cisco and lake trout research theme hypotheses because little work has focused on sculpin, community, or ecosystem level hypotheses (Zimmerman and Krueger 2009). This report first summarizes the presentations, discussions, and priorities for cisco re-establishment followed by presentations, discussions, and priorities for lake trout re-establishment. Hypotheses from the theme paper are referenced in bold italic (e.g., ***H1***) and the workshop presentations are summarized in Appendix I (cited as AI-page number [e.g., AI-12]) and poster highlights are given in Appendix II (cited as AII-page number). Primary literature citations are limited to those either funded under the Re-establishment of Native Deepwater Fishes research theme or explicitly related to the theme.

Sixty-five attendees representing nine state, provincial, federal, and tribal governments, 10 academic institutions, two private consultants, two non-governmental organizations, and stakeholders (i.e., recreational anglers) participated in the workshop (Appendix III). The agenda featured two invited talks—one on the status of and changes in lower food webs across the Laurentian Great Lakes (Barbiero et al. AI-1) and one on potential impacts of changes in lower food webs on native fish re-establishment (Bunnell et al. AI-1)—11 cisco presentations, and 16 lake trout presentations (Figure 1). The morning of 14 December featured two separate facilitated discussions on cisco and lake trout re-establishment. Overall, participants rated the workshop experience positively and provided feedback on how to more effectively deliver the workshop in the future (Appendix IV).

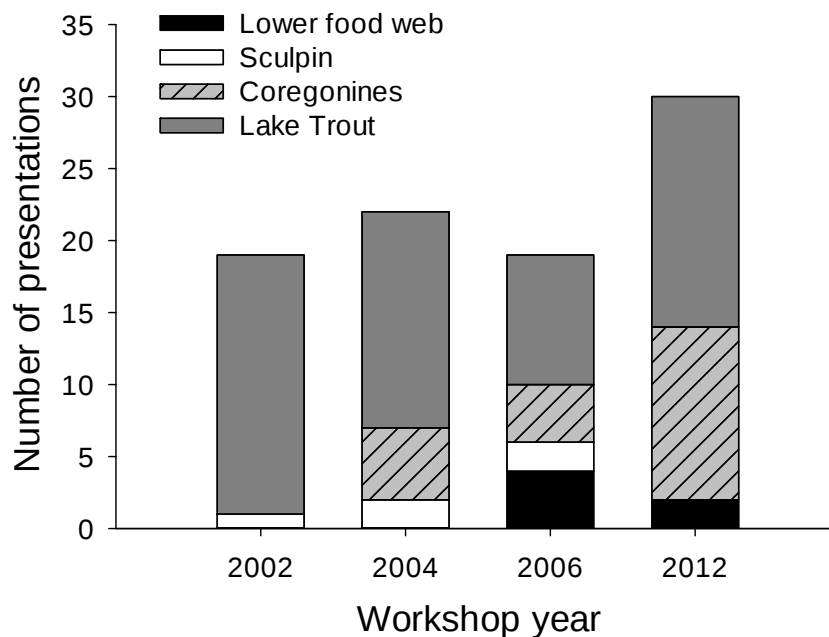


Figure 1. Number of presentations on lower food web, sculpin, coregonines, and lake trout for the four Native Fishes workshops from 2002-2012.

To avoid confusion about common names of the *Coregonus* spp., all species are referred to by their scientific names throughout this report. Cisco (formerly lake herring or lake cisco) is referred to as *C. artedi*; bloater is *C. hoyi*, kiyi is *C. kiyi*, and shortjaw is *C. zenithicus*. The generic terms “cisco” and “ciscoes” refer to all cisco species (*Coregonus* spp.) collectively and “deepwater ciscoes” collectively refers to *C. hoyi*, *C. kiyi*, and *C. zenithicus*.

CISCO RE-ESTABLISHMENT

Summary of cisco research presentations—No direct evidence shows that contemporary *C. hoyi* in lakes Michigan and Huron resulted from species introgression when deepwater ciscoes collapsed in these lakes (**H1**); however, evidence suggests that *C. artedi* from lakes Ontario and Nipigon are genetically different than those from Lake Superior (Pratt et al. AI-2).

Population regulation mechanisms for ciscoes remain largely unknown and how variation differs among species or lakes is poorly understood (**H2**), but predation likely plays some role (Bunnell et al. AI-2). Some evidence for intrinsic population regulation has been seen in *C. hoyi*, but among lakes, climate is also a likely source of variation (Bunnell et al. 2010).

Contemporary population structure of pelagic ciscoes within lakes is probably influenced by both passive dispersal of larvae and active homing behavior of adults (**H3**), but research is required to specifically address this hypothesis. Habitat quality is not likely an impediment to cisco re-establishment. Madenjian et al. (AI-3) showed that from a water quality perspective, Green Bay currently provides suitable habitat to support cisco rehabilitation in Lake Michigan. Workshop participants discussed how active fry dispersal and colonization ability may differ among *C. artedi* morphs with *C. artedi albus* and *C. artedi manitoulinus* being localized. Eshenroder (AI-7) presented a hypothesis explaining how pelagic ciscoes could be organized as metapopulations, with little homing tendencies required because of non-specific spawning site selection; therefore, it may not be necessary to stock at locations that had historical populations; but more important to re-establish schools.

Exotic planktivores (i.e., rainbow smelt, alewife, dreissenid mussels) probably have different effects on each pelagic *C. artedi* species (**H4**). Rainbow smelt predation may negatively affect *C. artedi* recruitment (Myers et al. 2009), but possibly only on small spatial scales, and adult diets of the two species overlap. Sculpins consume *C. hoyi* eggs (Bunnell et al. AI-2), but so do other species that have not been studied. Markham et al. (AI-6) showed that Lake Erie rainbow smelt populations are abundant; therefore, cisco restoration potential might currently be limited in that lake.

Pelagic ciscoes are undergoing parallel processes of differentiation in large, deep lakes (**H5**). Pratt et al. (AI-2), Howland et al. (AI-3), and Stott et al. (AI-3) presented evidence for parallel evolution of cisco morphs in lakes Great Slave, Great Bear, Superior, Huron, and Ontario, with at least two genetic groups occurring in each system and morphs being more closely related within lakes than between lakes.

Hatchery propagation is a feasible option for reintroducing pelagic ciscoes (**H6**); however, gamete collection is difficult, and feeding is challenging, but survival is high once fish begin feeding (Hanson et al. AI-4; Johnson et al. AI-4; Loftus et al. AI-5). Participants stressed the importance of developing shared standard operating procedures for cisco culture and that information transfer from northern Europe can improve culture techniques (e.g., Dettmers et al. AI-5). In general, workshop attendees saw a growing need for developing fish culture and stocking capacity to support cisco re-establishment in the Great Lakes; however, participants were cautious about jumping into large-scale culture operations at this time. Many participants, not aware of European culture history, expressed the need to invest in experimental culture techniques that were tied to a research agenda and used a common-garden approach to learning

about the relative contributions of genetics versus environment in the expression of phenotypic and physiological diversity among the cisco morphs.

Other key messages and uncertainties presented during the cisco session include the following: (1) what effect will lower food web changes have on extant cisco and how will they affect re-establishment (see Barbiero et al. AI-1; Bunnell et al. AI-1); (2) how should stakeholders be involved in re-establishment efforts (Kinnunen & Schroeder AI-6); (3) what are key knowledge gaps in moving forward with cisco re-establishment; and (4) with respect to the current theme paper (Zimmerman and Krueger 2009), new hypotheses and questions should be framed within a rehabilitation management context.

Summary of cisco discussions—Three highlights emerged from the cisco discussion: (1) progress on H5 (Are pelagic ciscoes undergoing parallel processes of differentiation in large, deep lakes?) and H6 (Is hatchery propagation feasible for reintroducing pelagic ciscoes?) is sufficient to partially answer the questions raised under the hypotheses; (2) major gaps in the understanding of cisco life history exist and should be addressed; and (3) three new hypotheses were developed on the basis of the discussions. In the following section, the discussions under each cisco re-establishment hypothesis identified by Zimmerman and Krueger (2009) are summarized and priorities are identified.

Assessment of cisco theme hypotheses—

H1. Did contemporary bloaters in lakes Michigan and Huron result from species introgression when deepwater species of cisco populations collapsed in these lakes?

The degree to which C. artedi and C. hoyi have introgressed is unknown, but could be explored in Lake Michigan, where during the 1960s population abundance of both species was low. The group agreed that the subgenus Leucichthys requires taxonomic revision.

Taxonomy—The taxonomy of the subgenus *Leucichthys* requires revision. Considerable work has been done on the complex over the past five years (Muir et al. 2011, Blackie et al. 2012, Pratt and Chong 2012, Vecsei et al. 2012, Muir et al. 2013, Yule et al. *In Press*) and a number of ongoing projects will contribute to these efforts (Pratt et al. AI-2; Howland et al. AI-3).

Introgression—The degree of introgression between *C. artedi* and *C. hoyi* is unknown. *C. hoyi* in Lake Michigan has been shifting to deeper habitat, which should be considered when selecting source populations for stocking. Bloaters have broad food habits, whereas the other deepwater ciscoes appear to be more specialized. From an introduction perspective, it makes sense that *C. hoyi* be used, but they have more potential for interaction with native remnants than other deepwater ciscoes. One debate revolves around the risk associated with restoring offshore ecological function versus the potential for hybridization with remnant *C. artedi*. This is an important management concern. In Lake Ontario, current *C. artedi* populations tend not to leave Prince Edward County area, so stocking sites could be selected to minimize overlap between stocked and remnant populations.

Opinions—Hybridization is observed in deepwater ciscoes—in an introduction program, we would avoid this, but is hybridization a normal part of the differentiation process? The conditions under which hybridization is most likely to occur should be determined.

H2: Are deepwater cisco populations (bloaters, kiyis, and shortjaw ciscoes) regulated primarily by intrinsic, density-dependent processes, or extrinsic processes?

Population regulation mechanisms for ciscoes are unknown and how variation differs among species or lakes is poorly understood, but predation likely plays a role. Evidence for intrinsic population regulation has been seen in C. hoyi, but when large ecosystem shifts occur, extrinsic factors could become important (Bunnell et al. AI-2).

Recruitment variation among morphs—Some data have been collected on cisco recruitment trends in Lake Nipigon, but only over a short timeframe. Population abundance has declined by about 50% over the last decade. Evidence suggested regional synchrony in recruitment dynamics among Great Lakes *C. hoyi* (Bunnell et al. 2010), but currently, recruitment seems to be asynchronous. Recruitment dynamics in Lake Huron are different from the other lakes, possibly due to ongoing food web change.

Recruitment regulation—The variables (e.g., sex ratio, lipid levels) regulating *C. hoyi*, *C. kiyi*, and *C. zenithicus* recruitment are largely unknown. Evidence for intrinsic population regulation has been seen in *C. hoyi*, but when large ecosystem shifts occur, extrinsic variables could become important (Bunnell et al. AI-2). Fish size has decreased—evidence from Lake Huron suggests extrinsic factors, such as predation from larger fish, are important. Alternatively, the small size of bloater could be from size-selective predation by the fishery that left only a small-sized genotype. Year-class strength for *C. zenithicus* and *C. artedi* appears synchronized in Lake Superior, suggesting that common variables regulate recruitment among the ciscoes. The notion of no interactions between *C. hoyi* and alewife (as suggested by Madenjian et al. 2008) should be revisited given recent recruitment events in lakes Huron and Michigan in the absence of alewife. Sculpin predation on *C. hoyi* eggs could be an important source of mortality (Bunnell et al. AI-2) and work on Lake Superior suggests that whitefish predation on *C. artedi* eggs is important (Stockwell et al. AII-2). The high variation in year class strength should be examined in a community context. What role do burbot play in cisco recruitment dynamics? Commercial fishermen in Lake Huron used to talk about peaks in burbot populations—are these peaks linked to *C. hoyi* population dynamics? In Lake Superior, *C. zenithicus* recover is suppressed by siscowet predation. Manipulation of predation pressure could facilitate cisco recovery.

Skipped spawning—Is spawning opportunistic on the basis of lipid stores? Is it density dependent? Can larval survival and egg quality be tracked back to maternal effects?

Opinions—During the past 5-10 years otoliths have replaced scales for aging ciscoes; therefore, our understanding of population dynamics is improving and we might have an opportunity to better address questions about year-class strength and population dynamics. Advanced age compositions and intermittent recruitment seen in Lake Superior *C. artedi* could have not supported the level of harvest documented during 1930-1960s. Efforts to collect gametes for a hatchery program should provide an opportunity to learn about spawning behavior of deepwater ciscoes.

H3. How are pelagic cisco populations structured? What are the roles of passive larval dispersal, active homing behavior of adults, and metapopulation structure?

Our understanding of cisco population structure and the roles of dispersal and homing in defining that structure in the Laurentian Great Lakes is insufficient.

Spatial scale—The spatial scale defining a cisco population or whether that spatial scale differs among morphs or species is unknown. Harford et al. (2012) presented some data on bloater seasonal habitat associations and suggested that predation pressure by lake trout and competition with non-native planktivores could be important in the observed seasonal patterns of habitat use. The ecology of body size and depth use by bloater was reviewed by Clemens and Crawford (2009). Are the ciscoes organized as metapopulations where the school functions as the habitat, and learning is through interactions with adults, or is learning innate via imprinting to habitat at the time of hatching and characterized by homing to natal spawning grounds (Eshenroder AI-7)? If ciscoes imprint on spawning grounds, when does it occur? Do their life history requirements and strategies even require homing? What is the survival advantage inferred for broadcast spawner with seemingly few specific habitat requirements? Answering these questions will determine life stage, locations, and densities for stocking (i.e., populations versus metapopulations; on top of extant populations versus in novel habitats).

The question of what spatial and density scales defines a cisco population is important and may provide some answers as to why extant populations do not expand to colonize new areas. For example, northern Lake Huron supported *C. artedii* harvests for years, but these populations have not expanded to colonize other areas. In terms of ecosystem function and services, why are extant *C. artedii* populations not providing the forage necessary to sustain lake trout and other piscivores?

Larval dispersal—Does larval dispersal (i.e., distance, direction, duration) differ among ciscoes? Do we fully understand the physical processes in terms of lake currents that would facilitate larval dispersal? For example, do we know where the deposition areas are in St. Marys River? What about currents, gyres, etc.? On a large scale, physical processes are important to understanding cisco dynamics. This research area relates to the GLFC Physical Processes and Fish Recruitment in Large Lakes research theme—hydrodynamic modeling coupled with larval dispersal. Could survival differ between those larvae advected offshore and those that remain nearshore, and if so, how do recent changes to the nearshore plankton community affect these processes?

Life history—Two major knowledge gaps in the life history of the ciscoes (pelagic and deepwater) include the following: 1) where do cisco morphs or species spawn? and 2) what happens to ciscoes between metamorphosis and recruitment to the fishery? Little is known about growth and survival after offshore advection, but year class at age-1 strength is indexed in spring bottom trawl surveys (see also Yule et al. 2007 for distribution data).

Opinion—Several hypotheses can be addressed in places where we have strong extant cisco populations and large vessels, trawling, and hydroacoustic capabilities, such as on Lake Superior—we just need to formulate the right questions.

H4. Do exotic planktivores (rainbow smelt, alewife) have different effects on each pelagic cisco species?

Information to assess the effects of exotic planktivores on ciscoes in the Laurentian Great Lakes is insufficient.

Effects of exotics—Barbiero's (AI-1) opening remarks suggest that loss of the spring plankton bloom could potentially impact survival of nearshore ciscos like *C. artedii* through reductions in prey for zooplankton and in turn less abundant food for larval fishes. These declines in zooplankton could also lead to increased predation by exotic species or increased competition with exotics for less abundant prey.

Will zooplankton community compositional changes affect native and invasive planktivores differently?
What are impacts of exotic versus native planktivores on community structure and ecosystem services?

Understanding the potential for interactions between rainbow smelt and ciscoes is critical to inform the development of stocking strategies. Lake Superior provides an information base that could be used to address this question. Smelt densities in Green Bay, Lake Huron's main basin, and Georgian Bay could be used to assess what level of smelt abundance precludes cisco re-establishment. Gobies are another benthic egg predator that could negatively impact *C. hoyi* survival if their distributions overlap (Bunnell et al. AI-2). Experimental releases of hatchery-reared ciscoes in different areas and life stages could be used to address questions about resource use, competition with non-native species, and differences in survival linked to exotic species. An adaptive management approach could help answer these questions; however, this approach would require an effective assessment approach to detect stocked fish in sufficient numbers and to assess impact and mechanism's perceived by exotic species.

Minimizing predation—Can stocking site characteristics be identified to minimize predation on cisco larvae based on emergence timing, current direction, and fish community composition? The group suggested that studying inland lakes might be a good way to address the question of non-native effects on ciscoes. Examples where smelt invaded and then cisco disappeared are common in inland Ontario lakes. A pilot project aimed at assessing the impact of smelt on ciscoes as a function of lake size should be undertaken. One participant noted that smelt effects over a gradient of densities were studied in inland Ontario lakes about 10 years ago—it would be interesting to revisit that dataset.

Opinions—Given the rebound of *C. hoyi* in Lake Huron in the absence of alewife – do we need to revisit our thinking on the impacts of alewife on bloaters? It would be nice to have a replicate system with bloater and alewife. Bloaters rebounded in Lake Michigan during the 1980s in the presence of alewife. Lake Superior currently supports both native and one non-native planktivores with similar zooplankton production and composition as is now seen in the other lakes. The levels of production the lake can sustain are lower than they were historically.

H5. Are pelagic ciscoes undergoing parallel processes of differentiation in large, deep lakes?

Pelagic and deepwater ciscoes are undergoing parallel sympatric differentiation in both large, deep lakes and small, inland lakes.

Sympatric speciation—Multiple cisco morphs occur outside of the Laurentian Great Lakes (Pratt et al. AI-2; Howland et al. AI-3; Muir et al. AII-2; Muir et al. 2011). Pratt et al. presented some evidence for differentiation of *C. zenithicus*, but not in the Laurentian Great Lakes. Despite considerable morphological variation, two spatially broad genetic groups were expressed, but these were linked to glacial refugia rather than specific ecomorphotypes. Genetic and morphological evidence suggests no support for the plasticity hypothesis. The sympatric speciation hypothesis was supported by Pratt et al. (AI-2).

Functional morphology—Although morphological variation appears parallel among lakes, the functional roles (e.g., energy transfer or interspecific interactions) of morphs may not be parallel among lakes. Do all morphs need to be re-established, or can ecological function be restored with fewer morphs? Can we predict function from morphology? How different were historical compared to contemporary morphs in terms of their ecological function? Schmidt et al. (2009) estimated trophic position and resource use among historical cisco morphs using stable carbon and nitrogen isotopes from museum fish collections. These data should be compared to contemporary data to understand niche shifts associated with non-

native planktivores and determine whether the ecological opportunity for re-establishment of cisco and shorthead cisco is feasible in Lake Erie, for example, where smelt populations remain abundant. What management approaches are available to conserve deepwater cisco diversity? If morphs fulfill distinct ecological roles, what are they and how can they be conserved?

Physiology—Do cisco morphs differ in physiology, and how do differences relate to stocking? The three *C. artedii* morphs from Lake Huron (i.e., *artedii*, *albus*, *manitoulinus*) should be reared in common-garden experiments to assess their local and physiological adaptations. Common-garden experiments can also facilitate assessment of sub-lethal stressors, such as food limitation, and how those effects vary among morphs. How do life history characteristics, such as fecundity, respond to various stressors? What are the critical life stages that are sensitive to stressors?

Spawning behavior—Little is known about the spawning habits of contemporary ciscoes. Do they differ in time (e.g., diel, season), space (e.g., depth, substrate), and behavior within and across lakes? A study using hydroacoustics and trawling targeted on suspected spawning sites to track gonadosomatic index (GSI) could provide insights into differences in spawning habits of the morphs. This information could help identify egg collection sites as well as provide a better understanding of stock structure to inform development of a stocking strategy.

Environment versus genetics—Common-garden experiments paired with experimental culture techniques can help to resolve many questions about the processes driving differentiation among cisco morphs. A hatchery environment provides opportunity to test the role of genetics versus environment in phenotypic expression. We do not know the relative roles of environmental plasticity versus genetics—when ciscoes are cultured and reintroduced, it is unknown what phenotype will be expressed. A small number of *C. hoyi* that were stocked offshore in Lake Ontario during November 2012 dove straight for the bottom, suggesting their adaptation for deep water was retained despite hatchery rearing. Some data, however, suggest that age-0 bloater are pelagic and should not have dove to the bottom. During the exploratory rehabilitation phase, we should consider raising *C. kiyi* in the hatchery.

Opinions—Perhaps inland lakes or quarries could be suitable for experimental stockings to test how stocked fish respond to their environment. Should conserving ecological function of cisco morphs be reflected in revisions to fish community objectives and rehabilitation plans?

H6. Is hatchery propagation feasible for reintroducing pelagic ciscoes?

Hatchery propagation is feasible for reintroducing pelagic ciscoes; however, some research and experimental culture is needed to refine egg collection, culture and rearing methods, determine appropriate brood sources, and develop a stocking strategy. In addition, more work must be done to determine if hatchery propagation is feasible for reintroducing deepwater ciscoes.

Egg collection & brood development—Current egg collection methods are insufficient to satisfy needs. Should a brood stock be developed? An effective way to obtain gametes is to partner with fishermen; Michigan Sea Grant (Kinnunen & Schroeder AI-6) and the USFWS (Hanson A1-4) have such partnerships in place. The Wave Glider is a new technology that can map fish distribution and help find source populations of deepwater ciscoes for egg collections when using boat-mounted hydroacoustic is not feasible. This technology is currently being tested on Lake Superior. Are we looking for optimum donor sources? Two studies focused on identifying genetically appropriate source populations for reintroductions (Fave 2007, Favé and Turgeon 2007) and one past workshop identified restoration needs

for *C. artedi* (Fitzsimons and O’Gorman 2006). *C. artedi* occur in many inland lakes adjacent to the Great Lakes. If inland populations (e.g., Torch, Elk, Charlevoix lakes) are genetically similar to remnant Great Lakes stocks, they could serve as gamete sources. Sampling inland populations would be logistically easier than sampling on the Great Lakes. Should reintroduction of morphs other than *C. artedi* and *C. hoyi* be considered? The current conceptual model starts with re-establishing *C. artedi*, but should deepwater forms, which may fulfill different ecological functions, be stocked simultaneously? For example, *C. kiyi*, which undertake deep diel vertical migrations (DVM) and cycle offshore nutrients, should be a candidate for experimental culture.

Culture techniques—Culture of the shallow-water form of *C. artedi* is feasible and Europeans have demonstrated that it can be done on a large scale with *C. lavaretus*. Culture and stocking have to be part of recovery programs. Experience with siscowet lake trout in the lab and humper lake trout in the hatchery demonstrates the importance of experimental culture for developing techniques and providing opportunity for learning (Goetz et al. AI-11).

Stocking strategy— In Europe, coregonine stocking is typically used to augment natural populations for increased food supply for humans; they are stocked on top of existing populations (i.e., augmentation). We need to examine the case histories to examine the efficacy of coregonine stocking (Dettmers et al. AI-5). The GLFC Science Transfer Program recently funded a project to assess such questions about European reintroduction efforts. Do cisco function as a metapopulation (Eshenroder AI-7)? If so, what are the implications for developing stocking strategies? Should each stocking event be considered the creation of a school of fish? This is in contrast to the lake trout restoration program, which is based on a model of lake-wide colonization attempts. Coregonine re-establishment will require more focused and strategic stocking. The depth of stocking should also be considered in relation to the morph being stocked. Should stocking occur on top of remnant populations or away from them? What are the risks? Cisco in Lake Ontario were genetically distinct from other lakes (Pratt et al. AI-2). Stocking large numbers of *C. hoyi* on top of remnant cisco or bloater populations could pose genetic risks via introgression.

Monitoring and assessment—An assessment program capable of detecting and measuring the success of re-establishment efforts is required.

Opinions—Cisco stocking is still a radical idea from a management perspective. Raceway space is available in Michigan due to the gap left by reduced Chinook salmon propagation. An experimental approach to establishing culture methods for deepwater ciscoes is necessary, but headway has been made with some current efforts to establish a *C. hoyi* brood stock.

Priorities for cisco re-establishment research—Discussions identified five priority research areas supporting cisco re-establishment.

1) ***Hypothesis 2: Are deepwater cisco populations (bloater, kiyi, and shortjaw) regulated primarily by intrinsic, density-dependent processes, or extrinsic processes?*** The group believed little progress had been made in understanding processes driving cisco recruitment dynamics; however, it was noted that contemporary density is much lower than it was historically so density-dependence may not operate at current population level. When is year-class strength set? Year class strength is probably determined by fall of first year of life. A positive correlation between spawning stock biomass and larval abundance suggests most mortality occurs after hatching, likely between hatching and the first spring. If age-0 juveniles are conspicuous in other fall sampling activities, may this be an indication of a strong year class? The North Channel of Lake Huron and Georgian Bay would be good areas to study recruitment

dynamics because these areas have healthy populations of multiple cisco morphs, yet they have not expanded to populate the rest of the lake. Why? Alternatively, Lake Superior, east of WI waters has abundant cisco populations that could be studied. What are the impediments to expansion and colonization of new areas by these populations? Is population density important to colonization potential? How does the structure of remnant or extant populations relate to the metapopulation concept? Can the study of maternal effects help answer questions regarding population regulation? What are the effects of alewife, smelt, and dreissenid mussels on recruitment? Acoustic surveys in lakes Huron and Superior show that areas with the greatest smelt densities overlap with cisco distributions. What is the effect of losing the spring plankton bloom on cisco population regulation? Historically deepwater ciscoes in lakes Michigan and Huron and pelagic ciscoes in all lakes were subjected to prolonged periods of large removals. Are contemporary intermittent recruitment patterns the same as historical patterns, and could these sustain the historical harvests observed? This question could be tested with a model. Aboriginal peoples talk about high annual variability in cisco abundance in the northern Canadian Great Lakes (Great Bear and Great Slave)—what can we learn from these “model” systems? Predictions of potential effects and interactions on the food web should be formulated before engaging in large-scale culture and stocking.

2) Hypothesis 5: Are pelagic ciscoes undergoing parallel processes of differentiation in large, deep lakes? A common-garden approach to studying cisco diversity should be employed. Understanding how cisco diversity is structured among lakes and the processes generating and maintaining that diversity will help identify appropriate source populations and predict responses of the system to stocking. Workshop participants also suggested that any laboratories rearing fish for stocking should collect and archive a fin clip for future genetic analysis. These tissues could be used to help track re-colonization and stocking success.

3) Hypothesis 6: Hatchery propagation is a feasible option for reintroducing pelagic ciscoes. Perhaps this hypothesis should be revised to include deepwater forms. Abandoned quarries should be explored as potential places to raise deepwater ciscos as they may be analogous to Finnish shallow ponds. Experimental stockings should be part of a research agenda. How will introduced forms function in the receiving environment? Can hatcheries be used to design and implement adaptive management experiments to answer these questions? How should restoration progress be measured and what lessons can we take from other systems, such as Lake Superior, where successful cisco sampling programs have been established? What does a long-term monitoring program look like? What are the impediments to and the benchmarks for success?

4) New Hypothesis: Cisco morphs fulfill unique ecological functions. New statistical and quantitative analyses, which use fatty acids and stable isotopes, could be used to help understand ecological function of cisco morphs in the Great Lakes food web, competitive interactions with non-native planktivores, and resiliency of the ecosystem to future invasions. The flexibility of morphs in filling these roles and the ecological function and potential differences among morphs should be better studied.

5) New Hypothesis: Ciscoes will adapt to climate change. The Great Lakes environment is expected to change considerably over the next century (e.g., ice cover, storm events). What are the potential effects of these changes on species with life stages that overwinter nearshore? We need to understand habitat change and loss and the potential impacts on cisco recovery to inform rehabilitation management plans.

6) New Hypothesis: Cisco monitoring and assessment will provide information on the efficacy of the re-introduction program. How best can stocked fish be detected in the wild and in harvests? What is the most effective method of tagging ciscoes? How can animals from different stocking events be identified? What will the design of a monitoring program look like?

LAKE TROUT RE-ESTABLISHMENT

Summary of lake trout research presentations—Diet diversity and bathythermal habitat use is greater in siscowet than lean lake trout, but humper diet has not been adequately assessed. Further, we do not know whether resilience to ecosystem perturbation differs among lake trout morphs (**H1**). We do know that diversity of habitat and trophic resource use in lake trout morphs changes over ontogeny (Zimmerman et al. 2009). Muir et al. (AI-8) showed that lean, humper, siscowet, and a fourth morph (redfin) were caught at all depths sampled around Isle Royale, Lake Superior, but leans were more abundant in shallow water (<50m), whereas siscowet were roughly five times more abundant than leans in deep water(>50m). These authors suggested that Isle Royale lake trout morphs may be undergoing homogenization or reverse speciation. We don't know what trophic niche is occupied by humper in Lake Superior; no new information was presented on how recruitment varies among lake trout morphs or variables influencing recruitment; and no new information was presented on response of lake trout morphs to differences in prey abundance.

Contrary to predictions, the Klondike strain of humper lake trout stocked into Lake Erie showed higher probability of sea lamprey attack reached smaller asymptotic size, but had comparable survival (~0.43; H2; Rogers et al. AI-13), compared to the other strains. This may indicate they are more resilient to sea lamprey predation. Murphy et al. (AI-11), in lab experiments, reported that both siscowet and lean lake trout from Lake Superior that were parasitized by sea lamprey showed faster growth rates and endocrine disruption, and parasitized siscowet had lower lipid storage, which suggests that parasitism affects bioenergetics. No differences were detected in parasitism rate between morphs. Murphy et al. (AI-11) also showed that laboratory-reared siscowets subject to sub-lethal sea lamprey parasitism mounted an immune response (detected by gene expression and hepatosomatic index), whereas lean lake trout showed more overt stress responses expressing genes related to circulatory compensation (e.g., hemoglobins) and bioenergetics.

The conditions under which lake trout and alewife can co-exist are unknown (**H3**); however, recent lake trout recruitment throughout Lake Huron has coincided with the near loss of alewife populations there (Riley et al. 2007). By contrast, localized recruitment has occurred in Lake Michigan in the presence of Alewife (Hanson et al. 2013). A management benchmark of $4 \text{ nmol} \cdot \text{g}^{-1}$ egg thiamine is required to avoid the sub-lethal effects and direct mortality from thiamine deficiency (Evans et al. AI-13). As alewife abundance in Lake Huron decreased, egg thiamine increased; however, the same trend was not seen in Lake Michigan, despite reduced alewife abundance. Presumably predation by alewife on age-0 lake trout has also declined during recent years. Coincident with the change in Lake Huron, lake trout parental biomass also increased.

No new information was presented under the hypothesis that metapopulation structure of wild lake trout within lakes reflects dispersal and natal homing tendencies of adult lake trout (**H4**). Outstanding questions under this hypothesis include the following: (1) does the spatial scale that defines a typical lake trout population differ among morphs; (2) does natal homing differ among morphs; (3) do fry or adult dispersal distances differ among morphs; (4) are morphs adapted to spawn at specific times or depths; (5) do wild lake trout have source and sink populations; and (6) what variables are associated with highly productive source populations?

We do not know if or how lake trout use visual, sound, and olfactory cues during spawning (**H5**); however, considerable progress on this hypothesis is expected over the next few years. An ongoing study of lake trout spawning behavior in the Drummond Island Refuge, Lake Huron identified six distinct spawning sites with very different apparent physical characteristics (Binder et al. AI-14). Preliminary analyses identified reproductive behavioral differences between males and females and possibly wild versus hatchery fish. In another study, preliminary data indicated that recently created artificial reefs in

Thunder Bay, Lake Huron attracted lake trout, but spawning activity on new reefs was erratic and colonization patterns varied among reefs (Marsden et al. AI-14). We know much more about the reproductive biology of lake trout morphs than we did a few years ago. Skipped spawning or “resting” occurs more at younger ages and more often in females from inland Ontario lakes; the proportion of adults resting can vary among years; and preliminary analysis suggests that fish from South Bay, Lake Huron also skip spawning, but more data are needed to fully understand reproductive physiology of lake trout (Morbey & Shuter AI-13). In Lake Superior, 24% of lean lake trout were resting compared to 63% of siscowets (on average; Sitar et al. AI-9). Reproduction by laboratory-reared lean and siscowet Lake Superior lake trout was synchronous with both morphs maturing during fall (Goetz et al. 2011); however, some wild siscowet populations appeared to spawn during spring (Sitar et al. AI-9). Siscowets also matured at a smaller size and older age than leans. Riley et al. (AI-11) used existing data to develop the hypothesis that lake trout spawning habitat in the Great Lakes is associated with drumlins and other glacial bedforms, but noted that more detailed bathymetry data are required to fully assess the hypothesis.

Large, deep lakes are probably characterized by parallel processes of incipient speciation of lake trout (**H6**). Several presentations described sympatric deep and shallow water lake trout morphs in several lakes across the range (see Hansen et al. AI-11; Jonas et al. AI-10; Muir et al. AI-8; Sitar et al. AI-9; and Stafford et al. AI-9). In addition, Chavarie et al. (AI-8) showed that in Great Bear Lake, as many as four morphs occur in shallow water (<50m), and Swanson et al. (AI-12) showed that in the far north, anadromous lake trout morphs occur. These recent results are consistent with those of others (Blackie et al. 2003, Alfonso 2004, Zimmerman et al. 2006, Zimmerman et al. 2007, Hansen et al. 2012) and support the hypothesis of parallel sympatric speciation. Common-garden experiments demonstrated a strong genetic basis for some aspects of morphology and physiology of siscowet and lean morphs (Goetz et al. AI-11). Goetz et al. (2010) demonstrated that growth, muscle lipid level, energy metabolism in general, and some morphological characters have a genetic basis because they differed between lean and siscowet lake trout reared in an identical laboratory environment. J. He (AI-12) highlighted the need to understand structural stability of ecosystems with continuous variations in life history parameters and developed a hypothesis based on existing life history theory.

A study on Lake Erie (Rogers et al. AI-13) showed that the humper lake trout morph can be successfully reintroduced from a hatchery environment (**H7**). Siscowet have not been experimentally cultured or stocked in any lake. We do not yet know the localities where siscowet lake trout gametes can be collected, how the hatchery environment influences early life history characteristics of humper and siscowet lake trout, how survival to maturity compares among lake trout stocked as eggs (turf incubators), fry, fall fingerlings, and yearlings, or whether spawning site selection behavior of reintroduced deepwater morphs differs from that of reintroduced leans. Evaluations of the latter are ongoing.

Summary of lake trout discussions—Three highlights emerged from the lake trout discussion: 1) progress on three hypotheses, H1 (Diet diversity and bathythermal habitat use is greater in siscowet lake trout than in lean or humper lake trout, and therefore siscowet lake trout will be more resilient to ecosystem perturbation), H2 (Is the humper lake trout morph less vulnerable to sea lamprey predation than the lean or siscowet morph?), and H6 (Are large, deep lakes characterized by parallel processes of incipient speciation of lake trout from an ancestral lean morph?) is sufficient to at least partially answer the questions raised under the hypotheses; 2) projects underway should allow us to answer several more questions raised under the remaining four hypotheses; and 3) new technologies (e.g., stable isotopes and pop-up tags) are powerful tools that should allow us to answer many of the outstanding questions. In the following section, the discussions under each lake trout re-establishment hypothesis identified by Zimmerman and Krueger (2009) are summarized and priorities are identified.

Assessment of lake trout theme hypotheses—

H1. Diet diversity and bathythermal habitat use is greater in siscowet lake trout than in lean or humper lake trout, and therefore siscowet lake trout will be more resilient to ecosystem perturbation.

We are much closer to answering this than we were a few years ago. The answers to these questions might be density-dependent. New tools, such as pop-up tags and stable isotope, offer exciting new approaches that will help address the question of diet and habitat use among the morphs.

*Trophic ecology—*Some general information is known about differences in diet, ecological niche, temperature, and depth among lake trout morphs. Diets from stomachs and stable isotopes from Lake Superior lean and siscowet have been described. The trophic ecology of humpers is unknown, yet they are being stocked in Lake Erie and Michigan. Several participants were unconvinced that the humper is a *Mysis* specialist throughout life history and indicated that more research is needed to understand the ecological role of the humper. Humper in Lake Mistassini, Quebec ate terrestrial insects even though the morph was only caught in deep water. Stable isotopes (C, N, S) are tools that integrate trophic resource use and changes over ontogeny (see Swanson et al. AI-12)—these tools should be applied to study differences in trophic ecology among Great Lakes lake trout morphs.

*Habitat use—*One participant commented that they had not seen siscowet on lean lake trout spawning reefs in Lake Superior. Little is known about the spawning habitats of siscowet. Pop-up tags could be used to answer questions about siscowet and humper habitat use. Siscowet retained pop-up tags for 3 months in the laboratory. With this technology, spawning sites, diel migrations, and much more than just depth preferences can be studied.

*Recruitment variation—*The degree of recruitment variation among morphs is unknown. Is the level of recruitment variation among Lake Superior lake trout morphs similar to that in other less-perturbed lakes (e.g., Great Slave Lake, Great Bear Lake, and Lake Mistassini)? How much recruitment is contributed by each morph to the overall lake trout population? Siscowet (shown by Bronte and Sitar 2008), and likely humper lake trout are more vulnerable to exploitation than leans, but seem more resilient to sea lamprey.

*Responses to prey abundance—*It is unknown whether lake trout morphs respond differently (e.g., diet shift, growth, fecundity) to changes in prey abundance. Does response time of predator to prey dynamics differ among morphs? Morphs likely respond to variation in their own abundance as well as prey abundance. Currently in Lake Superior, fat lean and skinny siscowet lake trout are common, suggesting differences in prey availability or differential ability to find alternate prey among individuals. In Lake Superior, lean lake trout now prey on lake whitefish, where this was rare before when rainbow smelt and benthopelagic coregonines were present in higher densities.

*Opinions—*One participant felt that microsatellites did not provide enough resolution to assess genetic diversity among morphs and suggested that single nucleotide polymorphisms (SNP) analysis should be used.

H2. Is the humper lake trout morph less vulnerable to sea lamprey predation than the lean or siscowet morphs?

Humper lake trout (i.e., Klondike strain) have comparable survival to some strains of lean lake trout in Lake Erie. Sub-lethal effects of predation differ among the

morphs, but more research is necessary to better understand differences in vulnerability and the effects of multiple stressors among lake trout morphs.

Sub-lethal effects—Sea lamprey parasitism is a major stressor, but we need to look at multiple stressors and understand how they interact. Siscowet appear less sensitive to sea lamprey parasitism than other morphs, but they do show endocrine disruption and other potential effects of parasitism. Reproductive investment should be strongly impacted by parasitism, but in Lake Champlain where parasitism is high, why is no negative response?

Survival—Differential vulnerability to parasitism may be more pronounced in Lake Superior where humper lake trout remain small and other large-bodied fishes are present. Humper lake trout (i.e., Klondike strain) in Lake Erie do not survive better than in Lake Erie do not survive better than Lewis Lake and Superior Marquette strains of lean lake trout but were similar to Seneca Lake strain (Rogers et al. AI-13). The recent survival rate for the Klondike humper was the lowest seen in Lake Erie ever.

Mechanisms—Predation by sea lamprey does differ among siscowet, humper, and lean lake trout, but the mechanism is unclear—that is, we don't know if vulnerability is related to differences in lake trout age structure, asymptotic size, maturity, or habitat use.

Opinions—Answering **H2** will help develop stocking and management strategies. Are sub-lethal effects being incorporated into population models? Understanding the effects of sea lamprey parasitism on reproductive physiology and life history is imperative to making total allowable catch and harvest recommendations. If we only stock the lake trout strain that best survives sea lamprey predation (i.e. only address one selection factor), we just shift the problem to other species. We just need to kill more sea lamprey.

***H3. Are lake trout and alewives capable of coexisting under specific conditions?
If so, what are those conditions?***

We don't know the relative effects of predation, competition for food, or early mortality syndrome on lake trout recruitment, but data suggest the two species are not co-adapted and negatively affect each other.

Thiamine—Thiamine concentration is lower in lake trout eggs from the Finger Lakes and Keuka Lake, where alewife are abundant, than lakes Ontario and Michigan. Why? In the Finger Lakes, thiaminase is a problem, but in Cayuga Lake where egg thiamine was low, embryos generated from the lake are viable. Why? Do Finger Lakes populations appear to be better at conserving thiamine during embryonic development? A strong positive correlation between lipid and thiaminase concentration has been found in alewife (Evans et al. AI-13). There was a time when Lake Michigan eggs were viable under a diet of alewives. Does the lipid/thiaminase relationship explain why Lake Michigan lake trout are no longer viable when feeding on alewife? We did see a drop in lake trout condition during 1995-1996 and condition has stayed low. Alewife might be producing thiaminase themselves—it is not necessarily coming from their diet. An issue with thiamine research is that it is laboratory based. In the wild, lake trout fry begin feeding upon emergence so they might be able to compensate for thiamine deficiency.

Predation—In general, the probability of finding lake trout fry in an alewife stomach is low because fry are rapidly digested in alewife stomachs. Under conditions when alewives are abundant relative to the number of emerging fry, detection in stomachs is difficult. When the opposite is true, a much higher percentage of alewife will have fry in its stomachs (C.C.K., personal observation). As such, understanding the role of alewife predation on lake trout recruitment is complicated and deserves more attention.

Competition—A third possible, and unstudied, effect of alewife on lake trout fry is competition for food.

Opinion—It appears that two camps exist—thiamine versus predation as the mechanism influencing lake trout mortality—but these mechanisms are not mutually exclusive and the dynamics are complicated. Regardless of the mechanism, reduced alewife abundance appears to benefit lake trout.

H4. Does metapopulation structure of wild lake trout within lakes reflect dispersal and natal homing tendencies of adult lake trout?

We have identified spawning locations for lean lake trout, but know next to nothing about where the other morphs spawn. The degree of reproductive isolation or gene flow among morphs has not been quantified.

Homing—Mark-recapture studies on lakes Superior and Michigan show that most adult lake trout are recaptured within 80km of their tagging location, although some trout will travel long distances. In lakes Superior and Michigan, we know that lake trout have high fidelity to spawning sites, but we do not know if it is truly homing—populations do move and co-mingle. Movement rates are large enough to generate sufficient gene exchange and segregation for lake trout to be structured as a metapopulation. Similarly, genetic structure of lake trout in Great Bear Lake suggests a small degree of migration between populations is sufficient to result in metapopulation structure.

Siscowet and humper spawning behavior, homing, and dispersal patterns are unknown. Specific sites for siscowet have yet to be discovered, but spawning aggregations of humper are known and sampled periodically for gametes to support USFWS hatchery brood stocks. Recent studies in Thunder Bay, Lake Huron (see Marsden et al. AI-14) and Drummond Island (see Binder et al. AI-14) may help answer questions about homing in the lean morph. Preliminary data show that individual spawning fish do move among reefs within a year and return to the same site over multiple years, and supports previous mark-recapture studies on Lake Superior, and elsewhere. Preliminary data suggest that stocked and wild fish may show differences in reproductive behavior (Binder et al. AI-14). Newly constructed spawning reefs in Thunder Bay were slowly colonized. Why did it take fish so long to find these habitats? Hatchery fish could be learning from wild fish that show homing behaviors.

Structure—Population structure could be related to distribution and availability of spawning habitat. For example, spawning habitat in the Apostle Islands, Lake Superior is a patch work of both onshore and offshore reefs that supported many spawning aggregations, with some interchange among them. Are these small groups functioning independently, or as a metapopulation? We don't know if lake trout show source-sink dynamics.

H5. Does lake trout spawning require visual, sound, and olfactory cues? If so, what are these cues?

We do not know if or how lake trout use visual, sound, and olfactory cues during spawning; however, considerable progress is expected on this hypothesis over the next few years.

Pheromones—The Commission has funded a project to extract and study lake trout pheromones, but results are a few years away. Is there anything about the way hatchery fish are raised that could affect the development of their olfactory system?

Behavior—Muir et al. (2012) synthesized and presented an updated lake trout spawning behavior model initially presented by Esteve et al. (2008). These authors summarized the uncertainties in spawning behavior and some of the hypotheses are currently being tested. Social cues, such as jumping out of water, should be added to the behaviors important for spawning. Preliminary data from the Thunder Bay, Lake Huron artificial reef project suggests behavioral differences between wild and hatchery spawners that could be evidence for social cues. Little is known about behavioral or reproductive differences among the morphs; do they mate assortatively?

Spawning habitat—Spawning was observed at six sites with very different physical characteristics (Binder et al. AI-14). One interesting behavior was spawning on gravel at the scoured base of giant boulders. Possibly, accelerated water due to the Venturi effect provides current and oxygenates embryos around these large boulders. These data show that slope and substrate size are not the only important characteristics of spawning locations. The key may be substrates with large interstices or substrates that generate enough water flow to oxygenate embryos. Spawning in Elk Lake, Michigan is focused in two areas that don't really have reef structure; could these fish be orienting on current or upwellings?

Opinion—Stocking to reestablish spawning populations on offshore reefs is required, as is already being done in Lake Michigan (Bronte et al. 2008, Dexter et al. 2011). If you don't stock them, the fish won't find the habitat on their own (Jonas et al. AI-10; Matthews AII-2; Krueger et al. 1986; Bronte et al. 2007(Bronte et al. 2007)).

H6. Are large, deep lakes characterized by parallel processes of incipient speciation of lake trout from an ancestral lean morph?

Large, deep lakes are probably characterized by parallel processes of speciation with sympatric deep and shallow water lake trout morphs occurring in several lakes across the range.

Genetics versus environment—On the basis of common-garden experiments, we know that differences in some aspects of morphology and physiology between lean and siscowet lake trout have a genetic basis; this is unknown for humpers, but could be inferred from the morphology of animals from paired stockings in lakes Erie and Michigan. The level of genetic differentiation among the morphs is only partially understood and little information on reproductive isolation or spawning habits of the morphs is available.

Diversity—Are siscowet and lean morphs hybridizing in Lake Superior? Older data on lipid content and fatty acids indicate a change. Are these fish with intermediate lipid levels a valid morph that occurred historically? Some participants felt that morphs other than lean, humper, and siscowet occurred in Lake Superior and that we should put more effort into quantifying the diversity (but see Muir et al. AI-8).

Some fish in Great Bear Lake appeared to function and look like siscowets, but they were not buoyant (i.e., did not have high body lipid content). One explanation for the occurrence of deepwater morphs with low fat content is that there is not enough energy in the system to accumulate fat. Populations in Great Bear and Great Slave lakes are old compared to the recently established populations in the western lakes (i.e., Yellowstone)—this could be an interesting comparison. More than one type of siscowet may occur in Great Slave Lake—do we see this elsewhere? Bronte & Moore (2007) showed that shape differences among siscowets from Lake Superior were related to capture location. Not only could siscowets be using

fat for buoyancy, but also as an energy reserve. We do see parallel evolution of deep-water morphs in multiple lakes, but lipids might be used for different purposes in these systems. Leans appear to use their lipids for reproduction whereas siscowets accumulate it in the body and use it to reduce specific gravity—these differences were shown to be influenced by genetics (Goetz et al. 2010).

Life history dynamics—Life history studies are underway to quantify (e.g., age structure, growth, age at first maturity) among lake trout morphs within and among lakes. Hansen et al. (2012) reported differences between lean and humper-like lake trout morphs from Lake Mistassini, Quebec. Asymptotic length does not differ between hatchery-reared fish in the Great Lakes and wild lake trout from Lake Mistassini, but growth rates did differ. This is not surprising because asymptotic size is likely genetically driven, whereas growth rate is more plastic.

Food web—The link between the shallow- and deepwater food webs represents a gap in knowledge. The humper morph could represent a major source of energy coupling between near- and offshore habitats. How might the production of one morph or depth zone influence the other?

Opinion—The northern Canadian Great Lakes provide an example of the lake trout diversity that historically occurred in the Laurentian Great Lakes.

H7. Can deepwater lake trout morphs be successfully propagated and reintroduced from a hatchery environment?

Deepwater lake trout morphs can be propagated, maintained, and reintroduced from a hatchery environment, but little is known about how the hatchery environment influences early life history characteristics, and production scale hatchery programs have not been undertaken, so a lot of uncertainties remain.

Gamete collection—The U.S. Fish and Wildlife Service has been collecting gametes and maintaining a brood stock for Klondike Reef (Lake Superior) humper lake trout since 1996. Little is known about locations siscowet lake trout that could serve as sources for brood stock development.

Culture—The U.S. Fish and Wildlife Service maintains a humper brood stock and has stocked them into Lake Erie since 2002 and begun in 2012 reintroducing them into Lake Michigan. Problems encountered were mostly associated with keeping brood stock reproductively viable (resting females, low eye-up, etc.) rather than rearing. In 2012, increased eye-up rates and egg expression were observed with treatments of females with luteinizing-hormone-releasing hormone (FWS, unpublished data). We know little about how the hatchery environment influences early life history characteristics of humper and siscowet lake trout. Goetz et al. (AI-11) and previously by the Michigan Department of Natural Resources (Stauffer and Peck 1981) showed that siscowet can be reared and maintained in a hatchery. We need to evaluate culture issues for each morph to be efficient at scaling up for production.

Stocking—While much is known for lean lake trout, little is known about how survival to maturity compares among other lake trout morphs, such as humpers, stocked as eggs (turf incubators), fry, fall fingerlings, or yearlings.

Priorities for lake trout re-establishment research—Time constraints prevented a thorough priority ranking of lake trout research hypotheses during the workshop; however, three key areas of research for lake trout re-establishment were identified.

1) Spawning behavior—A better understanding of spawning behavior and cues to spawning is required to improve stocking strategies and re-establishment plans. Much of this has been proposed before. How can we improve the effectiveness of stocking and get fish to use better spawning areas (see Bronte et al. 2007)? Should we be investigating alternative life stage stocking? How do various life stages relate to cues? How do lake trout relate to drumlins and other glacial land forms and does the hydrodynamic interaction with geology create acceptable spawning habitat? Detailed bathymetry is lacking, but data are available for certain areas and available side-scan sonar data need to be assimilated.

2) Community interactions—A number of potential impediments to lake trout re-establishment remain. Do alewife and round goby currently represent impediments to restoration? What is the interaction between deepwater lake trout and burbot? Do their diets differ? We have come to accept the current abundance of burbot as normal, but this might not be the case. How might reintroduction of deepwater lake trout affect burbot? A resistance to inter-basin transfers of live fish is apparent, but what about movement of animals within a basin? We could move extant populations as sources for other areas and use new tagging technology (i.e., pop-up tags) to address some interesting questions about spawning and homing. How do *Hemimysis* interact with age-0 lake trout and affect their growth and survival in nearshore spawning areas? Do they serve as a food source, a competitor for food, or as a negative stimulus? Swarms of *Hemimysis* aggregate in areas and fish are not observed associating with these swarms.

3) Ecosystem dynamics—The Re-establishment of Native Deepwater Fishes research theme paper (Zimmerman and Krueger 2009) outlines four hypotheses and fourteen questions associated with community and ecosystem processes structuring deepwater food webs in the Laurentian Great Lakes. Little work has been completed on ecosystem-scale dynamics and how these affect the inner circles in the re-establishment conceptual model (e.g., predicting effects of climate change; Zimmerman and Krueger 2009 pg. 1354). Changes in primary and secondary production in the offshore food web could influence our way of thinking about the ecosystem.

A SUMMARY OF FUTURE RESEARCH REQUIRED UNDER THE THEME

On the basis of the workshop presentations and discussions, M. Hansen provided a synthesis and wrap-up of the workshop. What follows is an attempt to capture the key messages from this summary talk. The International Conference on Restoration of Lake Trout in the Laurentian Great Lakes (RESTORE) was held in 1993—the mood among biologists and managers was not good at that time. Lake Superior was the only lake showing any sign of recovery. People felt that the recovery had nothing to do with stocking, rather populations rebuilt from remnant wild populations. Time has shown that stocking did help restore lake trout in Lake Superior and this success has changed our thinking about the role of hatcheries in restoration. No one could have predicted what happened in Lake Huron in recent years. Chuck Krueger's theory about lake trout interactions with alewife seemed crazy back then—time has shown he was on to something. In considering reintroduction of cisco and deepwater lake trout forms, we must think back to the original lean lake trout introductions. The program began as a mad scramble; fish were being dumped everywhere; but eventually, we came back to ask critical questions about how and where these fish should be stocked. We gained so much by slowing down and doing our homework, paving the way for the hatchery system to provide successful reintroductions. In terms of recent efforts, we should learn from our past; do the inventory of what forms of cisco we have and identify the impediments to re-establishment; and then thoughtfully propose rehabilitation plans. We must develop a strong means for measuring progress—this is crucial. We may be moving forward too quickly and not heeding the lessons we learned with lake trout.

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APPENDIX I. PRESENTATION SUMMARIES

Wednesday, December 12, 2012

LOWER FOOD WEB CHANGES

Status and changes in the lower food web across the Laurentian Great Lakes

R. BARBIERO, B. Lesht, G. Warren, T. Nalepa, D. Dolan, T. Johengen, and D. Warner

Barbiero presented results from the long-term monitoring program of the U.S. Environmental Protection Agency's Great Lakes National Program Office. Water quality data from 1983-present and lower food web biological data from 1998-present was analyzed. Trends in total phosphorus, chlorophyll, Secchi depth, and zooplankton biomass and community composition suggest that lakes Michigan and Huron shifted toward more oligotrophic conditions than in the past and are becoming similar to Lake Superior. In lakes Michigan, Huron, and Superior, zooplankton biomass has shifted so that a greater proportion is located deeper in the water column. The benthic amphipod *Diporeia* disappeared from shallow areas of lakes Huron and Michigan and was completely absent from Lake Ontario. The cause of this decline is unclear, but it has been linked to increases in dreissenid mussel populations. Trends in *Mysis* populations appeared stable, but data are insufficient.

Questions and Discussion

- If major changes in nutrients and chlorophyll were not observed in Lake Ontario, then why did the zooplankton community change?
 - Lake Ontario seems to be a different case than the other lakes. It typically does not have a spring phytoplankton bloom like the other lakes once did, the historical zooplankton community was different to begin with, and the crash in *Diporeia* populations was more extreme. It is possible that the other lakes are driven more by bottom-up processes while Lake Ontario is driven by top-down processes.

Potential impacts of changes in the lower food web on native fish re-establishment

D. BUNNELL

Bunnell presented trends in prey fish communities using data from numerous sources, and speculated on the potential ramifications of lower food web changes for native fish restoration. In particular, he examined how changes in invertebrate composition, distribution, and abundance have influenced fish diet composition and growth, and how changes in non-native alewife and smelt have influenced the recruitment potential of native fishes. Prey fish biomass has declined in all the Great Lakes except Lake Erie. Bunnell speculated that new benthic-oriented food webs will benefit fishes that can eat dreissenid mussels or show diet flexibility. Likely "winners" include round gobies, lake trout, juvenile bloater, and slimy sculpins, whereas deepwater sculpins and adult bloater might be "losers" in this new ecosystem. Further work is needed to understand recruitment bottlenecks for cisco and bloater. Bunnell concluded that predation is more likely than competition to drive native fish restoration and sustainability, and that top-down forces are likely to be more important than changes in lower trophic levels.

Questions and Discussion

- What might be the cause of the observed lower lipid content in adult bloaters and deepwater sculpins?
 - This might be an issue of quantity, not quality, of diet. The shift from larger diatoms to smaller diatoms and lower overall productivity could also impact lipids.
 - *Mysis* status and condition are largely unknown, but some evidence points to low lipids in Lake Huron. If they are declining or in poor condition, this would have important ramifications for native deepwater fishes.

CISCO RE-ESTABLISHMENT

Sculpin predation on bloater eggs—is it sufficient to drive bloater recruitment variability?

D. BUNNELL, J. Mychek-Londer, W. Stott, J. Diana, and C. Madenjian

Bunnell et al. examined whether benthivore egg predation explained variation in bloater recruitment among years. The project used a combination of field sampling for diet analysis and laboratory experiments to estimate the number of bloater eggs consumed per year by sculpin, and then extrapolated this to the population level. The results suggested that sculpin predation did not explain poor bloater recruitment for the 1995-2005 year-classes, but sculpin predation (especially by slimy sculpins) in recent years exceeded 40% of bloater egg production and could contribute to recruitment bottlenecks. This would be particularly important to consider if apparent sculpin recovery continues in Lake Ontario.

Questions and Discussion

- Have you considered the interaction between cannibalism and predation by sculpins?
 - We plan to look at this, but we need to determine what rates of cannibalism to use.
- Why did you use age-3 recruits to measure bloater recruitment? Might that be part of the problem in identifying relationships?
 - Age-3 fish provide a less biased estimate because of catchability. I don't think the pattern would change if you looked at other ages.
- With expanding bloater populations, perhaps bloater eggs are now spread out over a larger area. This would mean lower egg density in any one place, which could set the stage for density-independent effects.
 - We had not considered this. Very little is known about deepwater spawning behavior. When we found bloater eggs there tended to be few, whereas deepwater sculpin eggs would be in the hundreds – this is consistent with your theory.

Patterns of morphological and genetic diversity among ciscoes in deepwater lakes

T. PRATT, J. Turgeon, A. Bourret, S. Reid, A. Muir, C. Krueger, J. Reist, and K. Howland

Pratt et al. used both genetic and morphological approaches to describe cisco diversity across their range. Results supported the hypothesis that pelagic ciscoes are undergoing parallel processes of differentiation in large, deep lakes. Weak evidence for genetic differentiation of pelagic ciscoes in the Great Lakes was observed, but strong evidence of similar ecomorphotypes was found in some, but not all lakes outside the Great Lakes basin.

Questions and Discussion

- Could the pattern instead be explained by sequential invasion of the same genotype?
 - There is evidence for this in some of these lakes, but the data suggest that differentiation occurred in lakes after invasion.
- Is the use of Great Slave Lake as an “unperturbed” comparison valid? There is a lake trout fishery in Great Slave Lake, particularly in the Yellowknife area.
 - We don’t believe it has been perturbed at the level where we would expect to see a genetic signal. Also, we do not see evidence of genetic differentiation in several inland lakes where no fishing has ever occurred.

Phenotypic diversity of cisco in Great Bear Lake, NT: variation in morphology, diet and demographics

K. HOWLAND, C. Gallagher, D. Boguski, J. Reist, L. Chavarie, and S. Wiley

Howland et al. examined the morphological, meristic, life history, and dietary characteristics of ciscoes from Great Bear Lake, Northwest Territories to test the hypothesis that multiple forms, including shortjaw cisco, occur in the lake. The work represented the first comprehensive account of distinct cisco morphotypes in Great Bear Lake and is part of a broader, ongoing lake-wide analysis. The results of the research suggested that deepwater cisco were clearly distinct from shallow water types, supporting the parallel evolution hypothesis and suggesting a northern range extension for *C.zenithicus* or a *C.zenithicus*-like form.

Morphometric and genetic analysis of cisco (*Coregonus artedii*) from the Great Lakes

W. STOTT, D. Yule, M. Ebener, R. Claramunt, and S. Moore

Stott et al. used photographs of contemporary ciscoes to determine if and where historic forms persist. The project also examined if the morphological divergence was accompanied by genetic divergence. Results suggested that Lake Superior and Lake Ontario ciscoes were classified as *C.artedii* and Northern Lake Huron ciscoes were a mix of deep-bodied *C. albus* and *C. manitoulinus*. The largest genetic discordances occurred among lakes. Further work will compare contemporary and historic DNA samples and examine stable isotopes to provide more information about habitat use and trophic ecology. This information will be useful to define niche- and genetic-appropriate donor populations for reintroductions.

Questions and Discussion

- Are ciscoes lacking in the main basin of Lake Huron?
 - Historically, the *C. artedii* form was found in the main basin. We did not sample there, but we might expect to see that form if we did.

Spawning habitat unsuitability: an impediment to cisco rehabilitation in Lake Michigan?

C. MADENJIAN, E. Rutherford, M. Blouin, B. Sederberg, and J. Elliott

Madenjian et al. compared overwinter cisco egg survival and water quality characteristics, including dissolved oxygen, between a control site (St. Marys River) and a “treatment” site (Green Bay, Lake Michigan). The results showed that overwinter water quality and cisco egg survival were sufficiently high in lower Green Bay during the study years to suggest that adequate spawning habitat for ciscoes occurs in

the bay. In summer, dissolved oxygen concentrations in Green Bay were low enough to affect mayfly recovery, but hatched larval ciscoes should be able to actively avoid the hypoxic areas. Madenjian et al. suggested that Saginaw Bay would be a good location to repeat this study.

Questions and Discussion

- Was low dissolved oxygen in summer widespread or localized?
 - The low oxygen water mass actually moved from north to south through the bay and covered a large area. This is similar to what is observed in Saginaw Bay.

Experience and recommendations for bloater egg takes

D. HANSON, M. Holey, T. Treska, R. Gordon, and P. Haver

Hanson shared improved techniques for enhancing bloater egg takes that should help advance the goal of stocking 500,000 juveniles into Lake Michigan by 2015. Previous methods resulted in inconsistent fertilization rates, whereas new methods used stricter criteria for egg ripeness and 1:1 spawn pairings and resulted in better fertilization rates. The authors speculated that in the future, bottom trawling could be used instead of gillnetting to further improve egg collection methods.

Questions and Discussion

- The problem of getting water in the fishes' body cavities might not be a result of collection methods; it has been reported as a potential epizootic (i.e., waterbelly) in Lake Huron and thus might be disease related.
 - All samples sent to the fish health lab came back negative for disease screening, but this is worth further investigation.
- What is the primary purpose of the 1:1 spawn pairing method?
 - These fish might be used in a brood stock and we want to maximize genetic diversity.
- Are you collecting genetic data on the parents to understand the characteristics that result in higher hatch rates?
 - Yes, fin clips were collected for genetic analysis; however, many more fish were collected than anticipated so it might not be possible to run all the samples.

Pilot cisco egg take and culture study, Lake Huron, 2006-2011

J. JOHNSON, D. Fielder, M. Hughes, and R. Espinoza

Johnson shared experiences and lessons learned from a pilot study to develop and refine cisco culture practices. Egg stock was taken from a known spawning site in the St. Marys River, which was appropriate for the pilot study, but probably not the right location for developing nearshore or offshore stocks due to low abundance and river spawning life history. Results in all stages of the study, from egg take to culture to stocking and recovery were promising, and the experience will allow techniques to be refined and improved for future efforts.

Questions and Discussion

- Did you take photographs of the fish you recovered? What form did they look like?
 - Yes, we took photos and the fish looked mostly like *C. artedi*, with a few that looked like *C. albus*.

- Did you raise any fish in the hatchery to look at morphology?
 - We raised fish only for oxytetracycline quality control. We did not take genetic samples.
- Did you see benthivorous fish congregating in the spawning area?
 - We did catch some longnose and white suckers, but not many.
- The disinfection procedure you used was very rigorous. Is this standard?
 - We used the protocol for Chinook salmon. There was concern about VHS because of cases in the Apostle Islands in Lake Superior.

Thursday, December 13, 2012

CISCO RE-ESTABLISHMENT continued

Ontario's experience developing husbandry practices for *Coregonus hoyi*—lessons learned and next steps

K. LOFTUS, T. Drew, and G. Hooper

Loftus shared experiences rearing *Coregonus hoyi* at the White Lake Fish Culture Station in eastern Ontario beginning in 2011. The whitefish-rearing protocol was used as a starting point and gametes were collected from Lake Michigan. Issues with egg quality and larval feeding were encountered and solved during 2011, with a final survival rate of 90% by the fifth year-class. Overall objectives of the 2012 efforts were reduced egg loss due to pressure change, increased egg fertilization rate, and improved survival and growth following hatch. The researchers found that egg quality and viability was substantially improved due to an improved spawning process, but some spawners were still much better than others. Husbandry improvements increased survival from hatch to end of early rearing by a factor of three compared to 2011.

Coregonine culture and assessment in Finland—possible insights for North America

J. DETTMERS, G. Isbell, M. Holey, R. Gordon, and S. LaPan

Dettmers shared insights gathered from a recent visit to Finnish coregonine culture facilities. The objective of the initial visit was to understand the scope of Finnish propagation for coregonids, which has been conducted since the 1940s, and to evaluate whether additional information transfer would be helpful. The visiting team of scientists from North America gained several insights, including the importance of flow-through water sources, natural temperature cycles, and grow-out ponds. The appropriate age for stocking seems to be fall fingerlings of at least 8cm, with fish stocked primarily into rivers. Dettmers concluded that large-scale rearing of coregonids and holding broodstock are feasible for the Great Lakes region. A second trip to Finland is planned to gain further insights from European culture and stocking expertise.

Questions and Discussion

- What is the closest correlate to bloater that the Finns culture?
 - Vendace.
- What are the the depth preferences of vendace? Are they correlates to bloaters in this sense?

- The Finns do not have a deepwater analogue to Great Lakes deepwater coregonids. There are deepwater whitefish morphs that spawn at 20-30m, but most of the fish they culture spawn in shallow water and rivers.
- Is there any intensive pond rearing being carried out in Finland?
 - The government is doing a small amount of experimentation with this, but it is at early stages. There are some private partners in the food fish industry doing this on a larger scale.
- Is organic or inorganic fertilizer used in the grow-out ponds? Do they see variability in production?
 - They use inorganic fertilizer, and they do see variability. They sometimes have to re-fertilize or spot fertilize the ponds.

Understanding and engaging stakeholders in coregonine reintroductions

R. KINNUNEN and B. Schroeder

Kinnunen shared results of workshops held in 2005 and 2010 with the goal to bring fisheries research and management science to Lake Huron communities and stakeholders. The workshops were coordinated with research and management agency staff, along with the Michigan Department of Natural Resources (MDNR) Lake Huron Citizen Fishery Advisory Committee. The workshops were opportunities not just for outreach, but also to gather information through facilitated discussions and written surveys. In 2005, stakeholders identified declines in the forage fish base as the most important issue facing the Lake Huron fishery. In 2010, a strong majority of stakeholders agreed that the MDNR should invest resources in rehabilitating native forage fishes, including ciscoes; a majority also agreed that the MDNR should divert resources from raising game species for this purpose. Kinnunen emphasized that committed and supportive stakeholders are critical assets to the native fish restoration discussion, and that the public must be involved in the early stages of discussion.

Questions and Discussion

- How does the Michigan DNR respond to this input?
 - There are people working in the field who are very committed to rehabilitation. The challenge is communication between Lansing and the field.
- Are stakeholders dissatisfied with anything in particular?
 - Stakeholders want to see changes enacted right away and don't always understand the process required.

The future of cisco restoration in Lake Erie

J. MARKHAM

Markham discussed issues surrounding restoration of cisco in Lake Erie, which were once abundant. Over the past decade, few ciscoes have been reported in commercial catches and they have not been caught during agency sampling. Conditions in the lake are currently more suitable for cisco than they were several decades ago – other native species, such as whitefish and burbot, have increased in abundance, rainbow smelt abundance has declined below the long-term average, and water quality in the eastern basin has improved. Markham also discussed impediments to cisco restoration in the lake. Perhaps the most critical impediment is rainbow smelt, which are still extremely abundant even though the population has

declined. Lake Erie is managed for percids that eat rainbow smelt; therefore, concern has been raised about reducing the forage base without knowing if cisco restoration will be successful. Markham outlined a proposed approach for restoration that would require assessment of the current population and genetic testing to determine if remnant stocks exist, and would recommend stocking only if spawner abundance is found to be a limiting factor for restoration.

Questions and Discussion

- Do phosphorus levels in the lake need to decline for restoration to be successful?
 - This is difficult to answer and it depends on where stocking would occur. Water quality in the eastern basin is good, but the western basin is hypereutrophic. This could present a problem if the western basin is used as a spawning/rearing area – but perhaps it also means more food availability.
- What makes you think you are missing the ciscoes with current agency sampling?
 - We don't use midwater trawling or suspended gillnets, so we might be missing fish in summer in the eastern basin. The Ontario Ministry of Natural Resources does use suspended gillnets with good coverage in Canadian waters, but they haven't sampled a cisco yet.

Implications of the metapopulation concept for cisco reintroduction

R. ESHENRODER

Eshenroder introduced the metapopulation concept as an alternative model to natal homing for cisco. In this model, which has been proposed for Atlantic herring, spawning, feeding, and wintering distributions are not innate and instead juveniles learn migration routes from adults. Eshenroder suggested that the metapopulation concept could explain trends observed in the Great Lakes; for example, a loss of “tradition” (transmission of migratory patterns across cohorts) could explain the cisco population collapse in Lake Erie. The metapopulation concept has several potential implications for cisco reintroduction, including the need for a stocking strategy that will establish new schools and prevent adult schools of extant populations from attracting stocked juveniles. Also, egg stocking is only appropriate if natal homing occurs, so life stages should be stocked that maximize survivorship to the advanced juvenile stage.

Questions and Discussion

- Have you thought about pheromones and how that might play a role in communication of schools and spawning aggregations?
 - This seems like the most likely way that juveniles would locate adult aggregations. With menhaden you can see “oil slicks” where schools have been, so there is a lot of material coming out of a school.
 - This might also be part of the social learning that goes on with juveniles.
- You discounted egg stocking if homing is not the mechanism – what difference does it make if all the other “rules” hold true?
 - It would be difficult to get the number of eggs you need to overcome the bottleneck.
- There isn't much genetic differentiation in coregonines; walleye fry are just as small but their populations have a lot of genetic differentiation, so that points to natal homing.

- The metapopulation concept does not preclude natal homing; if tradition goes on long enough, natal homing could develop.
- Atlantic herring show some seasonality and shifting of spawning due to climate change. In Lake Superior there have been reports of early spawners. Is there a time component to the metapopulation concept as applied to cisco spawning?
 - I am not aware of spring-spawning ciscoes as has been observed with Atlantic herring. Dwarf herring and regular herring have been produced from the same spawning area and same populations but at different times.

LAKE TROUT RE-ESTABLISHMENT

Understanding sympatric diversification in lake trout: exceptional shallow-water diversity in Great Bear Lake, NT

L. CHAVARIE, K. Howland, W. Tonn, and C. Gallagher

Chavarie examined diversity of shallow-water lake trout in Great Bear Lake, Northwest Territories by drawing associations among morphology, food habits, habitat use, movement, and life history. Great Bear Lake is relatively pristine with low fishing pressure compared to the Laurentian Great Lakes, so it would be expected to have a full, intact assemblage of lake trout morphotypes and could be used as a model system. The project identified three separate lake trout morphs, with a rare fourth morph. There was significant morphological variation within each morph across lake arms, which suggests parallel evolution among arms or several colonization events. Stable isotopes and fatty acid analyses revealed differences in diets among morphs. These results support the hypothesis that large, deep lakes are characterized by parallel processes of lake trout speciation.

Questions and Discussion

- Can you speculate about the functional use of the thick jaw on the fourth morph?
 - We called these fish “bulldogs” because of the appearance of the jaw, but found their diet to be more pelagic, which was unexpected. These fish are seen in higher arctic areas as well and the functional use of the jaw is not clear.

Lake trout diversity at Isle Royale, Lake Superior

A. MUIR, C. Krueger, M. Zimmerman, C. Bronte, H. Quinlan, and J. Glase

Muir determined whether three currently recognized lake trout morphs occurred around Isle Royale in Lake Superior, and if there was evidence that historic morphological diversity persists at this site. Lean, humper, siscowet, and a fourth morph (redfin) were caught at all depths sampled, but leans were more abundant in shallow water (<50m), whereas siscowet were roughly five times more abundant than leans in deep water (>50m). The level of differentiation among morphs was low compared to historical anecdotal accounts from the Great Lakes as well as unperturbed systems where the distinction among morphs is high. A historical fingerprint of the diversity that once occurred in the lake remains evident, but it is less distinct as a result of low population numbers during the 1950s, introgression as a result of hybridization, and ecological reorganization. High levels of variation within morphs could be the result of ecological bottlenecks or ecological release from some of the pressures that led to reduced diversity.

Questions and Discussion

- Is the release from pressures independent from homogenization?
 - Not necessarily.
- Is there historical data that could be analyzed to see if the morphs grouped more clearly in the past?
 - We do have data from 1995, but the analysis is limited by the small sample size of 100 fish.

Differences between lean and siscowet lake trout: what we have learned from sampling wild fish in Lake Superior

S. SITAR, R. Goetz, C. Bronte, C. Murphy, and P. Swanson

Sitar et al. investigated the reproductive biology of lean and siscowet lake trout by sampling monthly in Lake Superior. Temporal overlap in fall reproduction of leans and siscowets, and also evidence of lake trout spawning in spring in two offshore areas (Isle Royale and Stannard Rock) was observed. A considerable proportion of fish underwent skipped spawning, particularly siscowets, with an average of 63% of females skipping spawning in a given year. Siscowet matured at smaller size and at an older age than lean lake trout. The results suggest that siscowets have a conservative (frugal) reproductive strategy that relies on management of energy balance. On the other hand, leans are more conventional in their reproductive strategy.

Questions and Discussion

- Do the fish that skip spawning in the fall go on to be spring spawners?
 - This is possible, but spring spawners might be staging in different areas than we sampled. There is no evidence that spring spawners are widespread.
- Is it possible that siscowets have become more frugal due to declines in lipid levels since the 1950s and 1960s?
 - Perhaps, but we are describing them as frugal in the context of comparing them with leans. Unfortunately we don't have a long-term data set that allows us to look at historical reproductive status.
- Do you have any condition data? Perhaps they skip spawning because they are in poor condition.
 - We did not look at this specifically; we did collect data on sea lamprey wounding the data were insufficient to do a proper analysis.
 - The histology shows some maturation around July/August where eggs start to develop and then degenerate. So the decision to skip spawning seems to be made around this time.

Introduced lake trout exhibit life history and morphological divergence

C. STAFFORD, M. McPhee, L. Eby, and F. Allendorf

Stafford examined whether high densities of fish and the presence of *Mysis* induce life history diversification by depth of lake trout in Flathead Lake, Montana. Deepwater fish were stunted in growth and matured at smaller sizes than shallow-water fish, and the two types showed morphological differences. Diet also varied, with deep dwarfs consuming mostly *Mysis* and standard leans becoming piscivores. However, the two depth groups did not differ genetically or in lipid levels. These results support the hypothesis that life history and morphology have a plastic component in addition to a genetic

component. Stafford suggested that in the Great Lakes, the restoration of ecosystem process is critical to lake trout restoration.

Questions and Discussion

- There was a study on Lake Louisa of a population of lake trout that fed on invertebrates. Some fish escaped stunting and began to feed on other lake trout, growing very large.
 - We did see some cannibalism in Flathead Lake.
 - This has been seen in other lakes where fish with bigger mouths are able to start feeding on other fish and grow large. These giants could be the result of delayed reproduction.
- Could this be density dependent? That is, if you reduce density, will the dwarfs move back in to shore?
 - This is an interesting question – when do life history patterns become fixed?
 - There have been studies that looked at this question and showed that dwarfism can disappear within a generation.
- From the graph it looked like some fish switched from dwarfism to lean. Is this the case?
 - These fish pre-dated *Mysis* introduction.

Results from preliminary population assessments of Elk Lake lake trout, an apparent remnant Lake Michigan form and deepwater spawner

J. JONAS and L. Mathews

Jonas & Mathews studied a population of lake trout in Elk Lake, Michigan to evaluate genetic stock structure and physical appearance, estimate population size, and determine spawning behavior. The Elk Lake strain was not genetically related to forms stocked in the Great Lakes. Head shape was similar to leans stocked in Lake Michigan, but the fish in Elk Lake were more fusiform and had shorter distance between fins. Lake trout seemed confined to deep water and mostly on the west side of the lake during the spawning season, but no obvious spawning habitat was found in that area.

Questions and Discussion

- Has the state stocked Elk Lake in the past? Or are the origins of the fish a colonization event?
 - It was stocked with Marquette strain for a few years, but there are no remnants of their genetics in this population. The genetic data was most similar to the historic Charlevoix strain.

The influence of life history on response to stressors: the sublethal impact of sea lamprey parasitism on siscowet and lean lake trout

C. MURPHY, S. Smith, R. Goetz, S. Sitar, and L. Reed

Murphy et al. used field and lab approaches to identify sublethal, physiological effects of sea lamprey parasitism on lake trout, identify changes in hepatic genetic regulation due to sublethal sea lamprey parasitism, and compare sublethal effects between siscowet and lean morphotypes. Field data showed that faster growing fish were more likely to be parasitized, suggesting that siscowet might have more “buffer years” of reproduction before being parasitized by sea lamprey because their length-at-age is smaller than that of the lean morph. In the lab study, siscowets were found to mount an immune response to sea

lamprey parasitism, whereas leans showed a more overt stress response. Murphy concluded that siscowet are less sensitive to sea lamprey predation than lean lake trout.

Questions and Discussion

- Has anyone looked at the effects of temperature in mediating survival of parasitism? Siscowets would be in colder water during the usual period of lamprey growth.
 - This is a good point. We held temperatures the same in these experiments, but cold water could make siscowets even less susceptible to sublethal effects in the wild.

Differences between lean and siscowet lake trout: what we have learned from six years of rearing in captivity and what we still don't know

R. GOETZ, D. Rosauer, A. Jasonowicz, S. Sitar, C. Bronte, P. Swanson, R. Johnson, G. Goetz, S. Roberts, C. Murphy, S. MacKenzie, and P. Biga

Goetz et al. conducted a “common-garden” experiment to raise siscowets and lean lake trout from eggs to adults under identical environments. The fish were assayed for growth, body shape, fat content, and other characteristics to determine if morphotypic differences are genetic. Differences in growth, muscle lipid levels, general energy metabolism, and some morphological characteristics were genetic. Fish were also bred in the laboratory, and differences between morphotypes persisted for the F1 offspring. These results support the hypothesis that differences in lake trout morphotypes have a genetic basis. The research team hopes to use the cultured lake trout to answer additional questions, including the causes of skipped spawning and whether the behavioral drive for depth selection is genetic.

Questions and Discussion

- Could the decline in lipid levels observed since the 1950s and 1960s be explained by hybridization between the morphotypes?
 - That seems likely. There has been an increase in siscowet populations, so if they are expanding to lean habitats, there is a greater possibility that hybridization is occurring.
- Relevant to the question of whether depth selection is genetic is work that has showed that the ability to secrete gas into the swim bladder (and thus better regulate buoyancy) is heritable.
 - We want to look at the genetic basis of the actual behavior, not the ability to exhibit traits.

Life history variation among lake trout morphotypes in North American lakes

M. HANSEN, N. Nate, C. Krueger, M. Zimmerman, H. Kruckman, and W. Taylor

Hansen et al. examined whether life history characteristics differed between deep-water (humper) and shallow-water (lean) forms of lake trout in Lake Mistassini, Quebec. Data were collected on multiple physiological and morphological characteristics of lake trout sampled at various depths. The results showed that deep-water, invertivore humper lake trout grew more slowly to a smaller asymptotic size, which suggests different habitat use. Gas retention and lipid levels were shown to be heritable instead of environmentally plastic. Individuals did not switch life histories based on growth histories. Hansen et al. concluded that the two morphs likely reflect genetic differences rather than phenotypic plasticity and that they function as separate ecological entities.

Questions and Discussion

- Did you notice a difference in the frequency of vaterite otoliths between the two morphotypes?
 - No, these occurred very rarely.

Life history plasticity in changing environments, ecosystem stability in changing environments, and lake trout rehabilitation in Lake Huron

J. HE

J. He analyzed and compared ecosystem stability under scenarios with Chinook salmon, walleye, and lake trout as top predators. The life-history plasticity of lean lake trout was studied to see how lake trout growth has varied over time and what factors contribute to changes in timing of first reproduction. The results suggest that lake trout contribute most to ecosystem stability through their ability to alter their life history parameters in response to multiple energy pathways or major changes in food web structure. J. He concluded that a management strategy that does not assume constant biological parameters should be developed.

Differences in egg size and lipid content between life history types of lake trout in the Canadian Arctic

H. SWANSON, B. Tonn, K. Kidd, M. Power, T. Johnston, J. Reist, R. Wastle, J. Babaluk, P. Yang, N. Halden, and C. Zimmerman

Swanson et al. collected lake trout from 4 coastal Arctic lakes and outflows with passable streams to the sea to determine if lake trout make annual marine migrations, and if so, how these migrations compare to those of Arctic charr and if the fish feed on marine prey items. Results showed that several Arctic lake trout populations are anadromous or amphidromous. Anadromous fish were in better condition, had lower mercury levels, higher PCB levels, larger eggs, lower fecundity, higher C:N ratio, higher lipids, and were more piscivorous than non-anadromous lake trout. Next steps in the project include investigations of the geographic extent of anadromy, the relative importance of marine prey items, the contribution of anadromous fish to population productivity, and the effects of oceanic feeding migrations on reproductive fitness.

Questions and Discussion

- How far from the river mouth have you sampled lake trout in the sea?
 - Up to 5km.
- What is the salinity of the waters you find them in?
 - Not full-strength sea water – a mean of about 13 ppt.
- Do you think that population density in the lakes could be forcing anadromy?
 - This is definitely a possibility, but based on diets, Arctic charr and lake trout in the same lake don't seem to be competing.
- Have you seen a marine signature in lake trout eggs? This could give you an idea of the reproductive contribution of anadromous fishes to the population.
 - This type of sampling would logistically be very difficult given the weather. We could look for a marine signature in the nucleus of otoliths, which would get at this question if fish are laying eggs when they still have the marine signal.

- Some lake trout in the Great Lakes move to rivers to feed, and there are some populations that spawn in rivers. Is it possible that these fish are spawning in the sea?
 - They all spawn together in the lake and only go to the sea to feed.
- Were any of the lakes proglacial?
 - No, their entrances were along the coast. Now that we know the lake trout are more saline tolerant than we thought, we can answer some questions about their dispersal.
- Why are there no seemingly obligate freshwater charr in Europe or Asia? Why didn't they disperse to Asia? Greenland?
 - I'm not sure – that is a very interesting question.

Skipped spawning in lake trout and implications for rehabilitation targets

Y. MORBEY and B. Shuter

Morbey presented a case study on lake trout in Lake Opeongo, an inland lake in Ontario, to explore patterns in skipped spawning across time. Gonadosomatic index (GSI) data from 1994-2011 were analyzed. Results indicated that the incidence of skipped spawning declined with fish age and was higher in females than in males, which is consistent with the hypothesis of skipped spawning as an adaptive life history strategy. Incidence of skipped spawning was not higher when condition was poorer. Additional work to analyze skipped spawning in lake trout from South Bay, Lake Huron showed evidence for skipped spawning, but more data were needed. The authors concluded that gonadosomatic indices are appropriate to measure skipped spawning in lake trout.

Questions and Discussion

- It seems that potential to allocate energy to somatic growth, rather than condition, is an important determinant of skipped spawning.
 - We need to disentangle the effects of both of these drivers.

An overview of thiamine deficiency with regard to lake trout restoration

A. EVANS, S. Riley, and D. Tillitt

Evans discussed past and ongoing work to examine the causes and consequences of thiamine deficiency complex on individual lake trout and on lake trout populations. From 1975-2003, decreased alewife abundance was associated with decreased lake trout fry mortality in Lake Michigan. Decreased alewife abundance was associated with increased egg thiamine levels in Lake Huron, but this relationship was not as pronounced in Lake Michigan. Decreased alewife abundance in Lake Huron was associated with increased lake trout recruitment.

Klondike strain lake trout in Lake Erie (lake trout status included)

M. ROGERS

Rogers compared life history and ecological traits between stocked Klondike and Finger Lake strains (i.e., a humper versus a lean strain) in Lake Erie. Between-strain differences were detected in length-at-age, sex ratio, lamprey wounding rates, and diet. Finger Lakes fish appeared less susceptible to lamprey wounding and reached a larger asymptotic size than Klondikes. Survival and age-at-maturity did not differ between strains. Rogers concluded by summarizing remaining critical questions for rehabilitation

and stated that Lake Erie, a lake with high prey abundance, provides an opportunity to contrast with restoration efforts in other lakes.

Artificial reefs in Thunder Bay, Lake Huron - restoration and research platform

J. E. MARSDEN, J. Johnson, and N. Dingledine

Marsden assessed recently-constructed spawning reefs in Thunder Bay, Lake Huron. Pre-construction assessment of natural reefs and post-construction monitoring of natural and restored reefs were used to determine whether lake trout and/or whitefish colonized new reefs for spawning, and to examine what reef characteristics were most attractive to spawning lake trout. Adult lake trout were attracted to the new reefs after some time, but were not attracted to natural, degraded reefs. Whitefish spawned on all reefs; lake trout spawned on new reefs, but only erratically. Marsden also shared preliminary results of another project that suggested lake trout were not attracted to fry fecal odor or other adults on spawning reefs.

Reproductive behavior of wild and hatchery lake trout in the Drummond Island Refuge, Lake Huron

T. BINDER, C. Krueger, H. Thompson, C. Bronte, S. Riley, M. Ebener, C. Holbrook, J. He, and R. Bergstedt

Binder presented preliminary results of a study in northern Lake Huron using acoustic telemetry to describe physical and environmental characteristics associated with lake trout spawning behaviors and to determine whether wild and hatchery lake trout differed in spawning habitat and behavior. Spawning was observed at six sites with varying habitat characteristics and the common feature of clean interstitial spaces ranging from 5 to more than 30cm, which suggests slope and substrate size are not the most important determinants of spawning locations. A clear difference in behavior between males and females was observed, with males apparently displaying more aggregation behavior than females. Some evidence of differences in behavior between wild and hatchery trout was observed, but the differences were inconsistent between years.

Is lake trout spawning habitat associated with glacial bedforms?

S. RILEY, M. Faust, C. Krueger, A. Muir, T. Binder, J. E. Marsden, C. Bronte, M. Hansen, T. Tucker, and H. Thompson

Riley presented evidence that drumlins, and potentially other glacial bedforms, might be important habitats for lake trout spawning in the Great Lakes. Lake trout have been shown to spawn on drumlins in northern Lake Huron, and evidence suggests other lake trout spawning areas in the basin are also associated with glacial outwash plains. Riley concluded that investigation of this hypothesis would provide important information for lake trout restoration efforts, but that existing bathymetry data is insufficient for further study.

APPENDIX II. POSTER HIGHLIGHTS

Lake trout spawning success: The first casualty of climate change?

John Fitzsimons, Golder Associates Ltd.

Research Highlights:

- The effects of climate change on lake trout reproduction are unclear, but will depend on the relative importance of temperature and photoperiod as reproductive cues and this may vary with latitude.
- Gametes just prior to, during, and immediately after spawning appear most at risk because of the timing of spawning which occurs in epilimnetic waters that are expected to show the greatest effects from climate change.
- With increasing latitude, the timing of lake trout reproduction seems less affected by variation in temperature and more affected by variation in photoperiod based on limited measures of egg deposition with negative consequences for egg viability.

Temporal variation of lake trout egg deposition in Parry Sound and possible causes

John Fitzsimons, Golder Associates Ltd.

Research Highlights:

- Natural reproduction by lake trout in Parry Sound between 1994 and 2011 increased, but subsequently declined, based on measures of egg density at three spawning reefs.
- Declines in egg density appeared unrelated to the effects of predation by crayfish, sculpins, or gobies, or to the effects of physical disturbance.
- Declines in egg density were most likely related to declines in adult abundance associated with increased levels of lamprey mortality.

Comparative ecology and life history characteristics of Lake Superior ciscoes

Owen Gorman, USGS Great Lakes Science Center, Lake Superior Biological Station

Research Highlights:

- The four cisco species of Lake Superior showed contrasting life history differences in size, growth, maturity, and sex ratios.
- Cisco and shortjaw cisco showed delayed maturity, larger size at maturity, larger adult size, and moderate bias in female abundance with age.
- Bloater and kiyi showed early maturity, smaller size at maturity, smaller adult size and strong bias in female abundance with size.
- The interplay of the life history characteristics of these species with predation by lake trout result in further ecological differences and likely contributes to coexistence.

Deepwater lake trout spawning habitat: a river runs through it?

John Janssen and Tom Hansen, University of Wisconsin – Milwaukee

Research Highlights:

- On Lake Michigan deep reefs, lake trout spawn on cobble slopes, as in coastal spawning lake trout. But, they also spawn on flat (plateau) areas if the cobble is near a dropoff and can intercept currents.
- For coastal spawning, hyporheic water exchange is driven by wave surge, so is pulsed on a scale of seconds. For deep reefs the currents are more continuous in direction. Dropoff edges do

reduce boundary layer effects due to nearness to a dropoff edge and turbulence due to flow acceleration at the edge. This can create scour at reef edges, but also at reef bases.

- Hence deepwater spawning is likely more similar to stream spawning with regards to substrate and flow requirements.

Truss type morphometric comparison of remnant lake trout from Elk Lake (Antrim County), lean forms from Lake Superior, and stocked Lake Michigan populations

Laura Mathews, Central Michigan University

Research Highlights:

- Elk Lake lake trout are morphologically different than stocked forms in Lake Michigan and lean forms in Lake Superior.
- The lean form from Lake Superior was compressed in head shape, while the Elk Lake and Lake Michigan forms were similar in head shape.
- The Elk Lake lake trout had a compressed body shape, while Lake Superior was intermediate, and Lake Michigan more fusiform.

A field guide to the taxonomy of ciscoes in Great Slave Lake, Northwest Territories, Canada

Andrew Muir, Michigan State University / Great Lakes Fishery Commission

Research Highlights:

- A guide was developed as a tool for distinguishing among ciscoes in Great Slave Lake, NT.
- Five ciscoes are differentiated and described and their taxonomic affiliations are assessed.
- The field guide can be downloaded from: <http://www.glfsc.org/pubs/SpecialPubs/2011-02>.

Native fish communities and habitat coupling: delivery of a nearshore energy subsidy by an offshore planktivore

Jason Stockwell, University of Vermont

Research Highlights:

- Winter consumption of incubating cisco eggs represented a significant proportion of annual consumption by lake whitefish in western Lake Superior.
- Stable isotope analyses corroborated these results and suggest other nearshore fish species also may rely on energy-rich cisco eggs during the winter.
- This offshore-to-nearshore link no longer exists in other Great Lakes where cisco has been replaced by invasive planktivorous species.

Genetic identification of unclipped lake trout in Ontario waters of Lake Huron

Wendy Stott, USGS Great Lakes Science Center

Research Highlights:

- Genetic markers can be used to distinguish among hatchery strains of lake trout stocked into Lake Huron.
- Lake Manitou and Seneca Lake genotypes are observed most frequently among naturally produced lake trout from Ontario waters of Lake Huron although they are not the most frequently stocked strains of lake trout.

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APPENDIX IV. WORKSHOP EVALUATION

1. The information provided in the workshop packet was helpful (average score 4.4/5). Eighty-eight percent (14/16) of respondents felt they received the right amount of information in the workshop packet. Additional information that respondents would have found helpful includes the following: 1) presentation abstracts; 2) participant bios; 3) a draft agenda provided sooner; 4) timelines of research; and 5) expectations of participants.
2. Eighty-eight percent of respondents (15/17) were aware of the Great Lakes Fishery Commission's Re-establishment of Native Deepwater Fishes research theme prior to the workshop.
3. Overall, participants approved of the workshop agenda (4.5/5), but suggested it could be improved by "reducing redundancy in the lake trout session." One participant stated: *"Given its theme, native lake trout and coregonids, I thought the agenda was very top-down oriented - but thorough."*
4. Overall, participants enjoyed the discussions and thought they were well-run and achieved their objectives (average score 4.4/5). Overall, comments on the discussions were favorable. Participants would have liked to have seen a broader, ecosystem approach to the discussions. Specific suggestions for improvement included the following: *"I feel the discussion was great but somewhat biased in scope to life-cycle/population level"* and *"No revisit of ecosystem hypotheses or research needs as a standalone topic."*
5. The meeting space, food and beverages, lodging, service, and overall venue quality were considered excellent (average score 4.7/5). Participants greatly enjoyed the socials, both for the food and for the opportunities afforded for informal discussion. Specific suggestions for improvement including the following: *"Meeting room too cold," "No cell service in meeting room and hotel rooms," "Screen too low,"* and *"Hot breakfast items would be nice."*
6. At the conclusion of the workshop 81% (13/16) of respondents indicated they were more likely to apply for funding under the theme than before the workshop. None said that they were less likely to apply.
7. All respondents (17/17) indicated interest in attending future theme workshops.
8. Eighty-eight percent (15/17) of respondents felt that a symposium, such as RESTORE, should be held. No respondents answered that they did not support holding a RESTORE-type symposium. Specific comments were as follows: *"It is time to regroup and document progress to date and set future course"* and *"It should include all species; ecosystem approach."*
9. Sixty-four percent (9/14) of respondents thought that a larger RESTORE-type workshop would be useful to their agency or institution. No respondents indicated that it would not be useful.
10. Summaries of additional feedback for future workshops included the following:
 - a. Overall, comments were favorable and the steering committee was commended for a valuable and well-planned workshop.
 - b. A common theme emerged that participants would like to have seen a more holistic, ecosystem approach carried through the entire workshop. It was noted that processes at the community and ecosystem level were missing from this workshop. Several

respondents wanted to see future workshops deal with the entire suite of native fishes in the Great Lakes, including lake sturgeon and American eels; this suggests a failure to emphasize that the theme is focused on the deepwater community. Based on the feedback, a RESTORE-type symposium would be an appropriate venue for addressing all native fishes.

- c. Participants expressed strong interest in a future workshop to transfer science to managers. One respondent commented that “*administrators and managers appear to be viewing the list of native species hypotheses/questions as reasons why it is too soon to implement stocking.*”
- d. Several respondents felt that some experts were not in the room. One noted that there were too few attendees working in Lake Ontario. Several criticized the exclusive, invitation-only nature of the workshop and suggested that attendees be asked to offer names of any scientists that are missing and would add value.