An Ecosystem Perspective on Re-establishing Native Deepwater Fishes in the Laurentian Great Lakes

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Abstract.—Herein we examine scientific questions related to successful re-establishment of native deepwater fish communities in the Laurentian Great Lakes, and we (1) propose a conceptual model for native deepwater fish communities; (2) review current research and identify research hypotheses for lake trout *Salvelinus namaycush*, pelagic ciscoes *Coregonus* spp., and sculpins (*Cottus* spp. and *Myoxocephalus* spp.); (3) pose research questions emerging at community and ecosystem levels; and (4) identify high-priority research topics related to population re-establishment. The conceptual model is based on a generalized life cycle nested within processes at the population, metapopulation, community, and ecosystem levels. The conceptual model assumes that variation in population abundance is a natural phenomenon and that biodiversity contributes to ecosystem stability. Key research topics related to lake trout re-establishment include understanding recruitment variation over space and time, identifying sources of early life history mortality, determining the level of genetic differentiation among morphotypes and populations, and comparing the life history and ecology of lean lake trout with those of other lake trout morphotypes. Key research topics related to re-establishing deepwater species of cisco include resolving uncertainties in species identifications, understanding processes maintaining distinctiveness among species, understanding processes leading to cyclic and erratic recruitment, and developing effective propagation methods. Key research topics related to re-establishment of sculpin species include comparing spawning ecology and early life history of each species, determining population structure, and evaluating the feasibility of live-transfer methods. Key research topics related to community- and ecosystem-level interactions include understanding large-scale directional influences on community function, expanding current views on ecological succession in large lakes, and determining the evolutionary role of diel vertical migration in phenotypic diversification of deepwater fishes. Finally, we propose that research in four topical areas are most pertinent to re-establishing native deepwater fishes: life history bottlenecks, population and metapopulation dynamics, matching fish phenotypes to stocking sites, and propagation and stocking methods.

Entire communities of deepwater fishes were eliminated from nearly all five Laurentian Great Lakes by the mid-20th century. With few exceptions, deepwater fishes have remained absent from large volumes of deepwater habitat to the present day (Eshenroder and Burnham-Curtis 1999). The Great Lakes Fishery Commission (GLFC), a binational agency coordinating the research and management of Great Lakes fisheries, has stressed the importance of conserving biological diversity represented in the form of populations, species, and communities (GLFC 2001). Deepwater communities composed of lake trout *Salvelinus namaycush*, burbot *Lota lota*, ciscoes *Coregonus* spp., whitefish *Prosopium* spp., and sculpins (*Cottus* spp. and *Myoxocephalus* spp.) were once major components of this diversity. Present

conditions offer promise for future re-establishment of native deepwater fishes. For example, potential source populations exist in Lake Superior and elsewhere that could be used for reintroduction into lakes where species are extirpated. Many variables contributing to the initial decline (i.e., effects of predation by sea lampreys *Petromyzon marinus*; overharvest) are now managed cooperatively by state, federal, and tribal agencies. Furthermore, rainbow smelt *Osmerus mordax* and alewives *Alosa pseudoharengus* are presently lower in abundance than when they were believed to have contributed to native species decline (O'Gorman and Stewart 1999).

This paper identifies key scientific questions related to successful re-establishment of native deepwater fish communities in the Laurentian Great Lakes. Re-establishment refers to reintroduction followed by long-term persistence of populations through natural reproduction. The term "re-establishment" does not mean that previous conditions are recovered (i.e., "restoration") but rather acknowledges that native Great Lakes communities have been irreversibly altered and that native fish recovery must proceed

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TABLE 1.—Extirpated, rare, and potential donor sources of native, deepwater fishes in the Laurentian Great Lakes and Lake Nipigon. Nipigon Lake (Ontario) is a large lake (4,848 km^2) in the Lake Superior watershed (~50 km upstream) that contains many of the original species and forms native to the Great Lakes. A Great Lake where a fish has been extirpated but a form of the species is still present in another Great Lake or Lake Nipigon is denoted by an "E." A "P" indicates the presence of a native, deepwater fish in each lake and its potential use as a donor source for reintroduction of a fish species extirpated in another Great Lake. An "R" indicates a Great Lake where the species or morphotype occurs in very low numbers. A Great Lake where a species or morphotype may have been present (historical records are unclear) is denoted by a question mark (?). Of note, blackfin cisco in Lake Nipigon is assigned a subspecific status (*Coregonus nigripinnis regalis*) that differs from historical populations in potential recipient lakes (*Coregonus nigripinnis nigripinnis*).

Taxon or form	Lake					
	Superior	Michigan	Huron	Erie	Ontario	Nipigon
Lake trout *Salvelinus namaycush*						
Lean lake trout morphotype	P	E	R	E	E	P
Humper lake trout morphotype	P	?	?			
Siscowet lake trout *S. namaycush siscowet*	P	E	E	?	?	
Shortjaw cisco *Coregonus zenithicus*	P	E	R	E		P
Kiyi *Coregonus kiyi*	P	E	E		E	
Bloater *Coregonus hoyi*	P	P	P		E	P
Blackfin cisco *Coregonus nigripinnis*[a]		E	E			P
Deepwater sculpin *Myxocephalus thompsonii*	P	P	P		R	P
Spoonhead sculpin *Cottus ricei*	P	P	E	E	E	P

[a] Blackfin ciscoes in Lake Nipigon are a subspecies (*Coregonus nigripinnis regalis*) that differs from subspecific populations (*C. nigripinnis nigripinnis*) historically present in the two E-category lakes.

within this context. Deepwater communities are hypolimnetic and characterized by high hydrostatic pressures, nearly constant cold temperatures, and minimal ambient light (Janssen et al. 2007). Native deepwater fishes of concern (Table 1) include three lake trout morphotypes, four pelagic cisco species, and two sculpin species. Members of the deepwater community that generally remain abundant over their historical range in the Great Lakes will not be specifically addressed (i.e., burbot, lake whitefish *Coregonus clupeaformis*, round whitefish *Prosopium cylindraceum*, and pygmy whitefish *Prosopium coulterii*).

Our intent is to promote biological understanding of deepwater fish communities and to provide information useful to management for re-establishing species of concern. We recognize that successful re-establishment of deepwater fishes will ultimately rely on both biological understanding and social, political, and economic capital. Management decisions reflect the interplay between biological understanding and cultural values, which differ among species and lakes (e.g., Decker et al. 1996; Krueger and Decker 1999). Within this broader management context, we focus on biological issues related to the re-establishment of native deepwater fishes. Our conceptual approach goes beyond a population-level focus and challenges researchers to consider lake trout, pelagic ciscoes, and sculpins within a context of processes occurring at metapopulation, community, and ecosystem levels. In so doing, we aim to prompt research efforts at many levels of organization (i.e., life history, population, community, and ecosystem).

We identify key areas of scientific information needed to re-establish native deepwater fish communities in the Laurentian Great Lakes by (1) developing a conceptual model for native deepwater fish communities; (2) reviewing current research on lake trout, pelagic ciscoes, and sculpins in relation to the conceptual model and identifying important research questions for each taxon; (3) posing questions emergent at community and ecosystem levels; and (4) identifying high-priority research topics.

Conceptual Model

Background.—A conceptual model based on a set of assumptions can provide an organizational framework upon which questions and hypotheses are developed (NPRB 2005; AYK-SSI 2006). Based on trial and error in Pacific salmon restoration, managers have emphasized the importance of articulating a conceptual model and evaluating its underlying assumptions (Liss et al. 2006; Williams 2006; Martin, in press). Conceptual models, although incomplete by nature, provide a framework for discussion. Our conceptual model will be successful if it is tested, debated, and subsequently revised many times. The conceptual model originally used to shape management actions in regards to lake trout re-establishment provides a useful example of this process.

Earliest actions undertaken for lake trout re-establishment were based on a relatively simple
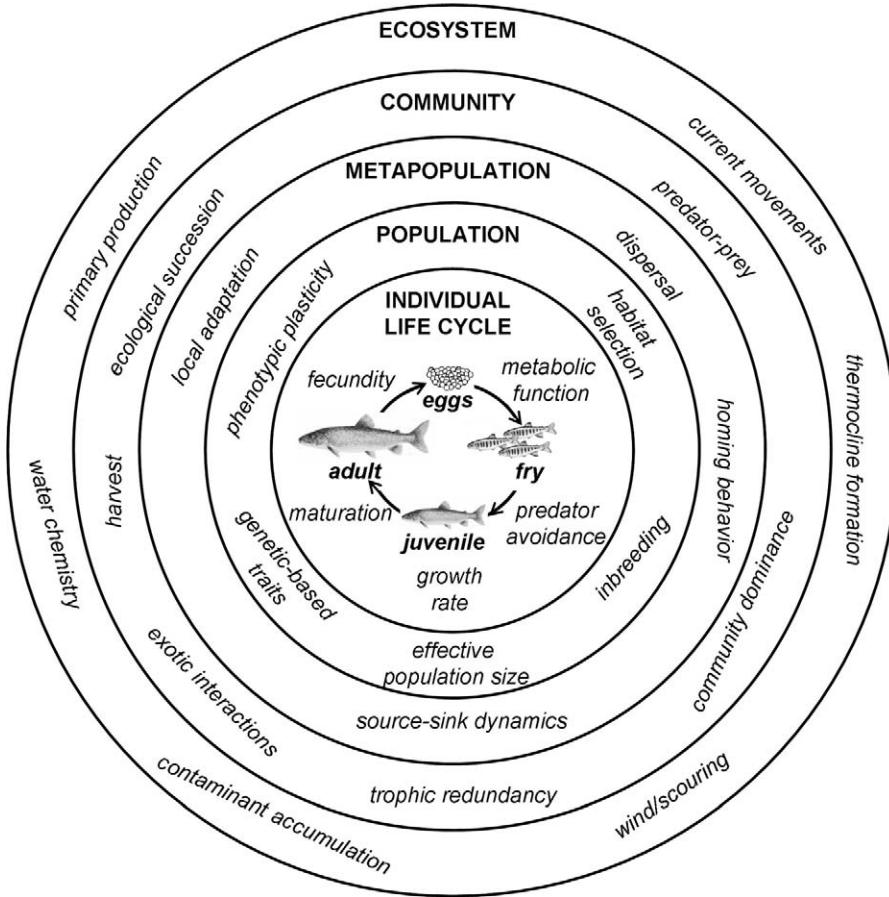
FIGURE 1.—Generalized conceptual model for the native deepwater fish community in the Great Lakes. Re-establishment of each species will involve sustained completion of the life cycle of individuals within the context of population, metapopulation, community, and ecosystem-level processes. The figure illustrates processes contributing to each organizational level. The list and arrangement of examples are not meant to be exhaustive or to emphasize connections among specific processes. Cascading effects of each process may be directed inward toward the population level or outward from the model center toward the ecosystem level. Environmental perturbations may initiate at any level and alter processes.

conceptual model that focused on increasing population abundance through (1) stocking and (2) mortality reduction via harvest limits and sea lamprey control (Burnham-Curtis et al. 1995; Hansen et al. 1995; Krueger and Ebener 2004). Other variables, such as juvenile mortality or habitat selection, were not assumed to limit lake trout recruitment. After four decades of experience, managers and researchers identified many additional variables as impediments to re-establishing lake trout, including incorrect identification of spawning habitats, interactions with native and nonnative species, disease, and predation (Bronte et al. 2003b). Thus, the conceptual model now used by managers and researchers is considerably different than the original model of the 1960s.

Conceptual model for native deepwater fishes.—Our generalized conceptual model is based on a life cycle nested within processes at the population, metapopulation, community, and ecosystem levels (Figure 1). We use ecological and genetic (when applicable) criteria to define these organizational levels. A population is defined as a breeding group of individuals from a single species that occupy a defined area and share a common gene pool that may be genetically different from the gene pools of similar groups. A metapopulation is defined as a group of semi-reproductively isolated populations whose dynamics and genetic structure are influenced by limited interpopulation migration and local environmental conditions. A community is defined as a group of species that occur in the same area and interact through

processes such as predation, competition, and mutualism. An ecosystem is defined as the interrelated set of biotic and abiotic variables that contribute to energy flow.

A life cycle model is easily communicated and facilitates concurrent consideration of critical life stages and influential variables. The research and management community already uses a comparable model for one lake trout morphotype, the lean lake trout. The life cycle model can be generalized to other forms of lake trout, such as the humper or siscowet morphotype, and to other species of deepwater fishes. Complexity is added by considering life cycles in the context of processes occurring at population, metapopulation, community, and ecosystem levels. Although the organization of the life cycle model is generalizable, the influence of different processes on native fish re-establishment is likely to be specific to species or morphotype.

Processes operate at different organizational levels and may vary in the scale and direction of their influence. For example, an ecosystem-level event influences all levels of organization but may occur at local (e.g., isolated chemical spill) or regional (e.g., warming surface temperatures) spatial scales. Temporal scales may vary among species because of species-specific generation times. The direction of influence across organizational levels may also vary. Metapopulation structure may be influenced by surface currents (ecosystem), prey availability (community), and effective population size (population). A major research challenge will be to correctly identify processes that are related to critical life history bottlenecks for each taxon and determine their appropriate spatial and temporal scales.

Assumptions.—Our conceptual model is based on assumptions that represent current ecological understanding as applied to conservation and restoration efforts. We have drawn from ongoing restoration efforts of two major systems, Pacific salmon in the northwestern USA and Canada (Williams 2006) and lean lake trout in the Laurentian Great Lakes (Selgeby et al. 1995b), as well as from community ecology research (McCann 2000). The stated assumptions are largely influenced by two emerging lines of discussion: (1) a definition of system stability and (2) the role of diversity in relation to long-term stability.

Stability is defined as either a set of equilibrium conditions or a response to environmental perturbations (Hollings 1973; Pimm and Hyman 1987; McCann 2000). How managers define stability will determine whether the goal of restoration is to re-establish a state or a process. The equilibrium (or steady state) definition of stability is measured as variability in population density over time, where a low coefficient of variation corresponds to high stability. The perturbation definition is measured as the duration (resilience) or magnitude (resistance) of a response after a disturbance, where short or small responses (i.e., high resilience or strong resistance) correspond to high stability. When managers focus on specific sustainable harvest levels, they assume that systems reach a stable equilibrium point and will persist in steady-state conditions (i.e., constant biomass or escapement; Hollings and Meffe 1996; Liss et al. 2006). However, natural systems rarely, if ever, display steady-state conditions. Alternately, considering stability with respect to resilience or resistance emphasizes the process of responding rather than an end point (Hollings 1973). A process-oriented approach to restoration has been promoted for Pacific salmon because managers were confronted with the prevalence of environmental variability and the complexity of natural systems (Liss et al. 2006; Martin, in press). A process-oriented approach focuses on the interconnectedness of elements within a system. This approach assumes that population variation is a natural phenomenon regulated at multiple spatial and temporal scales, which is inferred when the term "stability" is used (see below).

Many studies support the concept that diversity is positively correlated with stability (McCann 2000). Under fluctuating environmental conditions, diversity in behavior, morphology, or life history traits may contribute to differential survivorship of individuals, populations, or species. If responses of a set of populations to a fluctuating environment are asynchronous, the same variables that cause variation in population dynamics may result in overall stability at a metapopulation or community level (Tilman 1996; Chesson and Huntley 1997). For example, asynchronous variation in population densities of sockeye salmon *Oncorhynchus nerka* (i.e., intraspecific diversity) has resulted in metapopulation stability for this species over the last century in Bristol Bay, Alaska (Hilborn et al. 2003). Similarly, interspecific diversity in the form of food web complexity or functional diversity is positively correlated with community-level stability (Tilman et al. 1997; McCann et al. 1998). Several ecological studies have demonstrated that the diversity of ecosystems and communities—but not populations—is correlated with stability (Tilman 1996; McCann 2000; Worm et al. 2006). However, over evolutionary time scales, genetic diversity within populations may also improve resilience by increasing capacity of a population to adapt to changing environmental conditions.

As with the conceptual model, our seven assump-

tions are probably incomplete and are intended to be challenged:

(1) Research that involves a life cycle approach and focuses on recruitment bottlenecks will identify major impediments to species re-establishment.
(2) Fish re-establishment is influenced by variables operating in concert at different spatial and temporal scales.
(3) Population variability is an intrinsic property of natural systems that occurs to a higher degree than predicted by steady-state conditions.
(4) Species re-establishment will be affected by processes at population, metapopulation, community, and ecosystem levels.
(5) High genetic diversity and, hence, phenotypic diversity increase resilience and resistance of a species to environmental change.
(6) High species diversity within trophic levels increases resilience and resistance of a community to environmental change.
(7) Biological communities change over ecological and evolutionary time scales and represent an organized (i.e., nonrandom) assemblage of species.

The conceptual model and its assumptions lead to a series of questions related to re-establishment of native deepwater fishes. In the following sections, we review recent research findings and present hypotheses for three taxonomic groups (lake trout, pelagic ciscoes, and sculpins) and for processes influencing all taxa at community and ecosystem levels. We then suggest high-priority research in four topical areas: life history bottlenecks, population and metapopulation dynamics, matching fish phenotypes to stocking sites, and propagation and stocking methods. Research of high priority will be most likely to meet immediate information needs of managers charged with native fish re-establishment.

Lake Trout

Lake trout were once the dominant predator in the deep waters of each of the Laurentian Great Lakes. However, by the mid-20th century, lake trout were extirpated from each lake except Lake Superior and the Georgian Bay region of Lake Huron (Table 1). Key research topics related to lake trout re-establishment include understanding recruitment variation over space and time, identifying sources of early life history bottlenecks, determining genetic and morphological diversity, and comparing the life history and ecology of lean lake trout with those of other morphotypes. Seven research hypotheses and associated questions were developed to further understanding of these issues (Table 2).

In the Great Lakes, the lake trout life cycle begins with a spawning event in late fall, early spring hatching, and a 5–9-year maturation time. Lake trout are repeat spawners with a life span in excess of 20 years (Martin and Olver 1980). Fry are demersal after emergence. Juvenile diets include macroinvertebrates (opossum shrimp *Mysis relicta* and amphipods *Diporeia* spp.; Madenjian et al. 1998) and sculpins (Fisher and Swanson 1996). Adult lake trout are primarily piscivorous (Conner et al. 1993; Madenjian et al. 1998; Bronte et al. 2003a) and historically fed on sculpin and ciscoes (Van Oosten and Deason 1938; Dryer et al. 1965).

Lake trout recruitment is variable across spatial (Grewe et al. 1994; Perkins et al. 1995) and temporal scales (Richards et al. 2004; Linton et al. 2007). In some cases, a single variable explains regional differences in survival (e.g., gill-net fishery; Hansen et al. 1996). More often, key variables, such as stock abundances, are inadequate to fully explain variation in regional recruitment (Selgeby et al. 1995a). Variables affecting recruitment interact over different spatial scales. For example, recruitment of stocked versus wild lake trout may be mediated by the quality and connectivity among spawning habitats and by the behavior of stocked versus wild fish. Homing behavior, critical to maintaining population structure, is weaker in stocked lake trout than in wild lake trout (Swanson 1973; Krueger et al. 1986). Although offshore communities are thought to be more ecologically appropriate for lake trout re-establishment (Krueger et al. 1995a; Dawson et al. 1997), isolation from other spawning habitat may lead to low recruitment if reintroduced fish have weak homing abilities. Indeed, in regions where spawning habitats are offshore and more difficult for fish to locate (e.g., Apostle Islands, Lake Superior), wild lake trout contribute more substantially to recruitment than stocked lake trout (Krueger et al. 1986; Schram et al. 1995). In contrast, where spawning habitats are easily encountered (e.g., Michigan shoreline of Lake Superior), wild and stocked lake trout make equivalent contributions to the next cohort (Richards et al. 2004). This example illustrates how processes at multiple spatial (individual behavior, metapopulation structure, community composition) and temporal (habitat selection, habitat formation) scales interact to affect recruitment and the success of re-establishment efforts. Given these interactions, alternate stocking approaches may help to mediate the conflict between poor homing of stocked lake trout and ecological suitability of offshore spawning sites. Such alternate approaches include reintroducing eggs in artificial turf incubators (Swanson 1982; Bronte et al. 2002) or selecting

TABLE 2.—Hypotheses and associated research questions (Q) regarding lake trout re-establishment in the Laurentian Great Lakes.

Hypothesis 1. 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.

Q1.1 Do diets of shallow-water and deepwater morphotypes differ within and among lakes? Do humper lake trout occupy a different ecological niche than lean and siscowet morphotypes in Lake Superior?

Q1.2 Do trophic position and use of temperature or depth differ within and among morphotypes? Does the magnitude of this variation differ among morphotypes?

Q1.3 Do trophic relationships among lake trout morphotypes differ among regions within Lake Superior? What variables account for these differences?

Q1.4 Does recruitment variation differ among wild populations of each morphotype? Is level of recruitment variation among morphotypes in Lake Superior similar to that in other lakes with similar morphotypes (e.g., Great Slave Lake, Great Bear Lake, and Lake Mistassini)?

Q1.5 Do lake trout morphotypes respond differently (e.g., diet shift, growth, fecundity) to periods of low prey abundance? Does response time of lake trout populations to prey decline or recovery differ among morphotypes?

Hypothesis 2. The humper lake trout morphotype will be less vulnerable to sea lamprey predation than the lean or siscowet morphotype.

Q2.1 Does predation by sea lamprey differ among siscowet, humper, and lean lake trout because of differences in age structure, asymptotic size, maturity, or habitat use?

Q2.2 Do humper lake trout (i.e., Klondike strain) survive better than lean lake trout in Lake Erie?

Hypothesis 3. Lake trout and alewives are capable of coexisting under specific conditions.

Q3.1 Why do lake trout successfully reproduce in the Finger Lakes (e.g., Keuka Lake, Fitzsimons et al. 2005) where alewives are abundant?

Q3.2 Do fry predation and early mortality syndrome affect the recruitment of lean lake trout in Lakes Huron, Michigan, and Ontario? What are the relative effects of predation and early mortality syndrome?

Q3.3 Is increased lake trout recruitment in Lake Huron due to declining alewife populations? What variables in Lake Huron differ from those of the Finger Lakes?

Hypothesis 4. Metapopulation structure of wild lake trout within lakes reflects dispersal and natal homing tendencies of adult lake trout.

Q4.1 Does the spatial scale that defines a typical lake trout population differ among morphotypes?

Q4.2 Does natal homing differ among morphotypes?

Q4.3 Do fry or adult dispersal distances differ among morphotypes?

Q4.4 Are morphotypes adapted to spawn at specific times or depths?

Q4.5 Do wild lake trout have source and sink populations? What variables are associated with highly productive source populations?

Hypothesis 5. Lake trout spawning requires visual, sound, and olfactory cues.

Q5.1 Do females or males emit pheromones to elicit gamete maturation and trigger spawning behavior?

Q5.2 Do sound, lateral line reception, or visual cues trigger spawning behavior?

Q5.3 Do wild and stocked lake trout respond differently to reproductive pheromones, sound, or behavior?

Q5.4 Does assortative mating maintain differences among morphotypes?

Hypothesis 6. Large, deep lakes are characterized by parallel processes of incipient speciation of lake trout from an ancestral lean morphotype.

Q6.1 What is the level of genetic differentiation among lake trout morphotypes?

Q6.2 Does temporal or spatial reproductive isolation minimize potential for hybridization among lake trout morphotypes in Lake Superior?

Q6.3 Which processes (e.g., multiple colonizations, sympatric speciation) best explain repeated patterns of coexisting lake trout morphotypes?

Q6.4 Do life histories (e.g., age structure, growth, age at first maturity) of shallow-water and deepwater morphotypes differ within and among lakes?

Q6.5 In response to environmental variation, what role does phenotypic plasticity play in determining lake trout morphology and lipid content?

Hypothesis 7. Deepwater lake trout morphotypes can be successfully propagated and reintroduced from a hatchery environment.

Q7.1 What are the localities and seasons from which humper and siscowet lake trout broodstock can be collected?

Q7.2 How does the hatchery environment influence early life history characteristics of humper and siscowet lake trout?

Q7.3 How does survival to maturity compare among lake trout stocked as eggs (turf incubators), fry, fall fingerlings, and yearlings?

Q7.4 Will spawning site selection behavior of reintroduced deepwater morphotypes differ from that of reintroduced lean morphotypes?

stocking sites in close proximity to multiple potential spawning sites.

Two major sources of early life history bottlenecks are early mortality syndrome (EMS), which results from a thiamine deficiency (Tillitt et al. 2005; Riley et al. 2008), and alewife predation on lake trout fry (Krueger et al. 1995b). Relative effects of EMS and predation involve a sequence of interconnected temporal processes. Fry susceptibility to EMS is affected by parental diets, whereas the susceptibility of eggs and fry to predation by alewives is influenced by adult spawning site selection and by the timing of fry emergence (Savino et al. 1999; Baird and Krueger

2000; Fitzsimons et al. 2002; Strakosh and Krueger 2005). Furthermore, effects of EMS and predation are likely to occur at different spatial scales because the foraging behavior of adult lake trout encompasses a much broader area than localized spawning aggregations. Surprisingly, the negative effects of alewives on lake trout recruitment seem much less intense in Keuka Lake, New York, even though alewives are an important lake trout food item (Fitzsimons et al. 2005).

Genetic diversity expressed as functional traits is also important to lake trout re-establishment. For example, lake trout are capable of using all depths within the hypolimnion, and several genetically based traits are

associated with use of deep habitats, including high lipid content (Eschmeyer and Phillips 1965) and increased gas retention of the swim bladder (Eschmeyer and Phillips 1965; Ihssen and Tait 1974). In addition to depth, strains of stocked lake trout differ in their preferred temperature (Bergstedt et al. 2003), vulnerability to sea lamprey predation (Schneider et al. 1996; Madenjian et al. 2004; McKee et al. 2004; Bronte et al. 2007), and survival and recruitment (Madenjian et al. 2004; DeKoning et al. 2006). Given expected temporal fluctuations in community composition (e.g., sea lamprey abundance variations) and ecosystem characteristics (e.g., temperature increase), establishment of a combination of locally adapted strains should promote resilience of lake trout within a lake.

Comparative studies of lake trout genetic and morphological diversity outside the Laurentian Great Lakes are valuable because they afford a more complete understanding of ecological and evolutionary processes contributing to deepwater community function and of abundance variations expected for self-sustaining lake trout populations. Morphological diversity is often associated with the use of different habitat depths. The most common lake trout morphotypes in Lake Superior include the lean, siscowet, and humper lake trout (Khan and Qadri 1970; Moore and Bronte 2001). Lean lake trout occupy shallow-water habitat (<70 m), whereas humper and siscowet lake trout occupy deepwater habitat. Siscowet lake trout are capable of living at extreme depths and have been collected in the deepest waters (405 m) of Lake Superior (Sitar et al. 2008). Lake trout morphotypes also differ in body shape, lipid content, and osteological characters (Eschmeyer and Phillips 1965; Lawrie and Rahrer 1973; Burnham-Curtis and Smith 1994; Moore and Bronte 2001). Commercial fishermen have historically recognized locally specific stocks based on features such as coloration and spawning time (Brown et al. 1981; Goodier 1981; Krueger and Ihssen 1995). Lake trout morphotypes coexist in several other large, deep North American lakes, including Great Bear Lake (Blackie et al. 2003; Alfonso 2004), Great Slave Lake (Zimmerman et al. 2006), Lake Mistassini (Zimmerman et al. 2007), and Rush Lake (Hubbs 1929; M.S.Z. and C.C.K., unpublished data). Two of these morphological variants have received taxonomic status as subspecies, the siscowet lake trout of Lake Superior (Khan and Qadri 1970) and the Rush Lake trout *S. namaycush huronicus* (Hubbs 1929).

In comparison with lean lake trout, siscowet and humper lake trout probably face different obstacles to population re-establishment because they inhabit deep waters (>70 m) that are ecologically different from shallow-water habitat. Differences include thermal regimes, currents, substrate, prey, and exotic species abundances (Janssen et al. 2007). Deepwater morphotypes of lake trout also have different life histories (e.g., growth and maturation rates) than lean lake trout (Kitchell et al. 2000; Bronte and Sitar 2008) and may therefore respond differently to harvest. Recent studies indicate that lean and siscowet lake trout occupy different ecological niches (Conner et al. 1993; Harvey and Kitchell 2000; Harvey et al. 2003; Ray et al. 2007), humper and siscowet life histories differ significantly from that of lean lake trout (Burnham-Curtis and Bronte 1996; Miller and Schram 2000), and siscowet lake trout may have a longer or more variable spawning season than lean lake trout (Bronte 1993). Siscowet lake trout spawning locations have yet to be identified—a major obstacle to gamete collection and propagation of this morphotype.

Pelagic Ciscoes

The Laurentian Great Lakes once contained a diverse assemblage of pelagic ciscoes (Koelz 1929; Todd and Smith 1992; Eshenroder and Burnham-Curtis 1999). Before the arrival of the sea lamprey, alewife, and rainbow smelt, pelagic ciscoes supported major fisheries and were the primary prey for lake trout. At present, Lakes Michigan, Huron, Erie, and Ontario could serve as sites for re-establishment of pelagic cisco species (Table 1). Extant species include the cisco *Coregonus artedi* (hereafter referred to by scientific name to avoid confusion), a complex of three deepwater cisco species (bloater, kiyi, and shortjaw cisco), and the blackfin cisco. The blackfin cisco persists only in Lake Nipigon, although Lake Nipigon fish are currently classified as a different subspecies than the blackfin ciscoes described from Lakes Michigan and Huron (Table 1; Todd and Smith 1992). Key research topics related to re-establishment of deepwater species of cisco include resolving uncertainties in species diagnostic characters, understanding the process maintaining distinctiveness among species, understanding processes leading to cyclic and erratic recruitment, and developing effective propagation methods. Six research hypotheses and associated questions were developed in order to improve understanding of these issues (Table 3).

Over their life cycle, pelagic ciscoes use much of the lake environment. Habitat depth is a major variable that distinguishes pelagic cisco species. *Coregonus artedi* is typically collected at depths less than 50 m, whereas the deepwater species inhabit deeper waters, with the kiyi inhabiting the greatest depths (Smith 1964). For all cisco species in the Great Lakes, longevity is estimated between 6 and 11 years based on scale age data (Scott and Crossman 1973; Coffin et al. 2003), but otolith

TABLE 3.—Hypotheses and associated research questions (*Q*) regarding re-establishment of pelagic cisco species in the Laurentian Great Lakes.

Hypothesis 1. Contemporary bloaters in Lakes Michigan and Huron resulted from species introgression when deepwater species of cisco populations collapsed in these lakes.

    Q1.1 Should the subgenus *Leucichthys* be taxonomically revised?

    Q1.2 Does bloater morphology, ecology, or life history differ between lakes in which diversity did not collapse (i.e., Lakes Superior and Nipigon) and lakes in which diversity has collapsed (i.e., Lakes Huron and Michigan)?

Hypothesis 2. Population regulation of deepwater species of cisco (bloaters, kiyis, and shortjaw ciscoes) is primarily driven by intrinsic, density-dependent processes.

    Q2.1 Does recruitment variation differ among kiyi and shortjaw cisco populations in Lakes Superior and Nipigon and among *C. artedi* and bloater populations in Lakes Michigan, Huron, Superior, and Nipigon?

    Q2.2 Do similar variables (e.g., sex ratio, lipid levels) regulate recruitment of bloaters, kiyis, and shortjaw ciscoes?

    Q2.3 Do bloater females retain eggs and forego spawning when sex ratios are imbalanced?

    Q2.4 How much is the lipid content of bloaters, kiyis, and shortjaw ciscoes regulated by genetics as opposed to environmental variables?

Hypothesis 3. Contemporary population structure of pelagic ciscoes within lakes is influenced by both passive dispersal of fry and active homing behavior of adults.

    Q3.1 What spatial scale defines a pelagic cisco population, and does this differ among species?

    Q3.2 Does fry dispersal differ (i.e., distance, direction, duration) among species of pelagic ciscoes? Does adult homing behavior differ among species?

    Q3.3 Are spatial patterns in gene flow among populations correlated with physical variables like bathymetry or current direction?

    Q3.4 Do pelagic ciscoes have source and sink populations? Which variables are associated with highly productive source populations?

    Q3.5 Do variables such as dispersal and habitat quality limit population expansion of pelagic ciscoes in Lakes Huron and Michigan?

Hypothesis 4. Exotic planktivores (rainbow smelt, alewife) have different effects on each pelagic cisco species.

    Q4.1 What are the relative effects of exotics on fry, juvenile, and adult life history stages of pelagic ciscoes?

    Q4.2 Can site characteristics be identified that minimize predation on pelagic cisco fry based on emergence timing, current direction, and alewife or rainbow smelt distributions?

Hypothesis 5. Pelagic ciscoes are undergoing parallel processes of differentiation in large, deep lakes.

    Q5.1 Are pelagic cisco species genetically different?

    Q5.2 Does multiple colonization or sympatric speciation explain morphological diversity patterns in pelagic ciscoes?

    Q5.3 Do pelagic cisco species coexist in large, deep lakes outside of the Great Lakes? Are species pairs or complexes outside the Great Lakes similar to those observed within the Great Lakes?

    Q5.4 Do spawning habitats of sympatric pelagic cisco species differ in time (e.g., diel, season) and space (e.g., depth, substrate) within and across lakes?

Hypothesis 6. Hatchery propagation is a feasible option for reintroducing pelagic ciscoes.

    Q6.1 What is the most effective method for collecting gametes from wild populations?

    Q6.2 What is the most effective method of culturing pelagic ciscoes?

    Q6.3 What are the appropriate life stages and habitats for stocking pelagic ciscoes?

    Q6.4 What stocking densities and environmental conditions are conducive to re-establishment?

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data indicate that the maximum age of *Coregonus artedi* is closer to 20 years (Yule et al. 2008). Spawning seasons differ among species within lakes and differ among lakes for a given species (Koelz 1929; Scott and Crossman 1973; Smith and Todd 1984). Spawning depths range from 10 to 90 m (Scott and Crossman 1973), but deepwater spawning (up to 180 m) has been observed for *Coregonus artedi* in Lake Superior and for kiyi in all lakes (Scott and Crossman 1973; Smith and Todd 1984). Fry and juveniles are pelagic (Smith 1970; Crowder 1980) and feed on zooplankton (Wells and Beeton 1963; Wells and McLain 1973). Adult bloaters feed on benthic and pelagic macroinvertebrates (Wells and Beeton 1963; TeWinkel and Fleischer 1999), and adults of the deepwater species of cisco are known to undertake diel vertical migrations to prey on migrating opossum shrimp (Eshenroder et al. 1998; Hrabik et al. 2006).

Re-establishment of deepwater species of cisco is complicated by spatial and temporal differences in species characteristics. The apparent capacity of these deepwater species to homogenize morphologically under environmental stress (Smith 1968; Todd and Stedman 1989), combined with an environmental role in producing phenotypes (Todd et al. 1981), suggests that selection of stocking sites and densities will have a large impact on the ability of reintroduced stocks to maintain distinctive characteristics. With the exception of Lake Superior, species identities have been obscured by character introgression across species groups (Todd and Smith 1992) and secondary contacts among genetic lineages (Turgeon and Bernatchez 2003). For example, bloaters presently found in Lakes Michigan and Huron are hypothesized to be an introgressed form of the historical deepwater complex of cisco species that collapsed by the mid-20th century (Smith 1968; Todd and Stedman 1989). Collections from the early 1960s revealed that bloaters in Lake Michigan were more frequently captured in deep waters and attained larger body sizes than those collected in the early 1930s, when other deepwater species of cisco were still extant (Smith 1964).

Pelagic ciscoes are undergoing a process of ecological divergence (Smith and Todd 1984; Turgeon et al. 1999). Species in the deepwater complex of ciscoes are distinguished from each other and from

Coregonus artedi by their morphology, gill raker counts, and depth distributions (Smith 1964; Bailey and Smith 1981; Eshenroder et al. 1999). Existing relationships among cisco species morphology, ecology, and genetics are complex and suggest that both local adaptation and introgression have contributed to the current diversity of pelagic ciscoes (Turgeon et al. 1999). Species-level assignments of pelagic ciscoes are inconsistent with the hypothesis that ecotypes have arisen from parallel evolution within each lake (Turgeon and Bernatchez 2003). Therefore, an evolutionarily significant unit approach focused on re-establishing evolutionary processes within each lake (Turgeon and Bernatchez 2003) may be an appropriate framework for re-establishing pelagic cisco diversity in the Laurentian Great Lakes.

Sporadic, cyclic recruitment is a characteristic of pelagic ciscoes (Wells and McLain 1973; Bronte et al. 2003a) that will present a challenge for interpreting the success of any reintroduction efforts. Cyclic recruitment may result from variables intrinsic to the population (e.g., energy stores, size-dependent over-winter survival, and biased sex ratios; Madenjian et al. 2002; Pangle et al. 2004; Bunnell et al. 2006b) or from external variables (e.g., interactions with exotic planktivores; Smith 1970; Wells and McLain 1973; Crowder 1980; Fleischer 1992) and abiotic, density-independent variables (Bronte et al. 2003a). Although intrinsic variables will be difficult for managers to manipulate, the effects of extrinsic variables could be minimized by appropriate selection of sites and species for reintroduction. For example, interannual fluctuations in alewife abundance in response to ecosystem-level changes (e.g., temperature regimes) may have cascading effects on native pelagic ciscoes through predation on the young and competition with adults (Crowder 1980; Fleischer 1992). However, relative effects of predation and competition by exotics may differ among species of pelagic ciscoes because adults of species inhabiting the greatest depths (kiyi) are less likely to be impacted by exotic planktivores than those at moderate depths (shortjaw cisco and bloater). Indeed, the introduction of planktivorous alewives into Lake Michigan was associated with a dramatic feeding shift for bloaters, which inhabit relatively shallow depths (Crowder and Crawford 1984; Crowder 1986).

Sculpins

Unlike pelagic ciscoes and lake trout, no fishery exists for any sculpin species. However, sculpins are an important component of deepwater predator–prey interactions in the Great Lakes. Lakes of interest for the re-establishment of sculpins are Lakes Erie and Ontario for the spoonhead sculpin and Lake Ontario for the deepwater sculpin (Table 1). Key research topics related to re-establishment of these species include comparing spawning ecology and early life histories, determining population structure, and evaluating the feasibility of live-transfer methods. Five research hypotheses and associated questions were developed to address these issues (Table 4).

Sculpin species stratify by depth in a manner analogous to that of lake trout and pelagic ciscoes. Mottled sculpin *Cottus bairdii* inhabit shallow depths (<5 m), slimy sculpin *Cottus cognatus* and spoonhead sculpin inhabit moderate depths (common at 50–90 m), and deepwater sculpin inhabit the greatest depths (abundant at 75–90 m and as deep as 407 m in Lake Superior; Wells 1968; Scott and Crossman 1973; Selgeby 1988; Selgeby and Hoff 1996). Unlike lake trout or pelagic ciscoes, sculpin have no swim bladder for regulating buoyancy, and their depth distributions are not likely to be associated with diel vertical migration. Sculpin life span averages 5–10 years, with a maximum of 24 years (Selgeby 1988; Sheldon et al. 2007). Juveniles and adult sculpin are bottom-dwelling (Scott and Crossman 1973), whereas fry use pelagic and benthic habitats depending on species (Mansfield et al. 1983; Lantry et al. 2007). Adult sculpin mainly prey on opossum shrimp and the amphipod *Diporeia affinis* (Kraft and Kitchell 1986; Wojcik et al. 1986; Selgeby 1988; Owens and Weber 1995).

Improved understanding of life history differences among sculpin species within lakes and differences among lakes for a given species will aid selection of appropriate donor populations and stocking sites. Reproductive timing is a variable aspect of sculpin life history. Spawning of deepwater sculpin has been reported to occur in all seasons (Scott and Crossman 1973; Wojcik et al. 1986; Selgeby 1988). In Lake Michigan, eggs of deepwater sculpin hatch between March and May (Mansfield et al. 1983). Slimy sculpin and spoonhead sculpin are found with eggs throughout the year (C. Bronte, U.S. Fish and Wildlife Service, Green Bay, Wisconsin, personal communication), and spawning for these species has been observed during spring in Lake Superior (Selgeby 1988) and during late summer and fall in Quebec and Ontario (Scott and Crossman 1973).

Ecological variables influencing sculpin survival and population structure are especially formative during early life history stages, when survival is known to be low (e.g., deepwater sculpin; Geffen and Nash 1992). Alewives are a major predator of pelagic sculpin fry (Smith 1970; Wells and McLain 1973; Crowder 1980), whereas lake trout (especially deepwater morphotypes) and burbot are major predators of juvenile and adult sculpin (Owens and Bergstedt 1994; Madenjian et al.

TABLE 4.—Hypotheses and associated research questions (*Q*) related to re-establishment of sculpins in the Laurentian Great Lakes.

Hypothesis 1. Temporal and spatial differences in sculpin spawning and early life history are adaptations to local spawning conditions.
  Q1.1 Does the spawning of slimy, spoonhead, and deepwater sculpins differ temporally and spatially within and among lakes? What environmental variables (e.g., substrate, depth, temperature) are associated with these differences?
  Q1.2 Does emergence time of fry differ among slimy, spoonhead, and deepwater sculpins within and among lakes? What environmental variables are associated with these differences?
Hypothesis 2. Benthic versus pelagic habitats of sculpin fry influence dispersal distances and contemporary population structure within and among lakes.
  Q2.1 What is the typical population structure of slimy, spoonhead, and deepwater sculpins? Does the spatial scale that defines a population differ among species?
  Q2.2 Are spatial patterns in gene flow among populations associated with physical characteristics, such as bathymetry or current direction?
  Q2.3 Do sculpins have source and sink populations? Are environmental variables (e.g., food availability, temperature, or contaminant levels) associated with highly productive source populations? Are downstream populations of deepwater sculpin (e.g., Lake Huron) regularly infused by drift of larvae from upstream populations (e.g., Lake Superior)?
Hypothesis 3. Variables influencing early life history events (egg and fry life stages) have a larger influence on slimy, spoonhead, and deepwater sculpin population dynamics than variables influencing juvenile and adult survival.
  Q3.1 How does recruitment differ among sculpin species and lakes, and why?
  Q3.2 Does juvenile and adult survival differ among species and lakes? What variables account for these differences?
  Q3.3 Why have spoonhead sculpin populations declined in Lake Michigan?
  Q3.4 Are contemporary conditions compatible for successful reintroduction of spoonhead sculpin in Lakes Erie and Ontario and for reintroduction of deepwater sculpin in Lake Ontario?
Hypothesis 4. The decline of amphipods *Diporeia* spp. and the increase of quagga mussels in the profundal zone will affect sculpin species.
  Q4.1 Will the change in invertebrate production have a larger effect on slimy sculpin than on deepwater sculpin (the former are more reliant on *Diporeia*)?
  Q4.2 In response to *Diporeia* declines, have sculpins shifted to feeding on opossum shrimp in deeper waters than previously observed?
  Q4.3 Does the increased complexity of benthic habitat afforded by quagga mussel shells reduce lake trout and burbot predation on sculpins?
Hypothesis 5. Live transfer is a feasible option for reintroducing sculpins to Lake Ontario.
  Q5.1 What are the logistical challenges of collecting, handling, transporting, and introducing sculpins to new locations?
  Q5.2 How does the genetic diversity of the relict population of deepwater sculpin in Lake Ontario compare with that of populations in the upper Great Lakes?
  Q5.3 What are the genetic and ecological risks of transplanting deepwater sculpin from upstream populations to downstream populations?

2002). For each sculpin species, basic descriptions of population structure in each of the lakes are lacking, and even less is known about metapopulation organization. Ecosystem processes, such as passive fry dispersal by currents and downstream drifting (Geffen and Nash 1992; Roseman et al. 1998), are more likely to affect the population structure of deepwater sculpin, which have pelagic fry, than slimy sculpin, which have benthic fry (Lantry et al. 2007). Indeed, slimy sculpin abundances in Lake Ontario correlate more closely with abundances of lake trout, which prey on juvenile and adult stages, than with the abundance of alewives, which do not prey on their benthic fry (Owens and Bergstedt 1994).

Sculpin species partition lake habitats by depth; however, their use of different depth zones is dependent on the presence and distribution of other species in the lake (Owens and Bergstedt 1994; Owens and Weber 1995; Madenjian and Bunnell 2008). Thus, lake-specific interspecific interactions will be an important component of successful sculpin reintroductions. Depth stratification of slimy sculpin and deepwater sculpin has been explained by competition (Kraft and Kitchell 1986; Owens and Weber 1995), predation (Owens and Bergstedt 1994; Madenjian et al. 2005), and spatial separation (Madenjian and Bunnell 2008). Opossum shrimp are more frequent in the stomachs of deepwater sculpin, and *Diporeia affinis* are more frequent in slimy sculpin diets (Kraft and Kitchell 1986). Predation by lake trout and other piscivores may assist or hinder deepwater sculpin recruitment. One study in Lake Ontario hypothesized that lake trout, as a keystone predator, positively impact deepwater sculpin abundance by suppressing slimy sculpin populations (Brandt 1986). However, a later study in Lake Michigan failed to support this hypothesis but rather concluded that deepwater sculpin abundance is influenced by alewife predation on fry and burbot predation on juveniles (Madenjian et al. 2005). The same study found that slimy sculpin abundance was influenced by lake trout abundance and predation.

Community and Ecosystem-Level Interactions

In this section, we propose ecological and evolutionary contexts for understanding abundance variations of self-sustaining native deepwater fishes. Spatial and temporal variations in species abundance are inherent in natural systems. For example, fisheries for self-sustaining populations of sockeye salmon in Bristol Bay (Hilborn et al. 2003) and walleye *Sander vitreus* in Lake Erie (Busch et al. 1975; Roseman et al. 2005) are characterized by large interannual fluctua-

TABLE 5.—Hypotheses and associated research questions (Q) related to community and ecosystem processes structuring deepwater native fish communities in the Laurentian Great Lakes.

Hypothesis 1. When lake trout are abundant, they function as keystone predators in deepwater communities and help maintain prey diversity.
   Q1.1 Do characteristics of pelagic ciscoes and sculpins (e.g., relative abundance, depth distribution, trophic position) differ in the presence and absence of lake trout?
   Q1.2 Within lakes, is one pelagic cisco or sculpin species competitively dominant in regions where lake trout are absent? Within lakes, are regional differences in predator (lake trout or burbot) abundance correlated with pelagic cisco or sculpin diversity?
   Q1.3 Does recruitment variation have a greater effect on pelagic cisco biomass than lake trout biomass (i.e., evidence for storage effect)?
Hypothesis 2. Temporal and spatial patchiness in invertebrate production has bottom-up effects on overall productivity of deepwater communities.
   Q2.1 Is early survival or growth of sculpins, pelagic ciscoes, lake trout, or burbot linked to spatial or temporal characteristics of invertebrate production (e.g., amphipods *Diporeia* spp., opossum shrimp, microzooplankton)?
   Q2.2 How do food web connections between sculpins, pelagic ciscoes, burbot, and lake trout differ (spatially or temporally) in response to low *Diporeia* or high dreissenid abundances?
   Q2.3 Does the presence or abundance of opossum shrimp create conditions that promote diversification of pelagic ciscoes and lake trout?
Hypothesis 3. Community dominance is a mechanism by which exotic fish species suppress native planktivores and piscivores in the deepwater community.
   Q3.1 What relative abundances of lean lake trout and burbot are needed to establish dominance of these species over alewives and round goby *Neogobius melanostomus*?
   Q3.2 Does burbot predation limit survival of juvenile or adult lake trout? What abundance of deepwater lake trout is required to minimize burbot predation and facilitate re-establishment of lean lake trout?
   Q3.3 What variables (e.g., food web characteristics, initial species diversity, stocking abundances or locations, and temperature regimes) contribute to successful invasion of deep lakes by lean lake trout outside their native range (i.e., Lake Tahoe, Flathead Lake, Lake Pend Oreille, and the Santa Cruz and St. Martin basins of Argentina)?
   Q3.4 Are differences in hatchery-origin lean lake trout survival or reproduction at nearshore versus offshore locations associated with environmental characteristics, such as alewife abundance, prey availability, or current directions?
   Q3.5 Why are burbot populations less affected by alewives than are lake trout?
Hypothesis 4. Two pelagic food webs exist within the deepwater community: one that is energetically connected to shallow-water communities and dominated by species feeding within a restricted depth zone, and one that is associated with deepwater habitat and dominated by species using a diel vertical migration feeding strategy.
   Q4.1 Do the frequency and distance of vertical migrations differ among pelagic ciscoes?
   Q4.2 Do feeding strategies (e.g., depths selected, use of benthic versus pelagic prey, diel vertical migration) differ among lean, humper, and siscowet lake trout morphotypes? Does the use of diel vertical migration change during lake trout ontogeny?
   Q4.3 What is the ecological role of species that do not exhibit vertical migrations (i.e., sculpins, burbot) in deepwater food webs? For lake trout, does the dietary importance of sculpins, as compared with pelagic ciscoes, vary with depth?

tions in yield. However, for the fishes considered in this paper, the scope of natural variation is poorly understood. When such variation has been studied (e.g., bloaters in Lake Michigan), key insights into the mechanisms of population regulation have emerged (e.g., Madenjian et al. 2002; Bunnell et al. 2006b). Herein, we review the ecological and evolutionary processes believed to structure deepwater communities under the assumption that re-establishing these processes will increase the resilience and resistance of native fish species to environmental perturbations. Four hypotheses and related research questions emerging from this review are listed in Table 5.

Ecosystem context for re-establishment.—Processes regulating population abundance and species diversity will affect how and whether reintroduced species become re-established within a lake. At a community level, top-down control and bottom-up control are two major pathways that influence community structure. Ecosystem-level influences on Great Lakes fishes are not well understood, although abiotic variables such as temperature and currents probably affect community dynamics.

Reintroduction of deepwater species of cisco and deepwater lake trout would greatly benefit from understanding top-down and bottom-up influences on survival and recruitment. Opportunities to study these inputs could come from intact ecosystems outside the basin (e.g., Lake Nipigon, Great Slave Lake), recovering ecosystems within the basin (e.g., Lake Superior or Georgian Bay), or adaptive management decisions (Walters and Holling 1990) associated with ongoing reintroduction efforts (e.g., humper lake trout in Lake Erie or bloaters in Lake Ontario). Top-down control is widely used as a paradigm in fisheries management (Hollings and Meffe 1996). Top predators influence community structure (i.e., top-down control; Evans et al. 1987; Pimm and Hyman 1987) by influencing prey body size, prey diversity, and the success of species invasions (Paine 1974; Thorp 1986; Evans et al. 1987). The overriding influence of top predators is partly due to a "storage effect," referring to biomass accumulated in a population after recruitment (Warner and Chesson 1985). In Great Lakes communities, storage will be greater in re-established populations of iteroparous, long-lived lake trout (native top predators) than in naturalized populations of semelparous, shorter-lived Pacific salmon (introduced top predators). Storage minimizes density fluctuations during years of low recruitment for long-lived top predators and buffers

entire communities against fluctuations in top-down control (Warner and Chesson 1985; Evans et al. 1987). Therefore, under periods of environmental stress, abundant, long-lived piscivore populations resist species invasions (Smith 1970; Christie 1974) and control exotic planktivores (Madenjian et al. 2002; Cox and Kitchell 2004).

Bottom-up effects are more likely to be temporally variable than are top-down effects. Abundance of invertebrate prey, such as zooplankton or epibenthic plankton, varies in space, depth, and time (Wells 1960; Watson 1974; Selgeby et al. 1994) in response to changes in primary production (Madenjian et al. 2002). Survival of native fishes with a pelagic fry stage depends on temporal coupling of peaks in zooplankton abundance and fry emergence. Variability in zooplankton abundance may lead to local adaptations of spatially separate stocks, a process hypothesized to influence the spawning behaviors of deepwater species of cisco (Smith 1964; Bailey and Smith 1981; Smith and Todd 1984). Temporal patterns of energy flow may also differ between lake trout morphotypes, an idea based on the observation that sources of primary production differ between food webs used by lean and siscowet lake trout (Harvey et al. 2003).

Important and recent bottom-up effects have been mediated by two invasive bivalves (the zebra mussel *Dreissena polymorpha* and quagga mussel *Dreissena bugensis*). Mussels have been proposed to redirect nutrient and energy flow between nearshore and offshore waters by way of a phosphorus shunt (Hecky et al. 2004). Changes in nutrient and energy flow have probably been exacerbated by an expansion of dreissenids into deep waters. Although initially restricted to water depths less than 50 m, dreissenids have now expanded their colonization to depths exceeding 100 m (Bunnell et al. 2009.). Concurrently, the abundance of native species of *Diporeia* has declined in Lake Michigan. As a result, the Lake Michigan benthic community is now a major energy sink in the form of dreissenids instead of an energy pathway (via *Diporeia*) to higher trophic levels, such as lake trout, pelagic ciscoes, and sculpins (Nalepa et al. 2009). Further, mean thiaminase activity in dreissenids from the Great Lakes is 25-fold greater than that in alewives collected from Lake Michigan; thus, dreissenids constitute a significant and previously unknown source of thiaminase in the Great Lakes food web (Tillitt et al. 2009). The effects of these recent changes in the benthic community on the potential for successful re-establishment of native fish species are unknown.

Ecosystem-level variables, such as climatic forcing and regime shifts, have potential to override effects of local and regional variables. Ecosystem-level variables are well-known contributors to population dynamics of Pacific salmon (Beamish et al. 1999; Finney et al. 2000, 2002). In the Laurentian Great Lakes, temperature patterns, water currents, water levels, and ice cover all have potential to override predicted interactions between a reintroduced native species and existing biota. For example, temperature increases in Lake Superior should expand the volume of feeding and reproductive habitat used by many native and exotic fishes whose ranges in this cold lake are currently restricted by their thermal tolerances (Bronte et al. 2003a). Currents can influence larval survival and population structure, yet the role of currents is only beginning to be understood (Dettmers et al. 2005; Hook et al. 2006; Bronte and Moore 2007). Furthermore, dramatic changes in water levels and ice cover, as observed over the past 30 years in Lakes Michigan and Huron, may affect recruitment success of alewives and rainbow smelt as well as that of native cisco species.

Ecosystem development and ecological trajectories.—Ecosystem development or ecological succession is a temporal process of community development in which the physical environment is modified by community-level processes, and eventually the system maintains some maximum biomass per unit energy flow (Odum 1969). Predictable spatial and temporal patterns of community organization in large lakes support the concept of such a predictable process. For example, similar feeding guilds have established in Old World and New World oligotrophic lakes, despite different casts of postglacial colonists (Evans et al. 1987). Furthermore, responses of native fish communities to overfishing and exotic invasions were nearly parallel in Lakes Huron, Michigan, and Superior (Smith 1970; Christie 1974). In addition, responses of native fishes to low alewife abundances in Lake Michigan changed in a consistent direction over time (Bunnell et al. 2006a).

A conceptual and biological tension exists between predictable outcomes of the ecosystem development model (Evans et al. 1987; Eshenroder and Burnham-Curtis 1999) and unpredictable variation observed in nature. Many community responses, especially those following major environmental perturbations, are not predictable from an ecosystem development model (Odum 1985). Unexpected consequences (e.g., stock collapses) may result from inadequate understanding of the ecological processes that maintain community structure (Liss et al. 2006; Martin, in press). Mid-20th century collapses of lake trout and pelagic cisco stocks in the Laurentian Great Lakes are an example of this. These communitywide stock collapses were

coupled with subsequent naturalization of nonnative planktivorous, piscivorous, and parasitic fishes. Today, the presence of exotic species results in an altered ecological landscape within which energy flows through altered pathways to native fish populations.

Whereas an ecosystem development framework focuses on the state of a mature community, a domains-of-attraction framework focuses on conditions necessary for the persistence or extinction of species (Hollings 1973; Hollings and Meffe 1996). Alternative domains of attraction are hypothesized to occur in lake ecosystems where species abundances undergo major disruptions (Hollings 1973). Community dominance, when the outcome of interspecific interactions is determined by the relative abundance of each species (Skud 1982; Walters and Kitchell 2001), is an example of alternate domains of attraction and may be a key process related to native fish re-establishment in the Great Lakes. Community dominance is a potential mechanism by which alewives maintain dominance over native fishes (Bronte et al. 2003b). Alewife dominance is maintained by interactions between alewives and native deepwater fishes over several life history stages. Adult alewives negatively affect egg and fry stages of lake trout and deepwater species of cisco through predation (Krueger et al. 1995b; Eshenroder and Burnham-Curtis 1999; O'Gorman and Stewart 1999). However, adult lake trout and adult ciscoes also affect adult alewives through competition and predation (Eshenroder and Burnham-Curtis 1999). Effects of these interactions on population abundance may depend on the initial abundances of alewives, ciscoes, and lake trout, thereby making stocking densities and selection of reintroduction sites important issues for native fish re-establishment (Bronte et al. 2003b, 2007).

Vertical migration and evolutionary trajectories.— The deepwater community of Great Lakes fishes includes at least two taxonomic groups, pelagic ciscoes and lake trout, undergoing concurrent processes of divergence (Smith and Todd 1984; Turgeon and Bernatchez 2003; Eshenroder 2008). Composition of the deepwater community is integrally connected by the ecology and evolution of these groups. For example, pelagic ciscoes (Koelz 1929; Smith 1964; Eshenroder et al. 1999) and lake trout morphotypes (Moore and Bronte 2001; Zimmerman et al. 2006; Eshenroder 2008) partition pelagic habitat according to depth.

Divergence of pelagic ciscoes and lake trout is associated with availability of deepwater habitat and presence of opossum shrimp in large, deep lakes (Eshenroder and Burnham-Curtis 1999; Eshenroder et al. 1999; Eshenroder, in press). Diel vertical migrations

of ciscoes and lake trout (Eshenroder et al. 1998; Hrabik et al. 2006) are associated with diel vertical migrations of opossum shrimp (Jensen et al. 2006). In deepwater habitats, where productivity and visibility are reduced, long vertical migrations may be necessary to encounter energy-rich pelagic prey. Therefore, traits that facilitate vertical migration should offer a competitive advantage in deepwater habitat. High fat content, a characteristic that distinguishes deepwater species of cisco and deepwater lake trout from their shallow-water counterparts (Eschmeyer and Phillips 1965; Krause et al. 2002), improves buoyancy regulation when swimming across depth zones by lessening dependence on the swim bladder (Henderson and Anderson 2002).

The hypothesis of vertical migration and buoyancy regulation is compelling as an organizing construct, but further explanations are needed to account for diversity within deepwater species complexes. For example, alternate hypotheses consider populations belonging to deepwater species of cisco as (1) semi-isolated stocks that are locally adapted to spawning times and temperatures and that synchronize emergence with local peaks in zooplankton production (Smith 1964; Bailey and Smith 1981) or (2) phenotypic variants with distributions reflecting refugia from lake trout predation (Ryder et al. 1981). Under the first alternative hypothesis, new populations are formed by individuals that stray to new habitat, and established population characteristics are maintained by local adaptation, homing behavior, and high density (Smith 1964; Bailey and Smith 1981). This hypothesis of homing and local adaptation could be tested with genetic, early life history, and distribution information from lakes in which deepwater species of cisco coexist (i.e., Lake Superior or Lake Nipigon). The second alternative hypothesis assumes a single gene pool among deepwater species of cisco, an assumption that is not supported by more recent data (Eshenroder and Burnham-Curtis 1999; Turgeon et al. 1999; Turgeon and Bernatchez 2003).

Deepwater lake trout are similar to the deepwater species of cisco in that they are morphologically and ecologically heterogeneous. Humper and siscowet lake trout morphotypes are caught deeper in Lake Superior than the lean morphotype (Khan and Qadri 1970; Moore and Bronte 2001); lake-wide variation also occurs within these morphotypes (Peck 1975; Bronte and Moore 2007). The prevailing hypothesis explaining lake trout morphological diversity is that deepwater morphotypes are adapted for improved buoyancy regulation in connection with diel vertical migrations (Eshenroder and Burnham-Curtis 1999). However, research on the trophic status and feeding behavior of deepwater

morphotypes is in its infancy. Siscowet lake trout have been observed undergoing diel vertical migrations (Hrabik et al. 2006); however, the periodicity and obligatory nature of this behavior are unknown. Feeding behavior of humper lake trout has not been well studied. Humper lake trout are slower growing and are smaller at maturity than lean lake trout (Rahrer 1965; Burnham-Curtis and Bronte 1996); they have been hypothesized to be deepwater invertebrate specialists, an ecological niche that would differentiate them from the piscivorous siscowet lake trout (Eshenroder, in press). This resource partitioning hypothesis needs to be tested by comparing diet and migratory behavior among morphotypes.

Research Priorities for Re-establishing Native Deepwater Species

We have proposed a conceptual model that links processes at multiple spatial and temporal scales, and we have identified many research questions on the ecology and evolution of native deepwater fishes in the Laurentian Great Lakes. The seemingly infinite number of identified research questions could create tension between time needed to address the diverse array of research topics and an immediate need to take management actions to re-establish extirpated species. The notion that each question must be answered before management can move forward is intractable. Priorities need to be established so that the most pressing research needs of management can be afforded the greatest effort. Therefore, we recommend that priority be given to research topics that meld the acquisition of conceptual ecological understanding with its application for re-establishing native species in the Great Lakes. Below, we propose research in four topical areas as being high priority: life history bottlenecks, population and metapopulation dynamics, matching fish phenotypes to stocking sites, and propagation and stocking methods.

Life history bottlenecks.—Management to re-establish natural populations of species requires identification of obstacles that stand in the way of success (Krueger and Decker 1999; Bronte et al. 2003b). Barriers to re-establishment are best investigated by identifying when in the life history and by what process natural recruitment is blocked. Natural recruitment of a species will be affected by population, community, and ecosystem-level processes. Priority should be given to research that (1) identifies life history bottlenecks for sculpins, pelagic ciscoes, and lake trout morphotypes other than the lean morphotype and (2) determines which variables contribute most to survival and reproduction. A multistage life history approach is especially needed to understand the processes and predict the outcome of community-level interactions between native species

(lake trout and pelagic ciscoes) and exotic planktivores (alewives and rainbow smelt; e.g., community dominance hypothesis).

Population and metapopulation dynamics.—Understanding the characteristics of self-sustaining populations (e.g., age-class structure, age at first maturity, growth, recruitment) will help establish realistic expectations (i.e., management objectives) for re-established populations. However, the accuracy of such benchmarks depends on how well the population unit itself is understood. Therefore, priority should be given to research that determines population and metapopulation structure for each species, documents patterns in population abundances, and identifies intrinsic or extrinsic processes associated with abundance fluctuations. Long-term population data from lakes representing a range of ecosystem perturbations (e.g., Lake Huron versus Lake Superior versus Great Slave Lake) will be especially valuable in developing objectives used to measure management success (Krueger and Decker 1999).

Matching fish phenotypes to stocking sites.—Re-establishment of native deepwater species will depend, in part, on the selection of reintroduction sites in the Great Lakes. Potential sources for reintroduction could be from Lake Michigan, Huron, Superior, or Nipigon (Table 1). Stocking should be undertaken only when natural recolonization will not occur within acceptable time frames and when other obstacles to survival and reproduction are solved (Reisenbichler et al. 2003). Appropriate phenotypes should be matched to environmental characteristics of sites where reintroduction will occur (Reisenbichler et al. 2003). Therefore, priority should be given to research that identifies adaptive traits with a genetic basis, as well as life history (spawning time and temperature, emergence timing), ecological (resource partitioning, antipredator defense), and behavioral (homing, dispersal) variables contributing to local adaptations. Understanding these variables and their relationship to and interaction with the physical and biological characteristics of the surrounding environment will help link donor populations to specific sites in recipient lakes.

Propagation and stocking methods.—Reintroductions of native species will not be possible without effective propagation and distribution methods. Information gaps regarding these methods differ among taxa. Priority should be given to (1) locating siscowet lake trout spawning sites, (2) developing propagation methods for pelagic ciscoes, (3) evaluating the efficacy of existing coregonid stocking programs (presently occurring in northern Europe), and (4) developing methods of collecting, handling, and transporting ciscoes and sculpins.

Conclusions

The complexity and connectedness of the native deepwater fish community in the Laurentian Great Lakes highlight the need to acquire and organize biological information related to the re-establishment of these species. Our conceptual model organizes biotic and abiotic topics associated with population re-establishment around a generalized life cycle. The life cycle is influenced by processes at population, metapopulation, community, and ecosystem levels. We challenge researchers to consider the temporal and spatial scales contributing to life history bottlenecks when forming their research questions. We also emphasize that ecosystem stability is most effectively achieved by re-establishing processes rather than achieving some designated invariant condition. On ecological and evolutionary time scales, native deepwater fish communities are in the process of change and are likely to change even in the absence of unforeseen environmental perturbations (Burnham-Curtis et al. 1995). However, proactive measures have the potential to re-establish processes degraded by environmental perturbations, such as overharvesting and exotic invasions. Efforts to re-establish a diversity of connections within the deepwater community in the Laurentian Great Lakes will improve resilience and resistance of native fish species to inevitable environmental change in the future.

Acknowledgments

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