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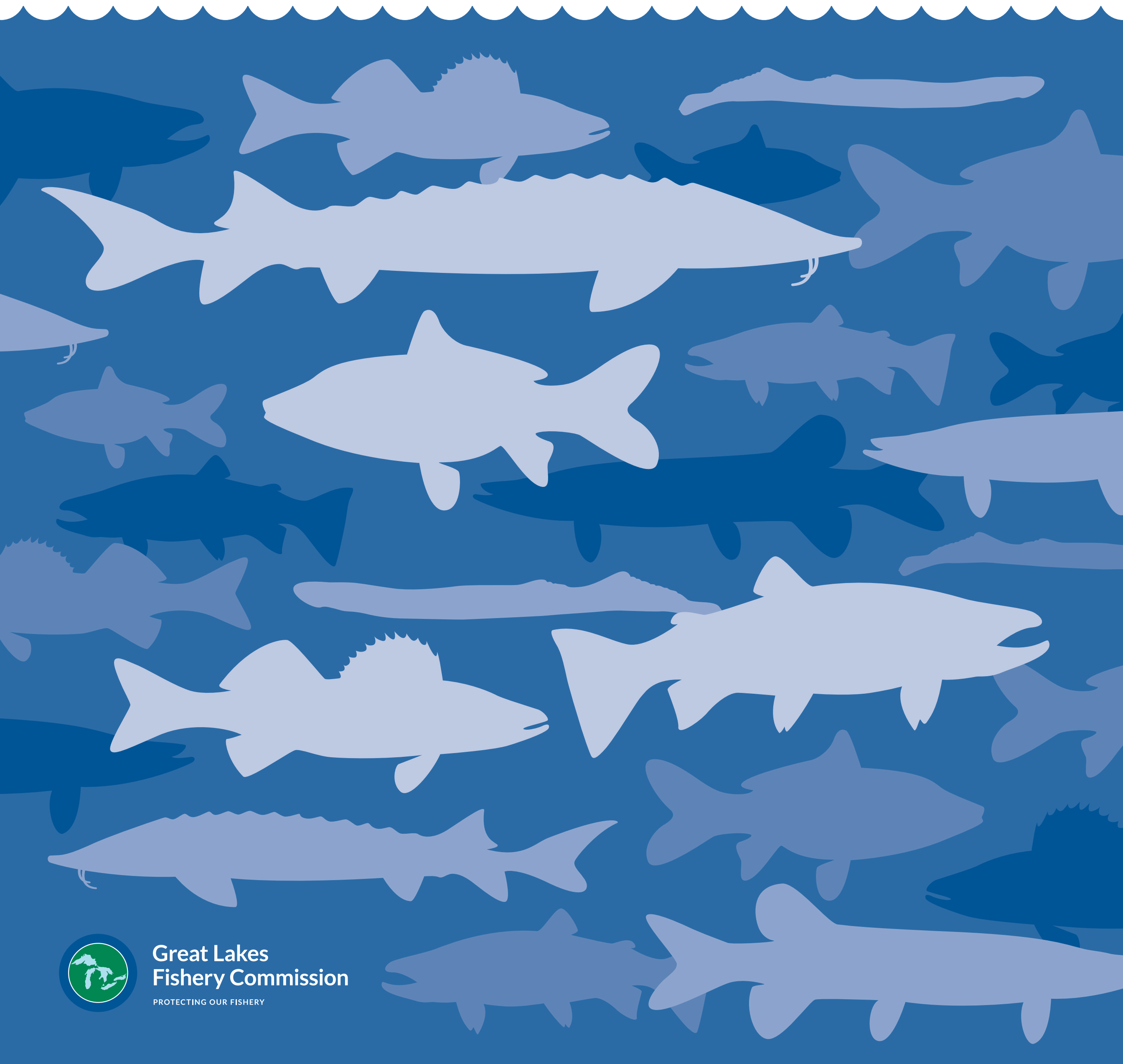

Great Lakes
Fishery Commission
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The Great Lakes Fishery Commission (Commission) was established by the Convention on Great Lakes Fisheries between Canada and the United States, which was ratified on October 11, 1955. The Commission was organized in April 1956 and assumed its duties as set forth in the Convention on July 1, 1956 (glfc.org/pubs/conv.pdf). The Commission has two major responsibilities: first, develop coordinated programs of research in the Great Lakes, and, on the basis of the findings, recommend measures that will permit the maximum sustained productivity of stocks of fish of common concern; second, formulate and implement a program to eradicate or minimize Sea Lamprey populations in the Great Lakes. The Commission is also required to publish or authorize the publication of scientific or other information obtained in the performance of its duties.

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Scope

Launched in 2022, *Laurentian* replaces three historically separate, irregularly published Commission journals: *Technical Report, Special Publication, and Miscellaneous Publication. Laurentian* will continue to serve as an outlet for publication of interdisciplinary review and synthesis papers; narrowly focused material with special relevance to a single but important aspect of the Commission's mandate under the Convention; and scientific reports from committees that work under the umbrella of the Commission. In addition, relevant papers that do not fit the format of mainstream journals owing, for instance, to length, extensive datasets, or nature of the material and its presentation, will be considered. For further clarification, authors are encouraged to review recent papers published under the three former titles, all available on the Commission's website (www.glfc.org).

Editorial Process

All accepted submissions to *Laurentian* will be citation indexed by ProQuest®. In continuing with this scholarly process, all submissions will be reviewed by external experts, freelance editors, or staff editors as indicated by the nature of the material. Manuscripts should be submitted to the Commission's Managing Editor (randye@glfc.org) to begin the editorial process. The editor may also be consulted in advance of submission, if authors are unsure regarding whether a proposed paper is suitable for *Laurentian*. After a submission is determined to be suitable for *Laurentian*, the Managing Editor will forward it to one or more freelance Technical Editors, who will arrange for peer review, as needed based on subject matter. Reviews by Technical Editors and the Managing Editor may satisfy the requirement for review, or additional reviews may be sought by a freelance editor. The Managing Editor will decide on acceptance and requirements for revision based on recommendations from technical editor(s) and the Managing Editor's own review.

Style

The style guide of the American Fisheries Society (A Guide to AFS Publications Style) has been adopted for *Laurentian* (https://fisheries.org/books-journals/writing-tools/style-guide/).

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Synthesizing Professional Opinion of Lake Whitefish and Cisco Recruitment Drivers across the Great Lakes

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ABSTRACT

Disentangling the suite of ecological drivers that explain recruitment variability for Lake Whitefish *Coregonus clupeaformis* and Cisco *C. artedi* is of critical importance for their conservation, management, and stewardship in the Laurentian Great Lakes. However, recruitment is inherently variable and can be regulated by many interacting processes, the relative importance of which can vary spatially, temporally, and ontogenetically. Given this complexity, comparisons across lakes and species that identify overarching hypotheses could efficiently guide future research. Using facilitated deliberations among fishery professionals (n = 57) with expertise in Great Lakes *Coregonus* spp., we synthesized current knowledge regarding (1) which biophysical processes are most important for driving contemporary recruitment between species, among lakes, and across life stages and (2) mechanisms by which those drivers regulate recruitment at key life stages. Participants affirmed the hypothesis that many drivers interact in complex ways to regulate Lake Whitefish and Cisco recruitment. Large-scale climatic processes affecting early life-stage growth and survival were consistently considered important. Other drivers were only deemed influential in certain lakes, highlighting perceived context-dependent recruitment dynamics. Notably, recruitment in Lakes Superior, Michigan, and Huron was considered limited during larval and early juvenile life stages by low productivity, whereas spawning-habitat degradation and reduced metapopulation diversity were hypothesized to limit recruitment during embryonic and larval stages in Lakes Erie and Ontario. Several drivers were hypothesized to similarly impact Lake Whitefish and Cisco during early life stages, while drivers acting on post-larval life stages were typically distinct between species. The hypotheses synthesized herein can guide future research on Lake Whitefish and Cisco recruitment dynamics in the Great Lakes.

INTRODUCTION

Lake Whitefish *Coregonus clupeaformis* and Cisco *C. artedi* are socioecologically important fish species across the Laurentian Great Lakes (Figure 1). These two species and other members of the coregonine subfamily (Salmonidae Coregoninae) contribute to native fish diversity in the Great Lakes (Koelz 1929; Eshenroder et al. 2016) and perform key ecosystem functions, such as transferring energy across trophic levels and habitats (Stockwell et al. 2014). Lake Whitefish and Cisco are also culturally and economically valuable. Since time immemorial, Indigenous communities of the Great Lakes region have nurtured ongoing relationships with these species—known by numerous ancient names—through singing, dancing, and ceremony with and for the fish (F. Ettawageshik, Little Traverse Bay Bands of Odawa Indians, personal communication) as well as for subsistence and commercial harvest (Gobin et al. 2022; Duncan et al. 2023). European settlers established commercial fisheries by the early 1800s that quickly became widespread and highly intensive (Smith 1995; Spangler and Peters 1995; Bogue 2000). Due to the cumulative impacts of overfishing, habitat degradation, and non-native species, many Lake Whitefish and Cisco populations across the basin declined precipitously between the late-19th and mid-20th centuries (Smith 1968; Eshenroder et al. 2016). After decades of harvest regulation and Sea Lamprey *Petromyzon marinus* control, many Lake Whitefish populations partially recovered, but they still exhibited wide fluctuations in abundance due to a combination of exploitation and unfavorable biophysical conditions (Christie

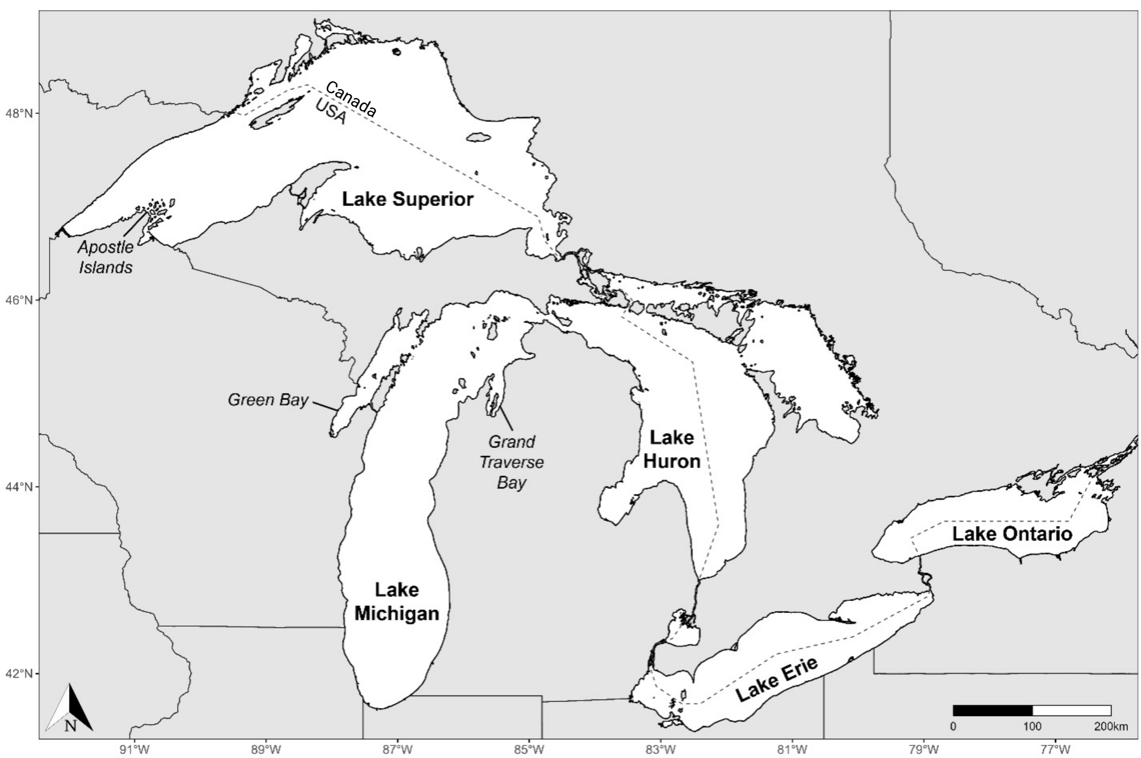

FIGURE 1. Map of the Laurentian Great Lakes with locations referenced in the text. The dotted line demarcates the international border between the USA and Canada.

1963; Cucin and Regier 1966; Jensen 1976; Taylor et al. 1987). Lake Whitefish populations in many regions then reached high levels of abundance during the 1990s (Ebener 1997), but recruitment and subsequent fishery yield for many populations declined again in the early 2000s (Mohr and Nalepa 2005). While Cisco has partially recovered in Lake Superior and supports viable fisheries (Stockwell et al. 2009; Rook et al. 2021), populations remain spatially fragmented and depressed in abundance in many regions of Lakes Huron, Michigan, and Ontario, and the species is considered extirpated from Lake Erie (Eshenroder et al. 2016). The socioecological importance of coregonine fishes has driven a growing number of management and restoration initiatives (e.g., Bronte et al. 2017; Weidel et al. 2022), including a basinwide adaptive conservation and restoration framework (Bunnell et al. 2023).

Understanding the processes driving recruitment variability is a critical knowledge gap for advancing management and stewardship of Lake Whitefish and Cisco populations (Fitzsimons and O'Gorman 2006; Zimmerman and Krueger 2009; CLC 2018; Ebener et al. 2021). It is unclear why recruitment is sporadic or declining for many populations of Lake Whitefish and Cisco while recruitment is consistent or improving for others. Notably, a few populations appear to be exceptions to widespread recruitment declines. For example, the Apostle Islands (Lake Superior; Carl 2021) and Green Bay (Lake Michigan; Hansen 2019; Ransom et al. 2021) support abundant Lake Whitefish spawning stocks with consistent recruitment, and Cisco populations in Grand Traverse Bay (Lake Michigan) are expanding (Claramunt et al. 2019). Meanwhile, population trajectories for some sympatric populations of Lake Whitefish and Cisco have recently diverged, including those in the eastern basin of Lake Ontario (Brown et al. 2022), northern Lake Michigan (Madenjian 2019; Modeling Subcommittee 2022), and northern Lake Huron (Riley and Ebener 2020; Modeling Subcommittee 2022). Increased understanding of the processes regulating the populations of these two species could help clarify the causes of declining, sporadic, and asynchronous recruitment, and may be needed to effectively design management interventions for both species (Bronte et al. 2017; Ebener et al. 2021; Bunnell et al. 2023). Unfortunately, understanding recruitment and its drivers is challenging because recruitment is regulated by a myriad of interacting processes (e.g., Ricker 1954; Subbey et al. 2014; Munch et al. 2018), the relative importance of which can vary spatially, temporally, and ontogenetically (e.g., Myers et al. 1997; Houde 2008).

Although fully disentangling the complex suite of biophysical recruitment drivers may be impossible, cross-species and cross-lake comparisons can help identify key drivers by highlighting common or divergent responses across gradients of habitats and environmental conditions. Lake Whitefish and Cisco overlap in their spawning habitat. Adults can spawn in a diversity of nearshore habitats in late fall where their fertilized embryos settle onto benthic substrates, incubate over winter, and hatch in early spring as planktonic larvae (Goodyear et al. 1982; Ebener et al. 2021; Paufve et al. 2022; Weidel et al. 2023). Consequently, the early life histories of these two species are generally similar during the embryonic and larval stages (Brown et al. 2023), but the species diverge by the juvenile stage when Lake Whitefish become demersal and benthivorous (>40 mm TL, approximately 3–4 months post hatch; Reckahn 1970; Claramunt et al. 2010), whereas Cisco continues using pelagic habitats (George 2019). This ontogenetic niche differentiation offers an opportunity to identify the life stages at which recruitment bottlenecks occur between species. Both species may be subject to similar recruitment bottlenecks if processes acting on the embryonic and larval life stages are most important for regulating their populations. Conversely, processes acting on later life stages after habitat use and ecological interactions have diverged between species may be important, which could explain observed differences in recruitment trends between species. Further, comparisons across populations and habitats can help to inform our understanding of how biophysical processes interact to regulate recruitment (Myers and Mertz 1998; Ludsin et al. 2014). Each of the Great Lakes represents a unique ecosystem that exists across gradients of biological community structures and physical regimes; comparisons within and across lakes can illuminate differences in the relative importance of biophysical processes that are not uniformly distributed across the Great Lakes basin. Together, cross-species and cross-lake comparisons show promise for identifying when recruitment bottlenecks occur and the ecosystem context under which various processes are important for regulating recruitment.

Given the complexity of recruitment dynamics, a synthesis of professional opinion aimed at hypothesis generation could efficiently guide future research on key mechanistic relationships (Drescher et al. 2013; Sethi and Hollmen 2015). Understanding which processes shape recruitment and influence population dynamics in Lake Whitefish and Cisco has been a long-standing challenge. Concerns over declining Lake Whitefish growth and condition prompted scientists from across the Great Lakes to organize a workshop to evaluate the role of declining *Diporeia* spp. (hereafter, *Diporeia*) prey resources (Mohr and Nalepa 2005) and to publish a special issue of journal articles assessing the health of Lake Whitefish populations (Brenden et al. 2010). More recently, fishery scientists and managers identified existing research gaps and priorities for Lake Whitefish in the upper Great Lakes during a 2018 management workshop (CLC 2018), culminating in a comprehensive review of declining Lake Whitefish recruitment by Ebener et al. (2021). In parallel, interest in Cisco restoration motivated the workshops in 2004 (Fitzsimons and O'Gorman 2006), 2016 (Bronte et al. 2017), and 2018 (George et al. 2018), all of which were broadly focused on summarizing an understanding of remnant stocks, identifying research needs, and highlighting key uncertainties for Cisco restoration. However, less attention has been devoted to comparisons of recruitment drivers between Lake Whitefish and Cisco and to understanding of context-dependent recruitment dynamics among lakes. A synthesis of professional opinion can efficiently summarize the current state of knowledge about a complex problem (e.g., Mohr and Nalepa 2005), integrate knowledge from both published literature and expert intuition (e.g., Krabbenhoft et al. 2023), and guide future research aimed at identified knowledge gaps (e.g., Bunnell et al. 2018; George et al. 2018; CLC 2018). Structured workshops are a common tool for synthesizing professional opinion, as they can facilitate collaborative hypothesis generation that incorporates a diversity of expertise and approaches (e.g., Lauber et al. 2016). This collective professional opinion, therefore, encompasses knowledge from the literature and unpublished observations, in addition to what individuals perceive to be important.

Here, we synthesize professional knowledge of important recruitment drivers and identify key similarities and differences in hypothesized drivers for Lake Whitefish and Cisco across the Great Lakes. Specifically, we (1) identify which biophysical processes professionals consider most important for driving contemporary Lake Whitefish and Cisco recruitment variability in each of the Great Lakes, and (2) propose specific mechanisms by which individual biophysical drivers are thought to regulate recruitment, including on which life stage(s) they act. We achieved these objectives through a workshop with facilitated deliberations among fishery professionals with expertise in Great Lakes *Coregonus* spp. We focus here on processes believed to regulate survival across key life stages to improve our understanding of recruitment for future research. This study bridges knowledge derived from individual research projects investigating a single driver, species, and/or lake to achieve a holistic review of recruitment drivers across lakes and species. Importantly, our utilization of professional opinion and focus on contemporary conditions allows us to gain valuable insight into the dynamics most relevant for current populations and ecosystems, including those not yet present in the published literature. This synthesis can be used to guide future research targeted at evaluating key hypotheses and fill knowledge gaps for management and stewardship of populations across the Great Lakes.

METHODS

For the purposes of this synthesis of professional opinion, we defined three key terms: recruitment, recruitment drivers, and mechanisms (Table 1). Given these definitions, each recruitment driver is related to one or more potential mechanisms based on the specific manner, timing, and ecosystem context in which they act to regulate recruitment across life stages. We expected that the specific mechanisms that relate each driver (cause) to recruitment variability (effect) likely differ between species, among lakes, and across life stages; for example, prey availability could be a key driver of recruitment at the larval stage in some populations and at the juvenile stage in others. We focused on the drivers thought to be most important for regulating recruitment under contemporary conditions in each lake because the relative importance of each driver is likely context-dependent and non-stationary due to interactions with other drivers and ecosystem changes. We note that Cisco as a species exhibits high intraspecific diversity across the Great Lakes, including multiple ecomorphs (Eshenroder et al. 2016, 2021). We expected that recruitment drivers would be similar across Cisco ecomorphs and, therefore, we did not consider ecomorph-specific dynamics, although it is possible that the relative importance of recruitment drivers varies across ecomorphs.

We designed our synthesis of professional opinion as a two-step process: (1) an online survey distributed to registrants prior to the workshop and (2) a virtual workshop held on February 22, 2023; both steps of the process are described in detail below.

TABLE 1. Definitions of key terms.

Term	Definition
Recruitment	Number of individuals from a given cohort entering the population at some age or life stage each year. Recruitment is considered “set” beyond the period when most early life-stage mortality has occurred (adapted from Ludsin et al. 2014).
Recruitment drivers	Physical and biological processes that interact, directly or indirectly, to regulate recruitment.
Mechanisms	Way(s) in which each recruitment driver acts to regulate recruitment, including at which life stage(s).

We adopted a virtual format for the workshop to facilitate broad participation across a large geographic area by avoiding barriers to travel (e.g., cost, international travel approval). Workshop registration was open to anyone, although participation was primarily solicited through targeted invitations to scientists and managers from natural resource agencies, academic institutions, and nongovernmental organizations with expertise in Lake Whitefish and/or Cisco populations across the Great Lakes basin. We prioritized participation of individuals actively working to elucidate contemporary recruitment dynamics or who are currently responsible for assessment or monitoring of populations, with the goal of representing scientific expertise across lakes, species, and life stages.

We designed the online survey (Appendix A) with the primary goal of identifying and prioritizing potentially important drivers of recruitment prior to the workshop. All questions were optional and specific to each species and lake. We requested that respondents only answer questions for the lake(s) and species with which they were knowledgeable. We first asked respondents to organize a list of processes hypothesized to be important for recruitment (i.e., putative drivers) into three categories: highly important, moderately important, or not at all important. The pre-defined process list included various biotic and abiotic processes previously implicated in the literature on Lake Whitefish and Cisco recruitment (see Appendix A for full list) with the option to include a user-defined “Other” process. In this way, we were able to capture participants’ individual hypotheses about contemporarily important recruitment drivers. Second, respondents identified the life stage(s) where the most important recruitment bottlenecks were thought to occur (multiple answers). Third, because important recruitment drivers may have shifted through time due to anthropogenic ecosystem changes (e.g., species introductions, productivity regime shifts), respondents named any important perturbations they believed led to major changes in recruitment dynamics (open response). Lastly, we gave respondents the option to include additional details to help contextualize their responses (open response). We used the survey results to retain the recruitment drivers most frequently ranked as highly important for each species in each lake (Appendix B) for further deliberation during the workshop.

During the virtual workshop, we asked participants to collaboratively (1) finalize the list of the most important contemporary recruitment drivers for each species in each lake and (2) propose specific mechanisms by which each driver acts to directly or indirectly regulate recruitment, including at which life stage(s) each driver is acting. We provided participants with the recruitment drivers from the survey most frequently ranked highly important as a starting point for deliberations during the workshop, although we encouraged participants to refine or remove drivers from that list or introduce additional drivers. Through this exercise, we retained for interpretation only those drivers that were collectively hypothesized to play a key role in determining contemporary recruitment. We then asked participants to propose detailed mechanisms by which each driver acts to regulate recruitment at specific life stages. These tasks were facilitated through parallel, lake-specific breakout groups, each group with a moderator and note taker. Lake-specific breakout groups had one hour of deliberation time for each species. Moderators were responsible for ensuring that tasks were accomplished within the allotted time, but the discussion itself was participant led. For Lake Erie, where Cisco is considered extirpated (Eshenroder et al. 2016), we asked participants to speculate on which recruitment drivers might be important for a reintroduced population of Cisco under contemporary ecosystem conditions.

Lastly, in an effort to summarize professional opinion across lakes, we developed a conceptual diagram of hypothesized biotic and abiotic drivers of Lake Whitefish and Cisco recruitment across the Great Lakes, based on Krabbenhoft et al. (2023). We endeavored to depict the current scientific understanding of each driver's degree of influence in regulating mortality across different early life stages: specifically, over which life stages each driver directly regulates mortality and the relative influence of each individual driver across life stages. Using this approach, we also sought to delineate which drivers are hypothesized to affect both species similarly versus which mechanisms are thought to be unique to each species. Importantly, we aimed to describe each driver's direct effects on mortality, recognizing that many of these hypothesized drivers interact with and influence one another. We also note that this approach is inherently limited to recruitment drivers that directly regulate mortality, and, therefore, we did not include important demographic drivers of recruitment (e.g., spawning stock biomass [SSB]).

RESULTS

Fifty-seven fishery professionals participated in the workshop activities (Appendix C), representing 21 US federal (*n* = 20 participants), Tribal (*n* = 6), First Nations (*n* = 1), state (*n* = 10), provincial (*n* = 7), academic (*n* = 11), and nongovernmental organizations (*n* = 2). Five individuals completed the survey but were unable to attend the live workshop. Participation was well-balanced among the lake-specific subgroups during the workshop, with Lake Huron having the most participants (*n* = 12), followed by Lake Michigan (*n* = 11), Lakes Superior and Ontario (*n* = 10 each), and Lake Erie (*n* = 9).

Based on the survey administered prior to the workshop, important recruitment bottlenecks across all lakes were most frequently hypothesized to occur during the larval stage, followed by the early juvenile and embryonic stages (Figure 2). Basinwide patterns were generally similar between species, highlighting the importance of biophysical conditions during early life stages for recruitment of both Lake Whitefish and Cisco. However, the specific life stages during which important recruitment bottlenecks were thought to occur differed among lakes. Bottlenecks during larval and early juvenile life stages were most frequently

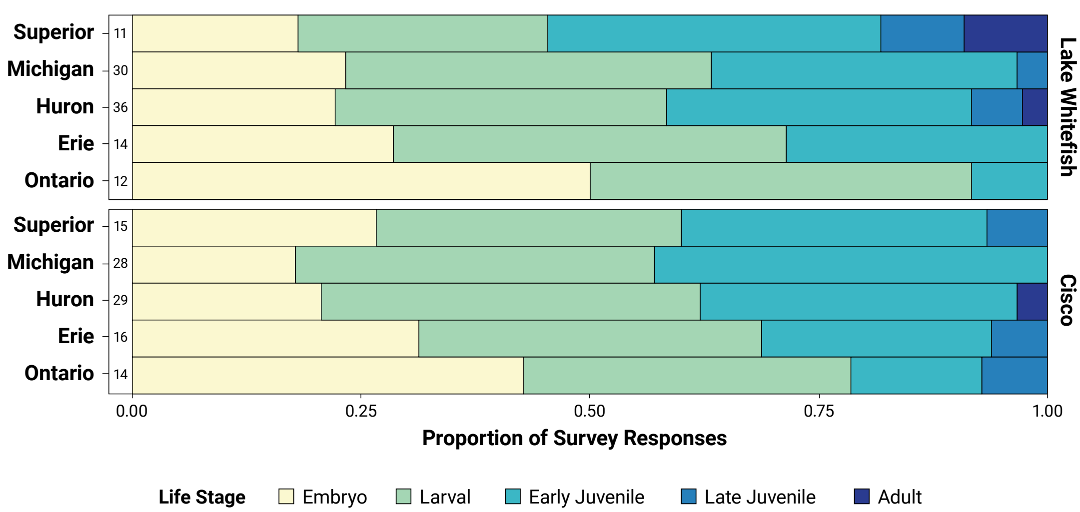

FIGURE 2. Distribution of responses to the pre-workshop survey question: "In general, during which life stage do you think the most important recruitment bottlenecks occur?" for Lake Whitefish and Cisco across the Great Lakes (see Appendix A). Respondents were able to select multiple answers, but they were asked to restrict their choices to those of equally high importance. Sample sizes are depicted to the left of each horizontal bar.

indicated for the upper Great Lakes (Superior, Michigan, and Huron), whereas recruitment bottlenecks were more commonly hypothesized to occur during embryonic and larval stages in the lower Great Lakes (Erie and Ontario). As with the basinwide patterns, results were generally consistent for Lake Whitefish and Cisco.

Prior to the workshop, participants identified major perturbations hypothesized to have led to the biggest changes in contemporary recruitment drivers and dynamics for each species (Figure 3). Responses to this survey question varied in the number of named perturbations and degree of detail; consequently, we report results based on all individually named perturbations from each response, retaining specificity from the original response when possible. Combining responses from all lakes, the establishment of dreissenid mussels (i.e., quagga mussel *Dreissena rostriformis bugensis* and zebra mussel *D. polymorpha*; hereafter, dreissenids) was the most commonly named perturbation for both Lake Whitefish (21%) and Cisco (13%). Unspecified non-native species were also frequently mentioned as perturbing Lake Whitefish (9%) and Cisco (10%) populations. Climatic change, such as decreased ice cover and increased water temperatures, was also among the most common perturbations identified across lakes for Lake Whitefish (17%) and Cisco (13%). Reductions in spawning stock biomass were frequently named for Cisco (11%) but not for Lake Whitefish (1%). Oligotrophication-induced shifts in primary productivity and declines in zooplankton prey availability for early life stages also were commonly reported for both species. Frequency of responses for important perturbations varied across lakes, reflecting differing ecosystems. For example, in Lake Superior, where dreissenids remain rare, harvest was the most common response for Lake Whitefish. Habitat degradation (e.g., sedimentation) was a commonly reported perturbation across lakes for both species, but most responses were specific to Lake Ontario.

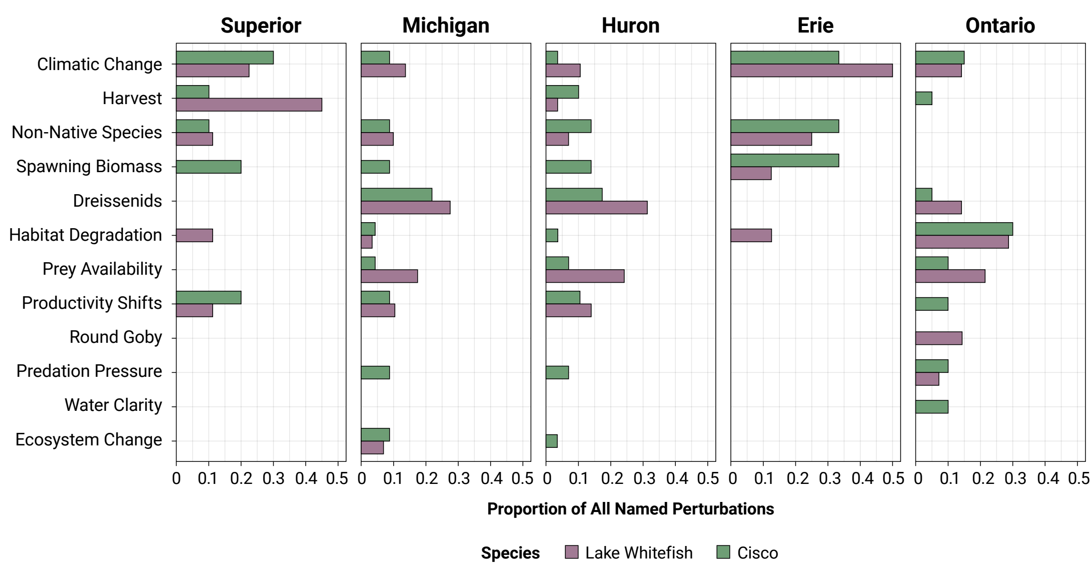

FIGURE 3. Distribution of categorized responses to the pre-workshop survey question: “Which perturbation(s) do you hypothesize have led to the biggest changes in recruitment drivers and dynamics?” for Lake Whitefish and Cisco across the Great Lakes (see Appendix A). The survey question was open-response such that answers differed in degree of specificity and number of named perturbations. Response proportions were calculated based on all reported perturbations, but only the most frequently named perturbations are visualized for clarity.

We preliminarily retained the drivers most frequently categorized in the online survey as highly important for each lake and species combination (Appendix B). Several of these physical and biological processes were consistently considered highly important for regulating contemporary Lake Whitefish and Cisco recruitment across the Great Lakes, the most prevalent of which were ice-cover concentration/duration, timing of ice-cover onset/offset, and zooplankton prey availability. Spawning habitat quality also was retained for both species in every lake except Lake Superior. For Lake Whitefish, benthic-prey availability was categorized as highly important for every lake except Lake Erie. Other putatively important processes were unique to specific lakes and species. For example, harvest and competition with benthivorous fishes were considered important processes affecting Lake Whitefish in Lake Superior, predation by piscivores on Cisco was considered important in Lake Superior, and competition with other planktivores was only important for Cisco in Lake Michigan. All preliminary drivers were retained for final determination of important recruitment drivers during the workshop.

Below, we detail the biological and physical processes that workshop participants selected as the most important drivers of recruitment variability for each species within each Great Lake (Table 2, Figures 4, 5). We also describe the proposed mechanisms by which each driver was hypothesized to regulate recruitment. Importantly, we note that the drivers and mechanisms identified here are those considered to be important by workshop participants and may or may not have empirical support in the literature.

TABLE 2. Summary of hypothesized important recruitment drivers and mechanisms for Lake Whitefish and Cisco in each of the Laurentian Great Lakes: Superior (SU), Michigan (MI), Huron (HU), Erie (ER), and Ontario (ON).

Driver	Mechanism	Life Stage	Lake Whitefish					Cisco				
			SU	MI	HU	ER	ON	SU	MI	HU	ER	ON
Spawning stock biomass	Directly affects reproductive output	All	✓		✓		✓	✓	✓	✓	✓	
Metapopulation diversity	Decreased resiliency to environmental variation through loss of spatial and/ or phenotypic diversity	All				✓				✓	✓	✓

TABLE 2. Continued.

Driver	Mechanism	Life Stage	Lake Whitefish					Cisco				
			SU	MI	HU	ER	ON	SU	MI	HU	ER	ON
Prey availability	Encounter rates (densities) and match-mismatch (timing) with zooplankton prey in spring regulates survival through direct starvation mortality	Larval		✓	✓				✓	✓		
	Encounter rates and match-mismatch with zooplankton prey in spring regulates growth, wherein slower growth increases vulnerability to predation, reduces swimming ability, limits gape size and/or decreases fitness in later life	Larval and Juvenile		✓	✓							
	Low availability of high-quality benthic prey (i.e., *Diporeia*) reduces growth with associated declines in condition, size-at-age, fitness, fecundity, and egg quality	Juvenile and Adult		✓		✓	✓					
	Shifts in zooplankton community composition, resulting in declining growth and survival	Adult								✓		

TABLE 2. Continued.

Driver	Mechanism	Life Stage	Lake Whitefish					Cisco				
			SU	MI	HU	ER	ON	SU	MI	HU	ER	ON
Predation	Predation by benthivorous Lake Whitefish, Lake Trout *Salvelinus namaycush*, and sculpins (Cottidae)	Embryonic						✓				
	Predation by planktivorous Rainbow Smelt *Osmerus mordax*, Alewife *Alosa pseudoharengus*, and/or Yellow Perch *Perca flavescens*	Larval				✓	✓		✓	✓	✓	✓
		Juvenile							✓	✓	✓	
	Predation by piscivorous Lake Trout and Pacific salmonids (*Oncorhynchus* spp.)	Juvenile and Adult					✓	✓				
	Predation by Sea Lamprey leads to direct mortality and/or morbidity	Adult			✓					✓		
Competition	Localized depletion of zooplankton (prey availability) and selective-feeding-induced-shifts in zooplankton prey community composition (prey quality) by planktivorous Rainbow Smelt, Alewife, and/or *Bythotrephes longimanus* (hereafter, *Bythotrephes*)	Larval	✓			✓		✓				
		Juvenile and Adult						✓	✓		✓	

TABLE 2. Continued.

Driver	Mechanism	Life Stage	Lake Whitefish					Cisco				
			SU	MI	HU	ER	ON	SU	MI	HU	ER	ON
Primary productivity	Pelagic primary productivity regulates the spring phytoplankton bloom, which in turn regulates the density and community composition of spring zooplankton for exogenously feeding individuals	Larval	✓	✓	✓	✓		✓		✓		
	Declines in pelagic primary productivity—mediated by decreased nutrient loading and intensified by dreissenid filtration and benthification—reduces available forage and limits overall carrying capacity	Larval, Juvenile, and Adult		✓	✓	✓						
	Increasing water clarity results in a higher vulnerability to visual predation and UV exposure	Egg, Larval, and Juvenile		✓	✓							

TABLE 2. Continued.

Driver	Mechanism	Life Stage	Lake Whitefish					Cisco				
			SU	MI	HU	ER	ON	SU	MI	HU	ER	ON
Ice cover	Protects from physical disturbance (dislodging/ advection) and sedimentation	Embryonic	✓	✓	✓		✓	✓		✓		✓
	Regulates light penetration and UV exposure	Embryonic	✓					✓				
	Affects spring water temperatures and subsequent timing of hatch and concurrent environmental conditions	Larval	✓					✓				
	Timing and duration influences match/ mismatch with prey	Larval			✓					✓		

TABLE 2. Continued.

Driver	Mechanism	Life Stage	Lake Whitefish					Cisco				
			SU	MI	HU	ER	ON	SU	MI	HU	ER	ON
Water temperatures during early life	Water temperatures from late fall to early spring regulate development, survival, size-at-age, and yolk-sac volume	Embryonic and Larval	✓		✓	✓	✓	✓			✓	✓
	Overwinter and early-spring water temperatures regulate the spring phytoplankton bloom, thereby affecting the timing and density of zooplankton prey for exogenously feeding individuals	Larval	✓		✓	✓	✓	✓			✓	✓
	Early-spring water temperatures mediate the risk of predation, where cold temperatures delay the inshore movement of predators into nearshore nursery areas	Larval and Juvenile						✓				
Wind forcing and water currents	Strong winds and resultant water currents during winter disrupts spawning substrates, particularly in shallow habitats without ice cover	Embryonic	✓					✓				

TABLE 2. Continued.

Driver	Mechanism	Life Stage	Lake Whitefish					Cisco				
			SU	MI	HU	ER	ON	SU	MI	HU	ER	ON
Wind forcing and water currents	Strong winds and resultant water currents in spring transport individuals into nearshore nursery habitats from offshore spawning habitats, or advect them away from nearshore nursery habitats	Larval	✓	✓				✓		✓		
	Water currents affect the distribution of zooplankton, thereby influencing encounter rates with prey	Larval		✓								
Spawning habitat quality	Infilling of interstitial spaces by silt, vegetation, and dreissenids reduces the quality of spawning substrates, resulting in poor conditions for development and survival (e.g., hypoxia, predation, advection)	Embryonic		✓	✓	✓	✓			✓	✓	✓
	Degradation of high-quality spawning habitats at a lakewide scale reduces spatial metapopulation diversity	Adult				✓				✓	✓	

TABLE 2. Continued.

Driver	Mechanism	Life Stage	Lake Whitefish					Cisco				
			SU	MI	HU	ER	ON	SU	MI	HU	ER	ON
Nursery-habitat quality	Shoreline hardening and beach erosion reduces habitat quality (e.g., reduced emergent vegetation) for foraging and protection from predators	Larval and Juvenile		✓								

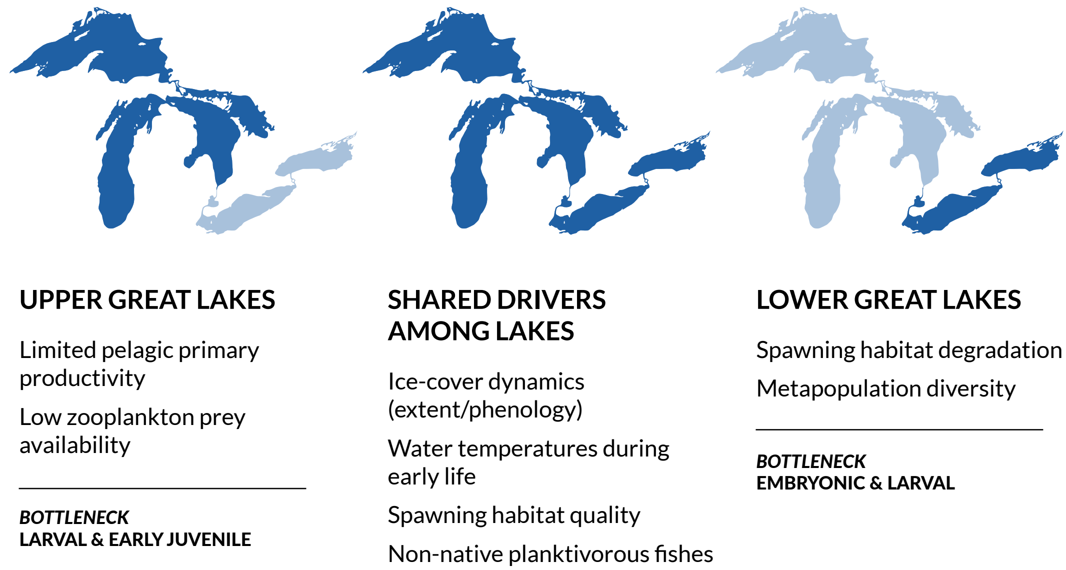

FIGURE 4. Cross-lake summary of biophysical processes and conditions considered important for driving contemporary Lake Whitefish and Cisco recruitment in the Great Lakes, including the life stages at which important bottlenecks were hypothesized to occur among lakes.

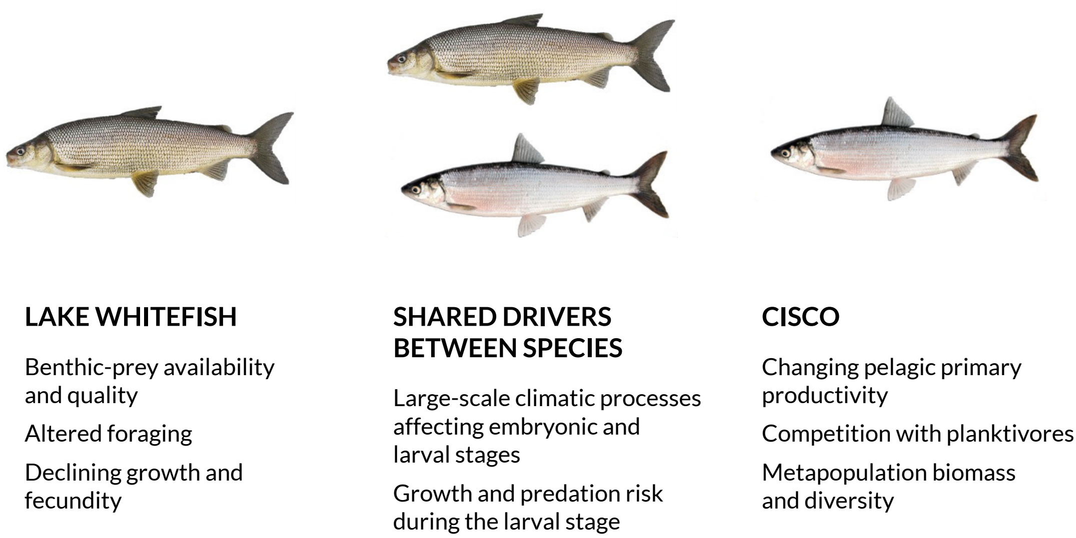

FIGURE 5. Cross-species comparison of biophysical processes and conditions considered important for driving contemporary recruitment of Lake Whitefish and Cisco across the Great Lakes.

Lake Superior

Recruitment of Lake Whitefish and Cisco in Lake Superior was hypothesized to be regulated during early life stages by interactions among climatic processes (i.e., ice cover, water temperature, wind), primary productivity, and competition with planktivores. Multiple abiotic processes during the embryonic and larval stages were thought to interact to regulate recruitment, including through indirect impacts on match-mismatch of larvae with zooplankton prey. For example, ice cover was hypothesized to reduce physical disturbance in nearshore embryonic incubation habitats, mediate light penetration to incubating embryos, and affect spring water temperatures. Fall water temperatures may affect the timing of embryo deposition, whereas overwinter water temperatures could affect the rate of embryonic development and the time of larval emergence, thereby influencing the quality of larvae at hatch and potential mismatch with spring zooplankton prey. Wind-driven water currents may affect planktonic larvae away from nursery habitats, with consequences for growth and survival. Physical disturbance during the embryonic stage may be more important for Lake Whitefish, which was understood to spawn in shallower areas than Cisco in Lake Superior. Participants also discussed how primary productivity can regulate zooplankton abundance, which, in turn, was believed to determine larval growth and survival; notably, because Lake Superior is oligotrophic, small increases in phosphorus were thought to result in large increases in productivity and, potentially, recruitment. Rainbow Smelt and *Bythotrephes* were hypothesized to induce local depletion of zooplankton or a shift in zooplankton community composition, which could reduce the quantity and quality of zooplankton prey. Competition with pelagic planktivores was identified as important for juvenile Cisco but not for juvenile Lake Whitefish, which transition to benthic habitats after the larval stage.

The hypothesized importance of SSB and predation pressure differed between Lake Whitefish and Cisco in Lake Superior. Participants agreed there is a minimum SSB needed to support a strong year-class for both species to capitalize on favorable environmental conditions. Environmental processes were thought to be more important than SSB alone for Cisco given the weak relationship between observed recruitment and SSB and its highly variable population dynamics. On the other hand, the magnitude of Lake Whitefish recruitment was thought to be tied more closely to SSB and may operate at more local scales relative to Cisco. Predation at the embryonic, larval, and juvenile life stages was also thought to be important for Cisco recruitment, whereas predation was not categorized as an important driver for Lake Whitefish. Sculpins, Lake Whitefish, and juvenile Lake Trout were highlighted as potentially significant predators on Cisco embryos. Rainbow Smelt were thought to consume larval Cisco, although abundant Rainbow Smelt populations were thought to shield juvenile Cisco from predation from Lake Trout and introduced Pacific salmonids. Participants hypothesized that cold water temperatures persisting through spring may mitigate piscivorous predation pressure on juvenile Cisco by delaying predator-prey habitat overlap.

Lake Michigan

Availability of zooplankton prey during the larval stage, primary productivity, climatic conditions (i.e., ice cover, advection risk), benthic-prey availability, and nursery-habitat quality were thought to be important drivers of Lake Whitefish recruitment in Lake Michigan. Recent declines in spring phytoplankton—thought to be mediated by lower nutrient concentrations and dreissenids (primarily quagga mussels)—were believed to be driving contemporary declines in zooplankton densities and altered zooplankton community composition. Limited zooplankton prey for larvae can cause starvation or reduce growth, potentially leading to increased size-dependent mortality; however, cold spring water temperatures and relatively large size-at-hatch could buffer against direct mortality due to starvation. Declines in pelagic production were understood to have resulted in increased water clarity, potentially magnifying vulnerability to ultraviolet radiation (UV) and predation across Lake Whitefish embryonic, larval, and juvenile life stages. Ice cover was thought to be important for protecting Lake Whitefish embryos from physical disturbance during incubation, particularly in areas with high wave energy. Climatic conditions during the larval life stage were hypothesized to influence Lake Whitefish growth, foraging, and developmental rates during the larval stage. Wind-driven currents were thought to affect the distributions of zooplankton and Lake Whitefish larvae, thereby regulating encounter rates with zooplankton and larval advection toward or away from nursery habitats. Nursery-habitat quality was thought to be declining due to shoreline hardening and beach erosion, thereby reducing quality of available prey and refugia from predation (e.g., emergent vegetation). Lastly, multiple changes in lower trophic levels due to the loss of *Diporeia* and proliferation of dreissenids were hypothesized to have led to a suite of impacts on Lake Whitefish recruitment. For instance, dreissenid colonization of spawning habitats could reduce habitat quality and embryonic survival. Additionally, reduced benthic-prey availability was thought to have reduced growth and condition of juvenile and adult Lake Whitefish, with potential lifelong consequences for parental condition, fecundity, egg quality, and spawning stock age and size structures.

Cisco recruitment in Lake Michigan, like Lake Whitefish recruitment, was thought to be regulated by zooplankton prey availability; in addition, participants identified SSB, larval predation, and competition with non-native planktivores as important drivers for Cisco. Availability of zooplankton prey may limit growth and/or survival through the same mechanisms as with Lake Whitefish, but participants considered Cisco to be less affected than Lake Whitefish by recent declines in primary productivity. In fact, participants thought that Cisco has directly benefited from these ecosystem changes, particularly during larval and early juvenile life stages. Abundances of two non-native planktivores, Alewife and Rainbow Smelt, were understood by participants to have declined in relation to decreasing productivity, which may have reduced their predation pressure on and competition with Cisco. However, participants noted that Cisco recruitment is likely limited by SSB in Lake Michigan, despite multiple strong year-classes observed regionally by participants over the past decade.

Lake Huron

Zooplankton prey availability, primary productivity, ice cover, spawning-habitat degradation, predation by Sea Lamprey, and SSB were identified as important recruitment drivers for both Lake Whitefish and Cisco in Lake Huron. Discussions centered on how declines in phytoplankton production—attributed to dreissenids—have reduced zooplankton densities, thereby influencing survival and/or growth of Lake Whitefish and Cisco during the larval and early juvenile stages. Participants also discussed how poor growth of Lake Whitefish and Cisco during the larval stage can have other impacts on fitness, such as increased vulnerability to predators, reduced swimming speed, and reduced gape size. Spawning-habitat degradation and interstitial depth reduction (i.e., sedimentation, colonization by dreissenids and *Cladophora*, a benthic alga) were thought to have decreased survival of both species through increased vulnerability to predation and hypoxia during incubation. Participants also hypothesized that colonization of spawning substrates by dreissenids might affect spawning-site selection. Consistent ice cover was thought to be important for protecting incubating embryos from physical disturbance and for minimizing advection to suboptimal habitats. Participants discussed how the timing and duration of ice cover also likely influences match/mismatch of emerging larvae with zooplankton prey, with effects extending to the early juvenile stage. Recruitment of both species was thought to be regulated through predation on adults by Sea Lamprey and resultant decreases in SSB. While the importance of SSB for Lake Whitefish was thought to differ among stocks in Lake Huron, Cisco SSB was considered to be greatly reduced, spatially fragmented compared to historical conditions, and highly important for lakewide recruitment.

Several drivers identified as important in Lake Huron were species specific. Changes in the diets of juveniles and adults were indicated as potentially influencing recruitment for both Cisco and Lake Whitefish, although the mechanisms differed between species. The loss of *Diporeia* prey for Lake Whitefish and the incorporation of non-native zooplankton species (most notably *Bythotrephes*) in Cisco diets were mentioned as potentially influencing growth or survival, thereby having an influence on SSB, female condition, and egg provisioning. While primary productivity was considered important for both species through a shared mechanism (i.e., impacts on pelagic zooplankton prey), primary productivity was also considered an important driver for Lake Whitefish through sequestration of energy to the benthos (i.e., benthification), which was understood to have altered the benthic-prey community in offshore habitats on which juvenile Lake Whitefish relies. Water temperatures during early life were thought to be important for Lake Whitefish through the effects of spring warming rates on match-mismatch between larvae and zooplankton prey. Wind-driven currents were identified as having the potential to move Cisco larvae and juveniles to or away from optimal nursery habitats, thereby contributing to variability in recruitment. Predation by Alewife and Rainbow Smelt during the larval and early juvenile stages was also considered important to Cisco recruitment. Additionally, the loss of phenotypic diversity was identified as being important for Cisco recruitment. The remnant ecomorphs of Cisco appear to be adapted for, and potentially limited to, nearshore environments; thus, the scope for Cisco recruitment could be limited relative to historical conditions when one ecomorph of Cisco dominated offshore waters.

Lake Erie

Overwinter water temperatures, primary productivity, spawning habitat, benthic-prey availability, interactions with Rainbow Smelt, and metapopulation diversity were all considered important for Lake Whitefish recruitment in Lake Erie. Overwinter water temperatures were thought to influence conditions during embryonic incubation and timing of larval hatching, primarily through regulation of ice-cover extent and phenology. Overwinter water temperatures were also considered important for mediating the timing and magnitude of the spring phytoplankton bloom, thereby influencing the availability of zooplankton prey for larvae. Lake Erie's elevated primary productivity compared to the other Great Lakes was thought to benefit Lake Whitefish recruitment through increased forage availability and growth rates; however, there also was a shared belief that dreissenids have reduced the carrying capacity for Lake Whitefish. Dreissenids were described as having reduced the quantity and energetic quality of benthic forage for Lake Whitefish, thereby limiting growth and fitness. A dearth of high-quality spawning habitat (i.e., clean, hard substrates in shallow water) in Lake Erie potentially limits successful embryonic development and could ultimately prevent the establishment of a metapopulation utilizing a diversity of spawning habitats. Participants debated if Lake Whitefish recruitment was limited solely by SSB, as low metapopulation diversity may play an important role. Lastly, Rainbow Smelt was considered an important predator and competitor of larval Lake Whitefish.

Participants hypothesized that important recruitment drivers for a reintroduced Cisco population would be similar to those for Lake Whitefish. Rebuilding an abundant spawning stock with high metapopulation diversity was identified as a major challenge to achieving Cisco recruitment. As was the case with Lake Whitefish, ample high-quality spawning habitat, which promotes proper embryonic development, was considered critical for Cisco recruitment. Winter water temperatures were predicted to be important for Cisco in the same manner as for Lake Whitefish, given their similar embryonic and larval life-history strategies. Lastly, Cisco recruitment was also predicted to be regulated by interactions with Rainbow Smelt, although the mechanisms differed from those of Lake Whitefish. While both competition with and predation by Rainbow Smelt during the larval stage were thought to be important, the predicted effects of Rainbow Smelt were not limited solely to the larval stage for Cisco. Participants considered Rainbow Smelt to be a major impediment for Cisco restoration, as Rainbow Smelt is currently abundant in Lake Erie and occupies the niche that Cisco formerly held. Rainbow Smelt adults were understood to consume juvenile Rainbow Smelt, and thus may also prey on young, post-larval Cisco. Further, as both Rainbow Smelt and Cisco are pelagic planktivores throughout their lives, competition between these species for zooplankton prey was expected to occur across multiple life stages.

Lake Ontario

The hypothesized drivers of Lake Whitefish and Cisco recruitment in Lake Ontario, which included ice-cover dynamics, spawning-habitat quality, overwinter water temperatures, and predation on larvae, were thought to act on embryos and larvae. The presence of ice cover was believed to protect embryos from physical disturbance and to, consequently, improve survival during incubation for both species. Spawning-habitat quality was hypothesized to be limiting recruitment through reduced embryonic survival; infilling of interstitial spaces with silt, macrophytes, and dreissenid shells were thought to have shallowed incubation depth and resulted in increased physical disturbance, predation on embryos, and hypoxia. Cold winter water temperatures—considered to be tightly intertwined with ice-cover extent and phenology—were hypothesized to improve embryonic development and increase survival to hatch. Colder water temperatures through spring were also thought to align larval emergence more optimally with the bioenergetics of early development, yolk-sac utilization, and the spring plankton bloom. Predation on Lake Whitefish and Cisco larvae by Yellow Perch, Rainbow Smelt, and Alewife also was hypothesized to be important for regulating recruitment. Yellow Perch was understood to be abundant in nearshore spawning habitats, but spatial habitat overlap was considered less extensive during the larval stages of Cisco and Lake Whitefish. Rainbow Smelt was hypothesized to be a more likely predator on both larval and juvenile Lake Whitefish and Cisco than Alewife or Yellow Perch, as Rainbow Smelt was believed to typically be inshore earlier than Alewife and to occupy the metalimnion later in the season.

Important recruitment drivers unique to each species in Lake Ontario encompassed multiple food-web interactions and demographic processes. Participants discussed how declining benthic invertebrate forage has substantially reduced Lake Whitefish growth, most notably through the replacement of *Diporeia* with dreissenids and potential competition with Round Goby *Neogobius melanostomus* for benthic prey. These negative interactions were hypothesized to begin when older Lake Whitefish larvae begin utilizing benthic habitats and to continue throughout an individual's lifetime, ultimately reducing spawner fecundity.

In contrast, changing productivity (i.e., declining nutrients, increased water clarity, re-establishment of the deep chlorophyll layer) was believed to have increased zooplankton densities in the metalimnion where juvenile and adult Cisco forage, potentially benefitting Cisco growth and survival. Commercial harvest of Lake Whitefish and predation by Lake Trout were considered important for regulating Lake Whitefish SSB and may limit the scope of Lake Whitefish recruitment. Metapopulation diversity was thought to be more important for Cisco than for Lake Whitefish because strong year-classes have been observed despite low SSB, and reduced spawning stock diversity was thought to have diminished Cisco resiliency to environmental variation.

Synthesis of Professional Opinion

Using our conceptual diagram of hypothesized biotic and abiotic drivers of Lake Whitefish and Cisco recruitment across the Great Lakes (Figure 6), we infer, based on professional opinion, the following overarching hypotheses regarding which drivers underlie survival across early life stages. First, the relative influence of abiotic drivers is strongest during early life, whereas biotic drivers become more important later in life. This hypothesis reflects the pronounced importance of abiotic drivers in regulating embryonic survival (e.g., ice-cover dynamics), whereas many biotic drivers (e.g., prey availability) do not take effect until after larval emergence and the transition to exogenous

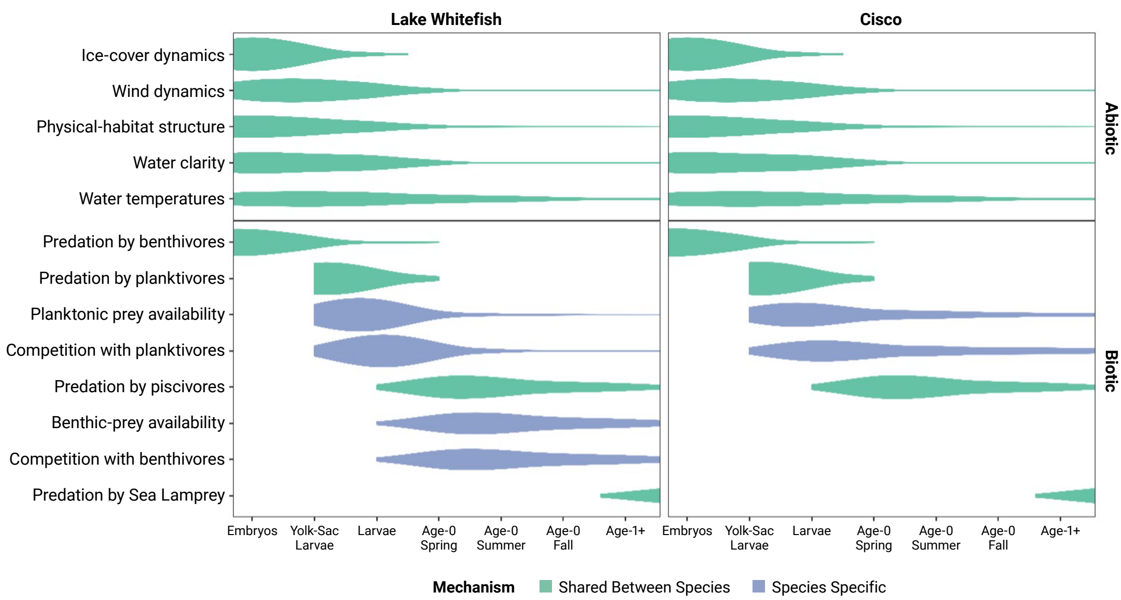

FIGURE 6. Conceptual model of hypothesized Lake Whitefish (left panel) and Cisco (right panel) recruitment drivers across the Great Lakes based on professional opinion. Violin plots describe each abiotic (top rows) and biotic (bottom rows) driver's (y-axis) degree of influence in regulating direct mortality across early life stages (x-axis). All violins have the same total area, but they differ in their extent and relative width. The extent describes life stages over which each driver regulates mortality, while the width depicts the relative strength of that driver at each life stage. Violin colors correspond to drivers for which mechanisms of regulating early life-stage mortality were hypothesized to be shared between species (green) or were species specific (purple).

feeding. While the relative impact of abiotic drivers is strongest in early life, the effects of some drivers persist through later life stages; for example, water temperatures influence growth throughout life. Second, abiotic drivers regulate recruitment based on the same mechanism(s) for Lake Whitefish and Cisco and, therefore, they exert similar influences on survival during early life. Third, biotic drivers exhibit species-specific effects, particularly on post-larval life stages. This hypothesis reflects the ontogenetic niche shift that separates Lake Whitefish and Cisco niche spaces between benthic and pelagic habitats, respectively, during their first summer of life. As a result, drivers affecting benthic food webs (e.g., benthic-prey availability) are unique to Lake Whitefish and are not expected to affect pelagic foraging of Cisco.

DISCUSSION

Our synthesis of professional opinion indicates that many different biophysical drivers are likely important for regulating Lake Whitefish and Cisco recruitment across the Great Lakes, and that these drivers likely interact in complex ways. Between four and eight drivers were deemed highly important for recruitment of either species among lakes, many of which encompassed multiple underlying mechanisms (Table 2). This finding is no surprise, given that the causes of recruitment variability in fishes are generally accepted as intricately complex across life stages and spatiotemporal scales (Houde 2008). Adding to the sense of complexity, participants often found it difficult to disentangle individual, direct effects of interacting processes. Nonetheless, clear themes emerged among lakes and between species (Figures 4, 5). Both ice-cover dynamics and water temperatures during early life were consistently considered important for regulating survival and growth potential. These processes are tightly intertwined, as cold water temperatures are necessary for ice formation, and both water temperature and ice cover influence other ecosystem processes (e.g., nutrient cycling and development of the spring plankton bloom; Cavaliere et al. 2021) that affect survival of early life stages. In addition, planktonic productivity, spawning-habitat quality, and interactions with non-native planktivores were considered highly important for both species in most—but not all—lakes. All these drivers likely exert strong influences on the growth and/or survival of embryos and larvae, highlighting the importance of favorable conditions during early life for governing recruitment to later stages.

Differences in the suite of drivers that participants identified as important among lakes emphasize the context-dependent nature of recruitment dynamics across the basin. Although individual drivers perceived to be important varied across lakes, clear commonalities emerged when comparing the upper (Lakes Superior, Michigan, and Huron) and lower (Lakes Erie and Ontario) Great Lakes (Figure 4). Low productivity in the upper Great Lakes (Barbiero et al. 2012; Dove and Chapra 2015) was thought to limit prey availability during larval and early juvenile stages and, consequently, recruitment of Lake Whitefish and Cisco. This bottleneck was thought to be most severe in Lakes Michigan and Huron due to declining productivity (Barbiero et al. 2018) and changing zooplankton community compositions (Barbiero et al. 2019). In contrast, because the lower Great Lakes are more productive than the upper Great Lakes (Dove and Chapra 2015), zooplankton prey was considered less likely to be limiting for early life stages. Instead, spawning-habitat degradation (Busch and Lary 1996; Koonce et al. 1996) and reduced metapopulation diversity (Brown et al. 2022) within the lower Great Lakes were hypothesized to limit recruitment at the embryonic and larval stages. Participants noted the uncertainty embedded within these perceptions, as empirical evidence to evaluate these hypotheses remains limited. Cisco ecomorphs also may vary with respect to important recruitment drivers within and among lakes due to differences in local adaptations (Eshenroder et al. 2016, 2021), although ecomorph-specific dynamics were not explicitly considered in this workshop (but see Lake Huron subsection). Further, participants stressed the importance of considering within-lake regional variation for understanding stock-specific recruitment dynamics (Zischke et al. 2017). For example, zooplanktonic productivity varies within, as well as among, lakes (Barbiero et al. 2019); this and other heterogeneity could result in local variation in key drivers (e.g., prey availability, spawning-habitat quality) and, therefore, recruitment (Ebener et al. 2021). More broadly, each lake represents a unique ecosystem that exists across gradients of biological community structures and physical regimes. While many of these biological and physical processes play a role in influencing recruitment, the unique set of conditions in each lake and region ultimately determines which drivers are most important for regulating recruitment.

Workshop outcomes suggest that management and stewardship actions targeting bottlenecks during early life stages (e.g., spawning-habitat restoration) could improve recruitment for both species, while interventions targeting impediments during juvenile and adult life stages may need to be tailored to each species' unique stressors and ecology. Many of the same recruitment drivers were thought to be highly influential for early life stages of Lake Whitefish and Cisco, while drivers acting on post-larval life stages were often hypothesized to be species specific (Figures 5, 6). Climatic processes that were important for regulating embryonic incubation success (i.e., ice cover, water temperature, physical disturbance) were frequently identified as important for both species, along with processes governing growth potential during early life (e.g., zooplankton prey availability) and risk of predation by planktivorous fishes during the larval stage. These patterns are consistent with the similar early life-history strategies of these fishes, as their embryos and larvae are subject to similar environmental conditions and interact with similar biological communities. That being said, the two species exhibit differences in their early life histories that could result in differential recruitment bottlenecks. For example, larval Cisco hatch at smaller sizes than Lake Whitefish and, therefore, may be more vulnerable to mortality during the larval stage. Moreover, many populations of Lake Whitefish and Cisco do not overlap in spawning habitat (e.g., Apostle Islands, Lake Superior; Goodyear et al. 1982) and would likely experience different conditions during early life. Drivers thought to be acting on juveniles and adults distinctly reflected their divergent post-larval life-history strategies. Notably, benthic-community disruptions in recent decades (i.e., replacement of *Diporeia* with dreissenids, Burlakova et al. 2022) have drastically modified Lake Whitefish foraging ecology, with subsequent declines in juvenile growth and spawner fecundity (Mohr and Nalepa 2005; Rennie et al. 2012; Fera et al. 2015; Trumpickas et al. 2022). Cisco being planktivorous do not rely on benthic forage (George 2019; Gatch et al. 2021) and were viewed by participants as having benefited from recent changes in primary productivity. While re-oligotrophication has reduced planktonic productivity, increasing water clarity has also shifted planktonic production deeper into the metalimnion (Barbiero et al. 2019; Scofield et al. 2020). The increasing importance of a deep chlorophyll layer associated with higher water clarity may have increased foraging opportunities for Cisco and potentially reduced competition with non-native planktivores (Riha et al. 2017). However, Cisco was generally thought to be more strongly limited by SSB and metapopulation diversity than Lake Whitefish across lakes, which may serve as an impediment to ongoing restoration of Cisco populations (Bunnell et al. 2023).

Climatic conditions during embryonic incubation and larval emergence were understood by participants to be among the most important determinants of Lake Whitefish and Cisco recruitment. Ice-cover dynamics (i.e., spatial extent and phenology of formation and breakup) encompass a broad range of physical, biogeochemical, and biological processes (Cavaliere et al. 2021) and are often proposed as a major driver of Lake Whitefish and Cisco recruitment variability, but the specific mechanisms by which ice cover acts to regulate recruitment are less clearly defined. Previous studies have found that Lake Whitefish and Cisco recruitment success is generally related to longer, colder winters with higher ice cover (Lawler 1965; Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993; Ryan and Crawford 2014; Lynch et al. 2015; Bonsall 2017; Amidon et al. 2021; Schaefer et al. 2022; T. Brown et al. 2022). However, other studies have found insufficient evidence to support the relationship between ice cover and successful recruitment (Cunningham and Dunlop 2023), or have found that other climatic processes during early life (e.g., water temperatures, wind dynamics) were as, or more, important than ice cover in explaining recruitment variability (Christie 1963; Taylor et al. 1987; Brown et al. 1993; Kinnunen 1997; Hoff 2004; Rook et al. 2013; Brown et al. 2022). Despite this uncertainty, ice-cover extent and phenology were frequently cited as important throughout the workshop. Participants proposed several mechanisms by which ice cover may act to regulate recruitment in concert with a suite of other climatic variables. Water temperatures are important for normal embryonic metabolism and development (Colby and Brooke 1970; Brooke 1975), timing of larval emergence (Mitz et al. 2019), and larval growth potential (Stewart et al. 2022; Cunningham and Dunlop 2023) for Lake Whitefish and Cisco. Importantly, water temperature is one determinant of ice-cover formation (Ozersky et al. 2021), which then serves to protect embryos from physical disturbance (Taylor et al. 1987) and UV exposure (Stewart et al. 2021). Ice cover also affects overwinter nutrient cycling, directly influencing planktonic production in spring (Cavaliere et al. 2021). However, the relative importance of these individual mechanisms remains unclear, and it is uncertain whether ice cover is a useful proxy for this complex suite of processes that could serve as the gateway for recruitment potential is uncertain. Regardless, climate change threatens to disrupt many of these individual processes, which could result in unfavorable conditions for recruitment through the decoupling of climate, embryonic incubation, and timing of larval emergence (Barta et al. 2024).

Workshop discussions highlighted the hypothesis that dreissenids influence multiple biotic and abiotic drivers of contemporary Lake Whitefish and Cisco recruitment dynamics, resulting in direct and indirect impacts across multiple life stages (Ebener et al. 2021). Zebra mussels established in nearshore areas of the Great Lakes in the 1990s, and quagga mussels established shortly thereafter, becoming widespread across the basin by the mid-2000s, except in Lake Superior where dreissenids remain rare (Karatayev and Burlakova 2022). Dreissenid filtration has sequestered production to the benthos, thereby reducing nutrients available for pelagic planktonic production (Hecky et al. 2004). Subsequent declines in pelagic zooplankton abundances (Barbiero et al. 2019) may limit foraging opportunities for larval *Coregonus* spp. (Cunningham and Dunlop 2023), while increasing water clarity may have increased vulnerability to UV exposure and visual predation (Bunnell et al. 2021). The effects of widespread dreissenid colonization on Lake Whitefish and Cisco spawning substrates remain uncertain. Dreissenids may degrade spawning-substrate quality by infilling interstitial spaces for incubating embryos (Marsden and Chotkowski 2001; Furgal 2019) and by enhancing *Cladophora* growth on substrates. Alternatively, dreissenid shell hash may provide novel hard substrates for embryonic incubation in areas without interstitial substrates (Weidel et al. 2023). The proliferation of dreissenids was associated with the loss of *Diporeia* (Mohr and Nalepa 2005), although the mechanism remains unclear (Watkins et al. 2007). In any case, the decline in *Diporeia* populations led to growth declines for juvenile and adult Lake Whitefish (Gobin et al. 2015; Fera et al. 2015), altered Lake Whitefish foraging behavior (Rennie et al. 2009; Fera et al. 2017), and shifted Lake Whitefish depth distributions (Rennie et al. 2015). While Lake Whitefish in some areas now consume dreissenids, the poor nutritional quality of dreissenids relative to *Diporeia* has reduced foraging efficiency (Rennie et al. 2012). While most of these perturbations are likely to affect both species similarly based on their life histories, Lake Whitefish interacts more directly with benthic habitats and, therefore, it could experience disproportionate impacts compared to Cisco. Additional research focused on understanding the mechanistic impacts on survival and growth across life stages could clarify their relative importance in influencing recruitment of each species.

Despite the wealth of insights gained during the workshop, our approach had limitations, and additional research is needed to further understand the causes of recruitment variability explored in this exercise. Importantly, the task presented to participants was not trivial, as they were asked to distill complex ecological dynamics into discrete categories. While this approach has the advantage of facilitating high-level comparisons among focus groups, it also runs the risk of oversimplification. Our focus group-style approach itself presents limitations, most notably the potential for groupthink (Cyr 2016) and limited diversity of perspectives (Drescher et al. 2013). While our online survey prior to the workshop was designed to capture individual perspectives in addition to the collective workshop deliberations, the drivers that emerged as important in each lake-specific group could have been influenced by who participated in the workshop. Further, professional opinion itself varies in its sources and quality of evidence, along with its degree of confidence in the face of uncertainty, making it difficult to interpret the knowledge of multiple professionals (Drescher et al. 2013; Morgan 2014). More broadly, the working hypotheses captured through this exercise are strongly influenced by the perspectives of the subset of scientists studying mechanisms of recruitment within each system, which ultimately influences what empirical data are collected and which hypotheses are tested between species and among lakes. On the other hand, some of the ecological processes discussed here are absent from the literature because they are difficult to measure or are of emerging concern. This information would, therefore, be absent from an analysis based solely on published empirical evidence.

This synthesis can be a springboard for future research on the causes of Lake Whitefish and Cisco recruitment variability. Opportunities abound to test the underlying hypotheses by leveraging existing datasets and prioritizing future research in areas where empirical data are lacking. One of the major insights generated through this workshop was that the suite of drivers considered to be highly important for recruitment differed among lakes and between species. Statistical support for this perception could be assessed through a quantitative, comparative study of recruitment and its drivers. Such an analysis would first require estimating standardized recruitment indices, which also could prove useful for monitoring temporal and spatial trends in recruitment (Ebener et al. 2021; Weidel et al. 2021). As well, a meta-analysis of Lake Whitefish and Cisco recruitment drivers could evaluate available published evidence for these hypotheses. Importantly, this synthesis is a step towards the development of a comprehensive conceptual model of the recruitment process that includes interactions among drivers, the influence of demographic factors (e.g., SSB, fecundity) on recruitment potential, and areas of uncertainty. Lastly, future research could explore recruitment dynamics at finer scales than in this workshop; for example, by assessing the extent to which the relative importance of hypothesized recruitment drivers varies within lakes, among life-history strategies (e.g., tributary-spawning), and among ecomorphs.

Understanding the causes of Lake Whitefish and Cisco recruitment variability will likely remain a persistent challenge. Fishery scientists and professionals have been studying recruitment trends of *Coregonus* spp. in the Great Lakes for nearly a century (Van Oosten 1928), resulting in a massive body of knowledge (e.g., Ebener et al. 2021). While many lessons have been learned during that time—sometimes the hard way (Stockwell et al. 2009)—many of the same questions persist, especially those focused on disentangling biotic and abiotic effects on recruitment (Ebener et al. 2021). In addition, the processes responsible for controlling recruitment variability may have changed throughout time in response to ongoing ecosystem change (Feiner et al. 2015). Unfortunately, the "recruitment problem" is near universal in fisheries science (Houde 2008) and limits our ability to generate predictive models of recruitment based on mechanistic relationships involving biophysical conditions (Subbey et al. 2014). However, recruitment models and forecasts do not need to be perfect to be actionable (Plagányi et al. 2014; Kiaer et al. 2021) and would benefit decision-making for Great Lakes fisheries (DeVanna Fussell et al. 2016). Continuing to augment our knowledge of coregonine recruitment and its drivers will be integral for understanding how these socioecologically valuable populations respond to environmental variability and future ecosystem change.

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APPENDICES

Appendix A: Online Survey[15]

Online survey distributed to registrants with the primary goal of identifying and prioritizing potentially important drivers of recruitment prior to the workshop.

Biographical Information: Name, Email, Organization/Affiliation

Goals for this Survey: This questionnaire is designed to capture participant ideas and facilitate conversation at the upcoming workshop focused on recruitment drivers and mechanisms for cisco and lake whitefish in each of the Great Lakes. Responses will be anonymously summarized and used as the foundation for discussions during the workshop. All questions are optional.

We will ask that you complete the following for each species within a lake-specific context based on your own expert opinion:

- Categorize hypothesized recruitment drivers according to their importance
- Identify life-stages where the most important recruitment bottlenecks occur
- Name perturbations that have led to major changes in recruitment dynamics

Note: We are primarily interested in synthesizing expert opinion on which drivers and processes are thought to be most important for each species in each lake. This is a brainstorming exercise based on your hypotheses. We are not looking to formalize conceptual models of coregonine recruitment or focus on technicalities. Please try to complete the survey from a "high-level brainstorming" perspective. Thank you!

Please select which lake(s) you would like to complete. We ask that you please only select lakes that you are familiar with. You may revisit this survey to complete multiple lakes.

○ Lake Superior
○ Lake Michigan
○ Lake Huron
○ Lake Erie
○ Lake Ontario

[15]In the survey, “thermal conditions” refers to water temperatures and “egg” refers to the embryonic life stage.

APPENDIX A. Continued.

Definitions:

- **Recruitment:** Recruitment is the number of individuals entering the population at some age or life stage in a given year and is typically defined as set beyond the period when most early life-stage mortality has occurred (Ludsin et al. 2014).
- **Drivers:** The physical and biological factors and processes that interact to directly or indirectly regulate recruitment. Many of these factors and processes are important for influencing recruitment in some way, but some have outsized influence on tipping the scales from recruitment success to failure; thus, important recruitment drivers are those which tend to play a key role in determining year-class strength. That being said, it is important to recognize that the relative importance of each driver is likely non-stationary and context-dependent (e.g., interactions with other drivers, ecosystem change).
- **Mechanisms:** Mechanisms describe how, and under which conditions, each driver acts to regulate recruitment and at which life stage(s). The specific mechanisms that relate each driver (cause) to recruitment variability (effect) likely differ across lakes (e.g., prey availability can be limited by intraguild competition and/or oligotrophication). We will discuss mechanisms for important recruitment drivers during the upcoming workshop.

Q1.

Please group the following processes based on which you **hypothesize** are important for regulating **contemporary** recruitment of [species] populations in [lake].

Ordered rankings within groups will not be considered. You do not have to categorize processes that are not at all important.

You may use the *Other* category to include a process not listed here. If you include *Other*, please be sure to specify the process in the next question.

Rankings:

- Highly Important
- Moderately Important
- Not at All Important

APPENDIX A. Continued.

Items:[16]

- ○ Wind dynamics
- ○ Timing of ice cover onset/offset
- ○ Ice cover concentration/duration
- ○ Primary productivity
- ○ Spawning habitat quality
- ○ Water levels
- ○ Water clarity
- ○ Contaminants
- ○ Hypoxia
- ○ Thermal conditions during early life
- ○ Other thermal dynamics
- ○ Prey availability – zooplankton
- ○ Prey availability – benthic invertebrates
- ○ Prey quality
- ○ Predation – piscivores
- ○ Predation – benthivores
- ○ Competition – planktivorous fishes
- ○ Competition– predatory invertebrates
- ○ Competition – benthivorous fishes
- ○ Morbidity – sea lamprey
- ○ Harvest
- ○ Spawning stock size
- ○ Hatchery supplementation
- ○ Parental condition and fecundity
- ○ Genetic diversity
- ○ Morbidity – bacterial kidney disease (BKD)
- ○ Morbidity – parasite loads
- ○ Morbidity – viral hemorrhagic septicemia (VHS)
- ○ Other

If you ranked *Other* as an important driver for [species], please specify.

[16]Processes were listed in random order within the survey.

APPENDIX A. Continued.

Q2.

In general, during which life stage do you think the most important recruitment bottlenecks occur for [species] in [lake]?

You may select multiple options, but we ask you to restrict your choices to those of equally high importance.

- ○ Egg
- ○ Larval
- ○ Early juvenile
- ○ Late juvenile
- ○ Adult
- ○ Other

If you ranked *Other* as an important driver for [species], please specify.

Q3.

Briefly, which perturbation(s) do you hypothesize have led to the biggest changes in recruitment drivers and dynamics for [species] in [lake]?

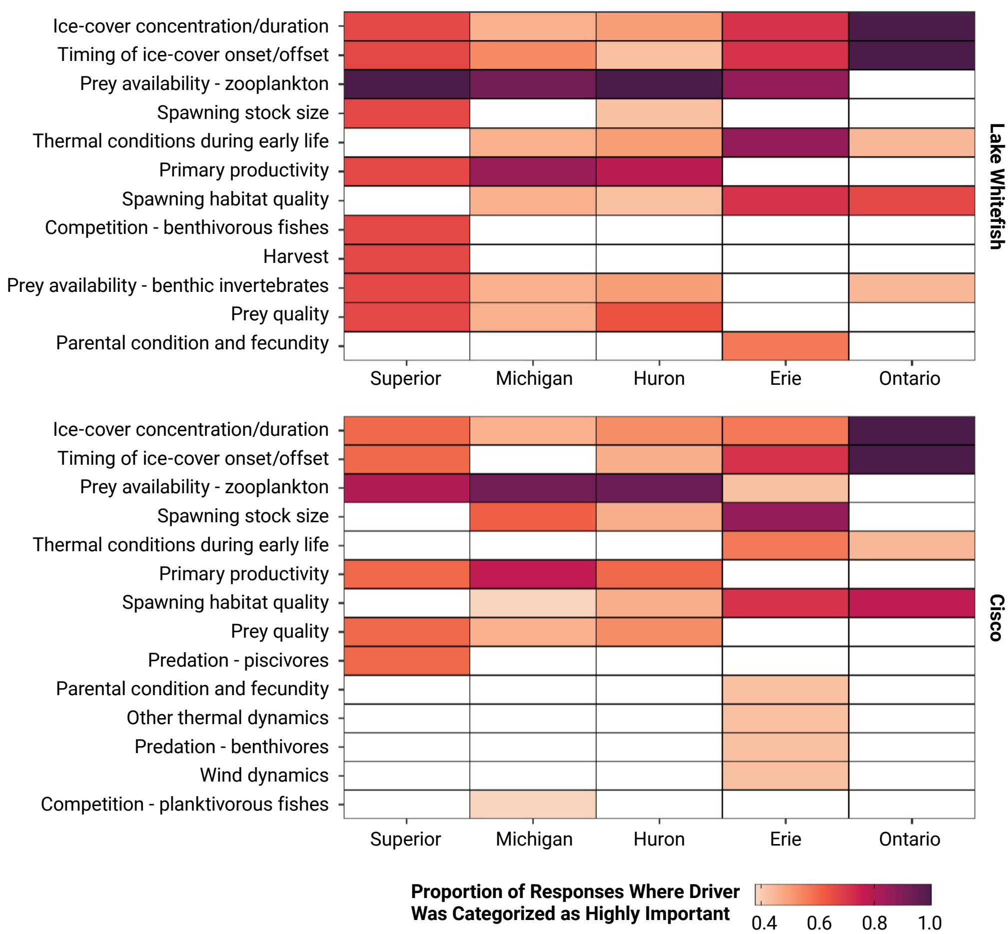
Optional

We welcome any additional details to help contextualize any of your responses for [lake] recruitment dynamics.

Thank you for completing this survey. We look forward to engaging with you and your ideas further at the upcoming workshop.

Appendix B: Online Survey Results

Physical and biological processes most frequently categorized by fishery professionals as "highly important" drivers of contemporary Lake Whitefish (top panel) and Cisco (bottom panel) recruitment in the Laurentian Great Lakes based on the pre-workshop survey (see Appendix A). These preliminary drivers were retained for further deliberation and a final determination of important recruitment drivers during the workshop (Table 2). Individual cells for each combination of driver (y-axis), lake (x-axis), and species (panel) are filled in color according to proportion of responses where a given driver was categorized as "highly important". Cells darkened in fill color with increasing frequency, whereas unfilled cells are those which were not among the top responses for a given species and lake.



Appendix C: Workshop Participation by Organization

Number of participants from each organization represented in the workshop activities (online survey and/or virtual workshop). Organizations are listed in alphabetical order.

Organization	Number of Participants			
	Survey and Workshop	Survey Only	Workshop Only	Total (n = 57)
Bay Mills Indian Community	1			1
Chippewa Ottawa Resource Authority			1	1
Chippewas of Nawash First Nation		1		1
Cornell University	3		2	5
Grand Traverse Band of Ottawa and Chippewa Indians	1			1
Great Lakes Fishery Commission	1			1
Lake Superior State University	1			1
Little Traverse Bay Bands of Odawa Indians	1			1
Michigan Department of Natural Resources	3	1		4
Minnesota Department of Natural Resources			1	1

APPENDIX C. Continued.

Organization	Number of Participants			
	Survey and Workshop	Survey Only	Workshop Only	Total (n = 57)
National Oceanic and Atmospheric Administration Great Lakes Environmental Research Laboratory	2			2
New York State Department of Environmental Conservation	1		1	2
Ontario Ministry of Natural Resources and Forestry	7			7
Purdue University	1			1
Sault Ste. Marie Tribe of Chippewa Indians	2			2
The Nature Conservancy	1			1
U.S. Fish and Wildlife Service	3			3
U.S. Geological Survey Great Lakes Science Center	12	1	2	15
University of Minnesota	2		1	3
University of Toledo	1			1
Wisconsin Department of Natural Resources	1	2		3

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