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Review

Advances in fish passage in the Great Lakes basin

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ABSTRACT

Addressing the impact of dams and other water control structures on fish communities and aquatic ecosystems is a major concern for fisheries managers in the Laurentian Great Lakes. Although nature-like and technical fishways (i.e., vertical slot, pool and weir, Denil) and, when suitable, barrier removals have been implemented across the basin, these fish passage applications are vastly outnumbered by barriers to fish movement. Lowermost barriers are the first structure that blocks fish passage within a tributary; and, in the Laurentian Great Lakes, they present a unique situation where restricting access to upstream habitat is a major component of a half a century long strategy to control invasive sea lamprey *Petromyzon marinus*. Solutions for passage at lowermost barriers must therefore consider alternative management actions surrounding increased connectivity and invasive species control. These actions are underlined by the primary management objective of enhancing production/diversity of native and recreationally desirable fishes. This review surveys the current state of fish passage technologies deployed in the Laurentian Great Lakes and other fish passage solutions under development, providing a reference for resource managers making decisions about barriers and fish passage that are critical for invasive species control and fishery restoration.

Contents

Introduction

Dams are a prevalent feature of the modern landscape. While many dams provide critical infrastructure services, such as flood

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control, water supply, and invasive species control, dams fragment aquatic ecosystems by blocking the free movement of water, sediment, nutrients, woody debris and aquatic organisms. In the Laurentian Great Lakes (hereafter referred to as the Great Lakes) alone, there are nearly 100,000 potential barriers to fish passage (Moody et al., 2017) impacting the movement of approximately 121 fish species known to show migratory movements between lakes and rivers or within rivers (Mandrak et al., 2003). The number of species impacted could be even higher as barriers block non-migratory movements as well. When fish passage is blocked by barriers, populations up- and down-stream can become genetically fragmented (Vrijenhoek, 1998), fish are unable to access habitat necessary to complete critical stages of their life cycle (Kruk and Penczak, 2003; Liermann et al., 2012), and areas upstream of the barrier can be starved of nutrients derived from migratory species (Childress et al., 2014). As a result, addressing the impact of dams and other water control structures on fish communities and aquatic ecosystems is a major concern for fisheries managers.

Dam removal or the installation of a fishway are the most common strategies to mitigate the impact of barriers to fish passage. The number of dams removed in the USA has increased to nearly 1600 since 1912 (American Rivers, 2019), but not all dams are ideal candidates for removal either because they still serve an essential function, there is social desire to keep them, or the cost of removal is too high (McLaughlin et al., 2013; Sneddon et al., 2017). In addition, impacts requiring thorough environmental assessment may result from dam removal, particularly involving accumulated sediments (Katopodis and Aaland, 2006). Fishways then become the next best solution to provide fish passage. Fishways can take many forms including technical fishways, nature-like bypass channels, fish lifts / elevators, or trap and haul operations (Katopodis et al., 2001). Development of modern fishways initially focused on passage of anadromous salmonids, species with well documented strong swimming and leaping abilities (Katopodis and Williams, 2012). Further, these designs typically accounted only for upstream passage of migratory adults, not the downstream movement of adults or bi-direction movement of other life stages. As early as the 1930s, salmonid-centric designs were adopted across the globe to pass non-salmonid species (Williams et al., 2012). While providing some level of passage, hydraulic conditions at these fishways did not match well with the behavior and physiology of targeted species. As a result, passage rates of fish with limited swimming or leaping abilities, compared to anadromous salmonids, is usually quite low (Mallen-Cooper and Brand, 2007). Even in cases where fish are able to ascend, fishways can delay migration timing (Van Leeuwen et al., 2016) and impose significant energetic costs that can reduce overall survival or spawning (Castro-Santos and Letcher, 2010). Around the world, efforts are underway to improve fishway designs that reduce migration delays and post-passage impacts for both salmonid and non-salmonid species by adapting designs to accommodate variable fish sizes, swimming performance, and behavior (Stuart and Marsden, 2019; Silva et al., 2018; Vowles et al., 2017).

Lowermost barriers are the first structure that blocks fish passage within a tributary and in the Great Lakes, they present a unique situation where restricting access to upstream habitat is a major component of a half a century long strategy to control invasive sea lamprey *Petromyzon marinus*. Due to their parasitism on large host fish, sea lamprey contributed to the decline and extirpation of lake trout (*Salvelinus namaycush*) from lakes Erie, Michigan, and Ontario (Siefkes, 2017). An invasive species control program, overseen by the Great Lakes Fishery Commission (GLFC), utilizes barriers to restrict migrating sea lamprey from accessing spawning habitat in tributaries and lampricides (i.e., TFM and niclosamide) to eliminate sea lamprey larvae (Siefkes, 2017). Currently, there are 1007 lowermost barriers in Great Lakes tributaries (Zielinski et al., 2019). A total of 77 barriers have been either constructed or modified for sea lamprey control, but most barriers are existing structures built for other purposes (Zielinski et al., 2019). Nearly 40% of sea lamprey barriers are fixed-crest barriers, which maintain a vertical differential between the spillway crest and tailwater level of at least 45 cm and has a 15 cm overhanging lip (Zielinski et al., 2019). These fixed-crest barriers block sea lamprey passage because sea lamprey are unable to swim, climb, or leap over the vertical face. With the exception of salmonids, which can leap over the barrier, most fish native to the Great Lakes have limited swimming and leaping abilities and are also blocked by fixed-crest barriers.

Great Lakes fishery managers and researchers have long been concerned with the impact sea lamprey barriers have on native fish passage in tributaries. At the Sea Lamprey International Symposium (SLIS II) held in 2000, the impact of barriers on sea lamprey control, native fish populations, and possible management actions were investigated. In a review of the sea lamprey barrier program, Lavis et al. (2003) emphasized the importance of sea lamprey barriers and proposed that 20 new barriers over the proceeding 10 years could help reduce lampricide use across the basin by 25%. Despite their clear role in sea lamprey control, researchers also acknowledged barriers alter fish distributions in streams (Hayes et al., 2003; Klingler et al., 2003; Porto et al. 1999). Dodd et al. (2003) found a net reduction in number of species upstream of barriers was primarily due to blocked fish passage and not changes to habitat due to impounding water. Seasonally operated barriers and fishways fitted with traps may provide some capacity for native fish passage; however, uncertainties in timing of seasonal operation limits the potential benefits, as both early or late season migrating sea lamprey may still trigger lampricide treatments with minimal improvements to passage on native species (Klingler et al., 2003). As a result, Klingler et al. (2003) recommended the GLFC focus research on fish passage devices to incorporate at sea lamprey barriers rather than fine-tune seasonal operation of barriers. Ultimately, any provision to increase connectivity/fish passage using fishways or other devices must consider the alternative management strategy to control invasive sea lamprey (McLaughlin et al., 2003; McLaughlin et al., 2013).

This paper provides a summary of the status of fish passage in the Great Lakes Basin and advancements made since SLIS II in 2000. We start by reviewing all fishway technologies currently employed in the Great Lakes Basin. Data on current fishway status were collected from the Sea Lamprey Barrier Database (data.glfc.org) for sites in the US and the CanFishPass database (Hatry et al., 2013) for sites in Canada. The initial review includes fish passage technologies at all barriers in the Great Lakes Basin, but emphasis is drawn to fish passage technologies tied to sea lamprey control (i.e., fish passage at lowermost barriers). Finally, we review future developments in fish passage technologies and their potential application in the Great Lakes.

Status of fish passage technologies in the Great Lakes Basin

Fishways

Fishways are relatively rare in the Great Lakes Basin, especially when compared to the 3,954 dams (Moody et al., 2017). There are currently 103 (53 US, 50 CAN) confirmed fishways in the Great Lakes Basin and another 184 sites, all in the US, with unconfirmed fishway status. Of the confirmed fishways, 32 (28 US, 4 CAN) are located at lowermost barriers (Fig. 1). There are several different types of fishway aimed at providing upstream passage to fish: Denil (baffled), pool and weir, vertical slot, nature-like, and others (Table 1). The most common fishway design is the pool and weir,

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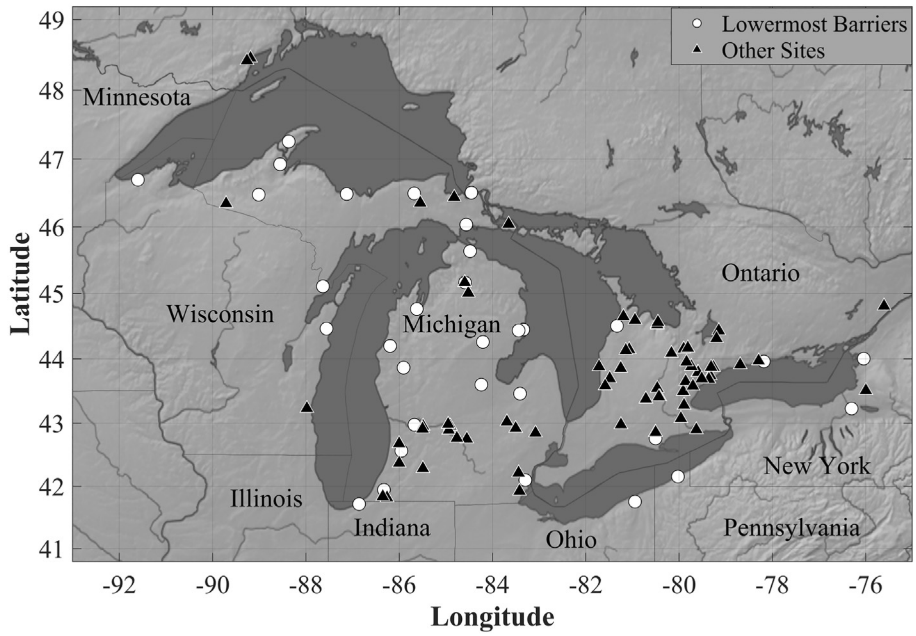

Fig. 1. The location of confirmed fishways at lowermost barrier sites (open circle) and other sites (closed triangle) on Great Lakes tributaries. 184 sites in the US have unconfirmed fishway status.

with a total of 45 (Table 1). When considering fishways at lowermost barriers only, the relative proportion of fishways types is consistent with all confirmed fishways. Unfortunately, evaluations of fishway performance are rare (9 case studies of seven fishways) and lack consistency in assessment tools and evaluation metrics. The methods used to evaluate fish passage include telemetry (radio and Passive Integrated Transponder), trap catch, mark-recapture, and video. The fishways are evaluated based on metrics of overall passage numbers or attraction and passage efficiencies. A summary of fishway evaluations for upstream passage at seven fishways is provided in Table 2.

Installations or additions of fishways at Great Lakes barriers began in the early 1900s (Fig. 2). Changes in the number of fishways built across each decade follow a cyclical pattern. We use information from the state of Michigan as an example. An initial peak in fishway construction at any barrier site occurred from 1910 to 1940, which overlaps with Legislation, Act 123, adopted in 1929 provisioning free passage of fish over or through dams and prohibit the obstruction in rivers and streams that block fish movement (Michigan Statutes Annotated., 1994). A decline in new fishways occurred from 1940 to 1970, a period that featured peak operation of mechanical and electrical sea lamprey barriers

Table 1
Description of fishway types within the Great Lakes Basin.

Fishway type (% of existing fishways)	Description	Reference
Denil (13%)	An open rectangular channel with closely-spaced vanes or baffles, sloping upstream at a 45° angle, located along the sides and bottom. Can be installed on relatively steep slopes and flow is highly turbulent.	Katopodis et al., 2001; Linnansaari et al., 2015
Pool and weir (44%)	An open channel containing a series of stepped pools separated by weirs (cross-walls). Depending on the design, water can pass over each weir, through orifices in the weir, or combinations of both. Fish move by leaping or swimming from pool to pool. Most common fishway worldwide.	Katopodis et al., 2001; Katopodis and Williams, 2012; Linnansaari et al., 2015
Vertical slot (19%)	A sloping open channel with connecting pools separated by slender top-to-bottom openings on one or both sides. Hydraulics remain stable during fluctuating water levels. Sometimes outfitted with rock substrate on the bottom to enable passage of species with low swimming performance.	Katopodis et al., 2001; Katopodis and Williams, 2012; Linnansaari et al., 2015
Nature-like (13%)	Constructed channels that mimic morphodynamic components of natural fish habitat like riffles. Greater complexity to design compared to concrete lined structures. • *Pool and riffle* types follow a stair-step configuration with pools separated by short steep reaches (riffles) or rock weirs. • *Rock ramp* types have a sloped, rock lined channel with intermittent boulders to provide resting areas for fish.	Aadland, 2010; Katopodis et al., 2001; Katopodis and Williams, 2012
Other (11%)	A variety of unique structures that provide fish passage including a navigational lock, fish elevator, eel ladder, and modified spillways that are passage by fish. • *Navigational locks* provide occasional passage opportunities when fish enter and pass with locked vessels. • *Fish elevators/lifts* move fish by capturing fish in a water filled hopper that is lifted over a barrier. • *Eel ladders* move eels through a series of ramps interspersed with rest boxes that prevent fallback.	Linnansaari et al., 2015; Whitfield and Kolenosky, 1978

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Table 2
Summary of Great Lakes basin fishway evaluations. Reported passage numbers and efficiencies are for upstream passage, unless otherwise noted. Fishway types include: pool and weir (PW), vertical slot (VS), Denil (D), nature-like (NL) and other.

Fishway *Location*	Type	Study year	Passage Metric	Method	Reference
Berrien Springs Dam *St. Josephs River, MI*	PW	1993	*Total passages in 234 d (11 species, mostly salmon spp.)* 29,993	Video	Dexter and Ledet, 1997
Brule River Sea Lamprey Barrier *Brule River, WI*	VS	1954–1979	*Total passages in 25 y* 6,347 Rainbow trout; 4,250,501 Rainbow smelt; 95,410 Longnose sucker; 11,696 White sucker	Trap-catch	Klingler et al., 2003
Dunville Dam *Grand River, ON*	D	1997 & 2003	*Walleye* Attraction Efficiency: 21–63% Passage Efficiency: 0%	Radio telemetry	Bunt et al., 2000; MacDougall et al., 2007
Mannheim Weir – East *Grand River, ON*	D	1995–1996	*White sucker* Attraction Efficiency: 59% Passage Efficiency: 38% *Smallmouth bass* Attraction Efficiency: 55% Passage Efficiency: 33%	Mark-recapture, Radio telemetry	Bunt et al., 1999
Mannheim Weir – West *Grand River, ON*	D	1995–1996	*White sucker* Attraction Efficiency: 50% Passage Efficiency: 55% *Smallmouth bass* Attraction Efficiency: 82% Passage Efficiency: 36%	Mark-recapture, Radio telemetry	Bunt et al., 1999
Thornberry Fishway *Beaver River, ON*	NL	2017	*Rainbow trout* Attraction Efficiency: 53% Passage Efficiency: 100%	Radio telemetry	Bunt and Jacobson, 2019
Menominee Dam *Menominee River, MI*	Other	2016–2018	*Total caught (29 species)* 1,228–2,535 *Lake sturgeon passed* 36–74	Trap-catch	Donofrio, 2016, 2017, 2018
Big Carp River fishway *Big Carp River, ON*	VS	2003–2005	*11 species (mostly white sucker)* Attraction Efficiency: 93–96% Passage Efficiency: 35–88%	Passive Integrated Transponder (PIT)	O'Connor et al., 2003; Pratt et al., 2009
Cobourg Brook fishway *Cobourg Brook, ON*	VS	2003–2005	*8 species (mostly white sucker)* Attraction Efficiency: 78–82% Passage Efficiency: 7–10%	Passive Integrated Transponder (PIT)	O'Connor et al., 2003; Pratt et al., 2009

in the upper Great Lakes (Lawrie, 1970). The latest peak in fishway construction from 1990 to 2000 also overlaps with the adoption of the Natural Resources and Environmental Protection Act in the Michigan State legislature in 1994. Act 451, Part 483 (Natural Resources and Environmental Protection Act, 1994) prescribes rules and regulations for existing and new dams to provide fish

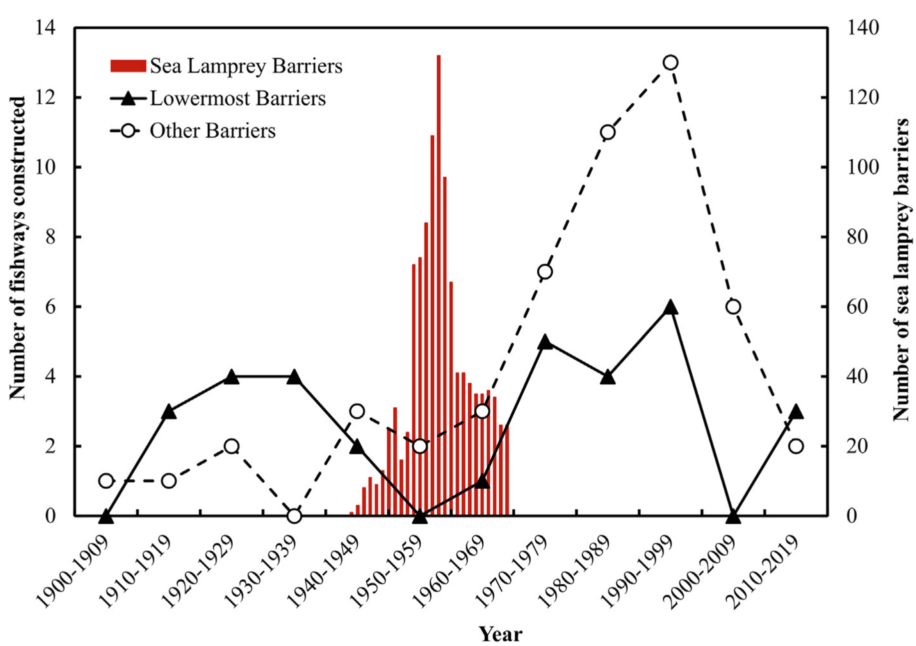

Fig. 2. Timeline of construction of fishways at lowermost barriers and other barrier sites within the Great Lakes Basin along with combined sea lamprey barrier operation in the Lake Superior, Lake Huron, and Lake Michigan (Lawrie, 1970). Fishway totals are summed across decades and sea lamprey barrier operation is shown yearly.

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passage. During the same time period, nearly one fishway was installed per year (Fig. 2). This rapid pace of fishway construction has slowed in recent years; only 5 fishways have been installed since 2010. While the changes in fishway construction appear correlated with major changes to Michigan legislation, this only applies to the 48 sites in Michigan. The impetus for fishway construction at all sites, including those in Michigan, is more likely a result of numerous environmental, societal, and legal actions. The major legislation that regulates fish passage in Canada is the Fisheries Act, which has continually evolved since its passage in 1868 (Katopodis and Williams, 2012; Kerr, 2010).

Barrier removal

In contrast to fishways, barriers can sometimes be entirely removed or replaced with nature-like fishways that restore migratory, nutrient, and sediment pathways with ecological and channel forming processes that utilize natural materials and mimic hydraulic and habitat features of natural functioning rivers (Katopodis and Aadland, 2006). Nature-like fishways, like rock-ramps, can maintain some hydraulic control similar to dams while improving fish passage (Aadland, 2010). Between 1967 and 2018, approximately 156 dams were removed on the U.S. side of the Great Lakes alone (American Rivers, 2019). The recent increase in barrier removals may have partially contributed to the reduced number of fishways constructed since its peak in the late 1990s. Since 2010, ten lowermost barriers were removed. For example, the Chesaning Dam on the Shiawassee River was removed and replaced with a rock ramp (rock arch rapids) in 2009. A post-construction assessment of the new rock ramp demonstrated improved ecosystem connectivity as evidenced by species richness, mean CPUE, and proportional species abundance of summer species (e.g., smallmouth bass *Micropterus dolomieu*, northern pike *Esox lucius*, channel catfish *Ictalurus punctatus*, and suckers *Catostomus* spp.) above the site that closely resembled levels of an undammed river (Stoller et al., 2016). A number of other projects in Michigan have utilized rock arch rapids, including the Potogannissing Dam and the Frankenmuth Dam on the Pottogannissing and Cass rivers, and the fisheries have had similar responses. Aadland (2010) also outlines numerous case studies that document upstream fish passage and usage of rock arch rapids, as high-quality habitat, by a myriad of fish species at different life stages during all times of the year. Removing dams or replacing them with nature-like fishways provides significant gains towards native fish passage and transport of sediments, nutrients, and woody debris; however, the hydraulic conditions (e.g., velocities, vertical differential) are unable to block sea lamprey.

The decision process behind removal of a lowermost barrier is largely site specific, but some of the common issues considered include public safety, barrier status (i.e., does it effectively block sea lamprey), presence of an upstream barrier, and potential habitat upstream of the lowermost barrier, and cost/benefit of modifying the structure. Of the lowermost barriers removed since 2010, four were small or in poor conditions and determined to not be complete barriers to sea lamprey. One structure was removed as a result of a court order due to resource damages, and the remaining dams were found to have limited or poor-quality habitat for sea lamprey.

Sea lamprey barriers

Some sea lamprey barriers essentially function as a filter to upstream passage. Fixed-crest barriers which intentionally block passage of invasive sea lamprey, unintentionally block native fish with limited leaping ability; but non-native salmonids are able to leap past barriers when a jumping pool is located immediately downstream (McLaughlin et al., 2006; Porto et al., 1999). Fixed-crest barriers act as a filter to upstream passage, essentially passing salmonids while blocking all remaining species. The following analysis demonstrates how fixed-crest barriers designed to block sea lamprey permit passage of salmon. The barrier height that salmon can pass depends on swimming speed and leap trajectory. A desktop analysis using a simplified ballistic model (Powers and Osborn, 1985) can provide approximate leaping height of non-native salmonids and subsequent ability to pass fixed-crest barriers. Assuming a constant leap angle among all species, the maximum leap height is ultimately proportional to an individual's maximum swimming speed. Numerous swim studies have examined swimming capabilities of chinook salmon *Oncorhynchus tshawytscha*, coho salmon *Oncorhynchus kisutch*, and steelhead rainbow trout *Oncorhynchus mykiss* (Katopodis and Gervais, 2016; Reiser et al., 2006), with the maximum swimming speed ranging between 8.2 and 9.5 body length per second (Table 2). Following Powers and Osborn (1985), when the downstream jumping pool is greater than one body length in depth, steelhead, coho salmon, and chinook salmon are all able to clear the standard 45 cm vertical differential required to block sea lamprey at fixed-crest barriers (Table 3). This analysis does not account for velocity conditions on either side of the barrier, which can both hinder or aid likelihood of passage. Examination of the distance to the apex of the leap trajectory also demonstrates that barriers in excess of 150 cm could be passed by all three species, but the fish must be relatively close to the barrier (<60 cm).

Seasonal barriers are also used sparingly throughout the basin (N = 46 seasonal- and adjustable-crest barriers) to selectively pass non-target fish before and after the sea lamprey migratory period. Seasonal barriers are comprised of structures with either an adjustable or removable crest or fixed-crest barrier with a fishway that can be closed during sea lamprey migrations. Unfortunately, the operational window for seasonal barriers cannot be generalized across the basin and must be defined on a stream by stream basis (Klingler et al., 2003). The operational window is identified using a combination of stream temperature, historical sea lamprey trap catches, distance of barrier the stream mouth, stream gradient, and isothermic zone (Zielinski et al., 2019). While seasonal operation of a barrier or adjacent fishway provides some passage opportunity to non-target fishes, the migratory window of sea lamprey overlaps significantly with many native fish. A modelling exercise by Velez-Espino et al. (2011) demonstrated that an operational window selected to block 99.9% of sea lamprey (75-day duration) would also block between 44 and 100% of non-target fish. This level of blockage would lead to declines in non-target fish upstream of the barrier similar to those expected for permanent barriers. While seasonal barriers could be appropriate for sites where the main fish species present are fall spawners (e.g., coaster brook trout), seasonal operations would still limit non-migratory movements of fish, which is an important aspect of life history for stream fish that has less seasonal predictability (Matthews, 1998). An alternative to seasonal barrier operation is trap-and-sort fishways, which combine traditional fishway designs with sea lamprey traps. These fishways allow trapped fish to be visually sorted with non-target fishes manually passed upstream and sea lamprey removed (Pratt et al., 2009). Only three trap-and-sort fishways operate in the Great Lakes Basin and while they can be 100% effective at blocking sea lamprey, non-target fish passage varies widely between 7 and 88% and those that are passed experience migration delays of 5–28 days (Pratt et al., 2009).

The concept of using elevated water velocity to selectively block/pass fish based on their swimming performance has often been suggested for sea lamprey control (See Zielinski et al. 2019 for a full description of velocity barriers). The lone field study of

Table 3
Summary of swimming performance and leap trajectories of chinook salmon *Oncorhynchus tshawytscha*, coho salmon *Oncorhynchus kisutch*, and steelhead rainbow trout *Oncorhynchus mykiss* (Katopodis and Gervais, 2016; Reiser et al., 2006; Weaver, 1963) with assumed leap angles of 40, 60, and 80 degrees. Leap height and distance to apex of trajectory calculated using Eq. 6 and 7 from Powers and Osborn (1985). Body lengths assigned from mean values for all three species in the Great Lakes (Scott and Crossman, 1973). Actual swimming speeds in m/s are calculated by multiplying the normalized swimming speed by mean body length.

Species	Mean body length (cm)	Max swim speed (BL/s)	Actual swim speed (m/s)*	Leap height (cm)	Dist. to apex (cm)
Chinook Salmon	88	8.2	7.2		
40°				109	260
60°				198	229
80°				256	90
Coho Salmon	64	8.7	5.6		
40°				66	157
60°				120	138
80°				155	55
Rainbow Trout	60	9.5	5.7		
40°				68	163
60°				124	143
80°				161	57

a velocity barrier in the Great Lakes basin occurred in the McIntyre River, Ontario (McAuley, 1996). Not only was the experimental barrier unable to completely block sea lamprey, but it also unintentionally blocked gravid white sucker passage (Chase, 1996). Despite the lack of past success, research continues to better understand sea lamprey locomotion in high water velocities with the goal of blocking passage (Zielinski et al., 2019).

Research and development of fish passage in the Great Lakes Basin

The most common solutions to fish passage at barriers in the Great Lakes Basin, technical fishways, dam removal, and dam replacement with nature-like fishways, are largely no different than solutions applied globally (Katopodis and Williams, 2012; Silva et al., 2018). Purposeful design of fixed-crest barriers with a jumping pool, seasonal barrier operations, and trap-and-sort fishways provide some passage to non-target species; however, their effects are limited in comparison to the number of lowermost barriers. The development of fish passage solutions in the Great Lakes has been tethered by the continued need for sea lamprey control. Thus, selectivity has been a major factor in the design of new fish passage technologies. This section provides a brief description of two fish passage technologies with selective capabilities under development, the Whooshh Fish Transport System and wetted ramps, and a side-baffle fish ladder designed to target passage of lake sturgeon *Acipenser fulvescens*.

Whooshh fish transport system

The Whooshh Fish Transport System (WFTS) is an emerging technology that transports fish using differential pressure to propel fish inside a low-friction, flexible tube. The WFTS has demonstrated successful, autonomous passage for Pacific salmonids along the west coast of the United States (Garavelli et al., 2019; Geist et al., 2016; Mesa et al., 2013) and, in a pilot test, successful passage of four teleosts found in the Great Lakes (Miehls et al., 2017). The benefits of the WFTS is the modular deployment and lack of infrastructure requirements. While the WFTS does not inherently provide any selective passage capabilities, development is currently underway to pair the WFTS with an imaging hood that captures multiple photographs so fish can be automatically identified and sorted before entering the WFTS (Garavelli et al., 2019; Miehls unpublished data). Garavelli et al. (2019) found the WFTS could scan and sort Chinook salmon and steelhead within 1.5–2 s, but fish separated by less than 0.5 s apart could not be scanned individually. An Alaska Steeppass fishway and false weir permits Pacific salmon to volitionally enter the system. Fish then slide through the imaging hood dewatered to ensure high quality images. The Alaska Steeppass fishway and false weir entrance design utilized with the WFTS have not been tested on fish native to the Great Lakes, and their ability and behavior to volitionally climb is unknown. Research is underway to develop alternative means to lift fish into the imaging system.

Wetted ramps

Wetted ramps, consisting of a smooth inclined ramp (10–60°) with a shallow sheet flow of water, have potential to pass fish with insufficient swimming or leaping abilities to overcome sea lamprey barriers (Sherburne and Reinhardt, 2016). Reinhardt et al. (2009) found sea lamprey would attach to the surface to hold position but not be able to progress further if their ventral fin was not fully submerged. Further laboratory tests found small fish (85–510 mm) native to the Great Lakes had modest success passing ramps inclined 10–20 degrees (Sherburne and Reinhardt, 2016). Between 31 and 47% of common white sucker *Catostomus commersonii* and smallmouth bass were able to successfully ascend a 0.6 m long ramp. In general, wetted ramps benefit passage of smaller fish that have a greater proportion of their body under water, and are able to generate more thrust than larger individuals with a greater proportion of their body out of the water. While preliminary data suggest wetted ramps have selective passage potential, further development is needed to characterize passage of both sea lamprey and non-target species at varying hydraulic conditions and within field-scale deployments.

Side-baffle fish ladder

In addition to development of fishway technologies with selective capabilities, research has also focused on modifying the design of existing fishways to improve passage efficiency of native fish. Kynard et al. (2011) recently developed a prototype, spiral, side-baffle fish ladder in response to the general poor performance of sturgeon species. to pass in most fishways (Bell, 1973). The spiral, side-baffle design was considered because it allowed continuous water flow while eliminating the need for cross channel walls (i.e., turning pools) that have been shown to significantly delay sturgeon passage at traditionally designed technical fishways (Thiem et al., 2011). Across a three-year laboratory study, Kynard et al., (2011) observed >90% attraction efficiency and 41–91% passage efficiency for cultured lake sturgeon juveniles and adults. While the results are promising, the experiments were conducted under tightly controlled laboratory conditions which may be difficult to maintain in the field.

Future of fish passage in the Great Lakes

While replacement of dams with rock arch ramps or nature-like fishways have been successful at restoring up- and down-stream passage for a myriad of fish species and life stages, the overall advancement of fish passage technologies that continue blockage of sea lamprey in the Great Lakes Basin since SLIS II has been slow. Despite new technologies having been investigated, none are ready for management scale applications. Consistent with other fishways around the globe, there is a general lack of monitoring data available to support the efficacy of Great Lakes fishways (Silva et al., 2018). While monitoring fishway attraction and passage efficiencies is necessary for assessment of river connectivity, it is not the only factor that determines fish population sustainability (Silva et al., 2018). Larger-scale factors like habitat loss upstream of a barrier and its fishway may have a more significant impact on reaching watershed fish community objectives. Increased monitoring of fish movement behaviors between lakes and their tributaries, as well as within rivers and streams will help managers assess which species are most impacted by barriers and likely candidates to target for passage solutions (Landsman et al., 2011).

Although considerable uncertainty exists on how to improve fish passage at lowermost barriers without detrimental impacts to sea lamprey control, there is common support from inland fisheries managers for an approach to barriers that seeks removal of structures no longer needed and are upstream of lowermost barriers. This approach has resulted in several restorations and improved connectivity across whole watersheds. For example, the Boardman River Dams Ecosystem Restoration Project (theboardman.org), the largest river restoration project in Michigan's history, recently removed three upstream barriers to fish movement and reconnected over 160 miles of free-flowing river.

Longitudinal connectivity is a two-way street in which fish migrate in both up- and down-stream directions (Calles and Greenberg, 2009). Downstream movement consists of both out-migrating adults and earlier life stages that either passively drift (larvae) or actively out-migrate (juveniles). While fishways provide pathways for upstream movement, they are usually not exploited for downstream movement due to low flows and narrow entrances relative to spillways (O'Connor et al., 2006). There is a paucity of studies on the impact of sea lamprey barriers on downstream movement of fish in the Great Lakes. Most lowermost barriers maintain a relatively small vertical drop and are unlikely to pose a significant mortality risk to adult fish passing downstream; however, their impact on earlier life stages is unknown. Further research on the impact of sea lamprey barriers on downstream fish movement and potential solutions, if a significant issue exists, are needed. We are unaware of any specific downstream fish passage solutions in the Great Lakes basin at non-hydropower barriers. Hydropower facilities represent the greatest threat to downstream migrating fish through screen impingement, turbine strikes, or passing over spillways with large vertical drops (Calles and Greenberg, 2009). There are 56 lowermost barriers in the Great Lakes that feature hydropower facilities (Zielinski et al., 2019), and many use vertical screens, or trash racks, to prevent debris and large fish from entering turbines. The only recent example of downstream fish passage mitigation is the angled fish guidance rack and surface bypass at the Menominee Dam, Marinette, WI, which was installed in 2016 to protect and pass downstream swimming adult lake sturgeon (https://www.menomineewatershed.com/fish-elevator.html).

To address the tension between invasive species control and connectivity surrounding lowermost barriers, the GLFC is leading the bi-directional selective fish passage (FishPass) project (http://www.glfc.org/fishpass.php). FishPass will be the capstone to the Boardman River restoration project, replacing the lowermost barrier, Union Street Dam, Traverse City, MI, thereby re-connecting the river with Lake Michigan. The mission of FishPass is to provide up- and down-stream passage of desirable fishes while simultaneously blocking and/or removing undesirable fishes. FishPass will replace the deteriorating lowermost barrier with an improved barrier featuring a fish-sorting channel and a nature-like river channel. Once constructed, scientists will be able to optimize various sorting technologies and techniques below the barrier to maximize efficiency of passing desirable fishes and removing invasive fishes. Research will follow an adaptive management framework (Williams et al., 2009) in which scientists and engineers will implement fish passage technologies informed from past experiments and will be annually monitored, evaluated, and adjusted in subsequent years. As a collaborative effort of fish passage biologists and engineers, all research at FishPass will emphasize ecohydraulic concepts that consider both biological and hydraulic components relevant to fish passage. Ecohydraulic studies may offer the most effective opportunity to evaluate and optimize selective fish passage technologies. FishPass will be a hub of fish passage technological development throughout the Great Lakes with a large (400 ft L × 30 ft W) adaptable flume and dual gate system to accommodate a wide variety of hydraulic conditions necessary to investigate selective fish passage technologies. The lessons learned from the optimization phase of FishPass may be applied to similar rivers across the Great Lakes and beyond.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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