



Fish movement and migration studies in the Laurentian Great Lakes: Research trends and knowledge gaps

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ABSTRACT

Resource management agencies in the Laurentian Great Lakes routinely conduct studies of fish movement and migration to understand the temporal and spatial distribution of fishes within and between the lakes and their tributaries. This literature has never been summarized and evaluated to identify common themes and future research opportunities. We reviewed 112 studies, published between 1952 and 2010, with the goal of summarizing existing research on the movement and migration of fishes in the Laurentian Great Lakes. The most commonly studied species were Lake Trout (*Salvelinus namaycush*), Walleye (*Sander vitreus*), and Lake Sturgeon (*Acipenser fulvescens*). Studies relied mainly on mark-recapture techniques with comparatively few using newer technologies such as biotelemetry, hydroacoustics, or otolith microchemistry/isotope analysis. Most movement studies addressed questions related to reproductive biology, effects of environmental factors on movement, stocking, and habitat use. Movement-related knowledge gaps were identified through the literature synthesis and a survey distributed to Great Lakes fisheries managers. Future studies on emigration/immigration of fishes through lake corridors, the dispersal of stocked fishes and of stock mixing were identified as being particularly important given their potential for developing lake- or region-wide harvest regulations and stocking strategies. The diversity of tools for studying fish movement across multiple years and various spatial scales gives researchers new abilities to address key science questions and management needs. Addressing these needs has the potential to improve upon existing fisheries management practices within the complexity of multi-jurisdictional governance in the Laurentian Great Lakes.

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Introduction

The Laurentian Great Lakes (hereafter referred to as the Great Lakes)—consisting of Lakes Superior, Huron, Michigan, Erie, and Ontario—are the largest group of freshwater lakes in the world and contain more than 150 species of fish. Collectively, a number of these species contribute to commercial, recreational, and tribal fisheries worth at least USD \$7 billion annually (ASA, 2008). The Great Lakes fisheries are shared by 34 million people in the United States and Canada (GLIN, 2010) with stakeholder groups representing government, industry, indigenous parties, and the general public. Management is conducted under the Joint Strategic Plan for Management of Great Lakes Fisheries, a voluntary agreement established by the Great Lakes Fishery Commission and signed in 1981 by most agencies in Canada and the United States (Gaden et al., 2008). The plan is grounded on the principles established by the Convention on the Great Lakes Fisheries, which strived for agency cooperation in

managing fisheries for maximum sustainable yield and the creation of a Sea Lamprey (*Petromyzon marinus*) eradication and control program (Selak, 1956).

History is replete with examples of changes that have affected the Great Lakes and its fisheries since humans first colonized the region. At the forefront is the invasion of Sea Lamprey (e.g., Hubbs and Pope, 1937; Smith and Tibbles, 1980), which led to much research contributing to the development of Sea Lamprey control strategies and initiatives aimed at rehabilitating affected fish populations. Historic problems associated with overfishing, eutrophication, loss of spawning habitat, pollution and contaminant discharge, exotic species introductions, and declines in native fish populations have also given rise to management challenges and research needs (as reviewed by Beeton, 1969; Christie, 1974; Johnson and Cooley, 1992; Mills et al., 2005; Dextrase and Mandrak, 2006; Shear, 2006). Many of these challenges and ecosystem stressors have been addressed to some extent (Mills et al., 2005). On-going management efforts, however, are essential to ensuring the long-term sustainability of the Great Lakes fisheries, particularly given emerging threats (e.g., climate change, Asian Carp invasion, viral hemorrhagic septicemia) and the potential for synergistic and cumulative effects of multiple stressors

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(Kelso et al., 1996; Rixon et al., 2005; Shear, 2006; Lumsden et al., 2007).

Knowledge of the movement and spatial ecology of fishes is of particular importance to managers as it provides information about how fishes are distributed in both space and time (Lucas and Baras, 2000). For example, knowledge of when and where spawning occurs as well as specific nursery habitat use by offspring informs management of critical habitats, which is important for the protection of threatened species (Cooke, 2008), and is also relevant in planning fisheries activities. Understanding the movements of fishes into and out of specific stocking sites can lead to refined stocking practices and enhanced rehabilitation programs (Cornelius et al., 1995; Fielder, 2002), and can also provide information on the natural history of invasive fishes (e.g., Sea Lamprey) for the establishment of control programs (Christie and Goddard, 2003).

Although movement studies have been conducted for some species in the Great Lakes, no formal compilation of research to date exists. As such, knowledge gaps are difficult to identify. Fish movement research in the Great Lakes has been limited by the immense size and depth of the lakes. However, considerable progress in recent years has been made in animal tracking technologies (Lucas and Baras, 2000; Cooke et al., 2004) that have coincided with advances in the analysis, application, and interpretation of increasingly large and complex datasets (Rutz and Hays, 2009). As a result, the study of fish movements over long distances is now possible where not previously feasible (e.g., transoceanic movements of Atlantic Bluefin Tuna [*Thunnus thynnus*] tracked with archival loggers, Block et al., 2001; coastal and watershed-scale studies of Pacific salmon [*Oncorhynchus* spp.] migration using telemetry, Welch et al., 2003). Other innovations such as otolith microchemistry enable researchers to reconstruct the movement history of individual fish (Brazner et al., 2004; Campana et al., 2007). Given these advancements in technological capabilities, a collation of all fish movement and migration studies from the Great Lakes would provide a resource for future research and development in this field, particularly given that the Great Lakes Fishery Commission is embarking on several large-scale and long-term research projects that are focused on quantifying and describing the movement and migration of key Great Lakes fishes (C. Krueger, Personal Communication).

This study compiled and synthesized the scientific literature on the movement and migration of Great Lakes fishes for the benefit of

fisheries managers and researchers alike. Our objectives were to: 1) characterize existing trends in research topics, techniques used to study fish movement, species studied, study sites, and publication sources for fish movement studies in the Great Lakes; 2) summarize the literature and techniques used for each research topic identified; 3) survey Great Lakes fisheries managers to identify knowledge gaps related to fish movement in the Great Lakes that, if addressed, could improve the understanding of ecological processes and inform fisheries management.

General approach

We examined studies that evaluated fish movements within and between the Great Lakes and their tributaries. The St. Lawrence River up to the occurrence of brackish water near Quebec City, Quebec, and the St. Marys, Detroit, and St. Clair Rivers were also included given their size and connectivity to the Great Lakes. Furthermore, studies examining adfluvial movements of Great Lakes fishes were also included (e.g., Haynes and Nettles, 1983; Huckins and Baker, 2008).

For this review, fish movement occurs when individuals or groups shift location along a horizontal or vertical plane. Studies employing methods that track individual or group movements are considered (e.g., telemetry, mark-recapture, hydroacoustics). Studies that were excluded from the review were those based on the presence or absence of an individual(s) or species, which studied range expansion, or that otherwise inferred movement from the collected data without the use of any particular tracking technology. Studies using mark-recapture techniques were excluded if the focus of the paper was only estimating abundance, survival, or rates of exploitation. Furthermore, studies in tributaries were excluded if fishes were not adfluvial or that were confined to sections of tributaries bordered upstream and downstream by non-passable dams (i.e., those without fishways or other fish passing devices). In total, 77 studies were excluded from analysis.

Primary and grey literature (i.e., technical reports, theses) searches were conducted from 15 January to 30 April 2010. Relevant papers were identified using various combinations of keywords to search academic journal databases, internet search engines, and government websites (Table 1) as well as referencing the literature cited sections of the papers covered in this review. In addition, members of the Great Lakes Fishery Commission Lake Committees, provincial and state

Table 1
Keywords and databases used to search for primary and grey literature of fish movement in the Great Lakes.

Keywords	Databases and Websites searched for primary and/or grey literature	URL
Adfluvial	Web of Science	
Behavior	Google	www.google.com
Diel	Google Scholar	http://scholar.google.com
Fish	Department of Fisheries and Oceans - WAVES database	http://inter01.dfo-mpo.gc.ca/waves2/index.html
Fish migration	Journal of Great Lakes Research	http://pubs.nrc-cnrc.gc.ca/eng/home.html
Fish movement	National Research Council Press Journals	http://pubs.nrc-cnrc.gc.ca/eng/home.html
Great Lakes	U.S. Fish and Wildlife Service Library	http://library.fws.gov/
Lake Erie	Michigan Department of Natural Resources and Environment	http://www.michigan.gov/dnr
Lake Huron	Minnesota Department of Natural Resources	http://www.dnr.state.mn.us/index.html
Lake Michigan	Wisconsin Department of Natural Resources	http://dnr.wi.gov/
Lake Ontario	Illinois Department of Natural Resources	http://dnr.state.il.us/
Lake Superior	Indiana Department of Natural Resources	http://www.in.gov/dnr/
Mark-recapture	Pennsylvania Department of Conservation and Natural Resources	http://www.dcnr.state.pa.us/
Migration	Ohio Department of Natural Resources	http://www.dnr.state.oh.us/
Migratory behavior	New York State Department of Environmental Conservation	http://www.dec.ny.gov/
Movement	Ontario Ministry of Natural Resources	http://www.mnr.gov.on.ca/en/index.html
Seasonal	Great Lakes Fishery Commission	http://www.glfsc.org/
Spawn	Scopus	
Tag	American Fisheries Society Online Journals	
Telemetry	Department of Fisheries and Oceans Canada	
Track	Biological Sciences Database	
Tributary		
Vertical		

agencies, and academic researchers involved in studying and/or managing the Great Lakes were contacted to obtain grey literature not readily available through library systems. The review procedure was conducted in the following order: selection of keywords; primary and grey literature database searches; screening of titles, abstracts, and full documents; selection of relevant documents; identification of research topics; and the data extraction and spreadsheet entry. Lastly, a short questionnaire was circulated via e-mail to the Great Lakes Fishery Commission Lake Committees to identify current management issues and research gaps that managers are facing.

The contents of each study in our database were organized by research topic, species studied, movement quantification technique (e.g., radio telemetry, mark-recapture), and study site. We found that many studies fit into multiple categories. For example, Caroffino et al. (2009) used multiple techniques to quantify movements of Great Lakes fishes and Kelso and Gardner (2000) covered multiple research topics in their study. Consequently, our summary statistics for each category or research section may exceed 100%.

We acknowledge that there may be relevant primary and grey literature that was not included in this synthesis. This is partly due to time constraints, the choice of keywords, databases, and limited access to full documents of certain studies. Nonetheless, we believe that the majority of the literature on this topic has been included and that the conclusions of our synthesis would not differ greatly with the addition of any studies missed. Discussion of the specific advantages and disadvantages of the techniques used to study fish movement have been covered by Lucas and Baras (2000) and Cooke et al. (In Press) and, therefore, these issues were not covered in this review.

Characteristics and trends in fish movement literature

General characteristics

The results of our literature search yielded 112 movement studies of Great Lakes fishes: 88 peer-reviewed studies and 24 grey literature reports (Table 2). Publication dates ranged from 1952 to 2010 with a general increase in the number of studies published since 2000 (Fig. 1). Of 88 studies published in the peer reviewed literature, 27.3% ($N=24$) were published in *Transactions of the American Fisheries Society*, 23.9% ($N=21$) in *Journal of Great Lakes Research*, 10.2% ($N=9$) in *Canadian Journal of Fisheries and Aquatic Sciences* including three studies in the journal's former title of *Journal of the Fisheries Research Board of Canada*, and 9.1% ($N=8$) in *North American Journal of Fisheries Management*. The remaining papers were distributed among several journals, including *Journal of Freshwater Ecology* (5.7%, $N=5$) and *New York Fish and Game Journal* (3.4%, $N=3$).

Research topics

Seven research topics were identified in the literature. Reproductive biology was the topic most commonly studied (41.1%; $N=46$), followed by environmental relations and disturbance (22.3%; $N=25$), and stocking (21.4%; $N=24$). Additional research topics included habitat use (17.0%; $N=19$), invasive species (14.3%; $N=16$), techniques for studying fish movement (6.3%; $N=7$), diet and trophic niche (5.4%; $N=6$), and barriers and fish passage (5.4%; $N=6$). Thirty-three studies (30.0%) incorporated multiple fish movement research topics. The research topic analysis and discussion section is organized in descending order from the most studied research topic to the least.

Research techniques

Results of our literature search yielded a number of trends in the techniques used to study fish movement. First, mark-recapture techniques (e.g., jaw tags, Wang et al., 2007; coded wire tags,

Adlerstein et al., 2007a,b; anchor tags, Behmer et al., 1993) were the most common approach for studying fish movement in the Great Lakes (43.8%; $N=49$). This trend may be explained by the pervasiveness of this technique prior to the development of newer technologies and the cost effectiveness of mark-recapture methods over other alternatives. Second, over the last 60 years it is evident that, although mark-recapture remains a popular technique for studying fish movement, biotelemetry and other methods have gained popularity amongst researchers in the last 20–40 years (Fig. 2). Radio telemetry (33.9%; $N=38$), hydroacoustics or sonar (8.0%; $N=9$), passive integrated transponder (PIT) tags (8.0%; $N=9$), acoustic telemetry (6.3%; $N=7$), and otolith microchemistry/isotope analysis (2.7%; $N=3$) were also used to infer fish movements. In addition, six studies (5.4%) used multiple techniques (Auer, 1999; McGrath et al., 2003a; Caswell et al., 2004; Binder and McDonald, 2007; Caroffino et al., 2009; Mandrak, unpublished).

Taxonomic patterns

Most publications focused on a single species (81.3%; $N=91$; Table 3) while 21 studies (18.7%) examined more than one species, including three that examined over 20 species (Porto et al., 1999; Klingler et al., 2003; Dolinsek et al., 2008). In total, 34 species of Great Lakes fishes were identified as being studied in the movement papers reviewed here (Table 3). There was a focus on three species (Table 3): Lake Trout (*Salvelinus namaycush*; 15.2%; $N=17$), Walleye (*Sander vitreus*; 14.3%; $N=16$), and Lake Sturgeon (*Acipenser fulvescens*; 13.4%; $N=15$). Sixty-four (57.1%) studies examined various salmonid species. A list of additional species studied can be found in Table 3.

Geographic patterns

Most studies were conducted in a single Great Lake or tributary (80.4%; $N=90$) and 21 studies (18.8%) considered more than one geographic location. Few studies (1.8%; $N=2$; Ferguson and Derksen, 1971; Todd and Haas, 1993) examined movements between Great Lakes (via river corridors). Most research took place in tributaries (38.4%; $N=43$) of the Great Lakes. The number of studies conducted in the Great Lakes themselves were highest in Lake Erie (24.1%; $N=27$) followed by Lakes Superior (19.6%; $N=22$), Michigan (17.0%; $N=19$), Ontario (10.7%; $N=12$), and Huron (8.9%; $N=10$).

Research topic analysis and discussion

Reproductive biology

Great Lakes fisheries have undergone dramatic change, with some having been pushed to near-collapse (Christie, 1974; Hansen, 1999). To both maintain existing and imperiled fisheries, researchers frequently conduct fish movement studies to understand and determine key attributes of the reproductive biology of economically important species. Studies in this section were separated into four sub-topics: movements to/from spawning sites (e.g., dispersal of juveniles and adults, fidelity, homing); location of spawning activities; spawning migrations of different fish species; and spawning behavior descriptions.

Movements of juveniles and adults away from or toward spawning sites is often assessed to inform rehabilitation procedures, elucidate key aspects of a given fishery, or enhance the scientific community's understanding of the ecology of a particular species. For example, juvenile dispersal from spawning sites/natal streams and nursery grounds has been studied for Walleye (Wolfert, 1963) and Lake Sturgeon (Baker, 2006; Lord, 2007; Caroffino et al., 2009), all with the common goal of rehabilitating populations. Two techniques have been used to examine juvenile dispersal: acoustic telemetry (Lord, 2007) and mark-recapture (Wolfert, 1963; Baker, 2006; Caroffino et al.,

Table 2Complete list of Laurentian Great Lakes fish movement studies ($N=112$), including primary and grey literature, and key characteristics of each study.

Reference	Research topic(s)	Study site(s)	Technique(s)	Specie(s)
Adlerstein et al., 2007a	Stocking	Lake Huron	Mark-recapture	Chinook salmon (<i>Oncorhynchus tshawytscha</i>)
Adlerstein et al., 2007b	Stocking	Lake Huron	Mark-recapture	Lake trout (<i>Salvelinus namaycush</i>)
Adlerstein et al., 2008	Stocking	Lake Michigan	Mark-recapture	Chinook salmon
Auer, 1999	Habitat use, Reproductive biology	Lake Superior	Radio telemetry, mark-recapture	Lake sturgeon (<i>Acipenser fulvescens</i>)
Auer and Baker, 2007	Reproductive biology	Sturgeon River, Michigan	Hydroacoustics	Lake sturgeon
Baker, 2006	Reproductive biology	Lake Michigan	Mark-recapture	Lake sturgeon
Behmer et al., 1993	Stocking	St. Marys River, Michigan; Lake Superior	Mark-recapture	Atlantic salmon (<i>Salmo salar</i>)
Benson et al., 2005	Habitat use	Peshtigo River, Wisconsin	Radio telemetry	Lake sturgeon
Bergstedt et al., 2003	Invasive species	Lake Huron	Mark-recapture	Sea lamprey (<i>Petromyzon marinus</i>)
Bergstedt and O'Gorman, 1989	Environmental relations and disturbance	Lake Ontario	Hydroacoustics	Alewife (<i>Alosa pseudoharengus</i>)
Bergstedt and Seelye, 1995	Invasive species, reproductive biology	Lake Huron tributaries	Mark-recapture	Sea lamprey
Binder and McDonald, 2007	Invasive species, reproductive biology, and habitat use	Lake Ontario	Radio telemetry, PIT tags	Sea lamprey
Brant, 1980	Invasive species, environmental relations and disturbance	Lake Michigan	Hydroacoustics	Alewife
Brazner et al., 2004	Technique	Lake Superior	Otolith Microchemistry/Isotope Analysis	Yellow perch (<i>Perca flavescens</i>)
Buettner, 1961	Technique, stocking	Lake Superior	Mark-recapture	Lake trout
Bunt et al., 2000	Reproductive biology, invasive species, barriers and fish passage	Grand River, Ontario	Radio telemetry	Walleye (<i>Sander vitreus</i>)
Caroffino et al., 2009	Reproductive biology	Peshtigo River, Wisconsin	Mark-recapture, PIT tags	Lake sturgeon
Caswell et al., 2004	Reproductive biology	Detroit River, Michigan	Acoustic telemetry, PIT tags	Lake sturgeon
Clark, 1990	Reproductive biology	Lake Erie	Mark-recapture	Northern pike (<i>Esox lucius</i>)
Cooke et al., 2004	Environmental relations and disturbance	Lake Erie	Radio telemetry	Smallmouth bass (<i>Micropterus dolomieu</i>)
Cooke et al., 2003	Reproductive biology, environmental relations and disturbance	Lake Erie	Radio telemetry	Smallmouth bass
Cooke and Schreer, 2003	Environmental relations and disturbance	Lake Erie	Radio telemetry	Common carp (<i>Cyprinus carpio</i>)
Cooke et al., 2000	Environmental relations and disturbance	Lake Erie	Radio telemetry	Smallmouth bass
Cooke and McKinley, 1999	Environmental relations and disturbance	Lake Erie	Radio telemetry	Channel catfish (<i>Ictalurus punctatus</i>), common carp
Cookingham and Ruetz, 2008	Invasive species, technique	Lake Michigan	PIT tags	Round goby (<i>Neogobius melanostomus</i>)
Crowe, 1962	Reproductive biology	Lake Michigan	Mark-recapture	Walleye
Dolinsek et al., 2008	Barriers	Lake Ontario tributaries	PIT tags	Sea lamprey, various ($N=23$)
Dufour et al., 2005	Invasive species	Lake Michigan	Otolith Microchemistry/Isotope Analysis	Alewife
Einhouse, 2008	Reproductive biology	Lake Erie	Mark-recapture	Walleye
Elrod and Schneider, 1987	Stocking	Lake Ontario	Mark-recapture	Lake trout
Elrod, 1987	Stocking	Lake Ontario	Mark-recapture	Lake trout
Elrod et al., 1996	Stocking	Lake Ontario	Mark-recapture	Lake trout
Eschemeyer et al., 1953	Technique	Lake Superior	Mark-recapture	Lake trout
Ferguson and Derksen, 1971	Stocking, reproductive biology	Lake Huron; Lake Erie; Lake St. Clair; Thames River, Ontario	Mark-recapture	Walleye
Fielder, 2002	Stocking, reproductive biology	Lake Huron	Mark-recapture	Walleye
Fielder and Thomas, 2006	Stocking	Lake Huron	Mark-recapture	Walleye
Fortin et al., 1993	Habitat use, reproductive biology	St. Lawrence River, Quebec; Ottawa River, Quebec	Mark-recapture	Lake sturgeon
Friday, in preparation	Habitat use	Black Sturgeon River, Ontario; Lake Superior	Radio telemetry	Lake sturgeon
Friday, 2007	Reproductive biology, environmental relations and disturbance	Kaministiquia River, Ontario	Radio telemetry	Lake sturgeon
Friday, 2006	Reproductive biology, environmental relations and disturbance	Kaministiquia River, Ontario	Radio telemetry	Lake sturgeon
Friday, 2005	Reproductive biology, environmental relations and disturbance	Kaministiquia River, Ontario	Radio telemetry	Lake sturgeon
Friday, 2004	Reproductive biology, environmental relations and disturbance	Kaministiquia River, Ontario	Radio telemetry	Lake sturgeon
Glass et al., in preparation	Habitat use	Lake Erie	Radio telemetry	Spotted gar (<i>Lepisosteus oculatus</i>)

Glover et al., 2008	Habitat use, reproductive biology, stocking	Lake Michigan	Mark-recapture	Yellow perch
Haas et al., 1988	Stocking	Lake Erie and tributaries	Mark-recapture	Walleye
Hansen and Stauffer, 1971	Stocking, reproductive biology	Lake Superior, Lake Michigan, Lake Huron	Mark-recapture	Rainbow trout (<i>Oncorhynchus mykiss</i>)
Haynes and Nettles, 1983	Stocking, reproductive biology	Lake Ontario	Radio telemetry	Brown trout (<i>Salmo trutta</i>)
Haynes et al., 1986	Environmental relations and disturbance	Lake Ontario	Radio telemetry	Rainbow trout
Haynes and Keleher, 1986	Environmental relations and disturbance	Lake Ontario	Radio telemetry	Coho salmon (<i>Oncorhynchus kisutch</i>), chinook salmon
Haynes and Gerber, 1989	Stocking, habitat use	Lake Ontario	Radio telemetry	Chinook salmon, coho salmon, rainbow trout, brown trout
Holtgren and Auer, 2004	Habitat use	Sturgeon River, Michigan; Portage Lake, Michigan	Radio telemetry	Lake sturgeon
Hrabik et al., 2006	Diet and trophic niche	Lake Superior	Hydroacoustics	Lake trout, various coregonids
Huckins and Baker, 2008	Reproductive biology	Lake Superior	Mark-recapture	Brook trout (<i>Salvelinus fontinalis</i>)
Janssen and Brandt, 1980	Invasive species, diet and trophic niche	Lake Michigan	Hydroacoustics	Alewife
Jensen et al., 2006	Diet and trophic niche	Lake Superior	Hydroacoustics	Deepwater ciscoes (<i>Coregonus</i> spp.), lake trout
Kelso and Gardner, 2000	Habitat use, reproductive biology, invasive species	Lake Superior	Radio telemetry	Sea lamprey
Kelso, 1976	Environmental relations and disturbance	Lake Erie	Acoustic telemetry	Yellow perch, white sucker (<i>Catostomus comersoni</i>)
Kelso, 1974	Environmental relations and disturbance	Lake Ontario	Acoustic telemetry	Brown bullhead (<i>Ameiurus nebulosus</i>)
Kelso and Kwain, 1984	Reproductive biology	Lake Superior	Acoustic telemetry	Rainbow trout
Kelso et al., 2001	Invasive species	Carp River, Ontario; Lake Superior	Radio telemetry	Sea lamprey
Kelso and Noltie, 1990	Invasive species, barriers and fish passage	Carp River and Pancake River, Ontario	Mark-recapture	Pink salmon (<i>Oncorhynchus gorbuscha</i>), coho salmon, Chinook salmon
Kennedy et al., 2005	Reproductive biology	St. Marys River, Michigan	Gill net	Pink Salmon
Klingler et al., 2003	Reproductive biology	Lake Superior tributaries	Trap	Rainbow trout, longnose sucker (<i>Catostomus catostomus</i>), white sucker, rainbow smelt (<i>Osmerus mordax</i>)
Kocik and Taylor, 1987	Diet and trophic niche	Lake Huron	Angling	Pink salmon
Kusnierz et al., 2009	Reproductive biology	Hurricane River, Michigan	PIT tags	Brook trout
Ohio Division of Wildlife, 2009	Reproductive biology	Lake Erie	Radio telemetry	Walleye
Ohio Division of Wildlife, 2008	Reproductive biology, habitat use	Lake Erie	Radio telemetry	Smallmouth bass, walleye
Ohio Division of Wildlife, 2007	Reproductive biology	Lake Erie	Radio telemetry	Walleye
Lallaman et al., 2008	Reproductive biology	Manistee River, Michigan	Mark-recapture	Lake sturgeon
Loftus, 1958	Reproductive biology	Lake Erie	Mark-recapture	Lake trout
Lonzarich et al., 2009	Environmental relations and disturbance	Onion River, Wisconsin	Snorkel Surveys	Coho salmon
Lord, 2007	Reproductive biology, habitat use	St. Clair River, Michigan	Acoustic telemetry	Lake sturgeon
MacCrimmon and Gordon, 1981	Environmental relations and disturbance	Lake Erie	Mark-recapture	Coho salmon, rainbow trout, brown trout
MacLean and Teleki, 1977	Habitat use	Lake Erie	Mark-recapture	Rock bass (<i>Ambloplites rupestris</i>)
MacLean et al., 1982	Environmental relations and disturbance	Lake Erie	Acoustic telemetry	Smallmouth bass, rock bass, yellow perch
Mandrak et al., in preparation	Habitat use	Beaver Creek, Ontario; Niagara River region	PIT tags, mark-recapture, radio telemetry	Grass pickerel (<i>Esox americanus vermiculatus</i>)
McGrath et al., 2003a	Technique	St. Lawrence River, New York	Acoustic telemetry, hydroacoustics	American eel (<i>Anguilla rostrata</i>)
McGrath et al., 2003b	Barriers and fish passage	St. Lawrence River, New York	PIT tags	American eel
McKinley et al., 2000	Environmental relations and disturbance	Lake Erie	Radio telemetry	Smallmouth Bass
Moore et al., 1974	Invasive species	St. Mary's River, Michigan; Lake Michigan; Lake Huron	Mark-recapture	Sea lamprey
Mraz, 1952	Reproductive biology	Lake Michigan	Mark-recapture	Yellow perch
Mucha and Mackereth, 2008	Habitat use, reproductive biology	Lake Superior	Radio telemetry	Brook trout
Murchie and Smokorowski, 2004	Environmental relations and disturbance	Magpie River, Ontario	Radio telemetry	Walleye
Nettles et al., 1987	Habitat use, reproductive biology	Lake Ontario	Radio telemetry	Brown trout
Newman et al., 1999	Habitat use	Lake Superior	Radio telemetry	Brook trout
Noltie, 1990	Reproductive biology, environmental relations and disturbance	Carp River, Ontario; Lake Superior	Mark-recapture	Pink salmon
Porto et al., 1999	Invasive species, barriers and fish passage	Lake Ontario	Mark-recapture	Various ($n = 42$)
Pratt et al., 2009	Barriers and fish passage	Big Carp River, Ontario	PIT tags	Rainbow trout, white sucker, rock bass
Pycha and King, 1967	Stocking	Lake Superior	Mark-recapture	Lake trout
Pycha et al., 1965	Stocking	Lake Superior	Mark-recapture	Lake trout

Table 2 (continued)

Reference	Research topic(s)	Study site(s)	Technique(s)	Specie(s)
Rahrer, 1968	Reproductive biology	Lake Superior	Mark-recapture	Lake trout
Ray and Corkum, 2001	Invasive species, habitat use	Lake Erie	Mark-recapture	Round goby
Romberg et al., 1974	Environmental relations and disturbance	Lake Huron, Lake Michigan	Mark-recapture	Brown trout, rainbow trout, lake trout, brook trout, chinook salmon coho salmon, common carp
Rybicki and Keller, 1978	Reproductive biology	Lake Michigan	Mark-recapture	Lake trout
Savitz and Treat, 2007	Reproductive biology	Lake Michigan	Radio telemetry	Smallmouth bass, largemouth bass (<i>Micropterus salmoides</i>)
Schmalz et al., 2002	Stocking	Lake Michigan	Mark-recapture	Lake trout
Schreer and Cooke, 2002	Environmental relations and disturbance	Lake Erie	Radio telemetry	Smallmouth bass
Smith and Elliott, 1953	Invasive species, reproductive biology	Lake Huron; Lake Michigan	Mark-recapture	Sea lamprey
Stockwell et al., 2010	Diet and trophic niche	Lake Superior	Hydroacoustics	Cisco (<i>Coregonus artedii</i>), kiyi (<i>Coregonus kiyi</i>)
Swanson, 1973	Reproductive biology, stocking	Lake Superior	Mark-recapture	Lake trout
Tewinkel and Fleischer, 1999	Diet and trophic niche	Lake Michigan	Hydroacoustics	Bloater (<i>Coregonus hoyi</i>)
Thompson, 2009	Habitat use	Lake Erie	Radio telemetry	Walleye
Todd and Haas, 1993	Stocking	Lake Erie; Lake St. Clair	Mark-recapture	Walleye
Wang et al., 2007	Stocking	Lake Erie; Lake St. Clair	Mark-recapture	Walleye
Wenger, 1982	Reproductive biology	Lake Erie	Radio telemetry	Brown trout, rainbow trout, coho salmon, chinook salmon
Wenger et al., 1985	Stocking	Lake Erie	Radio telemetry	Brown trout, rainbow trout
Whitledge, 2009	Technique	Lake Michigan	Otolith Microchemistry/Isotope Analysis	Does not describe
Wolfe and Marsden, 1988	Invasive species	Lake Michigan	Mark-recapture	Round goby
Wolfert, 1963	Reproductive biology	Lake Erie	Mark-recapture	Walleye
Wolfert and Vanmeter, 1978	Stocking	Lake Erie	Mark-recapture	Walleye
Workman et al., 2002	Technique, environmental relations and disturbance	St. Joseph River and Pere Marquette River, Michigan	Radio telemetry	Steelhead
Workman et al., 1999	Reproductive biology, environmental relations and disturbance	Pere Marquette River, Michigan	Radio telemetry	Longnose sucker, steelhead

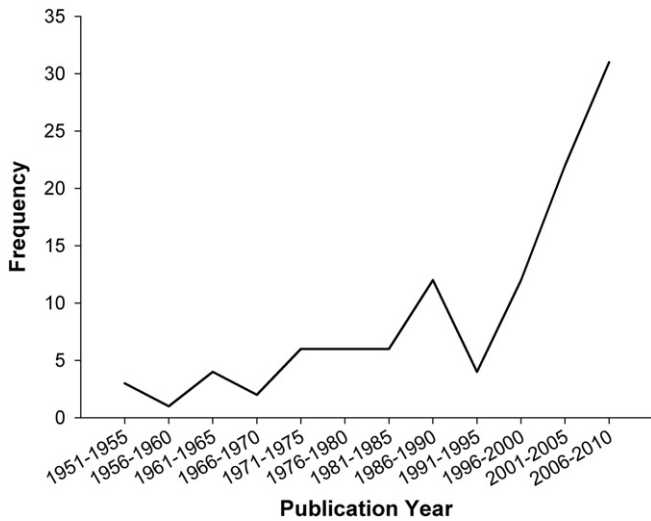


Fig. 1. The number of studies examining movements of Great Lakes fishes annually since 1951 to 1 March 2010. Each point represents the total number of studies for a given 4-year interval.

2009). In this case, mark-recapture may be advantageous over other telemetry methods because of the ability to tag smaller individuals (Caroffino et al., 2009). Mark-recapture techniques were used to show that large (i.e., >8 in.) Yellow Perch (*Perca flavescens*), important to Lake Michigan commercial fishermen, left spawning areas soon after spawning (Mraz, 1952). Long-term mark-recapture studies have been used to address both issues of dispersal (Rahrer, 1968) and migrations to and from spawning sites (Hansen and Stauffer, 1971; Auer, 1999; Baker, 2006). Savitz and Treat (2007) used radio telemetry to determine where Lake Michigan Smallmouth Bass (*Micropterus dolomieu*) move following spawning. For adult fishes, spawning movements (Smallmouth Bass, Savitz and Treat, 2007; Brown Trout (*Salmo trutta*), Haynes and Nettles, 1983; Walleye, Ohio Division of Wildlife, 2007, 2008, 2009) as well as pre- and post-spawn movements (Haynes and Nettles, 1983; Ohio Division of Wildlife, 2007, 2008, 2009) were assessed using radio telemetry. Acoustic telemetry

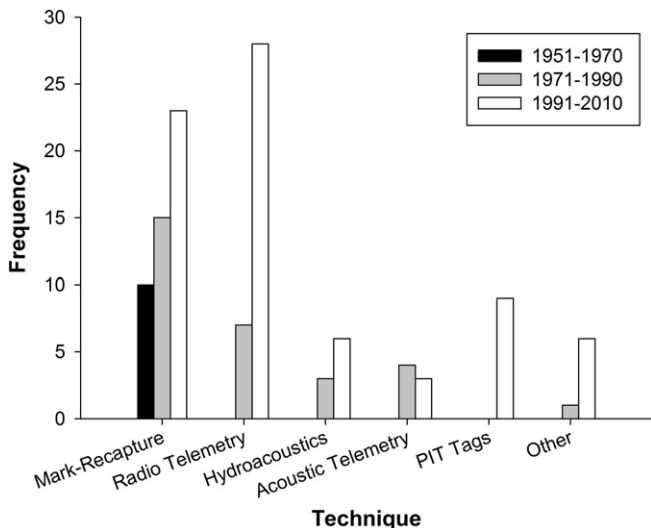


Fig. 2. Frequency of the techniques used to evaluate movements of Great Lakes fishes and the change in frequency over every 20 year period from 1952 through 2010. The category “other” consists of the following methods: otolith microchemistry/isotope analysis, snorkel surveys, traps, gill nets, and angling.

Table 3

Number and percentage of fish movement studies researching select species in the Laurentian Great Lakes and surrounding tributaries.

Species	Number of studies	Percentage of studies
Lake Trout (<i>Salvelinus namaycush</i>)	17	15.2
Walleye (<i>Sander vitreus</i>)	16	14.3
Lake Sturgeon (<i>Acipenser fulvescens</i>)	15	13.4
Rainbow Trout (<i>Oncorhynchus mykiss</i>)	11	9.8
Smallmouth Bass (<i>Micropterus dolomieu</i>)	9	8.0
Brown Trout (<i>Salmo trutta</i>)	8	7.1
Sea Lamprey (<i>Petromyzon marinus</i>)	8	7.1
Chinook Salmon (<i>Oncorhynchus tshawytscha</i>)	7	6.3
Coho Salmon (<i>Oncorhynchus kisutch</i>)	7	6.3
Yellow Perch (<i>Perca flavescens</i>)	7	6.3
Brook Trout (<i>Salvelinus fontinalis</i>)	6	5.4
Pink Salmon (<i>Oncorhynchus gorbuscha</i>)	4	3.6
Alewife (<i>Alosa pseudoharengus</i>)	3	2.7
Common Carp (<i>Cyprinus carpio</i>)	3	2.7
Longnose Sucker (<i>Catostomus catostomus</i>)	3	2.7
Round Goby (<i>Neogobius melanostomus</i>)	3	2.7
White Sucker (<i>Catostomus commersoni</i>)	3	2.7
Rock Bass (<i>Ambloplites rupestris</i>)	3	2.7
Steelhead	2	1.8
Northern Pike (<i>Esox lucius</i>)	2	1.8
Atlantic Salmon (<i>Salmo salar</i>)	2	1.8
American Eel (<i>Anguilla rostrata</i>)	2	1.8
Brown Bullhead (<i>Ameiurus nebulosus</i>)	2	1.8
Deepwater Ciscoes (<i>Coregonus</i> spp.)	2	1.8
Channel Catfish (<i>Ictalurus punctatus</i>)	1	0.9
Grass Pickerel (<i>Esox americanus vermiculatus</i>)	1	0.9
Kiyi (<i>Coregonus kiyi</i>)	1	0.9
Bloater (<i>Coregonus hoyi</i>)	1	0.9
Creek Chub (<i>Semotilus atromaculatus</i>)	1	0.9
Loggerperch (<i>Percina caprodes</i>)	1	0.9
Burbot (<i>Lota lota</i>)	1	0.9
Northern Hog Sucker (<i>Hypentelium nigricans</i>)	1	0.9
Rainbow Smelt (<i>Osmerus mordax</i>)	1	0.9
Spotted Gar (<i>Lepisosteus oculatus</i>)	1	0.9
Common Shiner (<i>Notropis cornutus</i>)	1	0.9
Largemouth Bass (<i>Micropterus salmoides</i>)	1	0.9

was used to demonstrate that movement of post-spawn Rainbow Trout (*Oncorhynchus mykiss*) in Batchwana Bay, Lake Superior, was minimal from spawning streams and that movements were often confined to shorelines (Kelso and Kwain, 1984).

Another approach to rehabilitating stocks, particularly Lake Sturgeon, is to identify spawning sites in the Great Lakes. For example, Fortin et al. (1993) studied Lake Sturgeon on three fluvial lakes of the St. Lawrence (Lac St. Pierre and Lac St. Louis) and Ottawa Rivers (Lac des Deux Montagnes) in Quebec, Canada, and used mark-recapture techniques to identify the spawning grounds located between the two rivers. Friday (2004, 2005, 2006, and 2007) confirmed that areas beneath Kakabeka Falls on the Kaministiquia River, Ontario were being used as spawning sites after radio tracking adults and observing larval drift. Finally, acoustic telemetry helped researchers reveal spawning grounds near Zug Island in the Detroit River, with additional movements indicating other potential but unverified sites (Caswell et al., 2004).

Identification of spawning sites has also been conducted for other species. For instance, river-spawning Lake Trout were marked and recaptured in a tributary of Lake Superior (Montreal River, Ontario) and were shown to return annually to this site to spawn (Loftus, 1958). Spawning sites were identified for Walleyes (Felder, 2002; Ohio Division of Wildlife, 2007, 2008, 2009) and Brook Trout (*Salvelinus fontinalis*; Mucha and Mackereth, 2008) to improve rehabilitation efforts following population declines. A 6-year mark-recapture study of Lake Michigan Yellow Perch was conducted to identify spawning areas and the amount of mixing occurring at these locations (Glover et al., 2008). Lake Erie fisheries managers will make

similar efforts to identify locations and habitat characteristics of spawning Walleye (Einhouse, 2008). Although both biotelemetry and mark-recapture have a range of advantages and disadvantages (see Lucas and Baras, 2000), biotelemetry allows users to make precise spatial localizations of fishes that recapture data may not provide users and may further be advantageous because mark-recapture methods cannot be used to continuously monitor movements.

Knowledge of migratory spawning behavior has been necessary for guiding management practices for a variety of species and enhancing our knowledge of a particular species' ecology. For example, understanding the migratory movements of fishes through proposed fishway locations is of importance to biologists and managers whose goal is to increase recruitment or rehabilitate stocks by improving connectivity (Workman et al., 2002; Bunt et al., 2000). Coaster Brook Trout migratory movements are an aspect of this species' ecology that is poorly understood, but PIT tagging efforts revealed peak activity occurring in October and again in late spring and early summer (Kusnierz et al., 2009). Migratory movements can also be used to improve fisheries regulations as demonstrated by Huckins and Baker (2008) where a combination of population estimates and movements of coaster Brook Trout indicated that current harvest rates were unsustainable. Wenger (1982) advocated enhancing the fall season salmonid fishery to increase angling opportunities after determining salmonid movements made them accessible to anglers. The migratory characteristics (e.g., group size, speed, and timing) and individual traits (e.g., length, weight, condition) of Walleye (Ferguson and Derksen, 1971), Pink Salmon (*Oncorhynchus gorbuscha*; Noltie, 1990; Kennedy et al., 2005), and Lake Sturgeon (Lallaman et al., 2008) have also been studied to further the understanding of these three species' reproductive biology. Lastly, studying the behavior of Sea Lamprey during the spawning migration using radio telemetry (Kelso and Gardner, 2000), mark-recapture methods (Smith and Elliott, 1953), and observation (Klingler et al., 2003) has helped inform and provide the necessary information for revising control programs (see Invasive Species section).

Determining homing movements in fishes is useful for adjusting stocking regimes, identifying potential spawning sites, or altering control programs for species such as Sea Lampreys. For example, the large number of recaptures and sedentary behavior of Northern Pike (*Esox lucius*) suggested evidence of homing during the spawning season and an inability to cope with the warm, less oxygenated waters of southern Lake Erie (Clark, 1990). The author used these data to implement a selective breeding program in an effort to identify and exploit a new strain of Northern Pike best suited for these waters (Clark, 1990). For Lake Trout, Swanson (1973) revealed that unlike native trout, hatchery-reared fish do not have distinct site selection abilities and can potentially fail to propagate. Lake Trout (Rybicki and Keller, 1978) and Walleye (Crowe, 1962) were marked and released in Lake Michigan and found to return to their stocking site (Rybicki and Keller, 1978) or spawning grounds (Crowe, 1962) during subsequent spawning seasons. Finally, Bergstedt and Seelye (1995) used coded wire tags to determine that homing behavior was not exhibited by Sea Lampreys from Lake Huron tributaries. Instead, Sea Lampreys appear to respond to olfactory cues which, if identified, could be manipulated to enhance control programs (Li et al., 2007).

Advances in telemetry tools have allowed researchers to compile fine-scale behavioral and activity data. For example, Cooke et al. (2003) used electromyogram (EMG) telemetry to determine the diel parental care activity and instantaneous swimming speeds of nesting male Smallmouth Bass in a thermal effluent canal at Lake Erie's Nanticoke Generating Station, Ontario. Binder and McDonald (2007) conducted an experiment using PIT tags and radio telemetry to evaluate the role of vision on the spawning migration of Sea Lamprey and found no differences in activity or movement rates between blind and fully-sighted (control) individuals.

Environmental relations and disturbances

Fish movement is often overlooked as a component of environmental monitoring. Environmental disturbances—natural (e.g., seasonal flooding, drought) or anthropogenic (e.g., power plant discharge, barriers to fish movement)—have the potential to affect fish movement, which could lead to long-term population level effects. Most studies assessing the effects of environmental relations and disturbances on fish movement in the Great Lakes were conducted on small-scales in localized systems (e.g., discharge canals), allowing for detailed behavioral assessments of individuals or populations. These studies have used EMG (Cooke and Schreer, 2003; Cooke et al., 2003; Murchie and Smokorowski, 2004), radio (e.g., Haynes et al., 1986; Cooke and McKinley, 1999; Workman et al., 2002; McKinley et al., 2000; Cooke et al., 2000; Schreer and Cooke, 2002) and acoustic telemetries (e.g., MacLean et al., 1982; Kelso, 1974, 1976), and observational surveys (Lonzarich et al., 2009). Studies assessing fish movement in response to long-term environmental changes or whole-lake disturbances are rare and often focus on basic fish biology, such as thermal tolerances, rather than behavioral changes in relation to environmental variables and disturbances.

The behavior of fish that migrate to and from Great Lakes tributaries can be influenced by stochastic environmental conditions. For example, Lonzarich et al. (2009) found that changes in abundance and movement patterns in juvenile Coho Salmon (*Oncorhynchus kisutch*) were highly correlated with summer flood events. Fish can also be affected by environmental conditions where flooding events are artificially manipulated, such as in Great Lakes tributaries that are regulated for flood control and power generation. Following manipulation of flow regimes on the Kaministiquia River, Ontario, the distance traveled by Lake Sturgeon migrating to spawning grounds was dependent on flow conditions and, overall, individuals were able to spawn regardless of flow (Friday, 2004, 2005, 2006, and 2007). Increased discharge rates (i.e., flow) were shown to increase the speed of upstream migration for salmonids (MacCrimmon and Gordon, 1981). In addition, Noltie (1990) found the effects of discharge rates, wind-generated turbulence, and water temperature on the migratory behavior of Pink Salmon varied between seasons and with sex, but the overall reproductive ecology of Pink Salmon paralleled anadromous populations.

Special attention has focused on power generating station operations and their influence on fish movement. Several generating stations exist in the Great Lakes but most research has been conducted in the discharge canal of the Nanticoke Thermal Generating Station, Lake Erie. Numerous fish populations have been studied to understand the effect of thermal discharge on activity and movement (Kelso, 1974; MacLean et al., 1982; Cooke and Schreer, 2003; Cooke et al., 2004), residency (Cooke and McKinley, 1999; Cooke et al., 2000) and reproductive activities (McKinley et al., 2000; Cooke et al., 2003). Research by Cooke et al. (2003 and 2004) and McKinley et al. (2000) on Smallmouth Bass revealed atypical behavior whereby nesting males vacated the canal once offspring reached the free-swimming fry stage (i.e., reproductive success) and over-winter residents did not return to reproduce in the spring. For other species (e.g., Channel Catfish [*Ictalurus punctatus*], Common Carp [*Cyprinus Carpio*]) within the canal, activity is minimally influenced by discharge rates because they mostly reside in areas away from the discharge canal (Cooke and McKinley 1999; Cooke et al., 2000). Similarly, fish encountering abnormally high water temperatures from a nuclear power plant's thermal discharge were later recaptured in high numbers outside of the discharge location, indicating little effect on migratory behavior (Romberg et al. 1974).

With global environmental disturbances such as climate change, there have been concerns about how fishes react to climatic fluctuation. After radio-tagging 28 adult Steelhead, Workman et al. (2002) created a model to demonstrate that increasing water

temperatures corresponded to increased upstream migratory movement, which has implications for predicting how other migratory species respond to atypical seasonal temperatures. Fluctuations in seasonal or annual temperatures (Haynes and Keleher, 1986; Bergstedt and O’Gorman, 1989) and lake-wide temperature stratifications (Brant, 1980) have been shown to affect fish movement within the Great Lakes and should be considered in the context of global climate change.

Stocking

This section illustrates the use of movement information to assess stocking success, strategies, and to delineate stock structures. For decades, fisheries biologists and managers have evaluated strategies for fish stocking and introduction. Stocking programs can create new fisheries, enhance or supplement existing stocks where recruitment is poor, rehabilitate over-exploited and depleted stocks, and mitigate effects of an activity on the productivity of a fishery.

Post-stocking survival of hatchery-reared fish is a primary indicator of stocking success. Conventionally, movement and recapture data have been used to assess optimal age and size to release stocked fish (Pycha and King, 1967; Behmer et al., 1993), identify appropriate seasons to plant fish (Buettner, 1961; Hansen and Stauffer, 1971; Elrod, 1987), assess the most appropriate genetic strain (Elrod, 1987; Elrod and Schneider, 1987), and employ tagging methods that ensure the greatest degree of stock survivability (Buettner, 1961; Behmer et al., 1993). Based on recaptures from recreational anglers, Behmer et al. (1993) suggested that stocking of Atlantic Salmon (*Salmo salar*) in the St. Marys River should occur in early June and at the largest size. Recapture data can also be incorporated into models to generate movement, survival, mortality, and abundance estimates (Fielder and Thomas, 2006; Glover et al., 2008; Haas et al., 1988). After marking Lake Trout with a variety of methods, Elrod et al. (1996) identified their geographical distribution in Lake Ontario and conducted genetic analyses for concentrations of Lake Trout found near stocking locations. It was determined that using pre-adapted genetic strains matched to a particular environmental condition (i.e., environmental matching) should be used as a stocking strategy (Elrod et al., 1996).

Mark-recapture techniques have been the basis for lake-wide mass marking programs in the Great Lakes. These mark-recapture data have been used widely to investigate the distribution and dispersal of hatchery-reared fish (Pycha et al., 1965; Schmalz et al., 2002). Information about when and where fish leave and return to stocking locations can help determine their contributions to respective fisheries and populations (Pycha and King, 1967; Swanson, 1973; Elrod et al., 1996; Schmalz et al., 2002). For example, Pycha et al. (1965) investigated the vertical distribution, dispersal, and return of hatchery-reared Lake Trout and found that neither shore nor boat stocking in inshore waters is effective for stocking offshore areas and that lake currents play an important role in fish dispersal. More recently, Schmalz et al. (2002) estimated Lake Trout movements using mark-recapture techniques and found that although stocking increased the number of Lake Trout, stocking may not increase the local population density because stocking densities influence dispersal.

Stock enhancement can be used to create or supplement fisheries and to rehabilitate populations of native species. For instance, identifying spawning migrations using mark-recapture has been shown to aid fisheries managers in determining stocking locations for hatchery-reared fishes and to enhance stocks where natural reproduction of wild stocks are poorly established (Hansen and Stauffer, 1971; Haynes and Nettles, 1983). Moreover, seasonal movements have been studied to determine dispersal of Chinook Salmon (*Oncorhynchus tshawytscha*; Adlerstein et al., 2007a) and Lake Trout (Adlerstein et al., 2007b). For example, Adlerstein et al.

(2008) revealed that Chinook Salmon movements correspond with increasing water temperature and prey distribution, but because these variables can change across jurisdictions, management initiatives should account for these factors. Although mark-recapture methods are a popular technique of estimating the contribution of stocked individuals to the population, radio telemetry has also been used to assess the contribution of stocked Brown Trout to fisheries in Lake Erie (Wenger et al., 1985) and Lake Ontario (Nettles et al., 1987). Oxytetracycline (OTC) is a less common method of marking fish and has been used by Fielder (2002) and Fielder and Thomas (2006) to help determine the recruitment of locally produced Walleye populations in Saginaw Bay, Lake Erie. Fielder (2002) used OTC to mark hatchery-reared Walleye and found that 79% of individuals contributed to the local population, indicating successful stock enhancement. Fielder and Thomas (2006) also used OTC and demonstrated that the majority of hatchery-reared Walleye spawning in the Tittabawassee River, Michigan remained in Saginaw Bay.

Traditionally, stocked fish have been treated and managed as distinct units. Migration patterns, however, have indicated trans-jurisdictional movements of hatchery-reared Lake Trout (Swanson, 1973; Elrod, 1987), Yellow Perch (Glover et al., 2008), and Chinook Salmon (Adlerstein et al., 2008). Therefore, understanding the spatial and temporal distribution of stocked fishes can help identify management zones (Schmalz et al., 2002). Stock mixing has been made evident by spawning migrations and inter-lake movements of Yellow Perch in the southern basin of Lake Michigan (Glover et al., 2008) and Walleye from Lake Erie, Lake St. Clair, and southern Lake Huron (Ferguson and Derksen, 1971; Wolfert and Vanmeter, 1978; Haas et al., 1988; Todd and Haas, 1993; Wang et al., 2007). Todd and Haas (1993) combined mark-recapture data with genetic analysis to determine the movement of Walleye stocks between Lakes Erie and St. Clair. The stock delineation demonstrated that genetic heterogeneity within each lake was sufficiently low enough to justify treating the population as a single unit, but that stocks between Lakes Erie and St. Clair were genetically distinct and should be managed separately (Todd and Haas, 1993). Glover et al. (2008) provided evidence of Yellow Perch straying from spawning sites and mixing throughout the southern basin of Lake Michigan which suggests potential increased gene flow. Furthermore, Glover et al. (2008) suggested that because movement of Yellow Perch is currently overlapping management boundaries in Lake Michigan, managers from adjacent jurisdictions should consider management boundaries that are complementary to movement ranges and patterns.

Identification of critical habitats and habitat use

Management efforts of both marine and freshwater fishes often characterize and identify critical habitats such as juvenile nursery areas or breeding/spawning grounds. Loss of habitat is recognized as one of the leading causes of imperiled fish stocks (e.g., Warren and Burr, 1994). Rehabilitation efforts, control programs, and fisheries enhancement plans could potentially benefit from the identification of critical habitats and the usage of these habitats by various species.

Most research in this area has been conducted on Lake Sturgeon and some of these investigations have demonstrated that habitat loss, coupled with overharvest and the introduction of invasive species can lead to population declines in the Great Lakes (Holtgren and Auer, 2004; Lord, 2007). Commonly reported issues for Lake Sturgeon include identifying Lake Sturgeon nursery habitats and their characteristics (Benson et al., 2005), protecting adult Lake Sturgeon migration corridors and spawning grounds (Auer, 1999; Fortin et al., 1993), and locating young-of-year (Fortin et al., 1993) and tributary habitats (Friday, unpublished).

Fish movement has also been used to identify critical habitats for species with conservation designations (Glass et al., In Preparation; Mandrak et al., in preparation), of special concern (Newman et al.,

1999; Mucha and Mackereth, 2008), and invasives (Kelso and Gardner, 2000; Ray and Corkum, 2001; Binder and McDonald, 2007; see also Invasive Species section). In Nipigon Bay, Lake Superior, radio telemetry was used to show that lake and stream habitats used by coaster Brook Trout during the reproductive and non-reproductive seasons require protection if rehabilitation of this unique strain of Brook Trout is to be successful (Mucha and Mackereth 2008). Recently, Glass et al. (in preparation) used radio telemetry to demonstrate that Spotted Gar (*Lepisosteus oculatus*) appear to prefer habitats with complex macrophytes including areas with more than one species of macrophyte present. Another recent study developed a habitat supply model to identify changes in available habitat and the effects on Grass Pickerel (*Esox americanus vermiculatus*) populations to assess and mitigate impacts of agricultural drain maintenance on fish communities connected to the Great Lakes (Mandrak et al., in preparation).

Identification of fish habitat also has applications in the management of other commercially and recreationally important fish species in the Great Lakes. Sex-specific habitat preferences and spawning habitat requirements of Lake Erie Walleye were determined using radio telemetry (Ohio Division of Wildlife, 2008; Thompson, 2009). More specifically, for example, males were more often found over gravel and cobble substrates compared to females, which may indicate that males begin staging in spawning areas before females arrive onto the spawning grounds (Thompson, 2009). Mark-recapture techniques were used to demonstrate the importance of potential Rock Bass (*Ambloplites rupestris*) nursery habitat in the Inner Bay of Long Point Bay, Lake Erie (MacLean and Teleki, 1977). Thermal habitat use by salmonids was quantified from radio-tagged individuals in Lake Ontario and found to be similar to those from other large waterbodies (Haynes and Gerber, 1989). Given the general failure of Brown Trout to reproduce naturally in Lake Ontario and the lack of information on the subject, Nettles et al. (1987) revealed Brown Trout occupied near-shore habitats within the thermocline region, indicating that Great Lakes salmonids may partition among available habitats. The authors recommended future research into habitat partitioning would help ensure the sustainability of Great Lakes salmonids.

Invasive species

Understanding the distribution and movement of invasive fishes is central to guiding their management and/or control in the Great Lakes. Although many invasive fishes of the Great Lakes have the capacity to alter and disrupt native fish communities, the literature identified in this review focuses on Sea Lamprey, Alewife (*Alosa pseudoharengus*), and Round Goby (*Neogobius melanostomus*).

One of the objectives under which the Great Lakes Fishery Commission is to develop and deliver a control program for Sea Lamprey control (Selak, 1956). To date, Sea Lamprey research includes detailing the migrations of parasitic phase Sea Lamprey (Moore et al., 1974; Smith and Elliott, 1953; Bergstedt and Seelye 1995; Kelso and Gardner, 2000), the effects of barriers to lamprey movement (Porto et al., 1999), spawning interactions (Kelso et al., 2001), estimates of abundance (Bergstedt et al., 2003), and migration physiology (Binder and McDonald, 2007). For example, Kelso et al. (2001) attached radio-transmitters externally to sterilized and fertile male Sea Lampreys to demonstrate interactions between individuals, competitiveness, and spawning activity for both types of male. Their data suggested that sterile males did not exhibit suppressed reproductive behaviors and that sterilization may be a worthwhile control method.

Alewives were first captured in Lake Ontario in 1873 and caused major ecosystem imbalances throughout the Great Lakes as they spread (Smith, 1970). Despite being an important source of food for salmonids, Alewives also alter the zooplankton forage base (Brooks, 1968), and out-compete native fishes (Smith, 1970). Most movement-based literature for Great Lakes Alewives has used hydroacoustics to

describe vertical migrations and feeding ecology (Janssen and Brandt, 1980), thermal distribution (Bergstedt and O'Gorman, 1989; Brant, 1980) and age segregation (Brant, 1980), but recently early-life movements were quantified using otolith microchemistry/isotope analysis (Dufour et al., 2005).

The discovery of Round Goby in the Great Lakes in the early 1990s led to a concerted effort among academic and government agencies to determine their effects on the native fish assemblage and its potential to spread throughout the Great Lakes and inland waters. The species' small size limits the effectiveness of mark-recapture techniques. Goby movement has been assessed using underwater observation to provide home range estimates (Ray and Corkum, 2001). In addition, external tags, dyes/paint, and PIT tags have been used both to record movement and examine the effectiveness of the method itself (Wolfe and Marsden 1998; Cookingham and Ruetz, 2008).

Our review revealed that relatively little attention has been given to studying the movements of invasive fish species. More specifically, we found no evidence of movement studies for some established invaders such as White Perch (*Morone americana*) and Eurasian Ruffe (*Gymnocephalus cernuus*; Mills et al., 1994). With the looming threat of Asian Carp (i.e., Silver Carp [*Hypophthalmichthys molitrix*] and Bighead Carp [*Hypophthalmichthys nobilis*]) reaching the Great Lakes and the continued range expansion of established invasives, future studies examining the movements of potential invaders and those that are already established could benefit management of Great Lakes fisheries. Based on our review, the research completed on Sea Lamprey has shown that studying movements of invasive species can help develop a more thorough understanding of their ecology and guide management or control programs.

Techniques for quantifying movement

Validating and improving techniques to study fish movement, address management issues, and further knowledge of fish ecology and behavior was another research topic area identified in the literature. For example, Eschemeyer et al. (1953) compared return rates of four tag types—Petersen, streamer, monel upper-jaw, and aluminum lower-jaw tags—for marking native Lake Trout in Lake Superior and found that Petersen tags had the highest return rate. Eschemeyer et al. (1953) and Buettner (1961) caution against, however, using Petersen tags as the pins projecting from the tags cause entanglement of fish and death among smaller-sized fish, despite high recovery rates. More recently, Cookingham and Ruetz (2008) used Round Gobies implanted with PIT tags and found 100% tag retention for 28 days, suggesting that PIT tags are suitable for individually marking Round Gobies at least over short-term periods.

Combining research techniques such as mapping and modeling with tracking technologies can help improve fishway design and predict migration patterns in relation to changing environmental variables. For example, a hydrosonic telemetry system was tested to continually map the position of American Eels (*Anguilla rostrata*) in the forebay of the Moses-Saunders Power Dam on the St. Lawrence River, New York and results indicated that 3-dimensional mapping of American Eel movements is a possibility (McGrath et al., 2003a). Workman et al. (2002) combined radio telemetry and camera-count data from a fishway to develop a new approach for analyzing upstream adult Steelhead migration in two Lake Michigan tributaries. This was based on probabilities of environmental cues (i.e., water temperature and stream flow) affecting upstream migration. Workman et al. (2002) suggest that this modeling approach can be used in other Great Lakes tributaries and for additional species whose migration behavior is influenced by water temperature.

Elemental and stable isotope analysis of fish otoliths and scales is an emerging technique used to record environmental histories of fish in the wild, such as their nursery habitat, population structure, and movement (e.g., Brazner et al., 2004; Rooker et al., 2003). Recent work

by Brazner et al. (2004) validated the use of elemental fingerprinting for quantifying movement of Yellow Perch in western Lake Superior. Otolith analysis of age-0 individuals from different coastal wetland nursery areas revealed nursery habitat locations which the authors suggested could be used to quantify the contributions of fish from coastal wetland nursery areas to surrounding lake populations (Brazner et al., 2004). In a multispecies study, Whitledge (2009) examined whether elemental compositions were distinct between Lake Michigan, the upper Illinois River, and three tributaries of the upper Illinois River. The results demonstrated potential applications of otolith microchemistry to determine inter-lake movement and transfer pathways of native and exotic species between the upper Illinois River and Lake Michigan (Whitledge, 2009).

All studies focusing on technique viability have solely quantified horizontal movement. None, however, have addressed how to improve methods of quantifying vertical movement and distribution. Mark-recapture and telemetry (e.g., radio and acoustic telemetry) are widely accepted methods for quantifying fish movement, and the recent advent of otolith microchemistry/isotope analysis presents a potential natural tagging method to improve mark-recapture estimates. Coupling multiple techniques (e.g., mark-recapture and telemetry) to quantify movement should be recognized as an improvement to existing methods and can increase the precision of survivorship and emigration estimates as well as estimates of fishing and natural mortality rates (see Pine et al., 2003).

Diet and trophic niche

When rehabilitating populations of fishes such as Lake Trout, Zimmerman and Krueger (2010) advocate an ecosystem approach that includes considering the diets and trophic niches of species within an ecosystem. Fish movements can inform biologists about diets and the relative position of fishes within the trophic structure (Janssen and Brandt, 1980; Kocik and Taylor, 1987; Tewinkel and Fleischer, 1999; Hrabik et al., 2006; Jensen et al., 2006; Stockwell et al., 2010). Advances in the understanding of trophic interactions and the behavior of Great Lakes fishes have more commonly been conducted on deepwater species. For example, Tewinkel and Fleischer (1999) used midwater trawls coupled with hydroacoustics to show diel vertical migration and the feeding habits of Bloaters (*Coregonus hoyi*) in Lake Michigan, and Jensen et al. (2006) created an energetic cost-benefit analysis for diel vertical migration for Opossum Shrimp (*Mysis relicta*), deep water Ciscoes (*Coregonus* spp.), and Lake Trout that showed the trade-offs between maximizing growth potential and predation risk. Stockwell et al. (2010) followed the diel vertical migration of Cisco (*Coregonus artedii*) and Kiyi (*Coregonus Kiyi*) and demonstrated that there may be a particular size at which Ciscoes are not predated upon.

Barriers and fish passage

In-stream barriers, such as dams, are often purposefully constructed for human needs (e.g., hydroelectric generation, flood control), but they can also be built to prevent the spread of invasive species. Because barriers restrict fish movements, there is concern for fish assemblages and other migratory species using the tributaries that barriers are erected on (Dodd et al., 2003). Harford and McLaughlin (2007) estimated that, after adjusting for non-random effects, an average of 2.4 fewer fish species were found upstream of barriers compared to tributaries without barriers. Understanding the timing and duration of fish movements in tributaries with barriers is vital to ensure that operations of barriers do not have negative effects (Workman et al., 2002). A mark-recapture study conducted by Porto et al. (1999) on four Lake Ontario tributaries compared movements of fishes in streams with and without low-head barriers and found that a significantly lower proportion of fishes moved through barrier streams. Kelso and Noltie

(1990) showed that a low-head barrier on the Carp River, Ontario allowed passage of Coho and Chinook Salmon, but precluded passage by Pink Salmon, although periods of increased flow did increase the probability of barrier passage. Finally, Dolinsek et al. (2008) demonstrated that, in Lake Ontario tributaries containing Sea Lamprey barriers, there is little inter-stream movement of Sea Lamprey and other non-target fishes and little evidence supporting *en masse* movements of fishes to new spawning grounds.

Passage and attraction efficiencies of fishways are other components of barrier research identified in the literature. Bunt et al. (2000) revealed that attraction efficiency of the Denil fishway used in the study was low and that none of the 24 radio-tracked Walleyes in Grand River, Ontario, passed through to successfully reach upstream spawning grounds. Their research highlights the need to increase attraction efficiencies and better pass individuals through the fishway (Bunt et al., 2000). In contrast, Pratt et al. (2009) demonstrated that modifications in compartment size and funnel design increased passage rates from migrating fish species in a vertical slot fishway on Big Carp River, Ontario. Conversely, the authors also found that similar improvements at a nearly identical fishway on Cobourg Brook, Ontario, did not yield increased passage rates because of poor attraction flow at that site (Pratt et al., 2009). Furthermore, PIT tagging efforts conducted by McGrath et al. (2003a) characterized the approaching movements and passage of American Eels at the Moses-Saunders Power Dam located on the St. Lawrence River, New York. Their findings indicate the addition of a second eel ladder would aid in passage efficiency (McGrath et al., 2003a). Continued research is needed to assess which species are most impacted by barriers, how their reproductive success is affected, and what modifications are needed to improve fishway passage efficiency.

Research needs

Members of the Great Lakes Fishery Commission Lake Committees ($N = 14$), primarily chairs and vice-chairs ($N = 8$), were sent a survey to identify the main concerns of Great Lakes management units, compile knowledge gaps within fish movement research in the Great Lakes, and assess the impacts of these research gaps on management. The short survey requested information regarding the organizations with which respondents are associated and the regions within which they work from a fisheries management perspective (Table 4). Participants were also asked to identify management issues of primary concern, research gaps relating to fish movement in the Great Lakes, and the resulting impacts on management goals (Table 4). The survey was used to determine whether the knowledge gaps identified by influential Great Lakes fisheries managers corresponded to those revealed in this review. The authors acknowledge that the survey is relatively coarse-scale and that the respondents do not represent all Great Lakes stakeholders. However, we speculate that the survey represents the collective voice of biologists, managers, and various agencies because of the respondents ($N = 11$), over half of the responses ($N = 6$) came from chairs or vice-chairs of Lake Committees.

Table 4

Survey questions given to Great Lakes fisheries personnel representing a range of agencies and management units. The survey was used to identify knowledge gaps related to movement of Laurentian Great Lakes fishes.

Questions
What organization(s) are you associated with?
What management issues are you primarily concerned with?
What region(s) do you deal with from a fisheries management perspective?
What research gaps relating to fish movement and migration do you believe exist for the Great Lakes?
What impact do these gaps have on your management goals?

Survey responses

Seven respondents identified species-specific research gaps. In particular, managers from Lake Michigan identified a lack of understanding and knowledge in movement and migratory patterns of Yellow Perch, Lake Sturgeon, and salmonids. One respondent suggested that current regulations for species such as Yellow Perch could lead to unsustainable harvest rates. Managers cited the lack of movement information for Lake Sturgeon as a potential hindrance in evaluating and prioritizing dam removal projects. Our review, however, shows Lake Sturgeon as the third most studied species, but none of these studies covered issues related to dam removal projects. In addition, two respondents identified knowledge gaps among various salmonid species. However, 31 species were studied in the papers reviewed here and over 25% ($N=9$) of those species were salmonids comprising 57.1% ($N=64$) of the Great Lakes fish movement studies. With the availability of so many species in the Great Lakes to study, the number of studies conducted on salmonids appears high and indicates an inconsistency between the opinions of managers and what has been published in the literature.

Four respondents, including one Lake Committee chair, identified knowledge gaps existing in our understanding of inter-lake movements, particularly immigration and emigration through lake corridors (e.g., between Lakes Erie and Huron) and the dispersal of stocked fishes from their original stocking locations. From the responses obtained in the survey, along with our findings from the literature review, it is clear that more research is required with regard to fish movements within and between the Great Lakes as well as movements and contributions of different stocks of fishes within fisheries. Our review also indicates that most literature on dispersal from stocking sites has focused on Lake Trout. We agree that expanding research into both inter-lake movements and the dispersal of stocked fishes would benefit Great Lakes fisheries management, particularly when applied to multiple species, issues with trans-jurisdictional movements, and the development of lake- or region-wide harvest regulations or stocking strategies.

Most studies focused on the movements of high profile species such as Lake Trout and Walleye, with relatively few studies examining movements of their forage species. We believe research gaps exist to study movements of forage fishes (e.g., coregonids) within the Great Lakes as movement relates to fish ecology and potential predator-prey interactions. Respondents from the Lake Huron and Lake Superior Committees also advocated the need to fill these research gaps. They emphasized the need for movement data during the non-reproductive periods of offshore forage fish species—particularly Cisco, Bloater, and Kiyi—because they are commercially harvested during this time. Survey respondents felt this information gap could potentially lead to mismanagement of native forage fish stocks, which could disrupt the predator-prey balance and influence the overall fish community structures in the Great Lakes. It is worth noting that maintaining the diversity among such fish communities as the coregonines is important to the overall biodiversity of the Great Lakes; only Lake Superior's coregonine community has maintained its full species complement. With fisheries management beginning to adopt a more holistic, ecosystem-based approach, it has become necessary to understand the biology of fishes located further down the food chain to fulfill this management strategy, particularly when formulating plans to reestablish important species (Zimmerman and Krueger, 2010).

Respondents to our survey expressed concern that the lack of information regarding fish movement could impact the ability of fish managers to place confidence on abundance measurements and understand the role of abiotic and biotic factors on life histories. Other concerns expressed by respondents included a lack of information on the emigration of American Eels, a threatened species that has been affected by barriers and turbine passage, and on movements of

recovering or developing stocks of fishes. Trap and transport programs for American Eels could be developed or improved based on movement information and understanding the movements of recovering stocks of fishes could lead to improved rehabilitation plans. Lastly, one respondent advocated for the development of new, cost efficient technologies to track fish movement and improve our understanding of Great Lakes fish ecology.

Summary and conclusions

Our review has revealed seven key research gaps that warrant further exploration, despite the history of well conducted movement studies to date. Inter-lake movement remains one of the largest research gaps for the Great Lakes fish movement literature. In addition, more information regarding the dispersal of stocked fishes from their original stocking locations was another identified gap. Broadening the species studied to include forage fishes, recovering fish populations, and predator-prey interactions are also research gaps that could be addressed in the future. Further studies on the movement of invasives are warranted as potential Asian Carp introductions threaten ecosystem function within the Great Lakes. Finally, few studies have examined the effect of barriers on fish movements, despite the prevalence of various types of barriers throughout Great Lake tributaries (e.g., Sarakinos and Johnson, 2003; Vélez-Espino et al., 2011).

As the advent of new and more powerful tracking technologies increases, so too will the application of these tools to address research questions such as large-scale movements (both spatial and temporal) and fine-scale behavior of fishes in and around fishways. There is a great need to advance our understanding of Great Lakes fishes and to improve the management of Great Lakes fisheries, especially in the areas of rehabilitation programs for native fishes, recreational fishery enhancement, and control programs for invasive species. Biologgers, acoustic telemetry (including both large-scale arrays to document gross movements and fine-scale arrays to provide detailed information on behavior and activity), hydroacoustics/sonar, and otolith microchemistry/isotope analysis are further expanding our ability to quantify fish movement in the Great Lakes. Biotelemetry and biologging devices can also be equipped with sensors (e.g., temperature, pressure, acceleration, muscle activity) with the potential to provide additional data on the environmental attributes fish encounter as they move (Cooke et al., 2004; Wilson et al., 2008; Rutz and Hays, 2009). There are already several examples of such devices being introduced in movement studies for Great Lakes fishes and great benefits could also arise from combining tools and approaches (see Cooke, 2008). Many of the uncertainties and corresponding challenges surrounding movement are biologically complex and vary in terms of spatial and temporal scale. Nevertheless, the options for tracking fishes are diverse in terms of the information they provide and the spatial and temporal scales at which they operate most effectively.

Unique features of the Great Lakes—geographical extent, geology, species richness, political jurisdictions, stakeholder involvement, and economic value—differentiate these lakes from the majority of other major freshwater systems. These aspects of the Great Lakes make them more similar to marine environments where scale and multi-jurisdictional governance also pose serious challenges to scientific research and successful fisheries management. We now possess the technology to better address issues related to fish movements across large spatial scales (e.g., acoustic telemetry, pop-up satellite transmitters) as well as technology to examine multiple facets of a species' ecology (e.g., biologgers, otolith microchemistry/isotope analysis). Our knowledge of fish movements can contribute significantly to the success or failure of management efforts (Dingle, 1996; Wilcove, 2008). The increased availability and continued improvements in the range and capability of tools to study fish movements offers the

potential to significantly and rapidly advance the science and management of Great Lakes fisheries.

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