STATUS OF WALLEYE IN THE GREAT LAKES: PROCEEDINGS OF THE 2006 SYMPOSIUM

Great Lakes Fishery Commission

TECHNICAL REPORT 69

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March 2010

Status of Walleye in the Great Lakes: Proceedings of the 2006 Symposium

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SPECIAL EDITOR'S FOREWORD AND ACKNOWLEDGMENTS

The case studies presented in this publication provide an update on the status of walleye populations in the Laurentian Great Lakes following Colby et al. (1991) and the proceedings of three international symposia on percid fishes (PERCIS). The papers presented in Colby et al. (1991) were produced as part of a walleye rehabilitation workshop held at the Franz-Theodore Stone Laboratory at Put-in-Bay, Ohio, during June 1990. The first PERCIS symposium was held at the Quetico Center in northwest Ontario, Canada, during 1976 with proceedings published in 1977 in the Journal of the Fisheries Research Board of Canada. The second PERCIS symposium was held in Vaasa, Finland, during August 1995 with proceedings published in Annales Zoologici Fennici the following year. PERCIS III was held in Madison, Wisconsin, during July 2003, and the proceedings of that symposium were published by the University of Wisconsin Sea Grant Institute.

The papers in this volume were presented during a symposium on Great Lakes walleye held at the 136th annual meeting of the American Fisheries Society in Lake Placid, New York, during August 2006. This symposium was organized by Ed Roseman, Patrick Kocovsky, and Chris Vandergoot, who all served as special editors, and was sponsored by the Great Lakes Fishery Commission and the Great Lakes Fishery Trust. Patrick Kocovsky, Chris Vandergoot, and Samantha Fedor moderated the session. The special editors are grateful to the following people who provided reviews of manuscripts: Bo Bunnel, Dave Clapp, J. Randy Jackson, Kevin Kayle, Ruth King, Roger Knight, Jeff Koppelman, Brian Lantry, Ashley Moerke, Rich O'Neal, Lars Rudstam, Jeff Schaeffer, Mike Seider, Wendy Stott, Maureen Walsh, Dave Warner, and Jay Wesley. Randy Eshenroder, Bob O'Gorman, and Jim Peck provided invaluable editorial assistance.

E. Roseman
March 2, 2010

STATUS OF WALLEYE IN LAKE SUPERIOR

Stephen T. Schram, Michael J. Seider[1], Patrick D. Furlong, and Michael J. Friday

Abstract

Walleye (*Sander vitreus*) is a top-level predator but only a small component of the overall Lake Superior fish community. Distribution of walleye is restricted to embayments and tributaries near suitable spawning areas. Walleye abundance in all areas of Lake Superior, with the possible exception of the St. Louis River, remains below historical levels. Rehabilitation strategies need to begin with collections of biological and ecological data from various Lake Superior walleye stocks to identify specific factors limiting recovery. Improving degraded tributary habitat and providing access to historical spawning areas in tributaries will be the key to walleye rehabilitation in Lake Superior.

Introduction

Walleye (*Sander vitreus*) are a small component of the Lake Superior fish community because suitable physical and thermal habitat (Jones et al. 2003; Eshenroder 2004) is absent in much of the lake. Walleye are currently found

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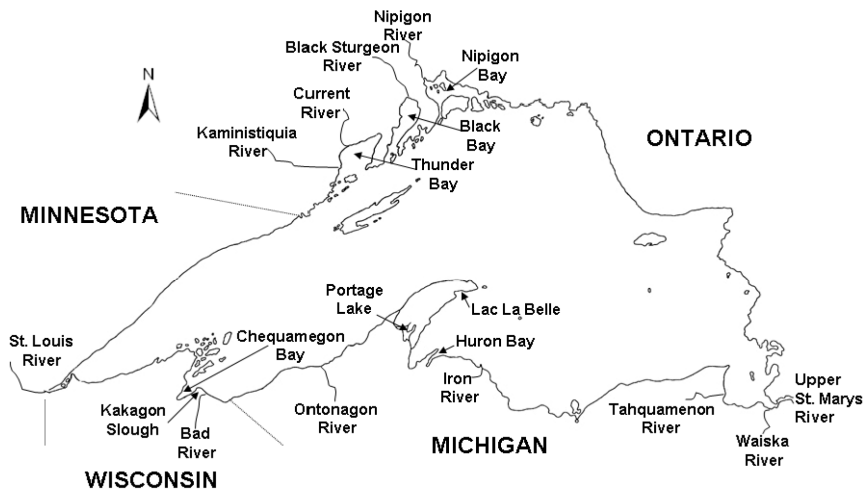
in approximately 79 tributaries and most bays (Horns et al. 2003), and viable populations are primarily associated with large bays and tributaries possessing suitable thermal, spawning, and nursery habitat. Discrete populations of walleye are known to spawn in at least 32 tributaries (Schram 2007). Historically, the largest populations were found in the St. Louis River, Nipigon Bay, and Black Bay (Fig. 1; Schneider and Leach 1979; Horns et al. 2003).

Fig.1. Location of walleye populations in Lake Superior and tributaries referred to in this report.



Walleye populations in U.S. and Canadian waters of Lake Superior once supported widespread commercial fisheries, but current populations support only limited commercial and recreational fisheries. Canadian commercial harvest peaked at 170,000 kg in 1966, whereas the maximum commercial harvest from U.S. waters was the 56,000 kg landed in Minnesota in 1885 (Baldwin et al. 1979). Walleye abundance eventually declined throughout the lake primarily due to overfishing and loss of connectivity to tributary spawning habitat due to dams (Schneider and Leach 1979; Schram et al. 1991). In U.S. waters, the state-licensed commercial fishery has been closed since 1955, but some walleye are still harvested by Native-American commercial and subsistence fisheries. Small commercial quotas are still allowed in specific zones of Canadian waters to allow for marketing of walleye caught incidentally in fisheries for major commercial species. Canadian First Nations walleye subsistence fisheries also occur in discreet areas, but no complete estimates of harvest exist. Lake Superior walleye populations provide recreational fisheries, where permitted, in tributaries, bays, and estuaries.

With the exception of the St. Louis River in U.S. waters, walleye populations in Lake Superior are well below historical abundance. The St. Louis River population is believed to be near historical abundance levels due to conservative fishing regulations enacted following improvements in water quality (Schram et al. 1992). In Canadian waters, Black Bay and Nipigon Bay have small resident populations supported by reproduction in the Black Sturgeon and Nipigon Rivers, respectively. Biological data sufficient to quantify other Lake Superior populations is lacking.

In 1994, the Lake Superior Committee of the Great Lakes Fishery Commission directed the Lake Superior Technical Committee to form a walleye subcommittee. The walleye subcommittee was charged with describing current population status (Hoff 1996) and developing a rehabilitation plan for walleye populations in the lake (Hoff 2003). The rehabilitation plan described the objectives for rehabilitation, identified issues limiting rehabilitation, and developed strategies for rehabilitation of walleye populations in Lake Superior. The 1990 fish-community objectives for Lake Superior (Busiahn 1990) encouraged agencies to re-establish depleted stocks of native species, including walleye. The objectives were revised in 2003 (Horns et al. 2003) to serve as a vision of what the future fish community should look like and to guide lakewide coordinated fishery management (Ebener 2007). The fish-community objective for Lake Superior walleye is to maintain, enhance, and rehabilitate self-sustaining populations of walleye and their habitat over their historical range (Horns et al. 2003). In this manuscript, we:

- Provide an update of the status of major Lake Superior walleye populations since the last status report in 1991 (Schram et al. 1991)
- Describe impediments to rehabilitation success
- Discuss potential walleye rehabilitation strategies

Populations and Status in Canadian Waters

Black Bay

Prior to its collapse in 1966, the walleye population in Black Bay (Fig. 1) supported the largest commercial walleye fishery on Lake Superior, with the majority of the spring harvest occurring near the mouth of the Black Sturgeon River. In addition to over-exploitation (Schneider and Leach 1979; Colby and Nepszy 1981), loss of access to spawning habitat was thought to be a factor in the collapse of the Black Bay population (Furlong et al. 2006). Construction of the Black Sturgeon Dam in 1960, which rendered most spawning habitat in the river inaccessible, was followed seven years later by an abrupt collapse of the population. A few walleye currently inhabit Black Bay, and a small population still exists in the lower river. Ontario Ministry of Natural Resources (OMNR) habitat surveys revealed that historical spawning grounds in the bay and the accessible river spawning habitat currently provide only limited spawning potential. Therefore, the lack of suitable spawning habitat is the major impediment to rehabilitation of this population. Genetic samples from the Black Bay population prior to its collapse and samples collected from fish currently in the Black Sturgeon River, both above and below the dam, indicated the presence of a single genetic population (Wilson et al. 2007), and it is likely that the Black Sturgeon River spawning population sustained most or all of the historical Black Bay population.

Although a zero-possession limit is in effect for the recreational fishery, rehabilitation of the Black Bay walleye population to historical levels cannot be accomplished without removal of the dam on the Black Sturgeon River. However, dam removal would also allow sea lamprey (*Petromyzon marinus*) unrestricted access to the system, and the population of northern brook lamprey (*Ichthyomyzon fossor*), a river resident and species of special concern, would be decimated by lampricides used to control sea lamprey. Management efforts are now under way to address the complex issue of loss of access to historical spawning habitat (Colby and Foster 2001; Petzold 2004; Furlong et al. 2006).

Nipigon Bay

The Nipigon Bay (Fig. 1) walleye population collapsed in the 1960s as a result of paper-mill effluent (Ryder 1968) and over-exploitation (MacCallum and Selgeby 1987). Pulp-mill discharges may have created an anoxic barrier (Ryder 1968) that disrupted walleye spawning migrations from Nipigon Bay to the Nipigon River, but this issue is believed to have been resolved through improved treatment of mill effluents. Eggs, fry, fingerlings, and, most recently, adults have all been stocked in the system as rehabilitation efforts. Based on genetic analysis, walleye collected during fall electrofishing surveys in the lower Nipigon River in 2001 and 2005 were progeny of four of the six source populations stocked into Nipigon Bay and one of unknown ancestry (Wilson et al. 2007). In addition to stocking, a zero-possession limit currently in effect for recreational anglers is also part of the management strategy aimed at rehabilitating walleye in Nipigon Bay.

Thunder Bay

At least two tributaries to Thunder Bay (Fig. 1), the Current and Kaministiquia Rivers, support spawning populations of walleye. Walleye were known to spawn near the mouth of the Current River, and, in 1991, spawning habitat was augmented in several portions of the river to mitigate habitat loss due to dredging in 1984 for dock construction. Estimates of walleye spawning at these sites were made annually during 1991-1993 and 1999-2000. Abundance increased from 1,167 in 1991 to 1,485 in 1993, but too few walleye were captured in 1999 and 2000 for reliable estimates, indicating that abundance had declined. More-recent survey data are lacking, but the long-term effect of the habitat-enhancement project may have been limited. Recent surveys provided evidence of natural reproduction in the Kaministiquia River. Mature walleye were observed spawning just below Kakabeka Falls in May of 2004, 35 km upstream from Thunder Bay, and larval walleye were collected below the falls in 2004 and 2006.

Populations and Status in U.S. Waters

Michigan Populations

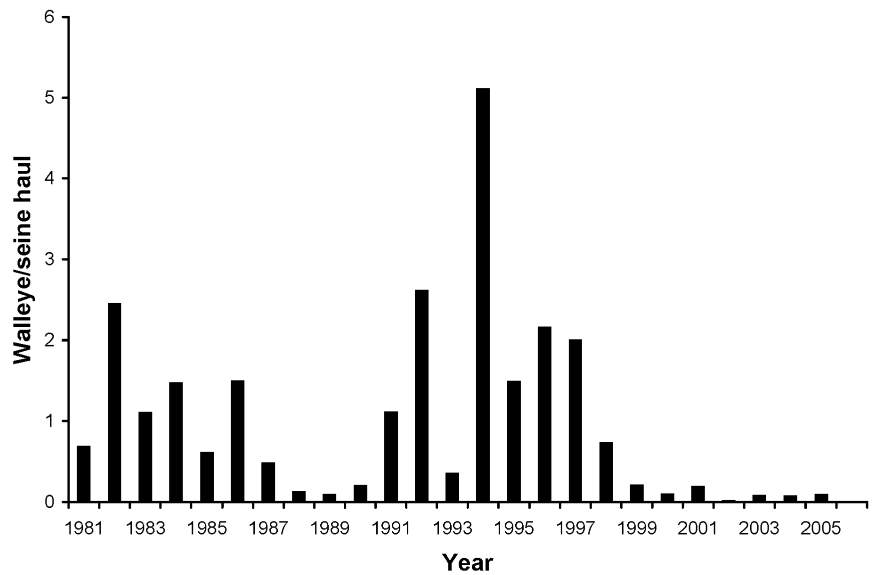
Walleye populations in the Ontonagon River, Huron Bay, Portage Lake, Lac La Belle, and the Tahquamenon River (Fig. 1) are maintained by stocking fingerlings periodically (G. Madison, Michigan Department of Natural Resources and Environment (DNRE), personal communication, 2007). Biological data for most of these populations are lacking, and the degree of natural reproduction is unknown. A spring fishery occurs near the mouth of the Iron River (Fig. 1), but whether these fish spawn in the river is unknown. Fishery and creel surveys were conducted on the Portage Lake population in 2007, and a creel survey was conducted on the Ontonagon River in 2006. Effort amounted to 10,334 angler hours, and 1,947 walleye were harvested from the Ontonagon River in 2006 (G. Madison, Michigan Department of Natural Resources and Environment, personal communication, 2007). The Chippewa/Ottawa Resource Authority (CORA) is evaluating the contributions of stocked fingerlings in the Waiska River area of the Upper St. Marys River (Fig. 1; M. Ebener, CORA, personal communication, 2007).

St. Louis River (Wisconsin/Minnesota)

Wisconsin and Minnesota share jurisdiction and management of a self-sustaining walleye population in the St. Louis River (Fig. 1; Schram et al. 1992). Prior to treatment of domestic and industrial wastes within the St. Louis River watershed in 1978, the fishery was catch and release for at least 80 years due to walleye being unpalatable. Water quality has improved since 1978, and walleye are now harvested in the recreational fishery. The population has been monitored for over two decades using the stock-status indicators suggested by Colby et al. (1994).

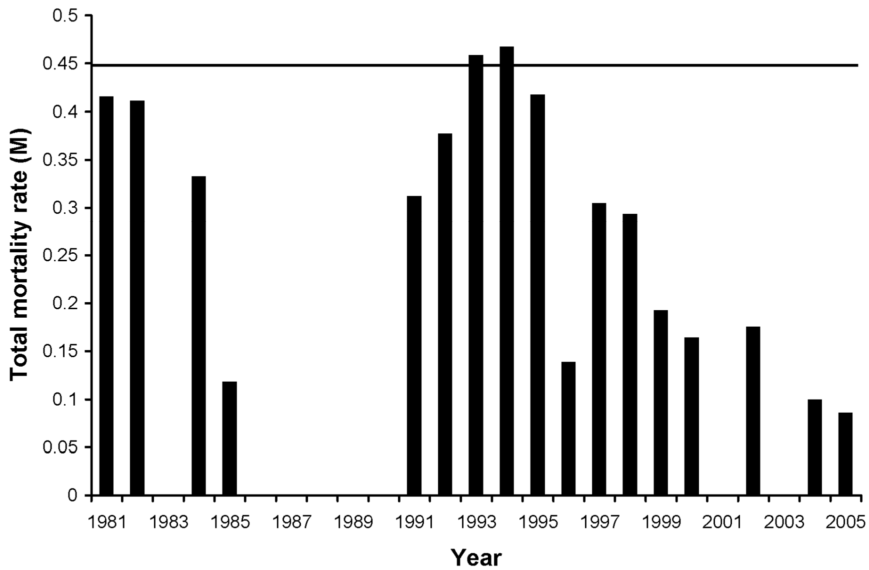
The St. Louis River population is characterized by long-lived individuals, slow growth rates, and highly variable recruitment. Data collected in 1980-1981, just two years after water-quality improvements, were indicative of a population without significant fishing mortality—some walleye were as old as age 22, and 63% of the mature males and 78% of the mature females were age 10 or older (Schram et al. 1992). Growth has been relatively stable over the past 25 years, as indicated by little change in the mean length of age-10 fish (MJS, unpublished data). Stronger year-classes have dominated the population in the St. Louis River but have often been separated by as much as 10 years. In 1981, 50% of the entire spawning population was represented by one year-class (Schram et al. 1992). Since 1981, results of standardized daytime seining of YOY walleye in the lower St. Louis River have indicated the production of strong year-classes in 1982, 1992, and especially 1994 (Fig. 2). The daytime seining catch was a reliable index of year-class strength until the river was colonized by zebra mussels (*Dreissena polymorpha*) in the 1990s, causing improved water clarity. The improved water clarity has made it harder to catch YOY walleye by daytime seining, and this metric is no longer a suitable index. However, recruitment is measured by examining the age structure of the spawning population.

Fig. 2. Young-of-the-year walleye catch (number•seine haul) from the St. Louis River, 1981-2006.



Management goals for the St. Louis River population include maintaining through harvest regulations a high catch rate and a size structure favoring bigger fish, protection of spawning and nursery habitat, and monitoring population dynamics (Blust et al. 1988; Schreiner et al. 2006). Regulations imposed on the recreational fishery are believed responsible for keeping the walleye total mortality rate generally below the 45% recommended by the walleye subcommittee (Fig. 3; Hoff 2003). Regulations since 1980 included a seasonal closure of the spawning grounds to angling and, since 1995, in the river, a two-fish-per-day limit with a 381-mm minimum-size limit, which, since 1995, was extended to the Minnesota waters of Lake Superior. In Wisconsin waters of Lake Superior, regulations since 1992 consisted of a five-fish-per-day limit and a 381-mm minimum-size limit with only one fish >508 mm allowed.

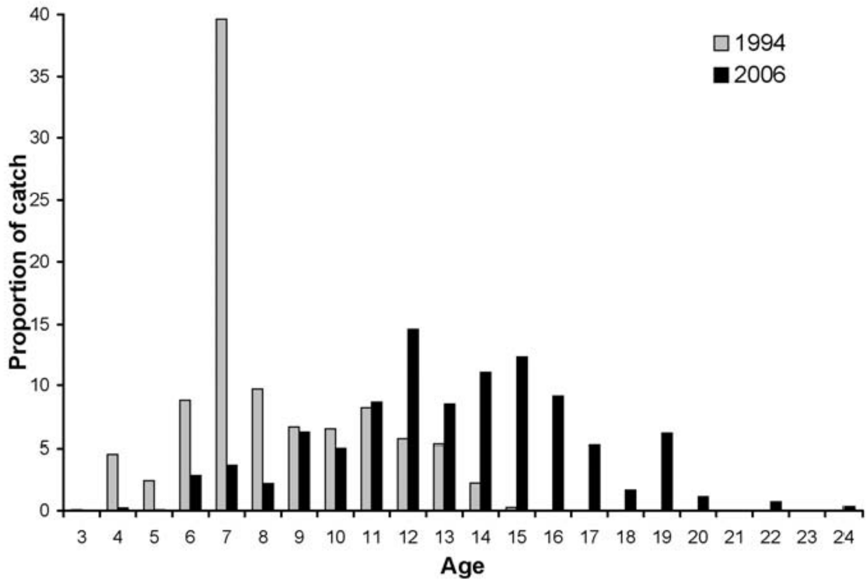
Fig. 3. Total annual mortality rates of walleye in the St. Louis River, 1981-2005. The solid horizontal line represents the maximum recommended total annual mortality rate (Hoff 2003).



Chequamegon Bay (Wisconsin)

Chequamegon Bay in Wisconsin waters (Fig. 1) supports a diverse fish community where walleye continue to play a dominant role as piscivore. Historically, production from the Kakagon Sloughs on the eastern end of the bay likely supported the entire walleye fishery. The fish community became disrupted during the 1940s-1960s as walleye abundance decreased due to predation on adults by sea lamprey and on larvae by rainbow smelt (*Osmerus mordax*) and overexploitation (Devine et al. 2005). The Wisconsin Department of Natural Resources (DNR) stocked fingerlings from 1980 until 2000 along the Ashland waterfront in an effort to create a localized fishery and reduce the abundant rainbow smelt population. Since 2001, walleye larval and fingerling stocking has been done in the Kakagon Sloughs by the Bad River Band of Lake Superior Chippewa. After fingerling stocking was initiated in the 1980s, walleye were observed using the Ashland shoreline for spawning. The age structure of this spawning population shifted from predominately young fish in a 1994 survey to older fish in a 2006 survey (Fig. 4). Although the proportion of walleye larger than 508 mm in the spawning population increased by 36% during these years, the estimated total number decreased from 7,196 (95% CI = 6,608-7,898) in 1994 to 4,715 (95% CI = 4,272-5,261) in 2006. The decreased abundance and the shift in age structure since cessation of stocking by the Wisconsin DNR suggest that natural recruitment along the Ashland shoreline and from the Kakagon Sloughs is limited and unable to support the bay's fishery; therefore, the population can be maintained only by stocking. Moreover, the stocking by the Bad River Band appears to have been inadequate. The current recreational fishing regulations for walleye (five-fish-per-day limit with a 381-mm minimum length and only one fish >508 mm) are believed responsible for the increased proportion of older and larger fish in the population. Despite decreased abundance and dependence on stocking, walleye remain the dominant predator in Chequamegon Bay. In a recent bioenergetics study (Devine et al. 2005), walleye accounted for 74% of prey consumption by predators in Chequamegon Bay.

Fig. 4. Age distribution of spawning walleye caught in Chequamegon Bay along the Ashland, WI, shoreline, 1994 and 2006.



Bad River (Wisconsin)

Walleye abundance in the Bad River (Fig. 1) has remained low for many years and is currently being supplemented by fish reared by the Bad River Natural Resources Department. The contribution of these stocked fish is unknown.

Conclusion

The Lake Superior fish-community objective for walleye of re-establishing a self-sustaining population is only being met in the St. Louis River. Improving degraded tributary habitat and/or allowing walleye unrestricted access to historical spawning areas will be the key to achieving the fish-community objective at many other locations. The same impediments to rehabilitation that existed in 2000 (Schram 2007) still exist today (e.g., limited biological data from many locations, fish passage and other habitat-loss issues, and highly variable recruitment along with slow growth). In Black Bay, walleye rehabilitation will require that remnant populations regain access to spawning habitat above the Black Sturgeon dam. In this and other tributaries, management agencies and sea lamprey control agents need to investigate options for fish passage that will meet the fish-community objectives for walleye, sea lamprey, and other species such as lake sturgeon (*Acipenser fulvescens*).

Schram et al. (1991), in an earlier status report, pointed out that walleye abundance in Lake Superior was below historical levels. Since then, agencies have attempted to rehabilitate a number of populations through stocking and implementing conservative fishing regulations. However, only a few populations are maintained by natural reproduction, and none, except that in the St. Louis River, has been rehabilitated back to, or near, historical levels.

Research and assessment needs identified by Hoff (2002) have not changed, and these needs should be considered by agencies as they develop rehabilitation plans. Rehabilitation strategies should start with collection of biological and ecological data from many populations to better identify specific factors limiting recovery. Management plans can then be developed to reconnect walleye with historical spawning and nursery habitat and to protect them from exploitation. The available data suggest that the majority of Lake Superior walleye populations are slow growing, old and late maturing, and unable to withstand high levels of exploitation.

Therefore, even when suitable habitat is not limiting, conservative fishing regulations will be necessary to rehabilitate and maintain walleye populations in Lake Superior.

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THE STATUS OF LAKE MICHIGAN WALLEYE STOCKS

Kevin L. Kapuscinski[1], Troy G. Zorn, Philip J. Schneeberger, Richard P. O'Neal, and Bradley T. Eggold

Abstract

We reviewed the status of 10 Lake Michigan walleye (*Sander vitreus*) stocks and the efforts to rehabilitate them since last described in 1991. Survival rates, number and age structure of spawning fish, and the amount of natural reproduction suggest that the Fox River stock is rehabilitated, the Little Bay de Noc stock is entering the late rehabilitation phase, and all the other stocks are either depressed or in an early rehabilitation phase. In addition, we found that abundance and age at maturity of most stocks remained stable or increased; growth was rapid, stable for most stocks, and similar to previous descriptions; survival and exploitation rates for all stocks were satisfactory for rehabilitation; and natural production of young was mostly low and, where present, extremely variable. These demographics were for walleye stocks in highly altered, habitat-limited systems. Additionally, predation by, and

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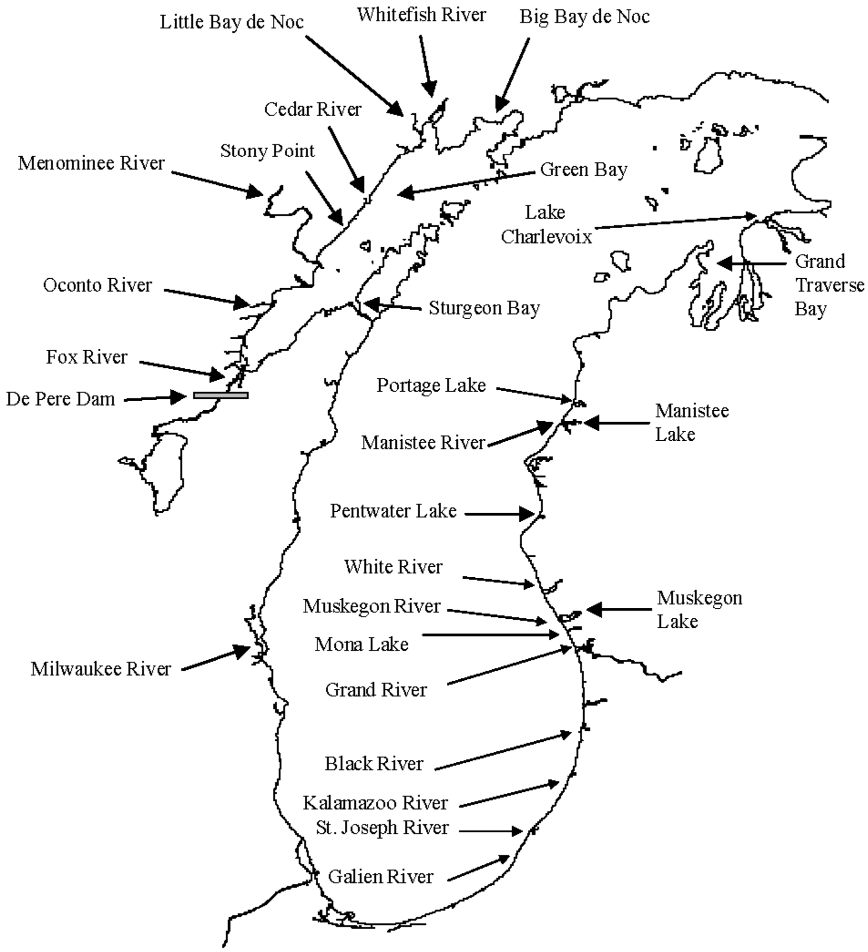
competition with, non-native species and large-scale processes such as increasing water clarity are occurring, but their affects on Lake Michigan walleye are poorly understood. Further population expansions are possible if spawning and nursery habitats are improved and augmented. Research needed to guide future rehabilitation efforts includes: evaluation of the efficacy of stocking walleye, especially in areas where natural reproduction occurs; identification of interactions between walleye and non-native species; and determination of the effects that dams and barriers have on walleye reproduction.

Introduction

The largest walleye (*Sander vitreus*) stocks in Lake Michigan exist in Green Bay and in the Muskegon River areas; smaller stocks exist elsewhere (Fig. 1). All Lake Michigan walleye stocks were diminished during the early- to mid-twentieth century, suffering the consequences of habitat destruction, pollution, interactions with non-native species, and over-exploitation (Schneider and Leach 1977; Schneider et al. 1991). Damming and pollution of tributaries used for spawning were identified as primary forces that impaired walleye reproduction (Schneider and Leach 1977). In addition, extensive destruction of wetlands (Whillans 1982) removed critical nursery habitats thereby decreasing survival of juvenile walleye. Interactions with non-native species (e.g., alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), and sea lamprey (*Petromyzon marinus*)) are also considered contributory to the decline of walleye stocks via predation and competition (Schneider and Leach 1977; Schneider et al. 1991). Northern Green Bay walleye stocks declined to very low levels by the mid-1960s, and, by 1973, only the Menominee River supported a self-sustaining stock in southern Green Bay (Schneider et al. 1991). By 1975, only about 2,000 adult walleyes were present in the Muskegon River, which had once harbored one of the largest walleye spawning runs in southeastern Lake Michigan (Schneider et al. 1991).

Fig. 1. Lake Michigan showing selected tributaries and locations of managed walleye stocks.



Efforts to rehabilitate walleye stocks began with limiting exploitation. Commercial walleye fisheries were eliminated in Michigan in 1969 and in Wisconsin in 1978. Lake Michigan water quality began to improve by the mid-1970s, following the passage and enforcement of the Clean Water Act. The Michigan Department of Natural Resources and Environment (DNRE) and Wisconsin Department of Natural Resources (DNR) began stocking fry and fingerling walleye into Green Bay and the Muskegon River during the early 1970s. As a result, stock sizes increased to levels that supported attractive sport fisheries in the 1980s (Schneider et al. 1991).

Substantial changes to the Lake Michigan ecosystem have occurred since 1989, just when Schneider et al. (1991) were concluding their analysis of the lake's walleye stocks. Nearshore food webs were altered by the establishment of zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis*; hereafter collectively dreissenids), white perch (*Morone americana*), and round goby (*Apollonia melanostoma*). Alewife, bloater (*Coregonus hoyi*), and rainbow smelt have decreased in abundance (Madenjian et al. 2002), while gizzard shad (*Dorosoma cepedianum*) remained very abundant in some tributaries. Phosphorus loadings to the lake were stable during the 1990s, but water clarity increased (Madenjian et al. 2002; Holey and Trudeau 2005; U.S. Environmental Protection Agency 2006). These changes, along with the proliferation of the filamentous algae *Cladophora gomerata*, suggest that dreissenids are sequestering nutrients in benthic food webs, and primary productivity in the littoral and pelagic waters of the lake may be decreasing (sensu Hecky et al. 2004). Despite these alterations of the ecosystem, walleye stocks have increased in abundance in many areas since 1989. Stocking likely contributed to the increases in northern Green Bay and the Muskegon River, whereas natural reproduction in the Fox River accounted for increases in southern Green Bay.

The purpose of this report is to describe the status of walleye stocks in Lake Michigan since last reported in Schneider et al. (1991). We discuss changes in demographics and rehabilitation efforts for walleye stocks in four areas of Lake Michigan: northern Green Bay (Big Bay de Noc, Cedar River, Little Bay de Noc, and Menominee River), southern Green Bay (Fox River and Sturgeon Bay), eastern shore (Grand, Muskegon, and St. Joseph Rivers), and the Milwaukee River (Fig. 1). We provide biological information on individual stocks, compare results to Schneider et al. (1991), discuss lakewide trends, and identify research and management needs.

Materials and Methods

We obtained data from published and ongoing studies, and additional information was incorporated from agency files and long-term assessments (Table 1). Walleye stocks were surveyed using several methods. Electrofishing surveys targeting spawning walleye were conducted in the Cedar and Menominee Rivers, whereas fykenet surveys were conducted in the Fox River and at Sturgeon Bay (Table 1). Spawner abundance was estimated in the Cedar and Menominee Rivers using the Schumacher-Eschmeyer mark-recapture method (Ricker 1975), in the Fox River using the Schnabel multiple-census mark-recapture method (Van Den Avyle 1993), and in the Muskegon River using the Chapman modification of the Peterson mark-recapture method (Van Den Avyle 1993; Table 1). Tag-return data from fish marked with jaw or Floy anchor tags were used to quantify walleye movement, growth, survival, and exploitation. We quantified growth of walleye from each stock (sex specific and year specific, where possible) with the additive-error von Bertalanffy growth model (Quinn and Deriso 1999). We used a Gauss-Newton least-squares method (SAS 9.1, SAS Institute Inc. or Systat 11, Systat Software Inc.) to estimate the parameters, approximate standard errors, and approximate 95% confidence intervals (CIs) of each parameter. We used sex-specific growth models, when possible, because walleye exhibit sexually dimorphic growth (Quist et al. 2003). Data were analyzed by year of collection to examine trends through time. For each stock, we considered growth rates and maximum length different between years if the 95% CIs on K (the rate at which length-at-age t, L_t, approaches the asymptotic average maximum length, L_∞) and L_∞ did not overlap. Data were combined when growth did not differ among years. We tested trends in growth of Fox River and Sturgeon Bay walleye, where multiple-year data were available, by regressing K, L_∞, and W_∞ (asymptotic average maximum weight; estimated from an unpublished weight-length relationship) on year. Parameter estimates for fitted von Bertalanffy growth models from individual years are available from the corresponding author.

Table 1. Summary of Michigan Department of Natural Resources and Environment and Wisconsin Department of Natural Resources walleye surveys and data sources.

Topic	Stock	Gear/method used	Years
Exploitation	Cedar River	Tag returns, Brownie et al. (1985)	1993-2004
	Big Bay de Noc	Tag returns, Brownie et al. (1985)	1990-2004
	Little Bay de Noc	Tag returns, Brownie et al. (1985)	1988-date
	Menominee River	Tag returns, Brownie et al. (1985)	1993-2004
	Muskegon River	Tag returns	1975-1987
	Muskegon River	Creel census, tag returns	2002
Growth	Big Bay de Noc, Cedar and Menominee River	Additive error von Bertalanffy growth models	1996, 1999, 2002
	Fox River	Additive error von Bertalanffy growth models	1991-1996, 1999-2004
	Sturgeon Bay	Additive error von Bertalanffy growth models	1991-1996
	Little Bay de Noc	Additive error von Bertalanffy growth models	1988, 1996, 1999, 2002
	Grand River	Additive error von Bertalanffy growth models	2004-2005
	Muskegon River	Additive error von Bertalanffy growth models	1947, 1955-1958, 1960-1962,
			1972-1976, 1986-1987, 1998,
			2002
	St. Joseph River	Additive error von Bertalanffy growth models	2003-2004
	Milwaukee River	Additive error von Bertalanffy growth models	1996-2006

Table 1, continued.

Topic	Stock	Gear/method used	Years
Movements	Big Bay de Noc	Tag returns, Brownie et al. (1985)	1990-2004
	Cedar and Menominee Rivers	Tag returns, Brownie et al. (1985)	1993-2004
	Little Bay de Noc	Tag returns, Brownie et al. (1985)	1988-date
	Fox River	Tag returns	1987-2004
	Sturgeon Bay	Tag returns	1989-2004
	Muskegon River	Tag returns	1948-1954, 1975-1976, 1981-1987, 2002
	Milwaukee River	Radio telemetry, Hirethota and Burzynski (2004)	1999-2003
Recruitment/ young-of-year relative abundance/ natural reproduction	Big Bay de Noc, Little Bay de Noc	Electrofishing, gillnets, OTC marking, Fielder (2002a)	2003-date
	Cedar River	Electrofishing, OTC marking, Fielder (2002a)	2004
	Little Bay de Noc	Statistical catch-at-age models, Schneeberger (2000)	1985-1996
	Fox River, southern Green Bay	Electrofishing, Kapuscinski and Lange (2005)	1990-2005
	Muskegon River	Electrofishing, OTC marking, Fielder (2002a)	1994-2005
	St. Joseph River	Electrofishing	2005

Table 1, continued.

Topic	Stock	Gear/method used	Years
Spawner abundance	Cedar River	Electrofishing, Schumacher-Eschmeyer method	2005
	Menominee River	Electrofishing, Schumacher-Eschmeyer method	2006
	Fox River	Fykenets, Schnabel method	1981-1984, 1987-2004
	Muskegon River	Seine, dipnets, Peterson-Chapman method	1954-1955
		Electrofishing, Peterson-Chapman method	1975, 1986, 1998, 2002
Survival	Cedar River	Tag returns, Brownie et al. (1985)	1993-2004
	Big Bay de Noc	Tag returns, Brownie et al. (1985)	1990-2004
	Little Bay de Noc	Tag returns, Brownie et al. (1985)	1988-date
	Menominee River	Tag returns, Brownie et al. (1985)	1993-2004
Survival	Fox River	Catch-curve regression	1991-2004
	Muskegon River	Tag returns	1975-1976
	Muskegon River	Catch-curve regression	1998, 2002
Spawning	Sturgeon Bay	Fykenets	1982-1996
Tag spawners	Big Bay de Noc	Electrofishing, fykenets	1990-2004
	Cedar and Menominee River	Electrofishing, fykenets	1993-2004
	Little Bay de Noc	Electrofishing, fykenets	1988-date
	Sturgeon Bay	Fykenets	1989-2003

The relative abundance of young-of-the-year (YOY) walleye was monitored via gillnet catches during the last week of August until the end of September (Little and Big Bays de Noc) and catch-per-hour (CPH) during electrofishing surveys in late summer and fall (Little and Big Bays de Noc, Fox River, and southern Green Bay). Gillnet, fykenet, and electrofishing surveys were conducted during September to document the occurrence of

YOY walleye in the Milwaukee River and Harbor. A larval tow net and a stationary drift net were used 1-3 weeks after walleye spawned to assess natural reproduction in the Milwaukee River. In Michigan waters of northern Green Bay and eastern Lake Michigan, the contribution of hatchery-reared walleye to stocks was assessed by marking hatchery-reared walleye with oxytetracycline and determining the proportion of YOY captured during fall electrofishing and gillnet surveys that were marked (Fielder 2002a).

Survival and exploitation of northern Green Bay walleye were estimated from cumulative tag-return data. For Fox River walleye, we used catch-at-age analysis to estimate total instantaneous mortality (Z) for male and female walleye captured during spawner surveys during 1991-2004. Ages were estimated for a sub-sample of walleye from scales and spines, and age-length keys were used to estimate the age frequency of the entire sample. Linear regression was used to estimate Z from the descending limb of the catch-at-age curve. We considered Z to differ among the sexes if the interaction term was significant ($\alpha \leq 0.05$). We calculated total annual survival rate and annual mortality from our estimates of Z (Quinn and Deriso 1999). For Muskegon River walleye, survival and exploitation are presented from the catch-curve analysis, creel census, and tag-return data reported by Hanchin et al. (2007).

Results

Northern Green Bay

Management. A primary management objective for Michigan waters of Green Bay is to restore self-sustaining walleye stocks to levels that support recreational fisheries. Sport-fishing regulations have remained essentially unchanged since summarized by Schneider et al. (1991), and they appear to protect stocks adequately. Current regulations consist of a 381-mm minimum length limit, daily bag limit of five fish, and closure during March 16-May 14. To further protect large fish, a regulation was enacted in 1994 for Little Bay de Noc making it illegal for anglers to harvest more than one walleye >584 mm each day. Special and more-complicated regulations were created for the Michigan-Wisconsin boundary waters and apply to the Menominee River.

Apart from regulations for state-licensed recreational anglers, there are tribal rules that apply to Native Americans who engage in recreational and subsistence fisheries for walleye in the 1836 Treaty waters of northern Green Bay. Tribal recreational fishers operate under rules that incorporate, or are substantially similar to, state recreational-fishing regulations (see http://www.michigan.gov/documents/dnr/Proposed_Consent_Decreepages1-144_209977_7.pdf and http://www.michigan.gov/documents/dnr/consent_decree_2000_197687_7.pdf for details). Tribal subsistence fishers with a permit may use gillnets (≤91.4 m long) and impoundment nets between May 15 and March 1 and have an aggregate (all fish species) catch of up to 45.4 kg (round weight) in their possession. In addition, the tribes may authorize harvest of walleye between March 15 and May 15 in specified tributaries of Little and Big Bay de Noc (i.e., Escanaba, Sturgeon, Days, and Rapid Rivers). The overall tribal harvest during this season is limited to no more than 2,500 walleyes ≥356 mm. Individually permitted participants in this fishery may harvest up to 10 walleyes daily with a hook and line or spear.

Stocking of walleye into northern Green Bay has been ongoing since 1989 (Table 2) at locations in the Bays de Noc, in the Cedar River, and in Green Bay proper at Stony Point (Fig. 1). More than 10.9 million fingerlings and 10.4 million fry were stocked into northern Green Bay during 1989-2005 (Tables 2, 3). Fishery managers discontinued planting walleye fry in northern Green Bay after 2000 due to dissatisfaction with perceived returns. Ripe adults collected off the mouth of the Whitefish River (Fig. 1) in Little Bay de Noc provided the brood source for all walleye planted into northern Green Bay.

Table 2. Numbers of walleye fingerlings (1,000s) stocked at various locations in Lake Michigan during 1973-2005 (*t* indicates <1,000 stocked). Stocking locations are grouped by geographic area: northern Green Bay, southern Green Bay (SGB), Milwaukee River (MR), and eastern shore.

	Northern Green Bay				**SGB**[a]	**MR**[b]	**Eastern shore**	
Year	**Big Bay de Noc**	**Cedar River**	**Little Bay de Noc**	**Stony Point**			**Northeast**	**Southeast**
1973	0	0	108	0	46	0	*t*	0
1974	9	0	84	0	150	0	0	12
1975	0	0	81	0	331	0	74	98
1976	0	0	122	0	134	0	0	1
1977	0	0	102	0	307	0	0	3
1978	0	0	132	0	57	0	0	25
1979	0	0	110	0	333	0	t	198
1980	0	0	118	0	0	0	3	335
1981	0	0	119	0	472	0	0	194
1982	0	0	14	0	0	0	0	222
1983	0	0	794	0	0	0	0	284
1984	0	0	230	0	382	0	36	329
1985	0	0	320	0	0	0	35	488
1986	206	0	255	0	0	0	44	742
1987	176	0	318	0	0	0	97	306
1988	73	72	85	7	0	0	64	334
1989	218	97	278	0	0	0	245	289
1990	0	158	506	93	0	5	216	402
1991	694	206	*t*	100	0	0	329	860
1992	0	33	426	167	0	0	603	795
1993	325	44	0	47	4	0	359	1,034
1994	0	217	264	307	174	0	262	1,004
1995	384	190	0	189	0	8	291	911

Table 2, continued.

Year	Northern Green Bay: Big Bay de Noc	Northern Green Bay: Cedar River	Northern Green Bay: Little Bay de Noc	Northern Green Bay: Stony Point	SGB[a]	MR[b]	Eastern shore: Northeast	Eastern shore: Southeast
1996	0	96	561	124	2	10	230	729
1997	264	161	0	59	41	0	403	1,019
1998	169	101	652	128	181	3	264	970
1999	544	0	0	0	158	8	418	1,934
2000	0	91	510	118	188	10	283	1,441
2001	463	0	0	0	0	10	457	1,381
2002	0	0	141	26	0	6	417	456
2003	607	0	0	0	249	11	406	757
2004	0	106	569	22	176	2	234	543
2005	749	0	0	0	1	10	239	525
Total	4,663	1,572	6,899	1,387	3,386	78	6,011	18,622

[a]59,000 fingerlings were stocked in the Fox River in 1977; all other fingerlings stocked in southern Green Bay were released in Sturgeon Bay.

[b]Fingerlings stocked in 1999; extended growth fingerlings (reared until 1 October, >17.8 cm total length) stocked in all other years.

Table 3. Numbers of walleye fry (1,000s) stocked at various locations in Lake Michigan during 1973-2005. Stocking locations are grouped by geographic area: northern Green Bay, southern Green Bay (SGB), Milwaukee River (MR) and eastern shore.

	Northern Green Bay			SGB		MR	Eastern shore	
Year	Big Bay de Noc	Little Bay de Noc	Cedar River	Fox River	Sturgeon Bay		Northeast	Southeast
1973	230	108	0	0	0	0	0	1901
1974	0	0	0	0	4,000	0	0	0
1975	300	0	0	0	5,000	0	4,629	2,000
1976	1,775	0	0	0	5,000	0	0	1,475
1977	0	0	0	0	5,000	0	0	0
1978	0	0	0	8,000	9,000	0	0	0
1979	0	0	0	10,000	0	0	2,350	866
1980	0	455	0	10,000	0	0	1,750	2,540
1981	0	1,692	1,125	10,000	0	0	1,750	10,447
1982	0	2,000	1,000	5,000	0	0	1,750	9,120
1983	0	1,350	1,000	6,000	0	0	900	3,510
1984	0	2,000	0	4,000	0	0	173	11,030
1985	0	1,900	0	0	0	0	213	9,700
1986	2,955	2,000	0	0	0	2,000	0	3,788
1987	0	0	0	0	0	0	5,000	7,069
1988	0	0	0	0	0	2,920	2,000	12,164
1989	2,775	0	0	0	0	0	6,114	9,226
1990	0	0	0	0	0	2,500	3,000	7,606
1991	0	0	0	0	0	0	6,600	3,240
1992	0	0	0	0	0	0	8,500	5,564
1993	0	0	0	0	0	0	1,998	0
1994	0	0	0	0	0	0	450	11,620
1995	0	0	0	0	0	0	6,500	6,500
1996	0	0	0	0	0	0	0	7,333
1997	0	0	0	0	0	0	0	1,650

Table 3, continued.

	Northern Green Bay			SGB		MR	Eastern shore	
Year	Big Bay de Noc	Little Bay de Noc	Cedar River	Fox River	Sturgeon Bay		Northeast	Southeast
1998	0	0	0	0	0	0	5,000	5,763
1999	5,300	0	0	0	0	0	3,200	1,600
2000	2,400	0	0	0	0	0	0	3,175
2001	0	0	0	0	0	0	5,500	1,200
2002	0	0	0	0	0	0	0	3,765
2003	0	0	0	0	0	0	0	3,250
2004	0	0	0	0	0	0	0	5,306
2005	0	0	0	0	0	0	0	0
Total	15,735	11,505	3,125	53,000	28,000	7,420	67,376	152,407

Abundance. Recruitment of stocked and wild-origin fish rebuilt walleye stocks in northern Green Bay to current levels. Based on multiple mark-recapture surveys, roughly 8,500 (±3,000 95% CI) walleyes spawned in the Cedar River in 2005, and 53,000 (±6,800) spawned in the Menominee River in 2006. The contribution of strong year-classes in 2003 was evident in the Menominee River in 2006, as 72% of walleye observed were males <510 mm total length (TL) (TGZ, unpublished data). Large numbers of female walleye from these same strong year-classes were expected to return to the river for their first spawning event during 2007 or 2008.

Sport-Fishery Harvest. Since 1988, sport-fishery harvests of walleye in northern Green Bay have generally increased in Little Bay de Noc and the Cedar and Menominee Rivers, whereas no discernable trend was evident in Big Bay de Noc (Table 4). Harvest in Little Bay de Noc increased 75% from an annual average of 17,490 fish during 1985-1989 to 35,700 fish during 2000-2004. In contrast, the sport fishery in Big Bay de Noc rarely harvested more than 3,000 fish in any one year during 1985-2004. Density of walleye in Big Bay de Noc is lower than in Little Bay de Noc because Big Bay de Noc has a shorter history of stocking, receives fewer fish per ha, and has lower levels of natural reproduction. Walleye harvest from the Cedar River and vicinity increased from an average of 360 fish per year during 1995-1999 to 1,830 during 2000-2003 (Table 4). Walleye harvest from the Menominee River and vicinity averaged 310 fish per year during 1985-1989, increased to an average of 22,220 during 1995-1999, and averaged 20,030 during 2000-2003.

Table 4. Numbers of walleye harvested by anglers from various Lake Michigan stocks during the open-water seasons of 1985-2005. Walleye stocks are grouped by geographic area: northern Green Bay, southern Green Bay (SGB), Milwaukee River (MR), and eastern shore (ES) (hyphens indicate no data).

	Northern Green Bay				**SGB**		**MR**	**ES**
Year	**Big Bay de Noc**	**Cedar River**	**Little Bay de Noc**	**Menominee River**	**Fox River**	**Sturgeon Bay**		**St. Joseph River**
1985	-	-	13,673	175	-	-	-	-
1986	518	-	19,598	278	27,367	878	191	-
1987	-	-	11,149	856	22,436	733	-	-
1988	1,168	-	12,534	35	14,891	6,596	-	-
1989	5,292	-	30,483	192	1,552	900	-	-
1990	2,408	-	31,017	-	1,409	249	-	-
1991	3,013	-	41,405	-	1,089	332	157	-
1992	906	-	17,704	-	3,074	-	-	-
1993	1,746	152	17,031	9,833	10,122	91	231	-
1994	8,228	236	21,042	18,728	19,627	98	-	-
1995	5,518	227	67,297	9,587	7,109	234	-	-
1996	1,960	434	56,270	11,792	8,455	192	-	-
1997	2,977	233	22,535	38,209	2,422	217	353	-
1998	4,245	665	19,769	27,887	1,784	1,132	194	4,347
1999	1,433	250	20,548	23,605	1,530	763	25	4,939
2000	902	977	30,769	10,037	1,688	465	-	5,204
2001	719	1,958	37,952	42,790	263	601	-	2,905
2002	1,658	3,454	35,958	15,138	617	218	469	4,231
2003	1,212	932	15,087	12,159	3,936	2,062	402	3,263
2004	704	-	33,436	-	2,558	33	77	-
2005	289	-	13,109	-	5,454	420	58	-
Mean	2,363	865	27,065	13,831	6,869	811	216	4,148

Movements. Two distinct movement patterns were evident for adult walleye marked with jaw tags in northern Green Bay. Walleye tagged in Little Bay de Noc, Big Bay de Noc, and the Menominee River showed relatively little movement away from tagging locations. Over 90% of tagged fish were recaptured within 20 km of the spawning areas where they were originally tagged. In contrast, walleye tagged in the Cedar River and near its mouth exhibited a bimodal movement pattern; only 31% of recaptured fish were observed within 20 km of the tagging site, whereas 66% were recaptured 40 km or more away. In and around the Menominee River, 51% of tagged walleye from the Cedar River were recovered, which is about 40 km away (Fig. 1).

Walleye generally showed high fidelity to spawning sites where they were originally tagged. Only 0.2% of walleye originally tagged in Big Bay de Noc strayed to other tagging locations during spawning periods in subsequent years. The percent of fish straying from tagging sites in Little Bay de Noc and the Cedar and Menominee Rivers was somewhat higher, ranging from 9.7 to 11.4% during 1994-2005. Schneeberger (2000) also reported high spawning-site fidelity (<4.5% straying) for northern Green Bay walleye during 1988-1996.

Growth. Growth of walleye in northern Green Bay did not change during 1996-2002. Furthermore, walleye growth was similar among stocks in northern Green Bay (Tables 5, 6). Growth of Little Bay de Noc walleye was not statistically different from that reported by Schneider et al. (1991) for 1988, but the growth coefficient, (K), was much higher during 1996-2002 than in 1988, and the asymptotic average maximum length, (L_∞), was much smaller (Tables 5, 6). Overall, growth of the northern Green Bay stocks changed marginally during a period when major changes occurred in Lake Michigan.

Table 5. Growth parameters estimated from additive error von Bertalanffy growth models for male walleye from four stocks in northern Green Bay, Lake Michigan. Also shown are the years data were collected, number of length-at-age samples, and the range of ages in the samples. Approximate standard errors (SE) and approximate 95% lower (LCL) and upper (UCL) confidence limits for each parameter are also provided.

Stock	**Year(s)**	*N*	**Age range**	**Parameter**	**Estimate**	**SE**	**LCL**	**UCL**
Big Bay de Noc	1996, 1999, 2002	134	3-16	L_∞	683.6	32.112	620	747.1
				K	0.2012	0.0509	0.1005	0.3019
				t_0	-1.042	1.0402	-3.0998	1.0158
Little Bay de Noc	1996, 1999, 2002	269	3-18	L_∞	634	18.758	597.1	670.9
				K	0.2341	0.0503	0.1351	0.3332
				t_0	-1.1265	0.9173	-2.9327	0.6797
Little Bay de Noc	1988	168	2-14	L_∞	730.7	50.193	631.6	829.8
				K	0.1284	0.0277	0.0737	0.1831
				t_0	-2.7705	0.7392	-4.2301	-1.3109
Cedar River	1996, 1999, 2002	196	3-14	L_∞	655	20.94	613.7	696.3
				K	0.2414	0.0434	0.1559	0.3269
				t_0	-0.9541	0.6333	-2.2033	0.2951
Menominee River	1996, 1999, 2002	252	2-16	L_∞	653.2	21.217	611.4	694.9
				K	0.208	0.0323	0.1444	0.2717
				t_0	-1.7558	0.5471	-2.8333	-0.6782

Table 6. Growth parameters estimated from additive error von Bertalanffy growth models for female walleye from four stocks in northern Green Bay, Lake Michigan. Also shown are the years data were collected, number of length-at-age samples, and the range of ages in the samples. Approximate standard errors (SE) and approximate 95% lower (LCL) and upper (UCL) confidence limits for each parameter are also provided.

Stock	**Year(s)**	*N*	**Age range**	**Parameter**	**Estimate**	**SE**	**LCL**	**UCL**
Big Bay de Noc	1996, 1999	84	3-13	L_∞	857.4	102.4	653.6	1061.2
				K	0.1277	0.0527	0.0229	0.2325
				t_0	-2.0062	1.6871	-5.363	1.3505
Little Bay de Noc	1996, 1999, 2002	219	5-22	L_∞	779.4	23.065	733.9	824.9
				K	0.1582	0.0276	0.1038	0.2127
				t_0	-0.9943	0.9947	-2.9548	0.9662
Little Bay de Noc	1988	65	4-15	L_∞	880.9	291.6	297.9	1463.9
				K	0.0662	0.0731	-0.0798	0.2123
				t_0	-8.9062	8.1501	-25.1981	7.3856
Cedar River	1996, 1999, 2002	217	3-14	L_∞	759.9	27.086	706.5	813.3
				K	0.1911	0.0347	0.1227	0.2595
				t_0	-1.615	0.7371	-3.0679	-0.1622
Menominee River	1996, 1999, 2002	236	3-19	L_∞	771.2	46.113	680.3	862
				K	0.1278	0.0386	0.0518	0.2038
				t_0	-4.7476	1.847	-8.3865	-1.1087

Maturity. Age at maturity of walleye in northern Green Bay was stable during 1976-2005. During 1989-2005, we examined 41,349 male and 15,436 female walleyes during the spawning period. Spawning runs during 1989-2005 contained few mature males younger than age 3 and <356 mm total length (0.2%), and only 3.0% of mature females were younger than age 5 and <508 mm. Schneider et al. (1991) reported that 0.3% of mature males were younger than age 3 and <356 mm, and 1.5% of mature females were younger than age 5 and <483 mm.

Recruitment. The amount of natural recruitment varied among the four walleye stocks in northern Green Bay. Natural recruitment was most evident in Little Bay de Noc, which was stocked in even-numbered years during 1990-2006. Walleye from year-classes formed in eight non-stocked years were well represented in samples collected during spring tagging and summer assessment surveys (Zorn and Schneeberger, in press). Fall sampling of age-0 walleye for oxytetracycline marks consistently yielded naturally reproduced fish in Little Bay de Noc during 2003-2007, with the naturally produced year-classes in 2003 and 2007 being roughly three times larger than the 2004 year-class, which benefited from a half million stocked fingerlings (TGZ, unpublished data). By way of comparison, Schneider et al. (1991) stated that modest numbers of wild juvenile walleye were collected in 1988 off the mouth of the Whitefish River located in Little Bay de Noc (Fig. 1).

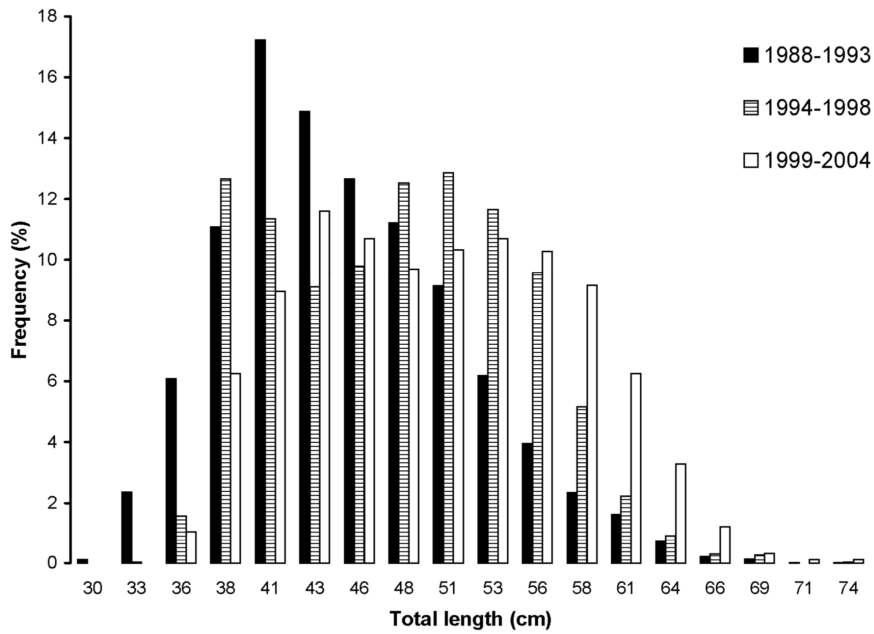
Ages of walleye collected during tagging studies in the Menominee River in 1996 confirmed that at least nine year-classes were present in the river prior to 1988, the year when stocking began (Zorn and Schneeberger, in press). These year-classes likely originated from the Menominee River because the samples were collected during the spawning run and spawning fidelity of northern Green Bay walleye stocks was over 95% during 1989-1996 (Schneeberger 2000). Fall electrofishing confirmed modest levels of natural reproduction in the Menominee River in 2006 and 2007 (TGZ, unpublished data).

The Big Bay de Noc and Cedar River stocks show evidence of natural reproduction, although levels observed may be inadequate for sustainability. In Big Bay de Noc, walleye older than age 10 and thus too old to have originated from stocking, which began in 1986, were rare in collections made in 1996 (Zorn and Schneeberger, in press). Moreover, little natural reproduction occurred in Big Bay de Noc in non-stocked years (2004 and 2006), and, when 749,000 fingerlings were stocked in 2005, naturally produced fish made up only 29% of age-0 walleye. However, preliminary data suggest that a strong year-class was naturally produced in 2007. In the Cedar River, fish from year-classes formed before the initial stocking of 1987 were absent, suggesting that natural reproduction was not occurring prior to stocking (Zorn and Schneeberger, in press). Modest numbers of age-0 walleye (44 and 20 fish) were collected in the Cedar River and off its mouth in 2004 and 2007, of which 36% and 100% were naturally produced (TGZ, unpublished data).

Survival. Based on cumulative tag returns since 1988 (Little Bay de Noc) or the early 1990s through 2004 (Big Bay de Noc, Cedar River, and Menominee River), average annual survival of walleye was 61% in Little Bay de Noc, 65% in Big Bay de Noc, 68% for the Cedar River, and 48% for the Menominee River (computed by the method of Brownie et al. 1985). Our annual survival estimate for Little Bay de Noc (61%) agrees well with an age-frequency-based estimate of 60% reported by Schneider et al. (1991) for fish collected in 1988. Colby et al. (1994) suggested that annual survival >50% is desirable for rehabilitation of walleye stocks, so our survival data are encouraging.

The high survival rates of northern Green Bay walleye caused a shift in size structure towards higher proportions of larger (older) fish. For example, the mean length of Little Bay de Noc male walleye tagged in spring increased 53 mm from 1988-1993 to 1999-2003, and the percentage of tagged fish >584 mm increased from 5 to 20% for males and from 61 to 92% for females (Fig. 2). Similar shifts in size structure were observed for all four northern Green Bay stocks.

Fig. 2. Length-frequency distribution of male walleye tagged in Little Bay de Noc, Lake Michigan during 1988-1993, 1994-1998, and 1999-2004.



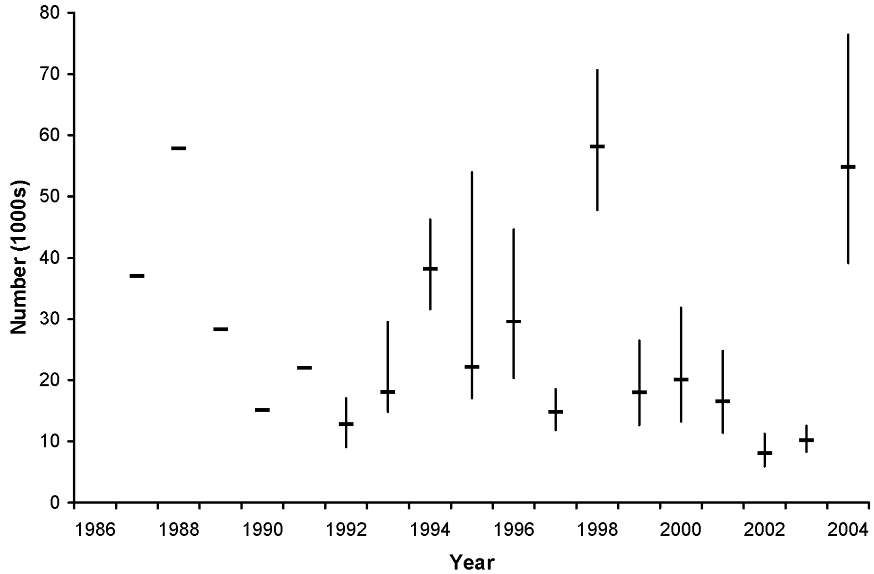
Exploitation. Based on cumulative tag returns through 2004, walleye exploitation rates were 3.9% in Little Bay de Noc, 3.0% in Big Bay de Noc, 2.7% in the Cedar River, and 4.4% in the Menominee River. These exploitation rates, however, were not corrected for non-reporting of tags. Thomas and Haas (2000) compared returns of reward with non-reward tags for walleye in Lake Erie and found that non-reward tags were under-reported by a factor of 2.7. Using this factor to adjust for non-reporting in Michigan waters of Green Bay, the exploitation rate was 10.5% in Little Bay de Noc, 8.1% in Big Bay de Noc, 7.3% in the Cedar River, and 11.9% in the Menominee River. These values are similar to the 8.1% exploitation rate of walleye in Saginaw Bay, Lake Huron, during 1992-2004 (Fielder et al. 2006) but considerably lower than the 18.3% exploitation rate of walleye in Lake Erie during 1989-2003 (Thomas and Haas 2005).

Southern Green Bay

Management. Crushed rock was installed at two locations during 1990-1992 in the Fox River and at two locations during 1999-2001 in southern Green Bay to increase the spawning substrate for the Fox River stock, which was reproducing at a level believed to be below full potential. To increase the abundance of the Sturgeon Bay stock, managers have relied on stocking the progeny of walleye taken from the Fox River during spawning. Sturgeon Bay was not stocked during 1985-1992 and thereafter was stocked intermittently (Table 2); Sturgeon Bay continues to support a put-grow-take fishery. The ban on commercial harvest of walleye in southern Green Bay that began in 1978 was continued, and angling regulations were unchanged during 1989-2006. Angling regulations for walleye in Wisconsin waters of Green Bay changed in 2007 to provide for consistent law enforcement off the mouth of the Menominee River, a boundary between the states of Michigan and Wisconsin. A no-minimum length limit for the Fox River continues to allow harvest of smaller walleye that are less contaminated with polychlorinated biphenyls (PCBs).

Abundance. The average number of walleye spawning in the Fox River during 1987-2004 was 28,000 and ranged from 8,100 to 58,100 (Fig. 3). The wide range of spawner abundances and large differences between consecutive years (e.g., 1998 and 1999) indicates that year-class strength was quite variable and mortality rates were high during the time series (see below). Spawner abundance exhibited no statistically significant trend during 1987-2004 (determined via linear regression: $F = 0.80$; $df = 1, 17$; $P = 0.39$). Spawner abundance was not available for the Sturgeon Bay stock.

Fig. 3. Numbers of walleye spawning in the Fox River during 1987-2004. Estimates for 1987-1991 are for all walleye; estimates for 1992-2004 are for all walleye ≥370 mm (surrogate for ≥age-3) and include 95% confidence intervals.



Sport-Fishery Catch and Harvest. The annual walleye catch (includes released fish) from the Fox River by anglers during 1986-2005 averaged 37,060 and ranged from 3,460 to 92,920. For Sturgeon Bay, the average catch was 1,420 and the range was from 180 to 7,520 (Table 7) (Kapuscinski and Lange 2005). Walleye catch was highest from the Fox River during the mid-1990s and again during 2003-2004, whereas catch from the Sturgeon Bay stock was highest during 1998-2005.

Table 7. Numbers of walleye caught by anglers (includes released fish) from three Lake Michigan stocks during 1986-2005 (hyphens indicate no data).

Year	Fox River	Sturgeon Bay	Milwaukee River
1986	33,124	878	285
1987	29,758	905	-
1988	24,409	7,520	-
1989	3,457	900	-
1990	45,648	661	163
1991	11,961	744	157
1992	17,515	-	7
1993	85,341	178	231
1994	65,190	223	-
1995	20,565	436	56
1996	92,915	759	-
1997	31,632	335	813
1998	11,354	4,147	265
1999	20,849	2,047	25
2000	14,953	562	-
2001	14,052	1,140	-
2002	13,779	1,539	903
2003	44,554	2,555	729
2004	89,704	1,126	491
2005	21,454	1,663	123
Mean	34,611	1,490	327

The annual walleye harvest from the Fox River during 1986-2005 averaged 6,900 and ranged from 260 to 27,370. In Sturgeon Bay during 1986-2005, the average harvest was 810, and the range was from 30 to 6,600 (Table 4). Walleye harvest from the Fox River was highest during 1986-1988 and high again during the mid-1990s, whereas harvest from the Sturgeon Bay stock was generally variable. Trends in walleye harvest from the Fox River did not always follow trends in catch. For example, in 2004, anglers caught 45,000 more fish than in 2003, but harvest declined by 1,300 fish. Kapuscinski and Lange (2005) concluded that this decline occurred because anglers were targeting trophy walleye (not the 2001 year-class that made up most of the catch), catching most of their walleye during the restricted spring season when only one fish >711 mm could be harvested, practicing catch and release, or some combination of these scenarios.

Movements. During 1987-2004, anglers voluntarily (no reward) returned 210 tags from walleye tagged in the Fox River. Of these returns, 80% were from the Fox River or southern Green Bay, 12% were from the Sturgeon Bay area, and the remainder were taken elsewhere. These results differ only slightly from the findings of Schneider et al. (1991), who found that 91% of walleye tagged in the Fox River during 1981-1983 were recaptured in the Fox River and 2.8% were recaptured in Sturgeon Bay. The minor differences between the two studies may have been caused by changes in the geographical distribution of walleye or by spatial or temporal variation in angler effort, which can easily bias recapture distributions (Wolfert and Van Meter 1978; Schwarz and Arnason 1990). Neither our study nor the Schneider et al. (1991) study accounted for spatial or temporal variation in angler effort.

During 1989-2004, anglers voluntarily returned information from 241 walleyes tagged in Sturgeon Bay. Of the returns, 94% were from the Sturgeon Bay area, 2% were from the Menominee River area, and the remainder were from elsewhere. These results are nearly identical to those of Schneider et al. (1991), who found that 94% of the tagged Sturgeon Bay walleye recaptured during 1984-1987 were caught within a 19-km radius of the tagging site, 1.8% had emigrated to the Menominee River, and 1.2% had emigrated to the Oconto River area (Fig. 1). Based on this comparison, movements of walleye tagged in Sturgeon Bay changed little from 1984-1987 to 1989-2004.

Growth. Growth changes differed for female and male walleye from the Fox River during 1990-2004. The growth coefficient, (*K*), of male walleye from the Fox River was higher during 1999-2004 than during 1990-1996 (Table 8) and regression indicated that *K* increased during 1991-2004 (r^2 = 0.63, P = 0.01). Conversely, regression indicated that *K* decreased for females during 1991-2004 (r^2 = 0.72, P = 0.001), but the estimates of *K* from the von Bertalanffy growth model did not differ from 1990-1996 to 1999-2004 (Table 8). The odd differences in growth history by sex may be attributed to the lower survival rates of males (see below), but this interpretation is speculative. We found no significant trends for the growth parameters (K, L_∞, or W_∞) of the Sturgeon Bay stock.

Table 8. Growth parameters estimated from additive error von Bertalanffy growth models for male and female walleye from two stocks in southern Green Bay, Lake Michigan. Also shown are the years data were collected, number of length-at-age samples, and the range of ages in the samples. Approximate standard errors (SE) and approximate 95% lower (LCL) and upper (UCL) confidence limits for each parameter are also provided.

Stock/ Year(s)	Sex	N	Age range	Para- meter	Estimate	SE	LCL	UCL
Fox River, 1990-1996	M	788	2-9	L_∞	975.2	51.05	875	1075.4
				K	0.0985	0.0103	0.0783	0.1187
				t_0	-2.4593	0.1962	-2.8445	-2.0742
Fox River, 1999-2004	M	721	2-14	L_∞	708.1	23.553	661.8	754.3
				K	0.1678	0.0173	0.1338	0.2017
				t_0	-2.0511	0.271	-2.5832	-1.519
Sturgeon Bay, 1990-1996	M	910	2-11	L_∞	771.1	17.963	735.8	806.3
				K	0.1723	0.0129	0.1469	0.1976
				t_0	-1.2042	0.2082	-1.6128	-0.7957
Fox River, 1990-1996	F	1,037	2-13	L_∞	894.5	12.844	869.2	919.7
				K	0.1501	0.0068	0.1368	0.1634
				t_0	-1.6278	0.136	-1.8947	-1.3608
Fox River, 1999-2004	F	758	3-14	L_∞	847.7	22.271	803.9	891.4
				K	0.138	0.0133	0.1118	0.1641
				t_0	-2.4659	0.3904	-3.2324	-1.6994
Sturgeon Bay, 1990-1996	F	902	3-14	L_∞	801.7	6.2428	789.5	814
				K	0.225	0.0096	0.2061	0.2439
				t_0	-0.351	0.1633	-0.6714	-0.0305

Schneider et al. (1991) concluded that growth of southern Green Bay walleye had not declined as a result of increased density, but a comparison of mean lengths of age-5 female walleye from the Fox River suggests density-dependent growth reductions may have occurred. Mean length of age-5 female walleye from the Fox River during 1987 was 571 mm (Schneider et al. 1991), whereas, during 1990-2004, mean length never exceeded 560 mm (Table 9). In contrast, mean length of age-5 females of the Sturgeon Bay stock was 543 mm during 1987, and this value was exceeded every year during 1990-1993 (Table 9). Therefore, the modest decline in growth rate of female walleye from the Fox River stock started during the 1980s, whereas the growth rate of females from the Sturgeon Bay stock may have increased during the 1980s, although it did not trend from 1990 through 1996. Growth of male and female walleye from Sturgeon Bay was more rapid than that of male and female walleye from the Fox River during 1990-1996 (Table 8), contrary to the findings of Schneider et al. (1991).

Table 9. Mean length (mm) of age-5 female walleye from two stocks in southern Green Bay, Lake Michigan during 1990-2004. The 95% confidence intervals about the means are in parentheses (hyphens indicate no data or $N < 5$.

Year	Fox River	Sturgeon Bay
1990	555 (548-562)	556 (550-562)
1991	554 (548-560)	557 (552-562)
1992	552 (546-558)	565 (552-578)
1993	554 (548-560)	557 (545-569)
1994	554 (546-562)	-
1995	557 (522-592)	-
1996	560 (554-566)	-
1997	-	-
1998	-	-
1999	542 (528-556)	-
2000	550 (535-565)	-
2001	531 (521-541)	-
2002	535 (519-551)	-
2003	542 (530-554)	-
2004	534 (520-548)	-

Maturity. From 1990-1996 to 1999-2004, the age structure of mature male walleye spawning in the Fox River did not differ, whereas the age structure of mature females shifted towards older fish (Table 10). During 1990-1996, age-3 and age-4 females comprised 28% of the run, and age-5 and older females comprised 72% of the run. During 1999-2004, only 12% of the females were ages 3 or 4, and 88% were age 5 or older. The increased proportion of older females in the spawning run is consistent with their decreased growth rates and high survival rates (see below). Schneider et al. (1991) did not provide maturity data for the Fox River stock, so we cannot compare age structure during 1990-2004 to that in the 1980s. However, the age structure of both male and female walleye spawning in Sturgeon Bay shifted towards older fish during 1990-1996 compared to 1980-1988 (Table 10). This shift towards an older age structure is inconsistent with the stable, yet high growth rates observed in Sturgeon Bay, and likely resulted from poor recruitment during 1985-1992 when no walleye were stocked.

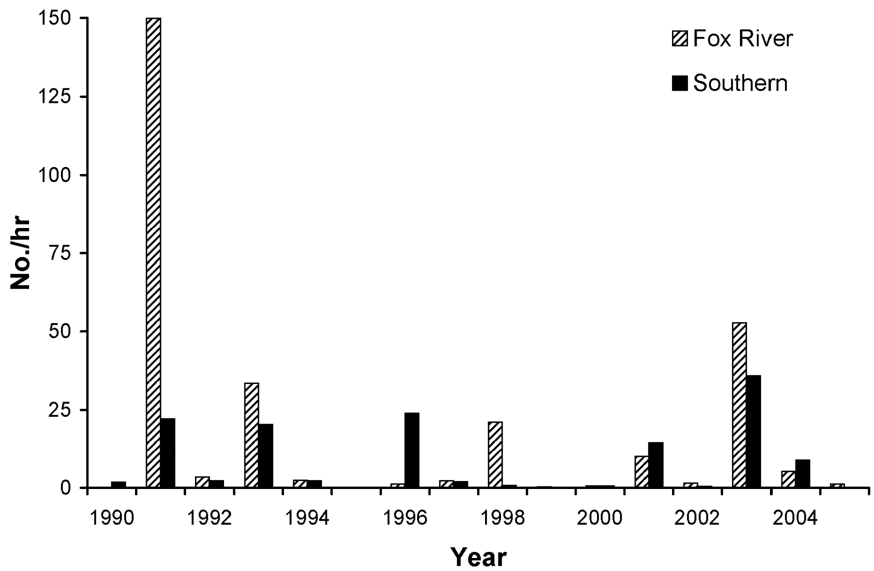
Table 10. Mean age composition (percent) of male and female walleye spawning in the Fox River during 1990-2004 and in Sturgeon Bay, Lake Michigan during 1990-1996. For Sturgeon Bay, mean age composition during 1980-1988 is from Schneider et al. (1991); age composition during 1976-1979 is not presented because of founding year-class effects.

		Age								
Year	***N***	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**≥10**
Fox River males:										
1990-1996	788	12	29	19	14	14	9	1	1	0
1999-2004	721	9	31	18	18	13	5	3	1	2
Sturgeon Bay males:										
1980-1988	13,650	8	30	20	20	11	6	3	1	1
1990-1996	911	1	4	8	26	27	19	8	4	2
Fox River females:										
1990-1996	1,037	0	9	19	13	18	20	10	5	5
1999-2004	758	0	2	11	17	20	15	12	12	11
Sturgeon Bay females:										
1980-1988	9,114	0	1	22	35	20	14	5	2	1
1990-1996	902	0	0	4	9	20	22	16	10	19

Poor natural recruitment in Sturgeon Bay relative to the Fox River likely resulted in differences in age structures of spawning walleye from the two stocks. During 1990-1996, males spawning in the Fox River were as young as age 2 and, on average, 2-year-old fish comprised 12% of the run, whereas ages 3 and 4 comprised 48% of the run, and the remainder (40%) were ≥age 5 (Table 10). In Sturgeon Bay, age-2 males comprised only 1% of the spawning run during 1990-1996, whereas ages 3 and 4 comprised 12%, and the majority (87%) were age ≥5 (Table 10). This comparison suggests that walleye from the Fox River stock matured considerably earlier than those from the Sturgeon Bay stock. However, Sturgeon Bay walleye grew faster than Fox River walleye during 1990-1996 and, therefore, should have matured earlier if growth is the mechanism that controls age at maturity.

Recruitment. The CPH of YOY walleye in late-summer and fall electrofishing surveys was highly variable across years, indicating large differences in year-class strength (Fig. 4). In the Fox River, CPH in the fall ranged from 0.1 to 149.8 during 1991-2005 with particularly large values (>50) in 1991 and 2003. In southern Green Bay, CPH in late summer during 1990-2005 was lower, ranging between 0 and 36, but the appearance of stronger and weaker year-classes usually followed the same pattern at the two locations (Spearman Rank Correlation; r_s = 0.71; P = 0.003). A relatively strong year-class (CPH ≥10) was typically produced once every two or three years at both locations, and a stretch of four consecutively weak year-classes occurred only once at each location: 1994-1997 in the Fox River and 1997-2000 in southern Green Bay. Variability in walleye year-class strength was likely caused by temperature fluctuations during spawning and hatching (Schneider et al. 1991; Hansen et al. 1998; Pitlo 2002).

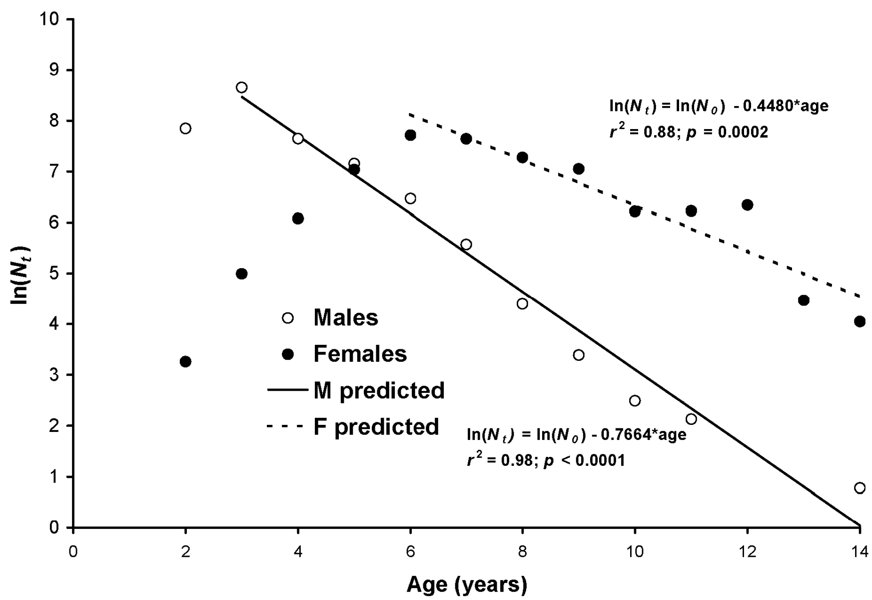
Fig. 4. Numbers of young-of-the-year walleye caught per hour of electrofishing in the Fox River and southern Green Bay, Lake Michigan, during 1990-2005. Electrofishing was conducted at index sites in the Fox River downstream from the De Pere Dam and in southern Green Bay within 8.9 km of the mouth of the Fox River.



Stocking was important for maintaining the Sturgeon Bay stock of walleye. The proportion of older spawners and the mean age of spawning females increased after stocking ceased. Sturgeon Bay received 46,000-333,000 fingerlings each year during 1973-1979 but no fingerlings during 1985-1992. Consequently, the proportions of older male and female spawners were greater during 1990-1996 than in 1980-1988 (Table 10). Mean age of females was 7.3 years in 1991-1992, 7.5 years in 1993-1994, and 9.0 years in 1995-1996. The increased proportion of older spawners and the progressive increase in mean age of female spawners were largely the result of relatively few wild-hatched fish recruiting to the spawning population.

Survival. Annual survival rate for male walleye spawning in the Fox River was 0.46 during 1991-2004 and that of females was 0.64. These survival rates are much higher than those reported by Schneider et al. (1991), which ranged from 15 to 33% during 1981-1985 (sexes not distinguished). Total instantaneous mortality (Z) differed among the sexes ($sex*t$ significant in general linear model; $P = 0.007$), and was higher for males ($Z = 0.77 \pm 0.1$; estimate ± 95% CI) than for females ($Z = 0.45 \pm 0.15$; Fig. 5). Both annual mortality and total instantaneous mortality for males were higher than the 50% threshold suggested by Colby et al. (1994) for healthy walleye stocks.

Fig. 5. Natural logarithm of catch-at-age $ln(N_t)$ for male and female walleye spawning in the Fox River during 1991-2004.



Eastern Shore

Management. Approximately 24.6 million walleye fingerlings and 219.8 million walleye fry were stocked into 22 tributaries along the eastern shore of Lake Michigan during 1973-2005 (Tables 2, 3). Most stockings of fry (69%) and fingerlings (76%) occurred in nine warm-water tributaries on the southeast shore of the lake from the White River to the Galien River (Fig. 1). The 13 tributaries north of the White River were stocked less intensely, and stocking often occurred in large cool-water lakes within these tributary systems. Stocking was the primary source of walleye recruitment for all eastern-shore tributaries, but some natural recruitment has been measured in the Muskegon and St. Joseph Rivers (R. O'Neal, Michigan DNRE, personal communication, 2008). The genetic integrity of eastern-shore stocks is considered by Michigan fishery managers when stocking walleye (Schneider et al. 2007). All walleye stocked into lakes and tributaries along the eastern shore of Lake Michigan are progeny of the Muskegon River stock. The Muskegon and St. Joseph Rivers historically supported the two largest stocks in this area of Lake Michigan.

The Michigan DNRE banned commercial harvest of walleye in 1969, although some commercial harvest in Great Lakes waters occurs by Indian tribes under treaty agreements. Subsistence fisheries for walleye by Indian tribes also occur in some areas and are regulated by a permit and quota system. Sport fishing is managed primarily using a minimum length, a daily bag limit, and seasonal closures to protect spawning adults (Schneider et al. 2007). The current Michigan sport-fishery regulations for walleye include a minimum length limit of 381 mm and a daily bag limit of five fish. The minimum length limit was established in 1976, and the bag limit was established in 1929. The season on Lake Michigan is open all year, whereas inland waters are open from the last Saturday in April through 15 March. The seasonal regulation was established in 1987, and the previous open season was from May 15 through February 28 for all Michigan waters. An exception, implemented for social reasons, exists for the St. Joseph River where no more than one walleye >584 mm may be possessed from below the first dam to the mouth of the river. Overall, sport-fishing regulations have not changed substantially since 1976, and changes in tribal harvest were relatively minor.

Abundance. Walleye spawning in the Muskegon River numbered 43,200 (±25,400 95% CI) in 1986, 46,500 (±4,500 95% CI) in 1998, and 38,000 (±7,300 95% CI) in 2002 (Day 1991; O'Neal 1998; Hanchin et al. 2007), indicating that the ban on commercial harvest initiated in 1969 and annual stocking initiated in 1978 has kept abundance stable since the mid-1980s. The 1986-2002 spawning runs averaged 42,600 fish, much greater than the roughly 2,000 fish in 1975 (Schneider et al. 1991) but less than the historic highs of 120,000-140,000 fish during 1953-1954 (Crowe 1955).

Sport-Fishery Harvest. The average annual harvest of walleye by the sport fishery from 24 eastern Lake Michigan ports (including charterboats), and specific tributaries during 1997-2005 was about 13,400 fish (Table 11). However, many areas were not surveyed every year. Furthermore, the harvest figures do not include some of the more-important tributaries (Lake Charlevoix, Portage Lake, Pentwater Lake, White Lake, lower Grand River, Black River, and Galien River), seasonally important early-spring and late-fall fisheries near harbors, nor some ice fisheries. Therefore, total annual harvest was likely higher than 13,400. Schneider et al. (1991) reported similar harvest levels for 1983-1987. Harvest occurs primarily in tributaries, and most of the harvest that occurs in Lake Michigan proper occurs near tributary mouths.

Table 11. Mean numbers of walleye harvested annually at different locations along the eastern shore of Lake Michigan by anglers fishing from charterboats, recreational boats, and shore during various time periods, 1997-2005 (SE = standard error). Harvest not labeled as being from charterboats is harvest from recreational boats and shore.

Location and harvest type	Period	Mean	SE
Lake Michigan (24 ports)	1997-2005	489	151
Lake Michigan charterboats	1997-2005	499	*
Manistee Lake	1999-2004	10	4.5
Manistee River	1999-2004	370	34.5
Muskegon Lake (summer & winter)	2002	2,082	527.5
Muskegon River (lower)	1999-2005	363	22
Grand River (portions of upper and middle)	2004	3,112	948
Kalamazoo River (lower)	2004	2,214	470
St. Joseph River (middle and lower)	1997-2004	3,833	558.5
St. Joseph River charterboats (lower)	1998-2003	434	*
Total		13,406	

*Charterboat harvest is based on a reporting system for which standard errors are not available.

Movements. Walleye tagged during spawning runs in the Muskegon River emigrated to Lake Michigan and tributaries other than the Muskegon River at a higher rate in 2002 than previously reported. Of tag returns, 50% came from Lake Michigan and other tributaries during 2002 (Hanchin et al. 2007), compared to 0.7-16.8% during 1948-1987 (Schneider et al. 1991). The increase in emigration to Lake Michigan cannot be explained, because tagging studies were not standardized and recapture effort was not quantified. The geographic distribution of 2002 tag returns ranged from the St. Joseph River to Grand Traverse Bay, with one from Green Bay, and was similar to that reported by Schneider et al. (1991) for 1948-1987. Annual migrations of Muskegon River walleye into Lake Michigan appear to be variable, but the geographic distribution of the fish within Lake Michigan appears relatively constant. Some adult walleye remained in the Muskegon River throughout the year. Their density in the lower river below the first dam was about $0.8 \cdot ha^{-1}$ (O'Neal 1997).

Growth. Growth of walleye from eastern Lake Michigan varied among stocks. Growth of walleye from the St. Joseph River was more rapid than for other stocks (Table 12). This finding is tenuous, though, because length-at-age information for the St. Joseph River stock was collected via creel census, whereas length-at-age for the other stocks was collected via experimental sampling. Thus, the growth rate of St. Joseph River walleye may have been overestimated at younger ages, because the 381-mm minimum-size limit on harvest made slow-growing fish less vulnerable to the creel. Trends in growth of eastern Lake Michigan stocks could not be analyzed because a time series of growth data was lacking.

Table 12. Growth parameters estimated from additive error von Bertalanffy growth models for male and female walleye from three stocks in eastern Lake Michigan and the Milwaukee River stock in western Lake Michigan. Also shown are the years data were collected, number of length-at-age samples, and the range of ages in the samples. Approximate standard errors (SE) and approximate 95% lower (LCL) and upper (UCL) confidence limits for each parameter are also provided.

Stock/Year(s)	Sex	*N*	Age range	Para-meter	Estimate	SE	LCL	UCL
Grand River, 2004-2005	F	177	5-15	L_∞	900.2	91.771	719	1081.3
				K	0.1104	0.0454	0.0208	0.1999
				t_0	-3.4638	2.313	-8.029	1.1015
Milwaukee River, 1996-2002	M, F	678	1-6	L_∞	645.2	25.056	596	694.4
				K	0.384	0.0356	0.314	0.4539
				t_0	0.1038	0.0505	0.0047	0.2029
Muskegon River, 1998, 2002	M	605	2-18	L_∞	842.2	53.3	737.5	946.8
				K	0.0969	0.0167	0.0641	0.1296
				t_0	-3.369	0.6321	-4.6104	-2.1277
Muskegon River, 1998, 2002	F	403	4-17	L_∞	859.3	46.144	768.6	950
				K	0.1082	0.027	0.0551	0.1613
				t_0	-5.2246	1.6963	-8.5595	-1.8897
St. Joseph River, 2005	M, F	209	0.5-9	L_∞	646.5	26.474	594.3	698.7
				K	0.3564	0.0454	0.2669	0.446
				t_0	-0.9875	0.15	-1.2833	-0.6917

Recruitment. Natural recruitment to the Muskegon River stock continues to be limited. All walleye stocked into this system since 1997 were marked with oxytetracycline. Hatchery-reared walleye comprised 35-100% of the YOY walleye collected during 1997-2004 (Fig. 6). Moderate percentages (35-50%) of wild walleye were found only in those years when stocking densities were low; hatchery-reared walleye dominated the catch when stocking density or survival of stocked walleye was high. Densities of YOY walleye in Muskegon Lake were variable and not related to numbers stocked during 1994-2005 (linear regression, $r^2 = 0.07$, $P = 0.45$; Fig. 7). Hanchin et al. (2007) also found that variability in year-class strength was relatively high in the Muskegon River system based on a catch-curve analysis of the 2002 adult spawning run. However, the age structure of the Muskegon River stock was stable from 1987 through 2002, with a modal age of 7 or 8. In 1998, walleye up to age 15 were observed, and, in 2002, many large age-8-18 walleye were observed.

Fig. 6. Percentage of young-of-the-year (YOY) walleye caught near Muskegon in fall that were of hatchery origin and the numbers of walleye stocked in Muskegon Lake and River during spring 1997-2004.

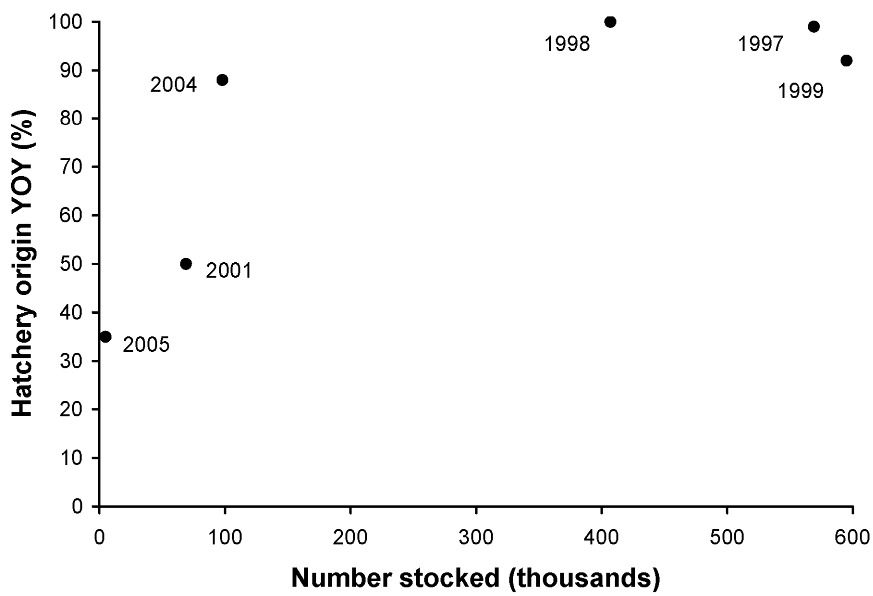
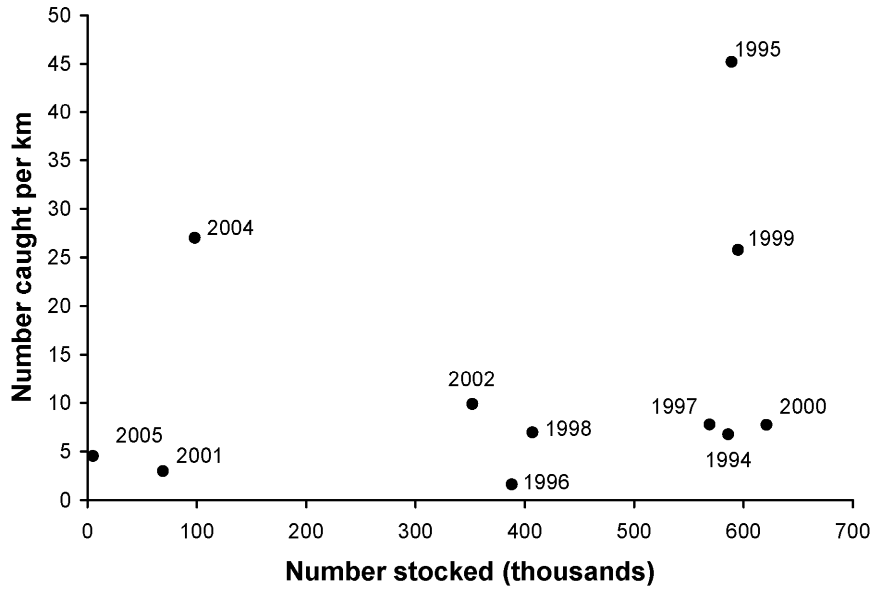


Fig. 7. Numbers of young-of-the-year walleye caught at Muskegon per km of shoreline electrofished during autumn and the numbers of walleye stocked in Muskegon Lake and River during spring, 1994-2005.



The recruitment bottleneck affecting Muskegon River walleye may occur between egg deposition and the hatching of larvae. Annual egg deposition was estimated at 4.0-4.9 billion in 1998 and 2002, based on mean number of female spawners and fecundity-length data from Day (1991). However, low larval densities were found in the river in 1986 ($0.166 \bullet m^{-3}$ during a 14-day period) (Day 1991) and in 2004 ($0.085 \bullet m^{-3}$ during a seven-day period; D. Jude, University of Michigan, personal communication, 2008). Based on average discharge from the Muskegon River during the 14-day sampling period, about 1.2 million fry were produced during 1986. Gamete viability does not appear to be limiting larval production, because the eggs collected for rearing by Michigan have about a 50% average hatch rate. Assuming egg deposition in 1986 was similar to that in 1998 and 2002 (mean = 4.45 billion), larval production during 1986 was very low compared to an estimated potential production of 724.6 million fry that would result from 4.45 billion eggs, assuming a 0.177 survival rate to the eyed-egg stage (reported for natural gravel/rubble substrates in a Minnesota lake by Johnson (1961) and a 0.92 survival rate from eyed-eggs to swim-up fry (observed under laboratory conditions by Schneider et al. (2003)). Poor fry production in the river may have resulted from egg predation, unfavorable thermal conditions for egg incubation due to dams, or unknown factors. Factors affecting recruitment in Muskegon Lake include pollution, habitat degradation, and predation from, and competition with, alewife and gizzard shad (O'Neal 1997).

The St. Joseph River was stocked with oxytetracycline-marked walleye fingerlings in 2005. YOY evaluations conducted during autumn found that 64% of the YOY were stocked, suggesting a fair level of natural reproduction and good survival of stocked fingerlings.

Survival. Based on infrequent observations, survival of adult walleye in the Muskegon River stock appeared relatively stable during the past 30 years. Survival of fish sampled during spawning runs was 65% in 1998 and 62% in 2002, as determined by use of a catch-curve regression (Hanchin et al. 2007). Schneider et al. (1991) estimated survival of walleye spawning in the Muskegon River stock at 62% during 1977-1982. These survival rates are relatively high for Michigan and well within acceptable limits; annual survival rates in other Michigan waters ranged from 35 to 80% (Schneider 1978; Miller 1997; Haas et al. 1985; Fielder and Waybrant 1998; Schneeberger 2000).

Exploitation. Exploitation of walleye in the Muskegon River stock was 11.1% in 2002, based on harvest from a creel census in Muskegon Lake and tag-return ratios, and was considered within acceptable limits (Hanchin et al. 2007). Generally, annual exploitation rates of ≤35% are considered acceptable in Michigan. Minimum exploitation rates for the Muskegon River stock from 1975 to 1987 ranged from 0.3 to 21.4% based on angler tag returns (Schneider et al. 1991). The high exploitation rate of 21.4% in 1981 was considered the best estimate of exploitation because of cash rewards for tag returns and extensive publicity of the reward program. Recent exploitation rates of walleye stocks from other Michigan waters ranged from 8 to 39% (Clark et al. 2004, 2005; Hanchin et al. 2005a, 2005b; Thomas and Haas 2000).

Milwaukee River

Management. The long-term management goal for walleye in the lower Milwaukee River and Harbor is to re-establish a self-sustaining stock (Wisconsin Department of Natural Resources 2005a). Walleye were extirpated, or nearly extirpated, because of habitat loss and degradation. A detailed rehabilitation plan was developed in 1998 with the help of public input (Wisconsin Department of Natural Resources 1998). As rehabilitation progressed, the following strategies were developed:

- Stock 10,000 extended-growth walleye fingerlings from Great Lakes stocks each year through 2004
- Evaluate predation, if any, by walleye on Chinook salmon (*Oncorhynchus tshawytscha*) smolts stocked in the same area
- Evaluate the use of Visible Implant Elastomer (VIE) technology to mark stocked walleye
- Document natural reproduction by walleye
- Estimate abundance of walleye
- Determine growth and survival of stocked walleye
- Determine movement and seasonal migration patterns of walleye using radio telemetry
- Assess the contribution of walleye to the nearshore fishery

Variable numbers of walleye fry and fingerlings were stocked in the Milwaukee River and adjacent harbor during 1986-2006 (Tables 2, 3), but fry stocking yielded only marginal results. The target of stocking 10,000 extended-growth fingerlings each year was achieved in 5 of 11 years during 1995-2005, and walleye stocked since 1998 were progeny of stocks in the Lake Michigan drainage (Wolf River and Lake Winnebago system or Puckaway Lake, WI). Stocking continues to be a management priority. Investigations of walleye preying on Chinook salmon smolts led to changes in salmon stocking locations that alleviated walleye predation on the smolts (Hirethota and Burzynski 2004). The VIE technique was used to mark stocked walleye, but it was abandoned after unfavorable evaluation in favor of a single fin clip (Hirethota and Burzynski 2004; Thompson et. al. 2005). Habitat in the Milwaukee River was also rehabilitated and enhanced. Water quality improved after several pollution abatement and prevention measures were enacted. The lowermost dam on the river was removed in 1997, opening an additional 9.6 km of river to fish moving upstream from Lake

Michigan and expanding angling opportunities. Additionally, the Wisconsin DNR improved in-stream habitat by adding 200 tons of fieldstone boulders to the river channel in the previously impounded area. Bank stabilization efforts included the use of 600 tons of limestone riprap as toe protection to prevent further erosion, live willow cuttings, and construction of nine bendway weirs (Wisconsin Department of Natural Resources 1994). These changes appear to have increased the diversity of native fish species and benefited anadromous trout and salmon by providing additional habitat (Wisconsin Department of Natural Resources 2005b).

Abundance. Walleye abundance in the Milwaukee River and Harbor was low during 1996-2006. The number of fish in all age-classes typically ranged from 430 to 880 between 1996 and 2005. The largest number of walleye, 5,340, was present in 2004. However, abundance was heavily influenced by survival of walleye stocked during the previous year because most fish were age 1. Numbers of walleye ≥age 2 ranged from 7 to 970 during 2002-2006. The scarcity of older walleye in the Milwaukee River could be due to dispersal, harvest, or both; we currently do not have evidence supporting the relative importance of these factors.

Sport-Fishery Harvest. A sport fishery quickly developed in the Milwaukee River due to the availability of creel-sized fish and interest by the public. Anglers targeted walleye in several areas, and creel surveys indicated a sharp increase in the angling effort for walleye in 1997 and 1998, just the second and third years after fingerling stocking began (Hirethota and Burzynski 2004). Although many anglers practiced catch-and-release fishing, liberal fishing regulations allowed a substantial harvest relative to the numbers of walleye present (Table 4). Current sport-fishery regulations for walleye in the Milwaukee River include a minimum length limit of 381 mm and a daily bag limit of five. The season is open all year.

Movements. Walleye movements, as determined from radio telemetry, exhibited a clear seasonal and spatial pattern. Walleye used the cooler Milwaukee Harbor as a thermal refuge in the summer and warmer canals in the winter (Hirethota and Burzynski 2004). Coincidentally, this movement pattern helped keep adult walleye away from Chinook salmon smolts that were stocked in the harbor in late spring. Radio telemetry also indicated that adult walleye took refuge in canals in the Menominee River (a tributary to the Milwaukee River) during late fall and winter. The canals receive discharges of warm water from an electric-generating plant.

Growth. Growth of Milwaukee River walleye during 1996-2002 was rapid and, on average, fish reached 433 mm at age 3 (Table 12). Rapid growth was attributed to two factors (Hirethota and Burzynski 2004):

- Sufficient forage available in the form of alewife, gizzard shad, shiners (*Notropis* spp.), and sticklebacks (Gasterosteidae)
- Movement to thermal refugia

Length-at-age was only available for ages 1-6, so it is likely that growth parameters will change as the stock ages and more data are acquired. Small sample sizes precluded sex and year-specific growth estimation.

Maturity. Only 19.7% of all walleye collected from the Milwaukee River during 1998-2001 were mature, and 87.5% of the mature fish were age 4 or age 5 (Hirethota and Burzynski 2004). Some (9.5%) male walleye matured as early as age 2, and some (37.5%) females matured as early as age 3. The early maturity of walleye in the Milwaukee River was most likely due to low densities and rapid growth (Colby and Nepszy 1981).

Recruitment. Successful natural reproduction by walleye in the Milwaukee River has not been verified. Spawning has occurred, as evidenced by the collection of a few spent female walleye during spring surveys. Larval and YOY surveys have not found naturally produced walleye. Identifying wild-hatched walleye fingerlings was possible because all stocked walleye fingerlings were marked (excluding walleye fingerlings stocked in 1999).

Community and Habitat Trends

Green Bay. The introduction and establishment of non-native species continued to alter the Green Bay aquatic ecosystem during 1990-2005. Invasion by dreissenids in 1990 has physically altered substrates, redirected nutrient pathways to the benthos (Hecky et al. 2004), and increased water clarity. For example, average Secchi-disk depth during August in Little Bay de Noc increased 36%, from 3.4 m in 1989-1990 to 4.6 m in 2004-2005. Concurrently, abundance of alewife and rainbow smelt declined, and the summer sport fishery for walleye in Little Bay de Noc moved farther offshore to deeper waters (Zorn and Schneeberger, in press).

White perch abundance in southern Green Bay increased during the mid- to late 1990s, decreased rapidly during the early 2000s, and, in 2006, was at a level much lower than the nuisance levels observed during the late 1990s (R. Lange, Wisconsin DNR, personal communication, 2006). White perch and threespine stickleback (*Gasterosteus aculeatus*), both first detected in Big and Little Bay de Noc during 1989-1990 (Schneeberger 2000), have not established large populations in northern Green Bay. The most recent fishes to invade were round goby and ruffe (*Gymnocephalus cernuus*). Round goby were first collected from Little Bay de Noc in 1998 (Clapp et al. 2001) and from Big Bay de Noc in 2002 (Zorn and Schneeberger, in press). In each bay, round goby made up >75% of the fish caught in summer trawl surveys within four years of initial detection, and the species was similarly abundant in southern Green Bay. Ruffe numbers have not increased sharply, although ruffe only recently became established. They were first observed in Little Bay de Noc in 2002 and in Big Bay de Noc in 2004 (Zorn and Schneeberger, in press). Two non-native zooplankters, *Bythotrephes longimanus* and *Cercopagis pengoi*, are established, but their affect on the aquatic community is currently unknown.

Riparian development and excessive sediment runoff from the Green Bay watershed continues. Contaminants, especially PCBs, persist in most, if not all, Green Bay fishes. Cleanup efforts have progressed since 1991 (Michigan Department of Community Health 2009; Pastor 2007; Wisconsin Department of Natural Resources 2007a), and contaminated sediments are now being removed from the Fox River upstream and downstream of the De Pere Dam (Fig. 1). Fish consumption advisories due to mercury and PCB contamination remain in effect for walleye, most other large-bodied piscivores, and bottom-feeding fishes.

Eastern Shore. Fish communities in Lake Michigan's nearshore waters and tributaries continue to change as summarized in Clapp and Horns (2008). Numerous non-indigenous species have established populations in Lake Michigan during the past 20 years. Examples include *Bythotrephes longimanus*, dreissenids, and round goby. Invasion by round goby coincided with severe reductions in two native inshore fishes, the johnny darter (*Etheostoma nigrum*) and mottled sculpin (*Cottus bairdi*). The filtering activities of dreissenids are affecting the base of the food chain by reducing zooplankton populations. The proliferation of dreissenid mussels coincided with severe reductions in populations of the burrowing amphipod *Diporeia* spp. The energy density of alewife, an important food of walleye (Diana 2006), was 23% less in 2002-2004 as compared to 1979-1981, which is likely related to the decline in *Diporeia* spp.. Overall abundance of prey fishes such as alewife, rainbow smelt, and bloater are at low levels. The abundance of yellow perch (*Perca flavescens*) is low, and its recovery to former levels of abundance is uncertain. Gizzard shad remain abundant in tributaries, and white perch abundance has increased (O'Neal 1997). Degradation of important littoral zone habitat in tributaries continues as a result of dredging and filling activities for development (O'Neal 1997).

Milwaukee River. Actions taken to rehabilitate walleye in the Milwaukee River have benefited native and non-native fishes. Native fishes increased in abundance and diversity following pollution abatement, dam removal, habitat enhancements, and bank stabilization (Wisconsin Department of Natural Resources 2005b). The improved environment in the river appeared to also benefit non-native anadromous trout and salmon by providing additional habitat (Wisconsin Department of Natural Resources 2005b).

Discussion

Actively managed walleye stocks in Lake Michigan have progressed along the rehabilitation continuum described by Colby et al. (1994). Stable abundance, stable or decreased growth rates, and natural recruitment suggest the Little Bay de Noc stock may be entering the late rehabilitation phase and that the Fox River stock is rehabilitated. However, these population dynamics were observed in systems with limited spawning and nursery habitat. If habitats are improved by removal of tributary dams and reductions in sediment runoff, the number of suitable spawning locations will increase, a higher proportion of eggs will hatch, and further population expansion may occur. The Little Bay de Noc stock may be self-sustaining, and the St. Joseph River stock has some natural recruitment, but both are still supplemented with stocked fish. Walleye stocks in Big Bay de Noc, Sturgeon Bay, and the Milwaukee and Muskegon Rivers are still classified as depressed due to persistent poor recruitment and reliance on stocking to maintain adult populations. The status of the Menominee River stock cannot be determined even though natural reproduction is occurring because spawning fish are of both hatchery and wild origin.

Some walleye stocks in Lake Michigan appear to mix extensively. As many as 50% of walleye tagged in the Muskegon River were caught in Lake Michigan proper or in other tributaries, primarily between the St. Joseph River to the south and Grand Traverse Bay to the north. The extent that eastern-shore stocks use Lake Michigan for refuge and foraging is currently unknown. About 20% of the Fox River walleye migrate north into Green Bay after spawning, crossing what was previously assumed to be stock boundaries. Cedar River walleye also migrated extensively, although movements of walleye from other northern Green Bay stocks are more limited. Colby and Nepszy (1981) warned against managing walleye stocks within artificial geographic boundaries, and many others have supported a stock-specific approach to management (Wolfert and Van Meter 1978; Todd and Haas 1993; Palmer et al. 2005). Tag-and-recapture and genetic studies can help identify the geographic range of walleye stocks, determine if remnant wild stocks persist (e.g., the Menominee River), and enhance rehabilitation and management efforts.

Growth of walleye from the Milwaukee and St. Joseph Rivers was very rapid. Rapid growth was probably due to relatively low abundance, large habitats with favorable thermal regimes (Hirethota and Burzynski 2004), and the availability of high-energy-density soft-rayed prey, such as alewife and gizzard shad (Quist et al. 2003), that walleye prefer (Knight and Vondracek 1993). Although growth rates were also high in the Fox River, length-at-age decreased for female walleye during 1991-2004. The smaller length-at-age were probably compensatory responses to high abundance of walleye relative to available prey, as previously observed for walleye stocks in the Bay of Quinte, Lake Ontario (Bowlby et al. 1991); in the Muskegon River (Schneider et al. 1991); and in western Lake Erie (Colby et al. 1994). In contrast, length-at-age of male walleye from the Fox River increased during 1991-2004. The slowed growth of females and increased growth of males from the Fox River may have resulted from differential mortality rates between the sexes. As compared to male walleye, the abundance of females likely increased over the study period due to their lower mortality rate, which was a result of females having reproductive behavior that was less energetically costly (Henderson and Nepszy 1994) and greater protection from harvest. Female walleye undergo brief spawning migrations into the Fox River, and spring sport-fishery regulations protect most females from harvest during this short period of time when they are accessible to river anglers. Conversely, male walleye spend more time in the Fox River and often remain in the river after the spring sport-fishery regulations expire, making them vulnerable to harvest. The harvest of small, slow-growing males in the Fox River may have contributed to the apparent fast growth of males.

Survival and exploitation rates of adult walleye from the various stocks in Lake Michigan that we examined appear satisfactory for rehabilitation. Survival rates ranged from 48 to 68%, were high and stable for the Muskegon River stock for nearly 30 years, and were typically >50%, as recommended for rehabilitation (Colby et al. 1994). Exploitation was <12%. High survival rates, low exploitation rates, and the fact that stocked fingerlings have re-established stocks (e.g., Sturgeon Bay) or increased abundances (e.g., Muskegon River) indicates that limitations to walleye rehabilitation occur between egg fertilization and the fingerling stage.

Growth, survival, and exploitation of adult walleye from most stocks appear suitable for rehabilitation, but self-sustainability has not been realized in most areas because of limited recruitment from natural reproduction. Among the walleye stocks in Lake Michigan, only the Fox River stock is totally self-sustaining. The potential of most stocks to produce recruits is probably a small fraction of what it was prior to industrialization, because critical spawning and nursery areas were destroyed or degraded by development of shorelines for industrial ports, pollution (Schneider and Leach 1977), sedimentation from watershed development, dredging of tributaries, and destruction of wetlands. Moreover, many walleye spawning sites were destroyed, degraded, or made inaccessible by dam construction (Schneider and Leach 1977). Reclaiming or constructing suitable spawning and nursery areas can enhance natural reproduction of walleye, but these efforts will be compromised if tributary sediment loads are not reduced. Nate et al. (2001) suggested that large amounts of sand might restrict walleye abundance in landlocked northern Wisconsin lakes by limiting recruitment. Some artificial spawning substrates installed in the Fox River and southern Green Bay during 1990-2001 have started filling with sediment. Future habitat construction should incorporate rigorous pre- and post-construction evaluations, as suggested for projects in Saginaw Bay, Lake Huron (Fielder 2002b). Pre-construction evaluation should determine the expected life of the project and its potential to increase walleye production.

Research and Management Needs

Compilation of this report allowed us to identify several information gaps that, if filled, would enhance the management of walleye stocks in Lake Michigan. Length-at-age data are needed for both sexes and all age groups before biologists can accurately estimate walleye growth and explore differences among stocks. Growth estimates for most stocks would have been improved with more data on age-4 and younger walleye. For walleye in the Milwaukee and St. Joseph Rivers, data were unavailable for older ages, and sex-specific data were limiting. The relatively young Milwaukee River stock offers an opportunity to quantify density-dependent growth responses as the stock ages and increases in abundance. For example, biologists may be able to describe how age at maturity changes as growth slows with increased abundance (Colby and Nepszy 1981; Schueller et al. 2005).

Collection of length-at-age data from all age-classes in the population will probably require sampling outside of the spawning season when mature and immature fish are mixed (e.g., fall electrofishing).

Further research is needed to guide stocking policies, especially in areas where walleye are stocked on top of naturally reproducing stocks (e.g., Little Bay de Noc and the St. Joseph River). The Michigan DNRE is quantifying contributions of stocked and wild walleye by marking stocked walleye with oxytetracycline and examining recaptures. Such studies should be continued or initiated to guide stocking when used as a tool for rehabilitation. In addition, investigation is needed into the discreteness and relative contributions of river- and reef-spawning walleye, particularly in Little Bay de Noc, which is a Michigan DNRE brood source. Palmer et al. (2005) caution that stocking walleye that are not adapted to local spawning areas (river vs. lake) can result in outbreeding depression, whereas stocking walleye that are adapted to local conditions may result in higher recruitment. For example, if Little Bay de Noc fish (the brood source) are primarily river spawners, then walleye rehabilitation in Big Bay de Noc (which lacks high-quality spawning rivers) might be more successful if walleye from a reef-spawning brood source were stocked.

Research identifying and quantifying interactions between walleye and non-native species will help guide walleye rehabilitation and non-native species management. Alewife can prey directly on walleye fry, compete with them during their planktivorous stage, and prey upon and compete with native prey fishes such as emerald shiner (*Notropis atherinoides*) and yellow perch (Wells and McLain 1973; Schneider and Leach 1977; Fielder et al. 2007; Madenjian et al. 2008). Although alewife numbers are currently relatively low in Lake Michigan (Madenjian et al. 2002), large aggregations of spawning alewife occur in tributaries when age-0 walleye may be vulnerable. Gizzard shad are currently abundant in the Fox River, but it is unknown if they restrict walleye recruitment via fry predation, as suggested for alewife. Round goby are abundant in many areas of Lake Michigan, and ruffe populations continue to build slowly in Big and Little Bay de Noc. However, the potential effect of round goby and ruffe on walleye rehabilitation is not well understood; ruffe do not appear to be voracious egg predators like the round goby (Ogle 1998; Steinhart et al. 2004).

The influence of dams and barriers on walleye rehabilitation efforts is likely significant but has not been fully addressed. Rehabilitation in northern Green Bay has progressed furthest in Little Bay de Noc, where the bulk of natural reproduction comes from walleye spawning in the largely contiguous Whitefish River and on reefs at the northern end of the bay. Most other key rivers in Green Bay have dams within a few kilometers of their mouths, which limit access to potential spawning areas. Sea lamprey barriers exist on other streams, and more barriers may be constructed on other tributaries to Green Bay. If river-spawning stocks historically produced most of the walleye in Green Bay, then dams and barriers may be a major impediment to rehabilitation of naturally reproducing stocks. For example, Jones et al. (2003) estimated that areas upstream of a dam on a Lake Erie tributary could produce eight times more larval walleye than the areas downstream of the dam that are presently connected to Lake Erie. Thus, most of the fry-producing potential of tributaries to Green Bay may be unavailable. Future research is needed to assess potential effects of dams and barriers on the ability to restore self-sustaining walleye stocks in Lake Michigan and to guide future decisions regarding dam removal, fish passage, and placement of sea lamprey barriers.

Predation by a growing population of double-crested cormorants (*Phalacrocorax auritus*) is having an unknown effect on the Green Bay fish community. Previous studies in Green Bay have shown that double-crested cormorants feed opportunistically on the most-abundant fish species (B. Belonger, Wisconsin DNR, unpublished data; S. Meadows, University of Otago, personal communication, 2008). Double-crested cormorant predation on walleye may be unimportant, but cormorant predation on other fishes that walleye eat, such as yellow perch and gizzard shad, may indirectly affect walleye. Research quantifying double-crested cormorant predation on fish populations in Green Bay will help adjust expectations for walleye rehabilitation and guide cormorant management.

Viral hemorrhagic septicemia (VHS) is the most-recent threat to walleye and other native fishes in the Great Lakes. It causes fatal anemia and hemorrhaging in many species of fish and was the suspected cause of fish kills in the Great Lakes during 2005-2007 (New York State Department of Environmental Conservation 2008; Michigan Department of Natural Resources 2007). The virus was detected in walleye from Lake Erie (P. Bowser, Cornell University College of Veterinary Medicine, personal communication, 2006) and the Thunder Bay area of Lake Huron (Michigan Department of Natural Resources 2007). The virus was also detected in freshwater drum (*Aplodinotus grunniens*) from Little Lake Butte des Morts and Lake Winnebago (Wisconsin Department of Natural Resources 2007b), which both drain into Green Bay via the Fox River. More than 30 species of fish are susceptible to VHS, including species that are potential walleye prey. Large-scale infections and fish kills would undoubtedly jeopardize walleye rehabilitation. Research is needed to determine how VHS might affect walleye rehabilitation. Initial research should attempt to determine if stress levels induce VHS outbreaks and if VHS resistance differs among walleye stocks or between wild-hatched and hatchery-reared walleye.

Research is needed on how recent changes in nutrient and energy flow and increased water clarity affect walleye abundance, behavior, and reproduction. Phosphorus loading to Lake Michigan has been relatively stable since 1990 (Madenjian et al. 2002; Holey and Trudeau 2005; U.S. Environmental Protection Agency 2006), yet water clarity has increased notably due to colonization by dreissenids. Increases in water clarity can result in reductions in walleye habitat and, therefore, walleye abundance. Lester et al. (2004) calculated that increased water clarity in Lake St. Clair resulted in a >50% loss of walleye habitat and that walleye abundance declined by a similar proportion. Tag-return data from Little Bay de Noc suggests that Lake Michigan walleye have responded to increased water clarity by moving further offshore to deeper waters during the summer (Zorn and Schneeberger, in press). In addition to increasing water clarity, dreissenids may be redistributing nutrients to the benthos and changing the lower-trophic community in ways that may influence walleye reproduction; increased abundance of *Cladophora* may further limit available spawning habitat, and reduced pelagic productivity can decrease carrying capacity (Hecky et al. 2004). Obtaining a better understanding of large-scale changes to the aquatic community will help forge more-effective strategies for rehabilitation of walleye stocks in Lake Michigan.

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STATUS OF WALLEYE IN LAKE HURON

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Abstract

Walleye (*Sander vitreus*) in Lake Huron comprise several localized populations and immigrants from the lower Great Lakes. The status of these populations and their fisheries varies across the lake. The contemporary (1992-2004) average annual walleye yield of 253,000 kg is still well below the target of 700,000 kg established as a fish-community objective. Many populations are depressed because of limited recruitment and, in some instances, because of excessive fishing. Recruitment has been limited due to loss of spawning habitat (particularly due to barriers on tributaries) and effects of non-native species. Newer sources of information include genetic identification of resident populations and of immigrants, quantification of consumption, and habitat assessment and planning for

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future remediation. Increased natural recruitment has been documented in Saginaw Bay since 2003 concurrent with the decline of the alewife (*Alosa pseudoharengus*) population in Lake Huron. Predacious and competitive effects of alewives have been a limiting factor in the past, and their amelioration is believed to have provided for better larval survival.

Introduction and History

The major walleye (*Sander vitreus*) populations and fisheries in Lake Huron are located in bays and littoral areas (Fig. 1; Schneider and Leach 1977; Schneider and Leach 1979; Reckahn and Thurstan 1991), because these areas provide suitable thermal habitat and proximity to reproductive habitat in rivers and their estuaries (Eshenroder 2004; Jones et al. 2003). Annual commercial yield of walleye during 1885-1945 averaged over 860,000 kg lakewide and often exceeded 680,000 kg in Saginaw Bay (Baldwin and Saalfeld 1962). By the mid-1900s, many of these populations and their fisheries were in severe decline for various reasons, including loss or degradation of physical habitat, declines in water quality, and overfishing (Spangler et al. 1977). These population declines may have been exacerbated by the predatory and competitive effects of non-native planktivores like rainbow smelt (*Osmerus mordax*) and alewife (*Alosa psuedoharengus*), which were abundant during this time (Schneider and Leach 1977; Schneider and Leach 1979). Most of the research and management of walleye in Lake Huron has been centered on recovery of these reduced populations. In 1995, the Lake Huron Committee of the Great Lakes Fishery Commission established a fish-community objective for walleye: to reestablish and/or maintain walleye as the dominant cool-water predator over its traditional range (in Lake Huron) with populations capable of sustaining an annual harvest of 700,000 kg (DesJardine et al. 1995). However, yields during 1992–2004 have averaged just 253,000 kg (Fig. 2).

Fig. 1. Historically important walleye populations in Lake Huron. Size of circle approximates relative size of contemporary populations.

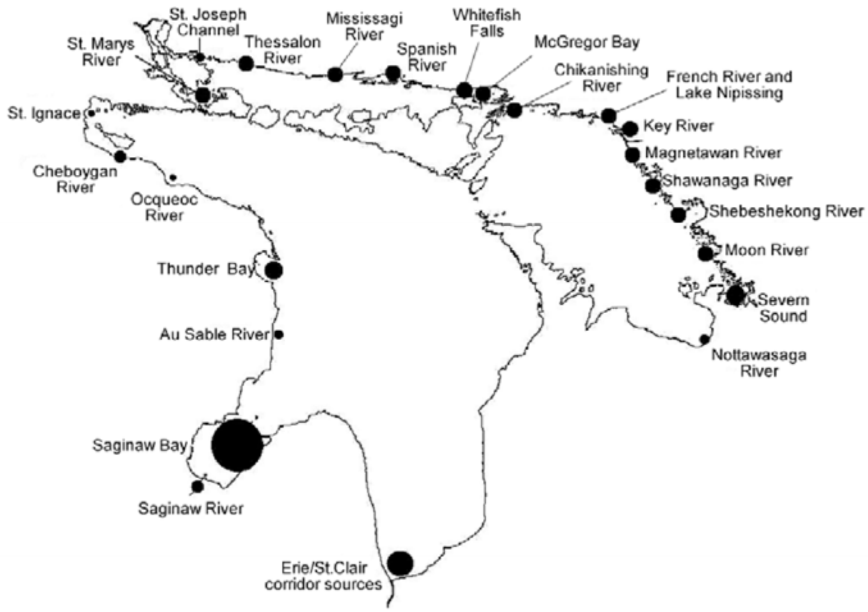
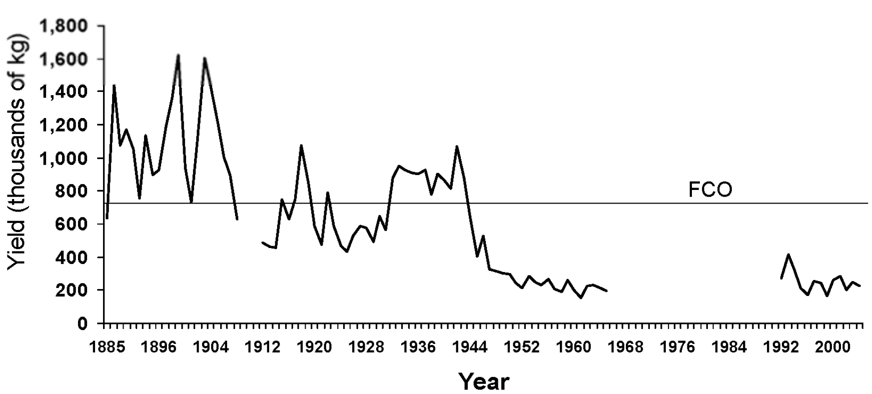


Fig. 2. Yield of walleye from all sources in Lake Huron, 1885-2004. FCO denotes the desired yield established as a fish-community objective (DesJardine et al. 1995).



Contemporary (1992-2004) walleye fisheries include recreational, commercial, and subsistence sectors. There is no commercial walleye fishing in Michigan waters with the exception of that allowed for Native American tribes under the 1836 Treaty, as described by the 2000 Consent Decree (Consent Decree Manual 2000). Yield from those tribal fisheries, in combination with some tribal subsistence fishing, has averaged 3,617 kg annually. Commercial yield in Ontario waters has averaged 107,109 kg. The estimated yield of the recreational fishery is about 142,000 kg, but this is likely an underestimate because recreational fisheries, although surveyed in Michigan waters, are not routinely surveyed in Ontario waters. In addition, subsistence catches (First Nations) from Ontario waters are typically not reported. However, it is unlikely that the total actual yield from all sources approaches the fish-community objective value of 700,000 kg.

Among the numerous walleye populations throughout Lake Huron, only the more-important 37 have been routinely assessed. Of these 37 populations, 29 are considered depressed, and some of these are being rehabilitated through various management actions, including stocking (Table 1). In this report, we discuss four factors that appear to be associated most with walleye population declines in Lake Huron: alewife, barriers in rivers, habitat degradation, and overfishing. Then we review the status of key populations.

Table 1. Status of 37 of the more-important walleye populations or spawning stocks within Lake Huron and known or suspected limiting factors coded as follows: (1) spawning habitat degradation; (2) spawning habitat access limitations (dams); (3) nursery habitat limitations; (4) seriously affected by exotic species; (5) heavy or excessive exploitation; (6) productivity limitations; (7) water-quality limitations.

Location	Basin	Status	Limiting factors known or suspected	Under active Rehabili-tation
St. Mary's River	Connecting waters	Moderate	6	Under study
Thessalon River	North Channel	Depressed	5	No
Mississagi River	North Channel	Depressed but stable	5	No
Serpent River	North Channel	Depressed	2,5,7	No
Spanish River	North Channel	Moderate	5,7	Yes

Table 1, continued.

Location	Basin	Status	Limiting factors known or suspected	Under active Rehabili-tation
Whitefish Falls	North Channel	Depressed but increasing	1,5	Yes
Little Current	North Channel	Depressed	2,5	Yes
McGregor Bay	Georgian Bay	Depressed	1,6,7	Yes
Sheguindah Bay	Georgian Bay	Depressed	1	Yes
Killarney Bay	Georgian Bay	Depressed	1,6,7	No
French River	Georgian Bay	Moderate	5	Yes
Key River	Georgian Bay	Depressed	1,2,5,7	Yes
Magnetawan River	Georgian Bay	Depressed	2,5	Yes
Naiscoot River	Georgian Bay	Depressed		Yes
Sucker Creek	Georgian Bay	Depressed but increasing		Yes
Shawanaga River	Georgian Bay	Depressed but increasing		Yes
Shebeshekong River	Georgian Bay	Depressed but increasing	5	Yes
Sequin River	Georgian Bay	Depressed	1,2	Yes
Boyne River	Georgian Bay	Depressed		Yes
Port Rawson Bay	Georgian Bay	Depressed	1	No
Blackstone Harbour	Georgian Bay	Depressed	5	No
Moon River	Georgian Bay	Depressed	1,2,5	Yes
Musquash River	Georgian Bay	Depressed	1,2	No
Severn River	Georgian Bay	Depressed but increasing	1,5	Yes
North River	Georgian Bay	Depressed but stable	5	Yes
Nottawasaga River	Georgian Bay	Depressed	2	No
Fishing Islands	Main Basin	Depressed		No
Point Clark	Main Basin	Depressed		No
Kettle Point	Main Basin	Moderate		No
Blue Point	Main Basin	Moderate		No

Table 1, continued.

Location	Basin	Status	Limiting factors known or suspected	Under active Rehabili-tation
Erie/St. Clair corridor sources	Connecting waters	Moderate		No
Cheboygan River	Main Basin	Moderate	2	No
Ocqueoc River	Main Basin	Moderate but small	2	No
Thunder Bay	Main Basin	Depressed	2, 3, 4	Yes
Au Sable River	Main Basin	Depressed	2	No
Saginaw Bay	Saginaw Bay	Depressed but increasing	1,2,3,4	Yes
Saginaw River	Saginaw Bay	Depressed but increasing	1,2,4	Yes

Factors Impacting Walleye Abundance in Lake Huron

Alewife

Alewives can be a formidable predator and competitor on fish larvae (Kohler and Ney 1980; Wells 1980; Brandt et al. 1987; Brooking et al. 1998) and may have been an obstacle to walleye recovery in some Great Lakes locations (Bowlby et al. 1991). The first evidence of an association between alewife abundance and walleye recruitment followed the collapse of adult alewife stocks, which started in 2003 (Bence et al. 2008). Walleye reproductive success surged in Saginaw Bay in the years immediately thereafter. Adult alewife abundance explained 59% of the variability in fall age-0 walleye abundance in the bay, and, in the absence of adult alewife, fall age-0 walleye abundance increased 50-fold (Fielder et al. 2007; Fielder and Thomas 2006). Adult alewife typically entered the bay for spawning (Carr 1962; Organ et al. 1979), and their residence may overlap with that of the larval stage of walleye; thus, we hypothesize predation on larvae by adult alewife. How long alewife abundance will remain low is unforeseeable, but, as long as it remains low, we expect that walleye reproductive success will be high. It is unknown if other walleye populations from around the lake have benefited from the decreased abundance of alewife.

Barriers to Fish Passage

Dams, spillways, and other barriers to fish passage affect walleye reproduction in Lake Huron by preventing access to spawning areas (Reckahn and Thurston 1991; Fielder 2002). There are 800 dams in the Michigan portion of the Lake Huron watershed alone, many of which were built in the early 1900s, and an estimated 86% of major tributaries in Michigan are fragmented by at least one barrier (Liskauskas et al. 2007). Jones et al. (2003) determined that providing fish passage for walleye in a Lake Erie tributary would increase spawning habitat eightfold. Walleye reproduction below barriers is also negatively affected when water releases at dams disrupt run-of-the-river flows and water-temperature regimes, affecting both adult fish and incubating eggs (Colby et al. 1979; Dimond et al. 1996; Liskauskas et al. 2007; Acres International 2006).

Degradation of Spawning Habitat

Walleye embryonic development requires flowing water with a gravel substrate in rivers or well-oxygenated open-water shoals (Colby et al. 1979). These habitats are subject to degradation from sedimentation, and such was the case in Saginaw Bay where sand and silt impacted offshore spawning reefs in the inner portion of the bay (Fielder 2002). Colby et al. (1994) list various strategies for improving walleye spawning habitat among their guidelines for rehabilitating Great Lakes walleye populations.

Overfishing

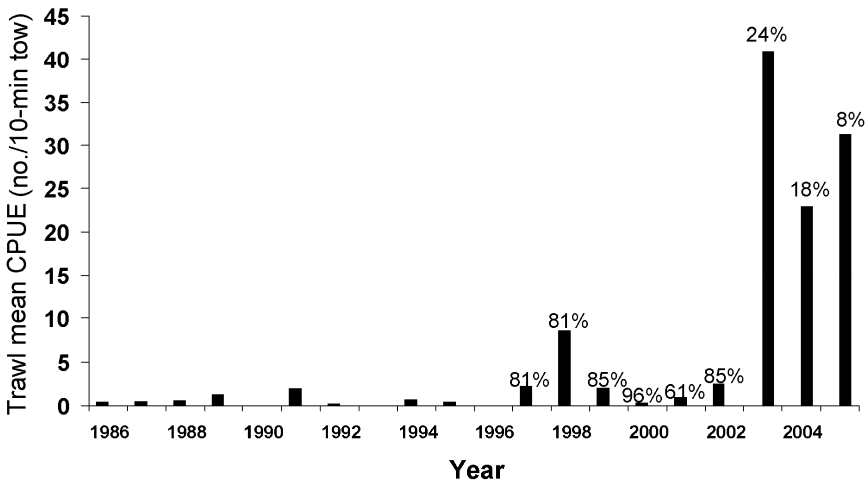
Although walleye fishing in Lake Huron is regulated, many populations and spawning stocks are subjected to intensive or excessive exploitation (Table 1), and competing commercial, recreational, and aboriginal subsistence fisheries present a challenge to management for achievement of sustainable populations. This challenge is sometimes exacerbated by a poor understanding of the identity and status of stocks that make up walleye populations. For example, walleye populations in the St. Marys River and North Channel are composed of a number of discrete spawning stocks (D. Caroffino, unpublished data), but the status of these individual stocks and their contribution to the fishery is unknown. Overfishing of individual stocks within a population is possible, compromising their fitness and sustainability.

Status of Key Walleye Populations in Lake Huron

Saginaw Bay

The walleye population in Saginaw Bay has substantially increased in recent years due to three consecutive years (2003-2005) of high production of age-0 fish (Fielder and Thomas 2006). Catch-per-unit effort of age-0 walleye in 10-minute trawl tows in the fall during 2003-2005 were 2.5 to 4.5 times higher than in 1998, the next best year (Fig. 3) since 1986. The major factor known to be associated with the production of these strong year-classes was the scarcity of adult alewives in those same years, but ideal climate conditions also may have been a factor in 2003 (Fielder et al. 2007). We suspect that a near absence of larval predation by adult alewives greatly improved the survival of larval walleye as egg deposition was not thought to have changed. The low incidence (8-24%) (Fig. 3) of oxytetracycline marks (infused on hatchery fish prior to stocking) on trawled age-0 walleye showed that most fish of the 2003-2005 year-classes were naturally reproduced. Prior to 2003, the walleye population in Saginaw Bay was relatively stable and was supported mainly by stocking (Fielder et al. 2000; Fielder and Thomas 2006). Stocking began in the early 1980s, and the number of year-classes in the population increased steadily before plateauing in the late 1990s. Prior to 2003, spawning habitat was thought to be the factor most limiting increases in population abundance (Fielder 2002), but the surge in age-0 abundance following the collapse of the alewife population indicates that predation by alewives may also have been a major limiting factor (Fielder et al. 2007).

Fig. 3. Mean catch-per-unit effort of age-0 walleye in fall trawling in Saginaw Bay, 1986-2005. Percentages indicate proportion of year-classes attributed to stocking, as indicated by oxytetracycline marking (from Fielder and Thomas 2006).



A walleye recovery plan for Saginaw Bay's population was adopted in 2002 (Fielder and Baker 2004), and it established, as a recovery goal, a self-sustaining population at a density that fully utilizes the capacity of the bay's adult habitat and prey base. Achievement of the goal was seen to have occurred when the density of walleye was high enough to cause the growth rate of age-3 walleye to decline to 110% of the state average rate (Great Lakes walleye typically grow faster than those inland) and remain at this rate for at least three of five consecutive years. This quantifiable measure of density is intended to be a measure of predator-prey balance. The growth rate of age-3 walleye in 2005 (2002 year-class) still exceeded the 110% level (114%), but growth of the 2003-2005 year-classes indicated a reduction close to the 110% target. However, the prospects for continued production of strong year-classes in Saginaw Bay are uncertain and depend on density-dependent factors and on adult alewives remaining scarce (Fielder et al. 2007). Even under the best of circumstances, a walleye population does not typically produce strong year-classes consecutively (Colby et al. 1979). Although density-dependent mechanisms have yet to affect walleye reproduction in Saginaw Bay, first-year survival of the large 2003-2005 year-classes was considerably less than that of earlier year-classes. As population density increases and growth declines, other factors, such as cannibalism (measured for the first time in Saginaw Bay in 2003) and lower overwinter survival may level out what would have been strong year-classes. In light of these density-dependent effects, walleye fingerling stocking in Saginaw Bay was suspended in 2006. Fingerling stocking may be resumed in the future if the alewife population recovers and walleye reproductive success declines.

Despite lower survival of walleye from age-0 to age-1 in recent years, production of strong year-classes (Fielder and Thomas 2006) suggests that Saginaw Bay's walleye population will continue to increase. The walleye population may reach a level that, through predation, precludes adult alewives from entering Saginaw Bay to spawn, should the alewife population in Lake Huron recover. By 2005, the strong 2003 year-class began to reach the 381-mm-minimum-length limit for the recreational fishery. The exploitation rate of walleye in this fishery averaged just 8% from 1992 to 2004, and total annual mortality rate averaged 36.1% from 1992 to 2003. How these metrics change once the stronger 2003-2005 year-classes recruit to the fishery remains to be seen.

St. Marys River

The locations where walleye spawn in the St. Marys River is not known, nor is the level of reproduction, but limited evidence suggests that the level is low in relation to historic levels. Spawning is thought to occur in the rapids below the compensating-works spillway, on shoals in Potagannissing Bay near the Seine Islands, and in five tributaries—the Munuscong, Garden, Echo, Bar, and Root Rivers (Gebhardt et al. 2002). With the exception of the Munuscong River, however, walleye spawning runs in the other tributaries are believed to have declined for reasons not fully known (Gebhardt et al. 2002). Overall abundance of walleye, though, has been stable from the mid-1970s through 2002 (Fielder et al. 2004). Walleye are stocked annually in the river, but it is not clear whether this practice accounts for the stability of the population.

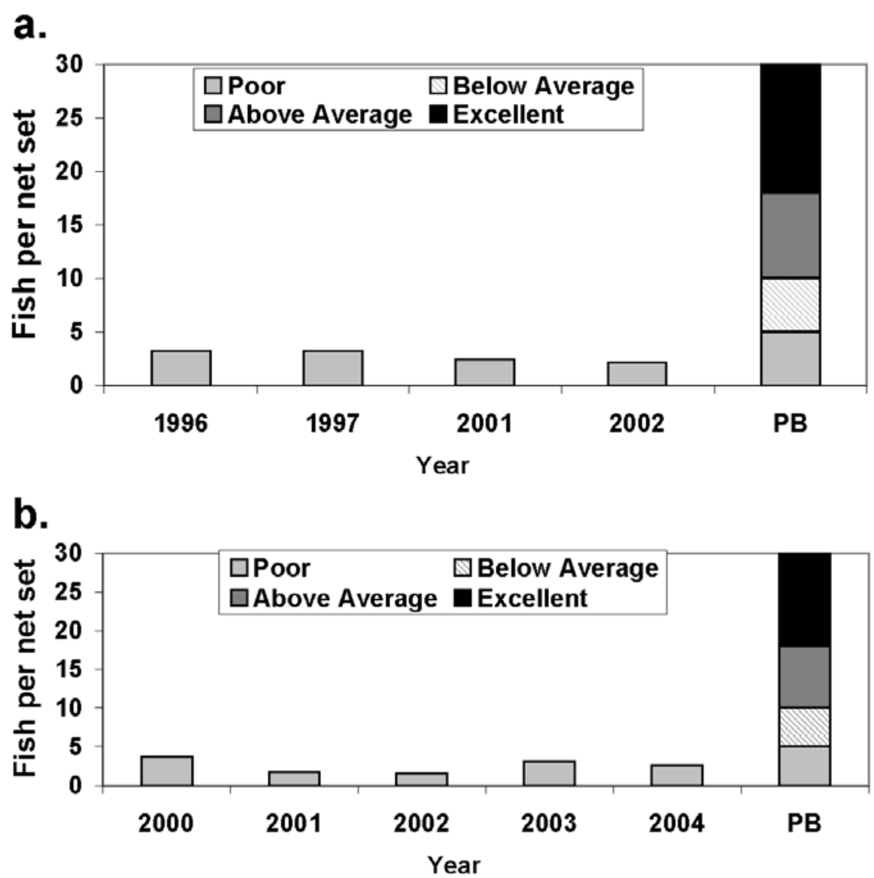
Hatchery fish stocked in 1998 were marked with oxytetracycline, and subsequent surveys indicated that 60% of the 1998 year-class was of hatchery origin. Genetic analysis of walleye in the St. Marys River indicates a considerable contribution from stocking sources outside of the river (D. Caroffino, Lake Superior State University, personal communication, 2003). Only the Bar River spawning population appeared to be unique and least affected by stocking.

In the St. Marys River, walleye are harvested in recreational, tribal/First Nation subsistence, and commercial fisheries (Ontario waters of eastern Potagannissing Bay). The total harvest in 1999 from all fisheries was estimated to be about 25,000 walleyes, mostly from the recreational fishery (Fielder et al. 2004).

Eastern Georgian Bay and the North Channel

Numerous walleye populations inhabit the vast littoral zone that comprises the eastern shore of Georgian Bay and the north shore of the North Channel, spawning in various tributaries (Fig. 1). Although historical yields were comparatively high, the effects of habitat alteration and over-exploitation have resulted in a gradual decline in the abundance of most populations (Spangler et al. 1977; Reckahn and Thurston 1991). For instance, relative abundance of the French River and Severn Sound populations has been consistently poor during the late 1900s and early 2000s, as compared to provincial benchmarks (Fig. 4; Morgan 2002; Skinner and Ball 2004), and age structure was dominated by young year-classes indicating over-exploitation (Liskauskas 2002). Current management efforts are aimed at restoring individual stocks.

Fig. 4. Walleye catch-per-unit effort from (a) the French River and (b) Severn Sound, Georgian Bay, Lake Huron (Upper Great Lakes Management Unit, Ontario Ministry of Natural Resources, unpublished data). The provincial benchmark (PB) column depicts provincial benchmarks for relative abundance (Morgan et al. 2003).



Studies on the population of walleye in Severn Sound (Fig. 1) demonstrate how excessive exploitation may be a more-important factor controlling walleye abundance than either water quality or habitat degradation. Severn Sound has undergone intensive remediation efforts aimed at improving water quality and aquatic habitat (Severn Sound Remedial Action Plan 1989). In 2002, Severn Sound was delisted as an Area of Concern because water-quality and aquatic-habitat improvement objectives were met (Severn Sound Remedial Action Plan 2002), even though the walleye restoration objective was not fully met. Although total harvest of walleye in Severn Sound in 2001 was estimated to be approximately 4,500 fish, 70% by the recreational fishery and 30% by the offshore commercial fishery (Gonder 2002), a fish-population forecasting model (Korver and Kuc 2002) indicated that the recreational harvest alone would compromise the sustainability of the population. In an effort to prevent further population declines, recreational-fishing regulations were made more stringent in 2003, and walleye quotas for the commercial fishery have been reduced.

The Moon River (Fig. 1) is a case study of habitat degradation having a profound effect on walleye reproduction. Because of hydropower development on its source, the Muskoka River, Moon River flows have been reduced by 75% (Acres International 2006). The remainder of the Muskoka River discharge is diverted to the Musquash River where two generating stations are located. Fluctuating flows as a result of quick increases and decreases of outflows from the Muskoka River frequently strand walleye eggs at a historically important spawning location just below Moon Falls. Winterton (1975) and Reckhan and Thurston (1991) concluded that such fluctuating flows accounted for over 85% of the variability in the year-class strength of the Moon River population and that high sustained flows are required for production of strong year-classes. Although a few strong year-classes have been produced by this population since 1968 when monitoring began, provincial records indicate that the spawning population has declined substantially over the ensuing years (Fig. 5). The development of a water-management plan for the Muskoka River watershed should provide an opportunity to redress the flow problem in the Moon River. Flows above 30 m^3/sec can increase appreciably the amount of spawning habitat available to walleye (Fig. 6).

Fig. 5. Average catch-per-unit effort of walleye in spring trapnet spawning-run assessments in the Moon River, 1968-2005. Zero catches indicate no netting effort conducted in that year (OMNR, Upper Great Lakes Management Unit, unpublished data).

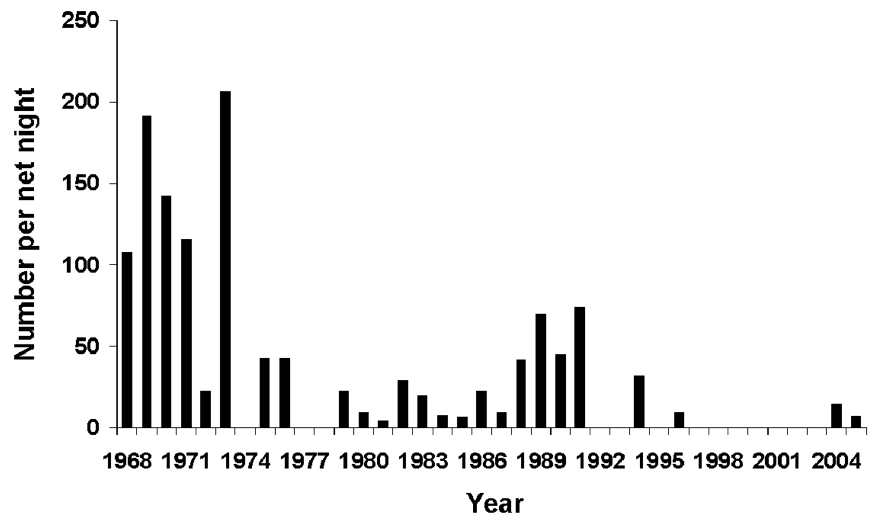
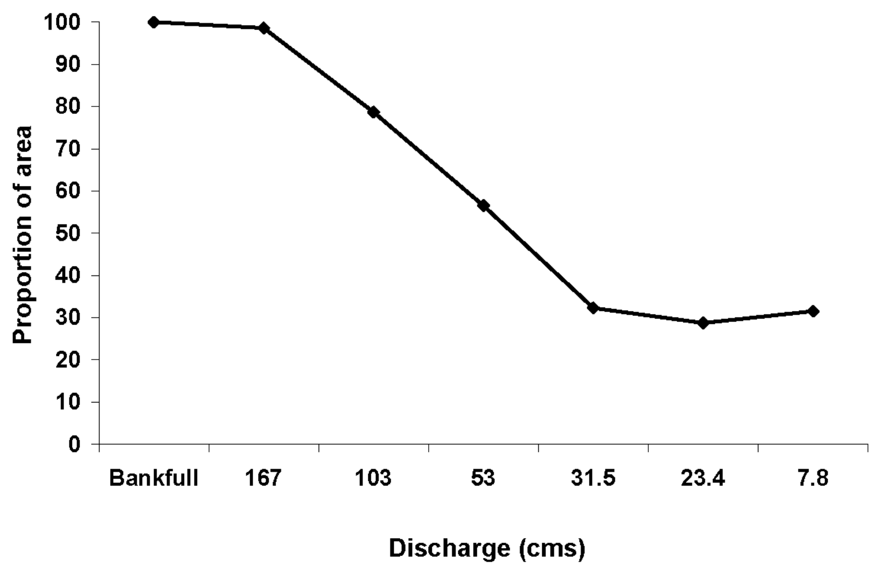


Fig. 6. Percentage of suitable walleye spawning habitat available at different flow rates in m^3/sec at a Moon Falls spawning site, Georgian Bay (from Acres International 2006).



Other management activities aimed at restoring the Severn Sound, Moon River, and other Georgian Bay and North Channel walleye populations include stocking and restrictions on exploitation. The effectiveness of rebuilding walleye populations by stocking has been unclear. Genetic surveys indicated reductions in diversity in some walleye populations in eastern Georgian Bay, likely caused by recent population bottlenecks and by reduced heterogeneity in stocked walleye populations (Gatt et al. 2002). Commercial quotas for walleye are reviewed annually, and current quotas are substantially lower than historical catches. In 2003, restrictive recreational-fishing regulations for walleye were approved and implemented for Georgian Bay and the North Channel, including reductions in daily limits, closed-season extensions, a protective slot limit, and added protection for spawning-sized fish.

Lake Erie-St. Clair Corridor and Other Sources

Walleye migrating from the Lake Erie-St. Clair corridor into Lake Huron (Haas et al. 1998), recovered from as far north as Thunder Bay (Fig. 1), are genetically distinct from resident Lake Huron fish (McParland 1996). Tagged fish from Lake Erie or other non-resident sources have not been detected spawning in the Tittabawassee River, an important spawning tributary to the Saginaw River. Immigrants apparently inhabit the lake only seasonally and out-migrate for spawning. Nevertheless, immigrants contribute substantially to the Ontario commercial fishery in southern and central Lake Huron (McParland 1996). How important these outside sources are to the recreational fishery is not known. Analysis of consumption by the predator community in Lake Huron indicated that walleye consumed as much as 7% of the total main-basin prey resources between 1984 and 1998 (Dobiesz and Bence 2005), but consumption may be underestimated if walleye populations occupy the open waters, which are not assessed for walleye.

Conclusions and Recommendations

Walleye recovery in Lake Huron must be evaluated on a regional basis because of the many localized populations and the contribution of immigrants. Populations are not now sufficiently abundant to support a sustained harvest of 700,000 kg recommended as a fish-community objective (DesJardine et al. 1995). Achievement of that level of harvest will require the Saginaw Bay population reaching near-historical numbers.

Recent trends in walleye reproductive success in Saginaw Bay, and possibly at other locations in the lake, suggest a new dynamic that may stem from the collapse of the alewife population. This dynamic, coupled with habitat improvement and control of exploitation, offers the greatest opportunity since the modern recovery period began to substantially increase walleye abundance and, at least, achieve local recovery objectives. Efforts to improve reproductive success and to increase abundance should be universal across all of Lake Huron as populations outside Saginaw Bay, especially those of the North Channel and Georgian Bay, are integral for achieving the lakewide fish-community objective.

We recommend development and implementation of recovery and/or management plans for each of the regionally important walleye populations. These plans should identify limiting factors such as impediments to fish passage at dams, other habitat deficiencies, or over-exploitation. These plans should become vehicles for investment and focused initiatives, not just by natural resource agencies but by partner organizations and stakeholder groups. The research needed to facilitate the development and evaluation of such plans includes quantifying the impacts of non-native species on a lakewide basis, identifying density-dependent factors influencing survival from age-0 to age-1 in Saginaw Bay, quantifying habitat impediments related to spawning and egg incubation for river-spawning populations, and quantifying commercial and recreational harvest by population. Catch data combined with regular assessment data can be used to develop sustainable harvest levels. Managers should, as part of an ecosystem approach, attempt to restore native planktivores, especially the cisco (*Coregonus artedi*), to fill the vacuum created by the collapse of the lake's alewife populations.

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STATUS OF WALLEYE IN LAKE ST. CLAIR AND THE DETROIT AND ST. CLAIR RIVERS

Megan Belore[1], Michael Thomas, and Brian Locke

Abstract

Lake St. Clair and its connecting rivers, the Detroit River and the St. Clair River, serve as an important habitat and migration route for many species of fish, including walleye (*Sander vitreus*). Using data collected by the Ontario Ministry of Natural Resources (OMNR) and the Michigan Department of Natural Resources and Environment (DNRE), we describe the abundance, recruitment, harvest, and distribution of walleye in Lake St. Clair and its connecting waters. During the 1980s, walleye abundance and recreational fishery catch-per-unit effort (CPUE) were high in Lake St. Clair. Walleye abundance decreased in the 1990s due to poor recruitment from the primary source stock that spawned in the Thames River. As angling CPUE decreased, angler preference for walleye diminished. The decline in walleye abundance in Lake St. Clair was due likely to decreased optimal walleye habitat caused by the invasion of zebra mussel (*Dreissena polymorpha*). Following the abundance decline in the 1990s, the walleye fisheries in Lake St. Clair and its connecting waters were largely dependent on walleyes emigrating from Lake Erie. Recent surveys have documented walleye spawning activity in the Detroit River, but the contribution of this spawning to adult walleye abundance remains unknown.

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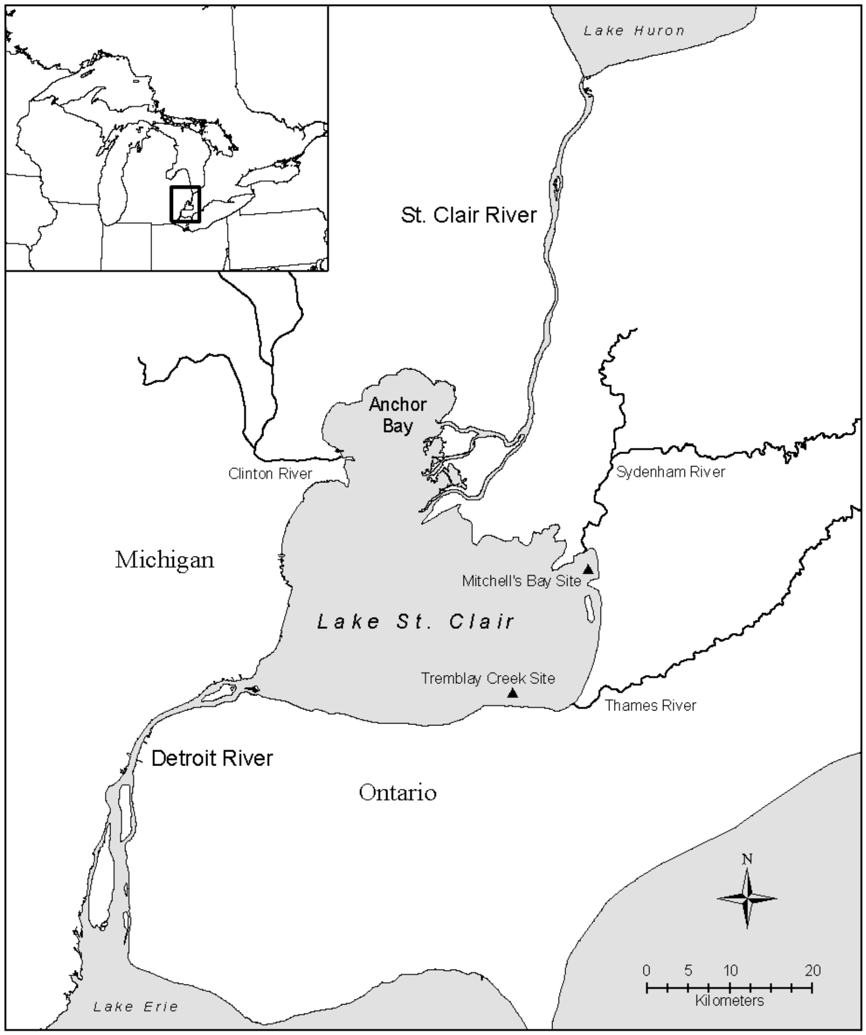
Introduction

Physical Description

Lake St. Clair has an area of approximately 1,114 km^2 and a shoreline length of approximately 272 km, in addition to a large semi-stable delta region in the northeast corner (Fig. 1). The Lake St. Clair drainage basin encompasses 12,616 km^2. The lake has a mean depth of only 3.0 m with a maximum natural depth of approximately 6.4 m; the navigation canal that traverses the lake is maintained at a depth of 8.2 m (National Oceanic and Atmospheric Association 1997). The lake has a short hydraulic retention time of about seven days (Bolsenga and Herdendorf 1993). The St. Clair River flows southward from Lake Huron for 64 km, having a mean flow rate of 5,100 $m^3 \bullet s^{-1}$, and accounts for 98% of the water flowing into Lake St. Clair. More than 50% of the water enters Anchor Bay through the most northerly of three channels, known as the North Channel and rapidly progresses down the western shore of Lake St. Clair and out through the Detroit River. The Detroit River is the only natural outlet from the lake. It is 50-km long and has an average flow rate of 5,300 $m^3 \bullet s^{-1}$ (Bolsenga and Herdendorf 1993). Two distinct water masses exist in Lake St. Clair. The northwestern (Michigan) portion of the lake is strongly influenced by water from Lake Huron and is cooler, clearer, and less productive than the southeastern (Ontario) portion of the lake, which has a longer retention time and higher productivity associated with nutrient loading from Ontario tributaries (Leach 1980).

Fig. 1. The St. Clair River, Lake St. Clair, and the Detroit River. Solid triangles indicate survey trapnet sites at Tremblay Creek and Mitchell's Bay.



The eastern shoreline of Lake St. Clair consists of low-lying agricultural land and contains diked and undiked marshes. The southern shoreline is largely agricultural with some urban development. The Thames (drainage area 5,807 km^2) and Sydenham (2,439 km^2) Rivers, together with several smaller tributaries, drain one of the most-productive agricultural areas in Canada into eastern Lake St. Clair (Appel et al. 2002). The largest tributary on the western side of Lake St. Clair is the Clinton River (drainage area 1,976 km^2), which drains mainly urban, suburban, and some rural areas (Appel et al. 2002).

Fish Community

Lake St. Clair, the Detroit River, and St. Clair River contain a wide range of aquatic habitats that support a diverse fish community. The present fish community is a mixture of warm-water and cool-water species with composition varying seasonally. Lake St. Clair and its connecting waters serve as a passage for fish migrating between Lake Erie and Lake Huron, and a number of species, including walleye (*Sander vitreus*), use Lake St. Clair and its connecting waters to migrate to spawning sites. Furthermore, a number of species in Lake St. Clair are found at the northern limits of their ranges and are not found elsewhere in Canada (i.e., northern madtom (*Noturus stigmosus*), ghost shiner (*Notropis buchananai*), and spotted sucker (*Minytrema melanops*) (Crossman 1963; MacInnis 1998; Committee on the Status of Endangered Wildlife in Canada 2005).

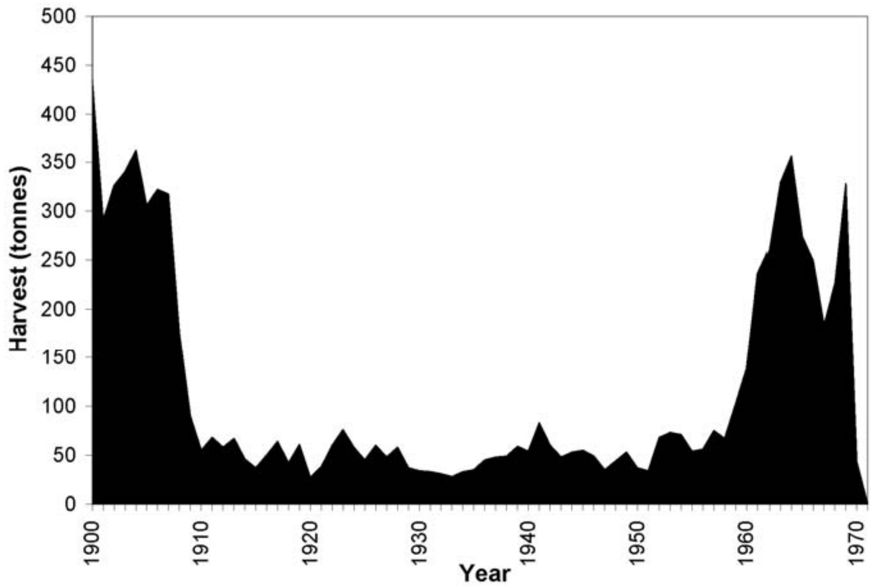
We believe that the fish community of Lake St. Clair changed during the 20th century due to exploitation by commercial and recreational fisheries, extensive nearshore modification (i.e., diking and draining of wetlands and shoreline hardening), increased human activities in the watershed, and introductions, as described generally for the Great Lakes by Christie (1974), Jude and Leach (1993), and Kelso et al. (1996). During the 1800s and early 1900s, cisco (formerly lake herring, *Coregonus artedi*), lake whitefish (*C. clupeaformis*), walleye, and lake sturgeon (*Acipenser fulvescens*) were important parts of the fishery (Baldwin et al. 2002). Since then, cisco and lake whitefish were nearly extirpated, and lake sturgeon stocks underwent decline (Smith 1972). In the past 30 years, the fish community underwent further changes likely in response to invasive species, continuing loss of habitat, nutrient inputs, and an intensive recreational fishery (MB and MT, unpublished data).

Walleye was the dominant piscivore in the fish community and most-sought-after recreational species during the 1970s and 1980s. In the 1990s, walleye abundance decreased and the distribution of walleyes became more limited. Over the same period, the abundance of muskellunge (*Esox masquinongy*) and smallmouth bass (*Micropterus dolomieu*) more than doubled, and these species replaced walleye as the dominant piscivore in the fish community. Collectively, walleye, muskellunge, and smallmouth bass have functioned as top predators despite changes in their relative abundances through time (Thomas and Haas 2007).

History of Sport and Commercial Fisheries

Lake St. Clair walleye stocks currently support important recreational and subsistence fisheries within the lake and its tributaries and are also exploited by the commercial fishery in southern Lake Huron. Commercial fishing for walleye began with the first settlers and continued until 1970 (Nepszy et al. 1991). Commercial harvest peaked at about 512 t (tonnes) per year in the late 1800s and then declined to an average of 319 t per year in the early 1900s. Following the closure of the commercial fishery in Michigan waters in 1908, the commercial harvest of walleye decreased to an average of 53 t per year through 1959. Commercial harvest later increased to an average of 258 t per year from 1960 to 1969 (Fig. 2) (Baldwin et al. 2002). The commercial harvest of walleye ceased in 1970 because of high mercury levels in fish flesh, and it never reopened.

Fig. 2. Commercial harvest of walleye in Lake St. Clair from 1900 to 1970 (Baldwin et al. 2002; MB, unpublished data) when the commercial fishery for walleye was closed.



A First Nations fishery operates on Lake St. Clair, the Thames River, and the St. Clair River using dipnets, roll nets, gillnets, and seine nets to harvest walleyes and other species. Annual harvests for walleye in the Thames River were estimated at 60,000 kg in the 1970s, 30,000 kg in the 1980s, and 13,000 kg through the mid-1990s. An additional harvest by the Walpole Island First Nation has not been measured but is believed to be low relative to sport yields (D. MacLennan (retired), OMNR, personal communication, 2003).

Lake St. Clair is a popular sport-fishing destination and supports both a summer- and winter-angling fishery. The summer walleye-angling fishery is lakewide, whereas the winter fishery is confined mainly to sheltered bays. Recreational fishing for walleye began in Lake St. Clair in the early 1900s. Since then, walleye have remained an important part of the lake's recreational fishery. However, the winter-angling fishery for walleye has been impacted by reduced ice coverage on Lake St. Clair during most winters since 1988.

Goals and Objectives of the Report

This report expands on the Nepszy et al. (1991) description of the status of walleye in Lake St. Clair. It describes the status of the walleye stocks in Lake St. Clair, the St. Clair River, and the Detroit River from the 1970s to 2006, including trends in abundance, recruitment, harvest, and patterns of movement within Lake St. Clair, its connecting waters, and the adjoining Great Lakes.

Methods

Trapnet Survey

The Ontario Ministry of Natural Resources (OMNR) has conducted a fall trapnet survey in the Canadian waters of Lake St. Clair with some regularity since 1974. Single trapnets were set at three fishing sites: Tremblay Creek (south shore), Mitchell's Bay (north shore), and St. Lukes Bay (east shore). Because the St. Lukes Bay site was not fished for the entire period of the survey, results in this report refer to the Tremblay Creek and Mitchell's Bay sites only (Fig. 1). Trapnet leads were set approximately 0.8 km from and perpendicular to the shoreline. The water depth at the netting sites averaged 3 m. Nets were generally set during the first week of October and fished until mid-November. The nets were lifted three times per week, weather permitting. Secchi-disk depth and water temperature were recorded at each lift. All walleye ages were estimated using scales. Number of fish per net day (catch-per-unit effort (CPUE)), mean fork length, and mean age of walleyes were estimated from the catch. Total mortality was estimated for age-5 and older walleyes using catch curves (Ricker 1975). A linear regression of $\log_e$ walleye CPUE on $\log_e$ Secchi-disk depth was used to determine the relationship between these variables.

Angler Surveys

Creel surveys were performed by the OMNR in the Canadian waters of Lake St. Clair from 1978 to 1983; 1985 to 1989; and during 1992, 1999, 2002, and 2006. A roving stratified sampling design was used incorporating mode (open water), spaces (areas), seasons (months), day-types (weekdays, weekend days), and periods (within-day time periods). In most years, the survey ran from June to August inclusive. However, in 1985 and 2006, the survey occurred only during July and August, and, in 1999, the survey occurred only during July. The survey was used to estimate targeted angler effort for walleye, targeted CPUE of walleye (targeted walleye harvest/targeted walleye effort), as well as the total catch (contains released fish) and harvest of walleye during the survey period.

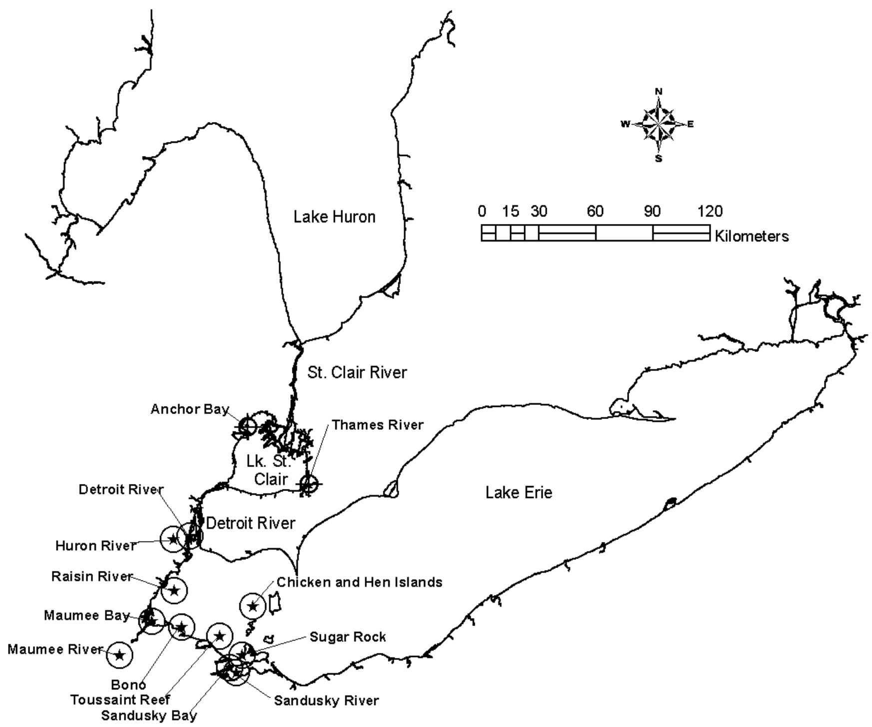
The Michigan Department of Natural Resources and Environment (DNRE) conducted an on-site creel survey from March 2002 through February 2005 along the U.S. sides of the St. Clair River, Lake St. Clair, and the Detroit River. However, 2002 is the only year for which data are available for both the connecting rivers and the lake. The survey region was divided into 20 grids, loosely based on a 10′ latitude by 10′ longitude grid. The creel survey employed a stratified design using simple random sampling within strata. Strata included grid-fished by month, weekdays/weekends (includes holidays), and mode of fishing. Catch and effort estimates were made for each stratum and then combined to give monthly and seasonal totals. Both weekend days and three randomly selected weekdays were sampled each week. Two types of data were collected for each area sampled: angler party interviews for catch rates and boat counts for effort. An angler party was defined as one or more anglers who fished together. Angler parties were interviewed at the completion of their fishing trips at various boat-launch ramps and at marinas. Fishing effort was determined through instantaneous counts of boats made from airplanes. That proportion of boaters interviewed by creel clerks who indicated they were not fishing was used to adjust the aerial counts for nonfishing effort. Standard mathematical formulas for creel surveys (Pollock et al. 1994; Lockwood et al. 1999) were used to calculate estimates. The creel estimates of harvest, catch, and effort are conservative and do not include night fishing or shore/pier fishing.

Additional recreational-fishing information was obtained from the Lake St. Clair Angler Diary Program. The diary program is a joint Michigan DNRE/OMNR sport-fish monitoring program for which volunteers report their fishing activity in Lake St. Clair and the St. Clair and Detroit Rivers. Volunteers complete a diary page for each fishing trip they make. Information recorded includes fishing location, duration, numbers of fish kept and released, and biological information (e.g., length). In addition, anglers collect scale samples that are returned to the OMNR for aging. This program has provided information on recreational walleye catches in Lake St. Clair each year since 1992 and is used to track trends in angler effort and catch rates. Because this is a volunteer program, the data may be biased.

Tagging Studies

Walleyes have been jaw tagged in the Thames River, Lake St. Clair's Anchor Bay, and several locations in the western basin of Lake Erie (Fig. 3). The Thames River was the principal spawning site for Lake St. Clair walleyes; fish were tagged there during spring from 1980 to 1983, 1993 to 1994, and 2002 to 2004. These fish were captured in seine nets set perpendicular to the banks. Scales were used to age the fish. The CPUE in the seine nets was used to estimate relative abundance of the spawning stock.

Fig. 3. Walleye tagging sites in the western basin of Lake Erie, the Detroit River, and Lake St. Clair. The Lake St. Clair (Thames River and Anchor Bay) tagging sites are indicated with a circle with crosshairs, the Detroit River and western Lake Erie sites are indicated with circles containing a star.



From 2002 to 2006, five trapnets were fished at the same sites in Anchor Bay, MI (Fig. 3) during May to capture walleyes for tagging. Global Positioning System (GPS) was used to locate the same sampling sites each year. The trapnets had 1.8-m-deep pots of 5.1-cm stretch-mesh, 7.6-cm stretch-mesh hearts and wings, and 91.4-m-long leads of 10.2-cm stretch-mesh. Trapnets fished an average of 52 hours between lifts. Upon capture, walleyes were immediately placed in an onboard live tank equipped with continuously circulating lake water. Most fish under 500 mm in length were tagged with size-10 or -12 monel metal strap tags affixed by overlapping the tag snugly around the dentary bone of the lower jaw. Most walleyes longer than 500 mm were tagged with size-12 tags affixed by overlapping the tag snugly around the maxillary and premaxillary bones. A total of 941 walleyes was tagged, and tag-recapture data were solicited from anglers and commercial fishermen on a voluntary basis.

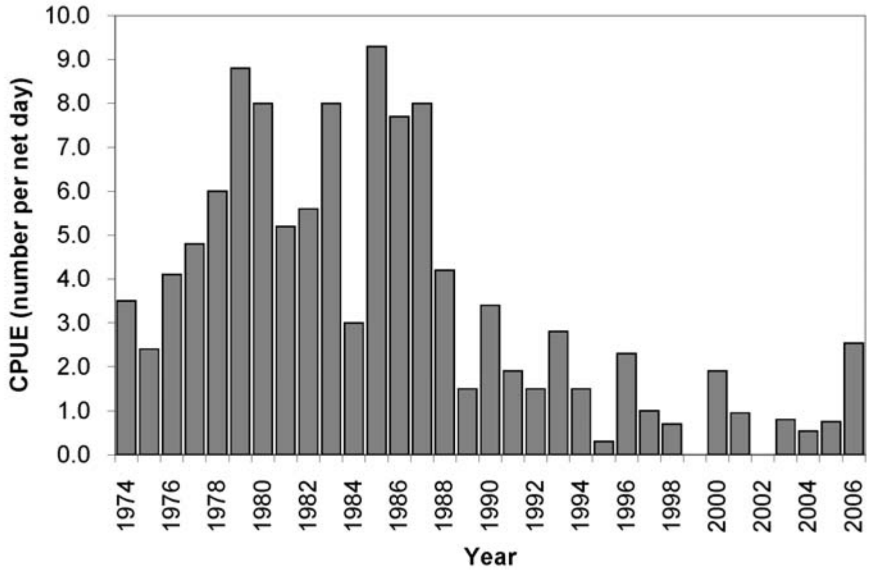
Walleyes were tagged in western Lake Erie spawning areas each year since 1989. Jaw tags were used until 2005, after which a combination of jaw tags and Passive Integrated Transponder (PIT) tags were used (Thomas at al. 2008). Tags were returned by anglers, commercial fishers, and agencies actively scanning for PIT tags. Tagging results were used to determine walleye migration patterns through the St. Clair River, Lake St. Clair, the Detroit River, and Lake Erie.

Results and Discussion

Trends in Abundance, Recruitment, and Mean Age

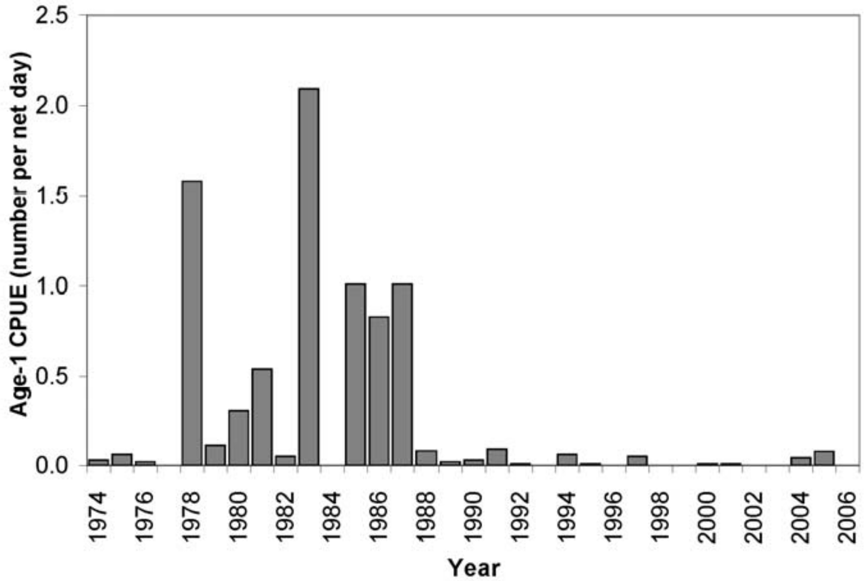
Catch per unit effort (CPUE) of walleye in the fall trap-net survey generally increased from 1974 to 1987, before the establishment of zebra mussels (*Dreissena polymorpha*) in Lake St. Clair in 1988 but decreased thereafter. The average CPUE of 6.0 fish•net day^{-1} from 1974 to 1987 decreased to 1.6 fish•net day^{-1} from 1988 to 2005 (Fig. 4). The CPUE in 2006 increased to 2.5 fish•net day^{-1}; however, many of these fish were likely migrants from the strong 2003 year-class in Lake Erie. The Thames River spawning run of walleye also declined in size after the late 1980s and early 1990s. Average CPUE from the seine nets used to tag walleye decreased from a mean of 25 walleyes per seine haul from 1980 to 1983, to 11 walleyes per haul from 1992 to 1994, and to less than 3 walleyes per haul from 2002 to 2004.

Fig. 4. Average walleye catch per unit effort (number of fish per net day) in Lake St. Clair from an OMNR fall trap-net survey, 1974 to 2006 (no survey in 1999 and 2002).



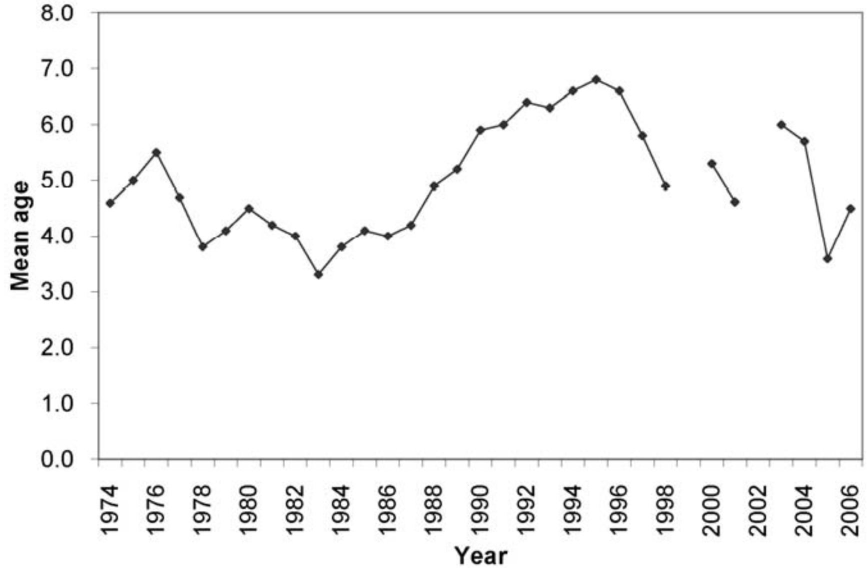
The high trapnet CPUEs during the 1980s reflected recruitment of the very strong 1977 and 1982 year-classes (Fig. 5). The last year-class of even moderate strength was produced in 1986. Since then, recruitment of age-1 walleye to the survey gear has been very low (Fig. 5).

Fig. 5. Average catch per unit effort of age-1 walleye (number of fish per net day) in Lake St. Clair in an OMNR fall trap-net survey, 1974 to 2006 (no survey in 1999 and 2002).



As the recruitment of walleye decreased in Lake St. Clair, the mean age of fish in the fall trapnet survey increased, as might be expected (Fig. 6). Mean age increased from 4.3 years from 1974 to 1987 to 5.6 years from 1988 to 2006 and was slightly lower from 2005 to 2006. The mean age of the Thames River spawning stock also increased as recruitment decreased. The mean age of walleye captured in seine nets during the spawning run was 5.5 years from 1980 to 1982, 8.1 years from 1993 to 1994, and 9.9 years from 2002 to 2004.

Fig. 6. Mean age of walleye in Lake St. Clair from an OMNR fall trap-net survey, 1974 to 2006 (no survey in 1999 and 2002).



Changes in Angler Fishery

The highest angler CPUE for walleye in Ontario waters during 1978-2006 was in 1988 (0.541 fish•rod-hour^{-1} (Table 1)), when CPUE in trapnets was also high (Fig. 4). By 1992, angler CPUE had declined to its lowest observed value (0.165 fish·rod-hour^{-1} (Table 1)). In the 1980s, the summer catch of walleye in Ontario waters was approximately 90,000 walleyes per year, but, by 1992, the catch had declined to only 18,000. The CPUE increased to 0.425 fish•rod-hour^{-1} in 2006, which was the highest CPUE since 1988. Nevertheless, catch remained low (approximately 10,000 walleyes caught in July and August (Table 1)).

Table 1. Walleye angler effort, catch, harvest, and targeted success rates in Ontario waters of Lake St. Clair during June to August, 1978 to 2006 (no survey in some years). Square brackets indicate years without all months and are not included in averages.

Year	Targeted walleye angler effort (rod-hours)	All angler walleye catch (number)	All angler walleye harvest (number)	Target success rate (number of fish caught per rod-hour)
1978	160,119	36,430	29,532	0.211
1979	227,391	90,002	80,472	0.386
1980	232,277	78,515	77,582	0.335
1981	240,548	81,441	76,116	0.332
1982	359,637	97,680	85,719	0.250
1983	253,525	77,296	64,164	0.291
1984	—	—	—	—
1985[a]	[236,663]	[94,971]	[91,437]	0.392
1986	212,038	68,349	60,555	0.317
1987	229,543	99,803	90,444	0.431
1988	268,770	148,762	134,412	0.541
1989	210,677	73,672	72,722	0.345
1990	—	—	—	—
1991	—	—	—	—
1992	106,175	18,013	16,510	0.165
1993	—	—	—	—
1994	—	—	—	—
1995	—	—	—	—
1996	—	—	—	—
1997	—	—	—	—
1998	—	—	—	—
1999[b]	[22,766]	[7,185]	[5,874]	0.294
2000	—	—	—	—
2001	—	—	—	—
2002	34,514	13,924	12,750	0.383
2003	—	—	—	—
2004	—	—	—	—
2005	—	—	—	—
2006[a]	[21,830]	[9,958]	[9,278]	0.425
Average	211,268	73,657	66,748	0.340

[a] July to August only.
[b] July only.

As walleye abundance and angler CPUE declined, so did angler preference for walleye. From 1978 to 1989, anglers targeting walleye accounted for about 69% of total angler effort in Ontario waters, but in 1992 and 1999 targeted effort decreased to 37% and 20%, respectively, of overall angler effort. In 2002, targeted walleye effort fell further to 17% of total effort, even though CPUE increased. In 2006, targeted angler effort remained low (25% of the total effort) despite catch rates near historic highs. In Michigan waters from 2002 to 2005, walleye remained the most-popular target species for anglers fishing the Detroit and St. Clair Rivers and ranked second only to yellow perch (*Perca flavescens*) among Lake St. Clair anglers (Table 2).

Table 2. Number of anglers fishing for a particular species of fish from creel surveys in the Michigan waters of the Detroit River (DR), Lake St. Clair (LSC), and the St. Clair River (SCR), 2002 to 2005.

Name	DR	LSC	SCR	Total
Anything	244	1,635	33	1,912
Salmon and trout (*Oncorhynchus* and *Salmo* spp.)	0	53	56	109
Largemouth bass (*Micropterus salmoides*)	46	169	4	219
Muskellunge	58	610	0	668
Northern pike (*Esox lucius*)	50	392	1	443
Panfish (*Lepomis, Pomoxis, and Ambloplites* spp.)	58	424	5	487
Smallmouth bass	209	1,941	93	2,243
Suckers (*Catostomus and Moxostoma* spp.)	0	1	0	1
Walleye	2,448	3,254	778	6,480
Walleye and yellow perch	72	646	10	728
Yellow perch	257	9,998	44	10,299
Total	3,442	19,123	1,024	23,589

In 2002, the walleye harvest from Michigan waters of Lake St. Clair and its connecting rivers was 220,500 (Table 3), with the Detroit River accounting for about 72% of the total. Of the legal-size walleyes caught by anglers in Lake St. Clair and connecting rivers in 2002, 95% were harvested. Targeted harvest rates were higher in the Detroit (0.29 fish•angler $hour^{-1}$) and St. Clair (0.23 fish•angler $hour^{-1}$) Rivers than in Lake St. Clair (0.13 fish•angler $hour^{-1}$). Peak walleye harvest in the Detroit River occurred in April, May, and June. Peak walleye harvest in Lake St. Clair and the St. Clair River occurred in June, July, and August.

Table 3. Estimated walleye harvest (number), catch (number), percent of catch harvested, total angler effort (angler hours), and nontargeted and targeted harvest rates (fish per angler hour) for the angler fishery in Michigan waters of the Detroit River, Lake St. Clair, and the St. Clair River, March through October 2002. Two standard errors of the point estimate in parentheses.

Water body	**Total harvest**	**Total catch**	**Percent harvested**	**Angler effort**	**Nontargeted harvest rate**	**Targeted harvest rate**
Detroit River	159,211 (55,411)	165,723 (57,108)	96.1	873, 388 (67,863)	0.1823 (0.1897)	0.2972 (0.1143)
Lake St. Clair	41, 973 (23,406)	46,361 (30,388)	90.5	1,368,563 (119,480)	0.0307 (0.0339)	0.1340 (0.1158)
St. Clair River	19,301 (13,200)	20,094 (13,875)	96.0	170,513 (14,336)	0.1132 (0.1178)	0.2391 (0.1704)
Combined	220,485 (61,582)	232,178 (66,160)	95.0	2,412,465 (138,153)	0.0913 (0.0260)	0.2285 (0.0669)

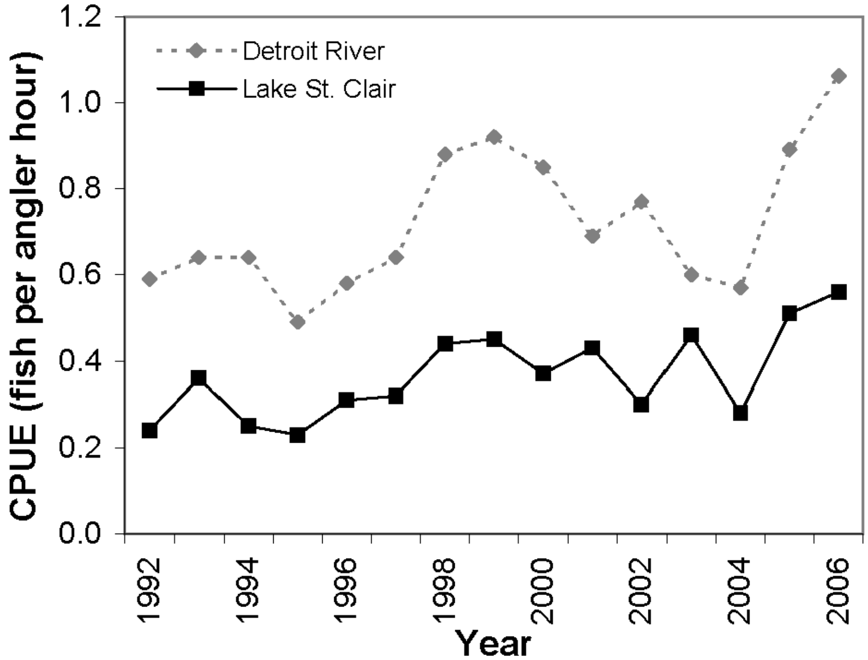
Ages for walleye sampled during Michigan DNRE creel surveys of Michigan's waters of the St. Clair River, Lake St. Clair, and the Detroit River during 2002 to 2004 ranged from 1 to 18 years with a mean age of 4.4 years (Table 4). The mean age for Detroit River walleye (5.1 years) was higher than for Lake St. Clair (4.0 years) or the St. Clair River (4.2 years). During these surveys, the 1999 year-class dominated the harvest at age 3 (63%) in 2002 and age 4 (49%) in 2003. In 2004, the 2001 year-class was most abundant in the harvest (40%), with the 1999 year-class next in importance (27%).

Table 4. Mean, minimum, and maximum age recorded for walleyes sampled by creel clerks during on-site creel surveys of Michigan waters of the Detroit River, Lake St. Clair, and the St. Clair River, 2002 to 2004. Two standard errors of the mean are given in parentheses.

	Age			
Water body	**Mean**	**Minimum**	**Maximum**	*N*
Detroit River	5.1 (0.2)	1	18	1,083
Lake St. Clair	4.0 (0.1)	1	18	2,245
St. Clair River	4.2 (0.2)	2	17	459
Total	4.4 (0.1)	1	18	3,787

Data collected from the angler diary program from 1992 to 2006 showed that walleye CPUE was consistently higher in the Detroit River than in Lake St. Clair, although CPUE trends were the same for both water bodies (Fig. 7). Both Detroit River and Lake St. Clair diarists reported an increase in walleye CPUE in the late 1990s, a decrease in the early 2000s, and an increase in 2005 and 2006. We suspect the later increase in CPUEs was because of an influx of migrants from the large 2003 year-class in Lake Erie. Angler diary information for the St. Clair River was not presented because of a lack of continuity, and no diary data were collected during the 1980s when walleye abundance was higher.

Fig. 7. Detroit River and Lake St. Clair walleye catch per angler hour from a joint Michigan DNRE/OMNR angler diary program, 1992 to 2006.



Growth and Total Mortality

Based on fall trapnet surveys, growth rates in Lake St. Clair have increased since the 1970s (Table 5). For example, the average fork length of age-1 walleye was 28.4 cm during the 1970s, 28.8 cm during the 1980s, 31.4 cm during the 1990s, and 32.1 cm from 2000 to 2006. Average fork length of walleye aged 3 to 7 was trending upward from 1970 to 2006, except during the 1980s when fork lengths at age were lower—apparently a response to the larger populations of that decade. Walleyes sampled by creel clerks in Michigan during 2002 to 2004 ranged from 31.5 to 78.0 cm in total length, with a mean total length of 47.5 cm (Table 6). The mean length of Detroit River walleyes was higher than those measured in Lake St. Clair or St. Clair River, but the longest measured (78.0 cm) came from the St. Clair River.

Table 5. Walleye mean fork length (cm) at age by decade in Lake St. Clair from an OMNR fall trapnet survey, 1970 to 2006 (no survey in 1999 and 2002).

	Mean fork length (cm) at age									
Years	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1970-79	28.4	35.1	41.0	45.2	48.6	51.2	55.1	58.2	61.7	66.1
1980-89	28.8	35.9	39.9	43.4	46.3	48.7	50.9	53.5	56.1	56.8
1990-98	31.4	39.6	43.8	46.7	49.7	50.4	53.4	53.3	56.4	59.0
2000-06	32.1	38.9	43.9	47.7	49.9	53.7	56.8	58.4	56.8	58.3
All years	29.7	37.0	41.9	45.5	48.4	50.7	53.7	55.6	57.3	59.0

Table 6. Mean, minimum, and maximum total lengths (cm) of walleyes sampled during on-site creel surveys on the Detroit River, Lake St. Clair, and the St. Clair River, 2002-2004. Two standard errors of the mean given in parentheses.

Water body	**Mean**	**Minimum**	**Maximum**	***N***
Detroit River	50.6 (0.5)	31.5	77.7	1,083
Lake St. Clair	45.9 (0.3)	31.8	75.4	2,294
St. Clair River	46.8 (0.6)	33.0	78.0	461
All water bodies	47.4 (0.2)	31.5	78.0	3,838

Based on trapnet data from 1974 to 2006, the instantaneous mortality rate (Z) of walleye aged 5 to 10 for the entire sampling period was 0.38. Total mortality, however, was declining during this period. From 1974 to 1987, total mortality was 0.63, and, from 2000 to 2006, total mortality was 0.37. Therefore, mortality and stock abundance were declining concurrently, suggesting exploitation was not a cause of the decline in abundance.

Movement of Walleye

Tagging studies have shown considerable movement of walleye between Lake Erie, Lake St. Clair, and Lake Huron (Todd and Haas 1993; Wang et al. 2007). Prior to the collapse of the Thames River walleye stock, genetic evidence suggested that Lake Erie stocks accounted for 14% and 37% of the nonspawning walleyes caught in Lake St. Clair in 1983 and 1984, respectively (Todd and Haas 1993). Todd and Haas (1993) also found that 29% of recaptured walleyes that were tagged in Lake Erie were recaptured north of Lake Erie in the Detroit River, Lake St. Clair, the St. Clair River, and Lake Huron. Further, they used tag-recovery data to confirm that each year large numbers of Lake Erie walleye entered Lake St. Clair and the connecting rivers during nonspawning seasons and returned to their Lake Erie spawning sites. Mixed-stock analysis of walleyes caught in southern Lake Huron from 1994 to 1995 indicated that walleye originating from Lake Erie spawning sites accounted for 68% of the catch, whereas the Thames River stock accounted only for 18% (McParland et al. 1999).

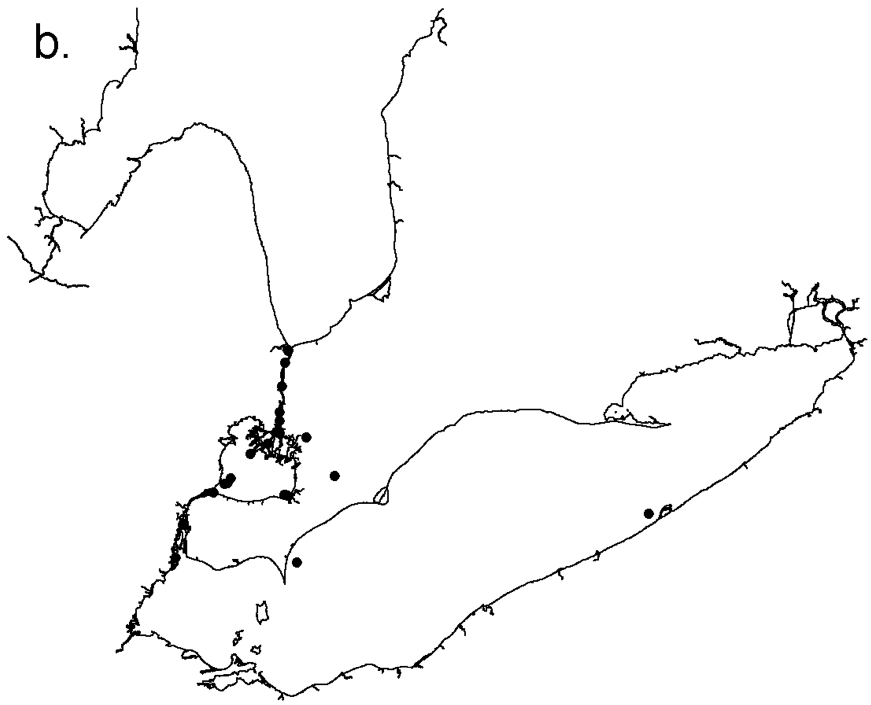
More recently, recovery data for walleye tagged on or near Lake Erie spawning sites from 2002 to 2006 demonstrated a continuation of the strong pattern of northward movement into Lake St. Clair and its connecting rivers (Fig. 8). In fact, about 30% of all tag recoveries reported for walleye tagged at Lake Erie sites from 2002 to 2006 came from the Detroit River, Lake St. Clair, or the St. Clair River (R. Haas, Michigan Department of Natural Resources and Environment, personal communication, 2008). This movement reflects a substantial northward movement of walleyes from Lake Erie spawning sites into Lake St. Clair and its connecting rivers, as well as intensive fishing effort targeting walleye on these waters. Although walleye move seasonally from the western basin of Lake Erie into Lake St. Clair, the Lake St. Clair spawning stock is genetically distinct from the Lake Erie spawning stock (Strange and Stepien 2007).

Fig. 8. Geographic distribution of tag recoveries of walleye tagged from 2002 to 2006: a) 1,558 recoveries (those with coordinates) from a total of 1,804 recaptures of 24,966 walleyes tagged at sites in the western basin of Lake Erie; b) 143 tag recaptures from a total of 941 walleyes tagged in Anchor Bay, Lake St. Clair. Data are from the Interagency Walleye Tagging Database maintained by the Walleye Task Group of the Lake Erie Committee.

Nonspawning walleyes tagged in the open waters of Anchor Bay, Lake St. Clair, were from unknown stock. We presumed that many of these walleye originated from Lake Erie spawning sites in the western basin. In contrast to the western-basin-tagged walleye recoveries, the geographical distribution of tag recoveries of Anchor Bay tagged walleyes was highly clustered along the western and northern shoreline of Lake St. Clair (Fig. 8). Furthermore, tag recoveries from the open waters of Lake Erie's western basin were rare, suggesting that few walleye tagged at the Anchor Bay site inhabited the western basin during the spring and summer fishing months in subsequent years. This pattern also suggests that walleye movements from western-basin spawning sites into the Detroit River, Lake St. Clair, and the St. Clair River are non-random. Our tagging data indicate that an individual walleye from a western-basin spawning site that migrates northward after spawning is unlikely to migrate eastward in subsequent years and probably follows the northward migration pattern annually. The factors that determine whether an individual walleye migrates northward or eastward from western-basin spawning sites remain unclear.

Based on tag recaptures, walleyes spawning in the Thames River migrate between Lake St. Clair, the St. Clair River, Lake Huron, the Detroit River, and Lake Erie. However, most emigrating walleyes move northward rather than southward, and this pattern has been consistent for two tagging periods: 1980 to 1982 and 2004 to 2006 (Fig. 9). Ferguson and Derksen (1971) also found that walleyes spawning in the Thames River moved northward into Lake St. Clair, the St. Clair River, and Lake Huron more often than moving south into Lake Erie. From 1980 to 1982, some 23,250 walleyes were tagged in the Thames River during spring spawning runs, and, from 2002 to 2004, only 324 walleyes were tagged. Of the walleyes tagged in the early 1980s, 4,113 were recaptured: 42% of the recaptured fish were caught in Lake St. Clair and the Thames River, 51% were caught north of Lake St. Clair (St. Clair River and Lake Huron), and only 7% of the fish were recaptured south of Lake St. Clair (Detroit River and Lake Erie). Of the 324 walleyes tagged from 2002 to 2004, 25 were recaptured; 44% were recaptured within Lake St. Clair and the Thames River, 36% moved north into the St. Clair River, and 20% moved into the Detroit River and Lake Erie combined (Fig. 9).

Fig. 9. Geographic distribution of tag recoveries reported for walleyes tagged in the Thames River during two time periods: a) 4,093 tags (those with coordinates) from 4,113 recaptures of 23,250 walleyes tagged from 1980 to 1982; b) 25 tags recaptured from 324 walleyes tagged from 2002 to 2004.

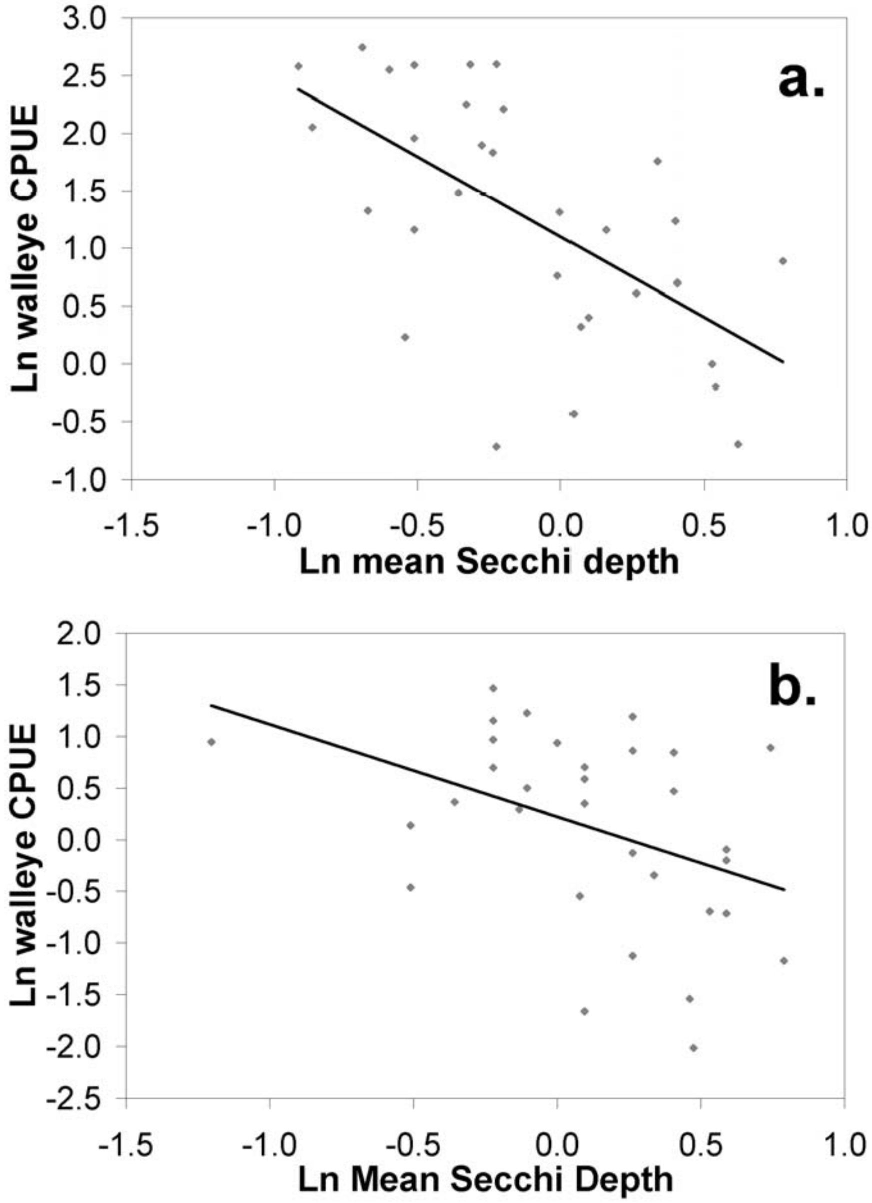


Recent surveys by the U.S. Geological Survey have documented walleye spawning activity in the Detroit River (Manny et al. 2007). A distinct Detroit River spawning stock may exist or walleyes may stray into the river from Lake Erie spawning sites. Progeny from these walleyes may contribute to adult walleye abundance in Lake St. Clair. Additional genetic and tagging studies are needed to better evaluate the role of the Detroit River as a source of walleye in these systems.

Changes in Ecology and Habitat

Changes in the ecology and habitat of Lake St. Clair have greatly influenced the walleye population during the last 30 years. Zebra mussels were first found in Lake St. Clair in 1988 (Hebert et al. 1989) and may be responsible for the decline in walleye abundance in the lake documented in this report. Filter feeding by zebra mussels increased water transparency (Holland 1993). Before zebra mussel colonization, Lake St. Clair Secchi-disk depth varied from 1 to 2 m, but, after zebra mussel colonization Secchi-disk depth more than doubled in many areas (Griffiths 1993). Secchi-disk depth increased at the Tremblay Creek and Mitchell's Bay trapnet survey sites by 80% and 40%, respectively, after zebra mussels colonized Lake St. Clair. Walleyes are light sensitive, and this increase in water clarity likely decreased the amount of optical habitat available for walleye (Lester et al. 2004). The trapnet survey showed that walleye CPUE decreased as Secchi depth increased at both the Tremblay Creek (r^2 = 0.38, p = 0.0002) and Mitchell's Bay sites (r^2 = 0.17, p = 0.019) (Fig. 10). The increase in water clarity also led to an increase in aquatic macrophytes in Lake St. Clair (Griffiths 1993; MacIsaac 1996; Schloesser et al. 1996). This increase in aquatic macrophytes improved the spawning and feeding habitat for species such as smallmouth bass and muskellunge. Both of these species have increased in relative abundance during the time in which walleye relative abundance decreased (MacLennan 1996; Thomas and Haas 2007). The population increase of smallmouth bass and muskellunge may have also increased predation on juvenile walleye. Other factors may have influenced walleye abundance from 1987 through the 1990s. However, fish-community and habitat changes associated with the invasion of the zebra mussel are the most likely cause, and exploitation was unlikely a factor as total mortality was declining during this period. Walleyes are no longer the top predator in Lake St. Clair, making achievement of historical levels of walleye yield unlikely.

Fig. 10. Relationship between mean Secchi depth (m) and CPUE of walleye in OMNR trapnet surveys at a) Tremblay Creek and b) Mitchell's Bay, Lake St. Clair.


a.
Ln walleye CPUE
Ln mean Secchi depth
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
b.
Ln walleye CPUE
Ln Mean Secchi Depth
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-1.5
-1.0
-0.5
0.0
0.5
1.0

Management Changes

After the decline of the Lake St. Clair walleye stocks in the early 1990s, management actions were taken to promote their recovery. In 1997, a size limit was placed on walleye caught in the Ontario waters of Lake St. Clair, the St. Clair River, and the Thames River in order to protect spawning walleye. The new regulation stated that no walleyes between 43 cm and 63.5 cm could be kept, and only one walleye over 63.5 cm could be kept. In later years, this regulation was simplified such that walleye of any size could be harvested, but only one walleye over 46 cm could be kept. Despite the management changes, the Thames River spawning stock has not increased in abundance. This fact also supports our view that changes to the environment, not exploitation, were the major causes of the decline in Lake St. Clair walleye abundance. In 2005, the walleye size limit was rescinded for Lake St. Clair and the St. Clair River, but it remains in place on the Thames River along with a spring (March 15 to April 15) closure to protect spawning fish. In 2001, the spring (March 1 to April 30) creel limit for walleye in the Detroit River was reduced from 6 to 4 fish in response to a reduced number of walleye in Lake Erie (the limit remained 6 through the remainder of the year).

From 1989 through 2003, Michigan walleye fishing regulations were consistent across all three waterbodies (Detroit River, Lake St. Clair, and St. Clair River). Those regulations included: no closed season, a six-fish daily possession limit, and a minimum size limit of 33 cm. In 2004, the regulations for only the Detroit River changed (matching the regulation changes made for the Michigan waters of Lake Erie) to include: no closed season, a five-fish daily possession limit, and a minimum size limit of 381 mm.

Walleye fingerlings were stocked into the Clinton River, a Michigan tributary to Lake St. Clair, starting in 1982 and continuing into the 1990s. The objective of the stocking effort was to establish a self-sustaining walleye spawning run. The fingerlings originated from spawning adults captured in the Muskegon River (Lake Michigan drainage) or Tittabawassee River (Lake Huron drainage). A total of just over 250,000 fingerlings were stocked before stocking was discontinued in 1997. A walleye spawning run was documented in the Clinton River in 1991 (Thomas 1995), but habitat conditions in the lower Clinton River and in Lake St. Clair near the mouth of the river were found to result in starvation of the resulting fry due to low zooplankton abundances (Haas and Thomas 1997). Since 1998, no walleye stocking has occurred in Lake St. Clair or its connecting rivers.

Conclusion

Habitat changes in Lake St. Clair caused by zebra mussels appear to have greatly reduced abundance of the Thames River spawning stock of walleye, which was the primary stock in the lake. These changes include increased water clarity, increased aquatic plant abundance and distribution, and increased abundance of potential predators on juvenile walleye, such as smallmouth bass and muskellunge. Although walleye from the western basin of Lake Erie migrate into Lake St. Clair and its connecting waters and the Thames River spawning stock persists, Lake St. Clair walleye fisheries are now largely dependent on immigration of walleye that spawn in Lake Erie. As walleye abundance in Lake St. Clair has declined, angler effort for walleye has decreased. Nevertheless, Lake St. Clair, the St. Clair River and the Detroit River continue to support an important recreational walleye fishery in both U.S and Canadian waters.

Acknowledgements

We thank Don MacLennan (retired) for his role in the collection, compilation, and analysis of walleye data at the Lake St. Clair Fisheries Assessment Unit. We thank Robert Haas for compiling and maintaining the Lake Erie and Lake St. Clair walleye tagging databases and preparing the tag recovery figures. We also thank two anonymous reviewers for their comments on the manuscript.

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STATUS OF WALLEYE IN WESTERN LAKE ERIE, 1985-2006

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Abstract

The abundance of walleye (*Sander vitreus)* in western Lake Erie has undergone dramatic fluctuations over the past century for a variety of reasons, including over-exploitation and the ever-changing characteristics of the lake's biological, physical, and chemical environment. Despite these fluctuations, western walleye have proven to be resilient and continue to support economically important recreational and commercial fisheries. This paper provides an overview of changes to the walleye population and fishery in the western waters of Lake Erie during 1985-2006 and discusses implications for the future. Over the past two decades, the abundance of walleye has oscillated from a historical high in 1988 to a steady decline in the 1990s to a secondary high in 2005. Concurrently, the forage base shifted from a community dominated by clupeids and other soft-rayed species, primarily emerald

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shiner (*Notropis atherinoides*) and gizzard shad (*Dorosoma cepedianum*), to spiny-rayed species, primarily white perch (*Morone americana*) and yellow perch (*Perca flavescens*). Additionally, the establishment of dreissenid mussels within Lake Erie resulted in increased water clarity and additional fish-community changes. Despite shifts in the prey community, walleye growth rates have not changed. A tagging study initiated in 1990 showed that some western walleye immigrated to eastern Lake Erie and also to Lake Huron via the Detroit and St. Clair Rivers. Declining walleye abundance in the 1990s prompted improved assessment techniques, including using sagittal otoliths instead of scales for age determination and estimating population abundance via statistical catch-at-age modeling. Declining walleye abundance also prompted a decision-analysis process and implementation of adaptive management strategies, including reduced harvest and minimum size limits in some jurisdictions. Walleye abundance in western waters has increased since 2004, and, although recruitment remains variable, walleye fisheries in western waters remain economically viable and sustainable.

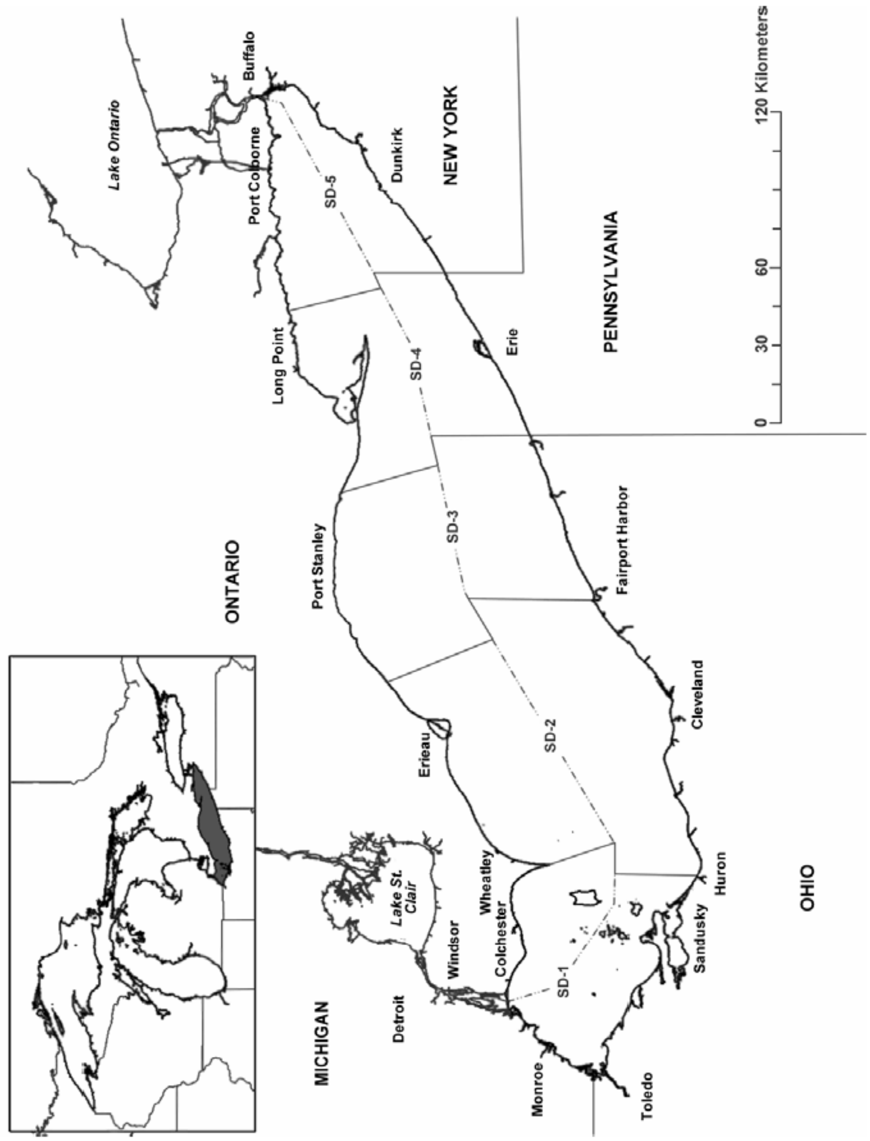
Introduction

The walleye (*Sander vitreus*) has always been an important fish in Lake Erie and was targeted extensively by the commercial fishery after the collapse of the valuable cisco (*Coregonus artedii*) fishery in the 1920s (Smith 1972; Hatch et al. 1987; Nepszy et al. 1991). As the commercial walleye fishery intensified in Canada and the U.S. and more-efficient fishing gear was developed, harvest in the western basin (see SD-1 in Fig. 1) increased steadily during the 1920s and 1930s and rapidly in the 1940s, reaching a peak harvest of nearly 7000 t in 1956 (Nepszy et al. 1991). A near-record harvest of over 6000 t was achieved in 1957 but was followed by declining harvests through the 1960s and closure of the fishery in 1970 (Baldwin et al. 2009; Nepszy et al. 1991). This decline in harvest was due to a major decline in walleye abundance attributed to nutrient enrichment, invasive species, exploitation, spawning-habitat degradation, dam construction blocking spawning runs on tributaries, and introgression with blue pike (*S. vitreus glaucus*) and sauger (*S. canadensis*) (Regier et al. 1969). Closure of the fishery in 1970 was due to high mercury levels in walleye tissue samples. By

1973, mercury levels had dropped below the human-health threshold (0.5 ppm) established by the U.S. Environmental Protection Agency (Colby et al. 1991), and recreational walleye fisheries were reopened in Michigan, Ohio, and Ontario waters. The commercial walleye fishery in Ontario waters was reopened in 1976 (Cowan and Paine 1997) but remains closed in Ohio and Michigan waters. Following the lifting of the fishing moratorium, walleye abundance and harvest, mostly recreational, increased rapidly during the late 1970s to 1985 (Hatch et al. 1987; Nepszy et al. 1991).

The objective of this paper is to review walleye population changes and describe the status of the walleye population and the walleye fishery in western Lake Erie (western basin and west-central basin) during 1985-2006 and to discuss current and possible future management strategies. Information regarding population status and fishery trends for Lake Erie's eastern walleye population is presented in Einhouse and MacDougall (Einhouse and MacDougall 2010).

Fig. 1. Map of Lake Erie showing fishery statistical districts (SD) (modified after Smith et al. 1961).


Lake Ontario
Buffalo
Port Colborne
SD-5
Dunkirk
NEW YORK
Long Point
SD-4
Erie
PENNSYLVANIA
ONTARIO
Port Stanley
SD-3
Fairport Harbor
Erieau
SD-2
Cleveland
Lake St. Clair
Wheatley
Colchester
Windsor
SD-1
Huron
Sandusky
OHIO
MICHIGAN
Detroit
Monroe
Toledo
0
30
60
120 Kilometers

Management Background and Data Sources

An interagency approach to management of the western walleye population was instituted during the early 1970s (Kutkuhn et al. 1976). Working under the auspices of the Great Lakes Fishery Commission (GLFC), the Lake Erie Committee (LEC) formed a Scientific Protocol Committee (SPC) to estimate the abundance of the walleye population, establish acceptable levels of exploitation that would allow recovery of the population, and allocate the surplus production of fish among management jurisdictions (Nepszy et al. 1991). All agencies with management authority on Lake Erie were represented on the SPC, including the Ontario Ministry of Natural Resources (OMNR), Michigan Department of Natural Resources and Environment, Ohio Department of Natural Resources (DNR), Pennsylvania Fish and Boat Commission, and the New York State Department of Environmental Conservation. However, quotas for western walleye were allocated only to Ontario, Michigan, and Ohio because walleye migration studies conducted in the early 1960s indicated that the western population was supported by separate spawning stocks that were largely confined to those jurisdictions in the western basin and portions of the west-central basin (Fig. 1).

In 1977, the Standing Technical Committee (STC) replaced the SPC both in name and function, and species-specific task groups were established within the STC, including the Walleye Task Group (WTG). The allocation process for the western population became more formalized under the LEC with the signing of A Joint Strategic Plan for Management of Great Lakes Fisheries in 1981 (Great Lakes Fishery Commission 2007). The responsibility for estimating the abundance of walleye and recommending allowable harvests was reassigned to the WTG (Knight 1997). To accomplish the charge of estimating population abundance, the WTG maintains and updates annually a centralized database of information collected from surveys of the commercial and recreational (sport) fisheries (fishery-dependent data) and from surveys conducted by agency personnel with agency gear and vessels (fishery-independent data). This information was used in this report to describe trends in population abundance and in fishery effort and harvest in western waters prior to and during 1985-2006.

Fishery-Dependent Surveys

Walleye harvest and fishing effort for the commercial (mandatory daily reporting) and recreational (mandatory daily reporting by charterboats and estimates by creel survey for individual anglers) fisheries in Lake Erie statistical districts (SDs) (Fig. 1) were compiled and reported annually by each management agency. Although numerous river- and reef-spawning stocks exist throughout the lake, these stocks have not yet been completely identified so walleye are assessed and managed according to two generalizations of "stocks," a western-basin stock and an eastern-basin stock. Historically, the western-basin stock has been considered to occupy SD-1, SD-2, and SD-3; the eastern-basin stock is considered to occupy SD-4 and SD-5 (Fig. 1). Data from Michigan (SD-1), Ohio (SD-1 and SD-2), and Ontario (SD-1, SD-2, and SD-3 were used by the WTG to estimate the abundance of the western-basin stock using statistical catch-at-age analysis (SCAA) and to monitor fishing effort and harvest by the commercial and recreational fisheries. Methods used to assess this effort and harvest vary among the management agencies and are described in their annual status reports (Michigan Department of Natural Resources 2007; New York State Department of Environmental Conservation 2007; Ohio Department of Natural Resources 2007; Ontario Ministry of Natural Resources 2007; Pennsylvania Fish and Boat Commission 2007).

Fishery-Independent Surveys

The abundance of age-0 western-basin walleye is assessed annually by bottom trawling in August, and these data have been used as a measure (or index) of year-class strength. This survey, initiated in 1969 by the Ohio DNR, has remained consistent through time with respect to the gear used, although the number of sites trawled and the spatial coverage has varied. The OMNR began a bottom-trawl survey employing similar gear in 1982. Each survey was treated as an independent index of age-0 western-basin walleye recruitment.

In 1987, the OMNR and Ohio DNR initiated the Lake Erie Interagency Trawl Survey (LEITS), using a similar trawl configuration and survey design, to assess percid (i.e., walleye and yellow perch (*Perca flavescens*)) recruitment at 77 fixed stations in Ohio and Ontario waters of SD-1. An interagency group, established in 1992 to review the LEITS, recommended that trawl catches among agencies be standardized to more-accurately describe walleye recruitment. A trawling comparison and calibration study conducted in 2003 has resulted in better methods to standardize catch rates of age-0 walleye among the different trawling vessels (Tyson et al. 2006). These methods will be employed beginning in 2007 and should result in improved age-0 walleye recruitment indices. In addition to percids, recruitment and growth indices for other species in the western-basin fish community (primarily white perch (*Morone americana*), gizzard shad (*Dorosoma cepedianum*), and shiners (*Notropis* spp.)) are also assessed with the LEITS. A detailed description of the LEITS is presented in Ohio Department of Natural Resources (2007) and in Forage Task Group (2007).

The relative abundance and biological characteristics of age-1 and older walleye were assessed annually during autumn using graded-mesh gillnets (Michigan Department of Natural Resources 2007; Ohio Department of Natural Resources 2007; Ontario Ministry of Natural Resources 2007). Because of differences in gillnet configuration and survey design, direct comparisons of catch rates among agencies are of limited value. However, these assessments provide usable year-to-year indices of abundance within agency waters, are a source for biological data (age, growth, etc.), and can be used to compliment other assessments. In Ontario waters, the age-0 walleye catch in bottom trawls (derived from the LEITS) correlated strongly with the catch of age-1 walleye in graded-mesh gillnets ($r^2 = 0.90$ $P < 0.01$; HAC, unpublished data) suggesting that year-class strength in the western basin is set by August of the first year. Biological information (age, growth, mortality) presented in this paper was from walleye collected in the Ohio DNR and OMNR fall gillnet surveys.

Walleye growth rates in the western basin were estimated for five time periods associated with increasing (1978-1983), peak (1984-1988), decreasing (1989-1996), low but stable (1997-2003), and increasing (2004-2006) walleye abundance to determine the influence of population abundance on growth rates and to compare contemporary growth rates with those prior to 1985. The Ohio DNR estimated growth rates from scales through 2003 and from otoliths thereafter, whereas the OMNR used scales prior to 2005 and otoliths thereafter. The switch from scales to otoliths was based on an interagency study in 2003, which concluded that scales underestimate age, especially for walleye age-3 and older (>500 mm), whereas otoliths did not (CSV, unpublished data).

Population-Abundance Estimates

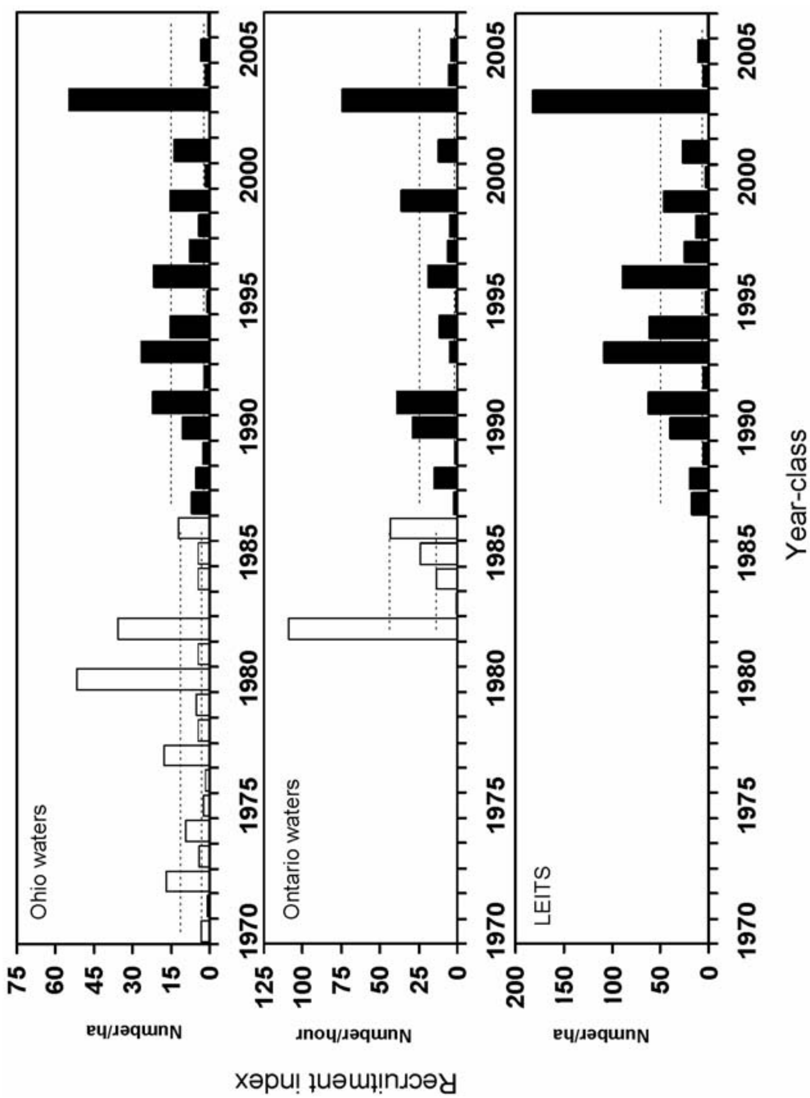
Estimating the population abundance of age-2 and older walleye in the western basin has been one of the primary responsibilities of the Lake Erie WTG since its inception. Early (i.e., 1980s) estimates of the walleye population were derived using virtual population analysis (VPA), but, due to uncertainties in the VPA estimates, the WTG began using a model based on a catch-at-age analysis under a Beverton and Holt $F_{0.1}$ yield-per-recruit management strategy (CAGEAN; Deriso et al. 1985) in 1990 (Walleye Task Group 1990). Although the population estimates obtained using the CAGEAN model were considered to be better estimates than from the VPA model (Knight 1997), the methodology used to estimate population abundance was changed to a SCAA model in 2000 (Walleye Task Group 2001). Similar to the CAGEAN model, the SCAA model utilizes fishery-dependent (harvest information) data, but the SCAA model is considered more robust because it incorporates fishery-independent data and is programmed in Auto Differentiated Model Builder (ADMB) software, which allows for the modification of output parameters (Walley Task Group 2001).

Population and Status Changes, 1985-2006

Recruitment and Abundance

Similar to recruitment patterns observed in other walleye populations in North America (Ney 1978), walleye recruitment in the western basin exhibited large inter-annual fluctuations (Fig. 2). Historically, strong (values greater than 3rd quartile) to moderately strong (values between 2nd and 3rd quartiles) year-classes were often followed by weak (values less than 1st quartile) to moderately weak (values between 1st and 2nd quartiles) year-classes (Fig. 2). Since 1985, strong year-classes have been followed by strong or moderately strong year-classes on two occasions (1990-1991 and 1993-1994).

Fig. 2. Recruitment indices for age-0 walleye based on number collected per hour or area (ha) in bottom-trawl surveys conducted in Ohio and Ontario waters of Lake Erie's western basin, reported by jurisdiction during 1970-1986 and collectively during 1987-2006 as the Lake Erie Interagency Trawl Survey (LEITS). The dashed lines in the two independent data sets (1970-1986 and 1987-2006) represent the 1[st] and 3[rd] quartile values. Note the different y-axis scales.

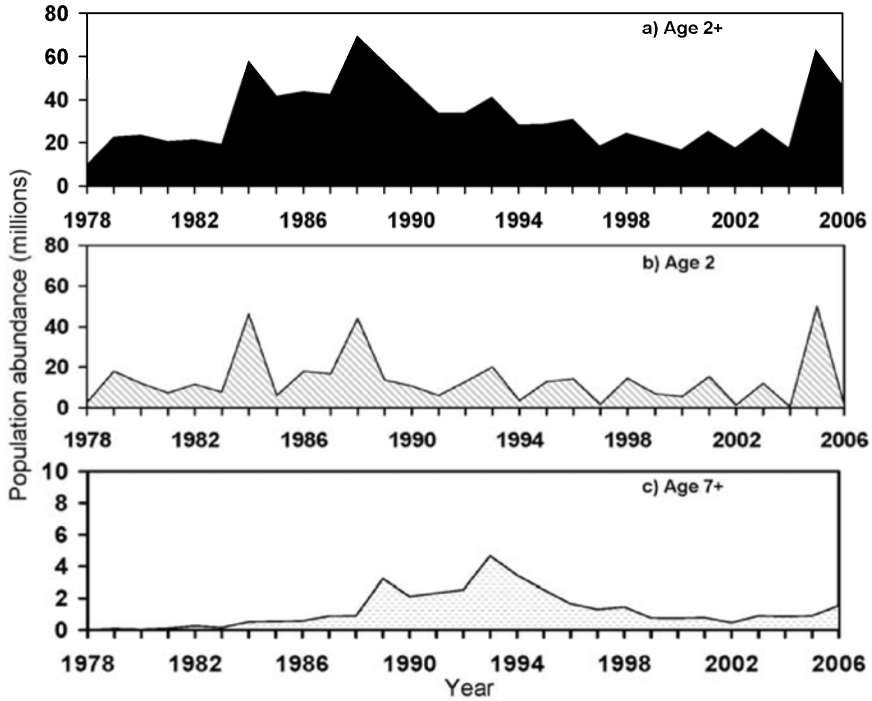


The western-basin walleye population has produced fewer strong year-classes in recent years, possibly due to changes in composition of the aquatic community and to physical changes in the lake. Only one strong year-class was produced during 1997-2006 compared to four during 1987-1996, although the frequency of weak year-classes was similar (3 versus 4, respectively). Factors affecting recruitment during the late 1980s to mid-1990s were believed to be river discharge (Reckhan and Thurston 1991; Mion et al. 1998), storm events (Roseman 2000), and gizzard shad abundance (Madenjian et al. 1996). However, physical changes (increased water clarity, decreased nutrient loading, decreased water level) and shifts in the aquatic community (establishment of non-native white perch, round goby (*Neogobius melanostomus*) and dreissenid mussels) may be the major factors affecting walleye recruitment after the mid-1990s (Ryan et al. 2003; Roseman it al. 2008).

Walleye recruitment in the western basin fluctuated similarly in Ohio and Ontario waters; the OMNR and Ohio DNR age-0 recruitment indices were highly correlated (r = 0.85) (Fig. 2). However, disparities occurred in 1993, 1994, and 1996 when the 1993 and 1994 year-classes were strong in Ohio waters but moderately weak (1993) or average (i.e., between 1st and 3rd quartiles in 1994) in Ontario waters. Also, the 1996 year-class was strong in Ontario waters but only moderately strong in Ohio waters.

Abundance of age-2 and older western-basin walleye has fluctuated considerably since 1970 due mainly to recruitment variation. Since 1978, the abundance of walleye age 2 and older (2+) peaked in 1988 at about 70 million fish then dropped to 20 million fish within 10 years (Fig. 3a). This decline, beginning in 1990 and continuing until 2002, likely was due to especially weak year-classes in 1992, 1995, and 2000 (Fig. 2). The abundance of age-2+ walleye fluctuated around 20 million fish during 1997-2004 then increased to about 65 million fish in 2005 with the influx of age-2 fish from the strong 2003 year-class (Fig. 3a). Abundance declined in 2006 due to poor recruitment from the weak 2004 year-class. Similar to age-2+ walleye, age-7 and older walleye (7+) were most abundant during the mid- to late 1980s, but, for reasons unknown, their abundance did not increase during the late 1990s and early 2000s despite strong 1991, 1993, and 1996 year-classes (Figs. 2 and 3c).

Fig. 3. Estimated abundance (millions of fish) of (a) age-2 and older (age-2+), (b) age-2, and (c) age-7 and older (age-7+) walleye in western Lake Erie (SDs 1-3; see Fig. 1), 1978-2006.

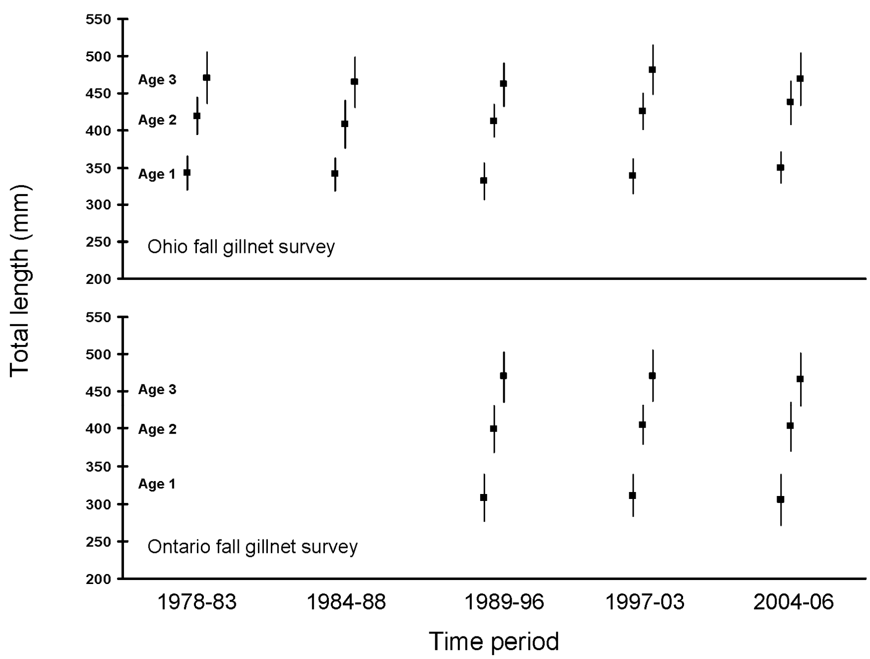


Growth

Growth rates for the western-basin walleye population have historically been higher than for other populations in North America (Colby et al. 1979), and during the mid-1940s and mid-1960s, a period of low population abundance, their growth rates (based on ages-1-3 fish) increased sharply (Wolfert 1977). Growth stabilized at a lower level during the early 1970s and mid-1980s as the abundance of walleye increased steadily (Hatch et al. 1987). During most of this period of stable growth, densities of walleye prey fishes, including clupeids (gizzard shad, alewife (*Alosa pseudoharengus*) and other soft-rayed fishes (i.e., emerald shiner (*Notropis atherinoides*), spottail shiner (*N. hudsonius*), and rainbow smelt (*Osmerus mordax*)) were high (Knight et al.

1984; Knight and Vondracek 1993). Knight et al. (1984) reported that age-1 and older walleye generally selected clupeids and other soft-rayed fishes as prey over similar-sized spiny-rayed fishes (i.e., white perch, yellow perch, freshwater drum (*Aplodinotus grunniens*), and white bass (*Morone chrysops*) throughout the year. Despite a considerable decline in soft-rayed fish abundance since the late 1970s and early 1980s and considerable variations in walleye abundance (Fig. 3), growth of ages-1-3 western-basin walleye (based on length at age) has remained relatively stable since 1978 (Fig. 4). As the abundance of soft-rayed fishes declined, walleye apparently utilized more of the increasingly abundant spiny-rayed fish (Knight and Vondracek 1993). Although growth rates have been shown to vary with shifts in the forage base in other North American walleye populations (Jones et al. 1994; Porath and Peters 1997), walleye in the western basin have shifted from soft-rayed to spiny-rayed forage with no apparent change in growth rate.

Fig. 4. Mean total length (mm) at age (with associated 95% confidence intervals) of age-1, age-2, and age-3 walleye averaged for five time periods during 1978-2006. Walleye were collected from the western basin of Lake Erie by the Ohio DNR and the Ontario MNR during fall gillnet surveys.



The specific factors affecting the shift in abundance from soft-rayed to spiny-rayed species has not been identified, but the most plausible factor is lower productivity due to reduced nutrient loading (i.e., measured as phosphorus) since the 1970s (Ryan et al. 2003). It is also possible that a portion of the shift may be due to gear bias, because increased water clarity associated with the establishment of dreissenid mussels (Nicholls and Hopkins 1993) may have resulted in some of the soft-rayed fishes becoming more pelagic and, therefore, less vulnerable to the bottom trawls used to assess their abundance.

Migration of Adult Walleye

The allocation of western-basin walleye quotas by the LEC since 1976 has been only to the management agencies within SDs 1, 2, and 3 (i.e., Ontario, Michigan, and Ohio), because migration outside of this area was deemed negligible from previous migration studies (Doan 1942; Wolfert 1963; Kutkuhn et al. 1976). However, tag returns from an interagency tagging program during 1990-2001 indicated that some large (and, consequently, older) female walleye from western-basin spawning stocks migrated north out of the western basin through the Huron-Erie Corridor (Detroit River-Lake St. Clair-St. Clair River) into Lake Huron and also migrated east into the eastern basin of Lake Erie (Wang et al. 2007). Males from the same western-basin spawning populations migrated much shorter distances than females. Wang et al. (2007) suggested that these migrations may be in response to changes in the spatial distribution of prey species (Parsons 1971; Knight et al. 1984) and/or to elevated water temperatures during the summer months (average 24°C) that exceed the thermal optima for larger walleye (i.e., 20-23°C; Coutant 1977; Kershner et al. 1999). Although the LEC has not yet determined if such migrations are sufficient to change quota allocations, information concerning the extent and direction of migration of western-basin walleye stocks is imperative for determining their contribution to lakewide harvest and for their sustainable management.

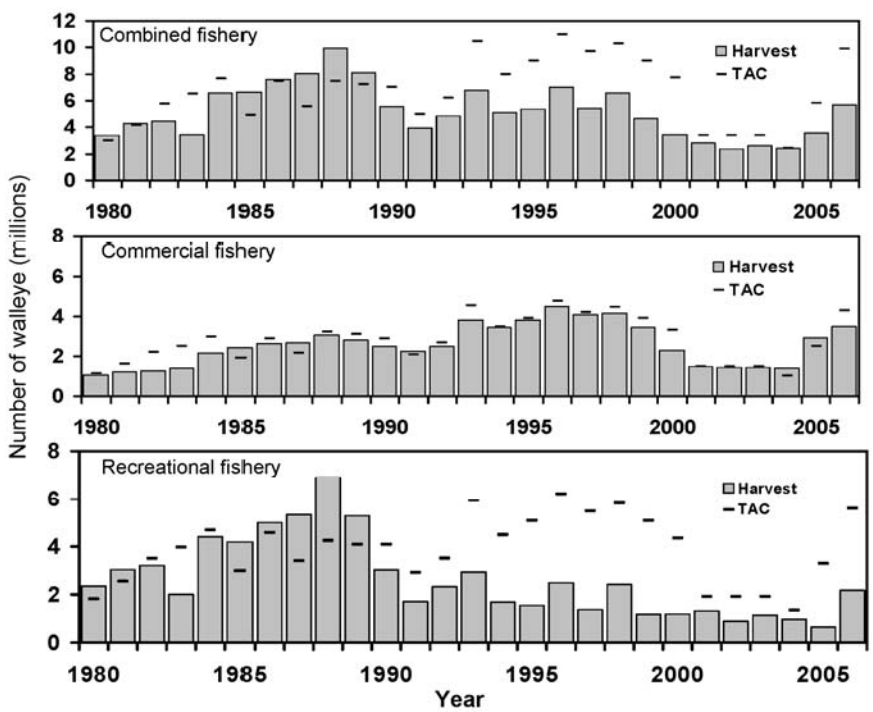
Walleye Management and Fishery Performance, 1985-2006

Walleye have been harvested commercially from Lake Erie since the late 1800s (Baldwin et al. 2009), but the only commercial fishery impacting the western-basin walleye during 1985-2006 has been in Ontario waters. Recreational fisheries extensive enough to influence walleye mortality were slow to develop in the western basin until 1975, after which catch rates, effort, and harvest increased dramatically both in U.S. and Ontario waters (Hatch et al. 1987). Historically, the majority of the recreational fishing effort and harvest for walleye has been concentrated in the western basin (Walleye Task Group 2008).

A process for developing western-basin walleye quotas was initiated prior to the reopening of the Ontario commercial fishery in 1976. Based on a consensus and working under the auspices of the GLFC, the LEC annually recommends an overall total allowable catch (TAC) based on findings provided by the WTG, which are based in part on a mortality rate determined to be low enough to prevent over-exploitation. Initially, the LEC allocated the TAC among agency jurisdictions based on their total surface area in SD-1 together with their surface area within the 13-meter depth contour of SD-2, which, at that time, was considered to encompass the range of most walleye in the western-basin population (Kutkuhn et al. 1976; Hatch et al. 1987; Walleye Task Group 1989). This surface-area factor was subsequently expanded to include waters in SD-3 that were within the 13-meter contour (Walleye Task Group 1990).

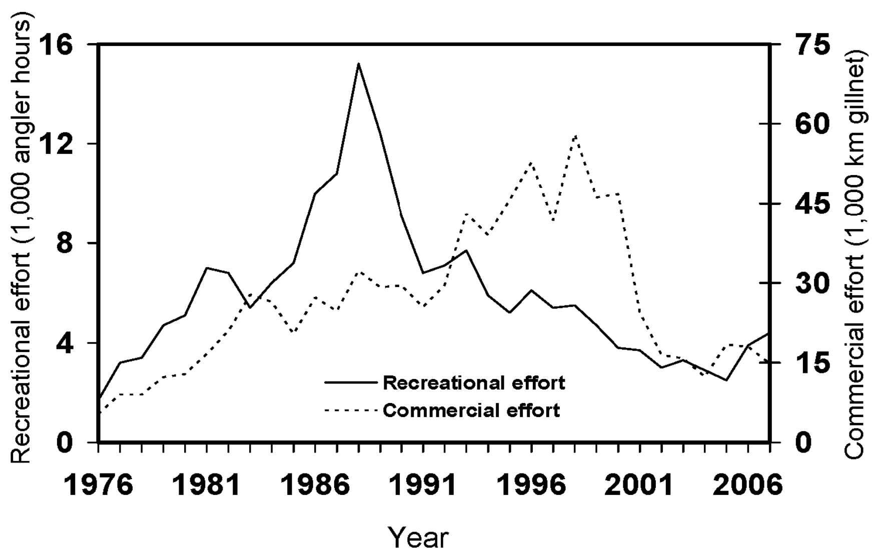
To comply with their share of the TAC, each western-basin agency constrains their respective fisheries by imposing restrictions. Recreational fisheries have been typically restricted by fish size and creel (daily possession) limits, whereas commercial fisheries have been subjected to effort and gear restrictions and individual quotas (Kohler and Hubert 1993). Recreational creel limits have ranged from 6-10 walleyes per day among western-basin jurisdictions, and minimum fish size limits have been used sparingly. Monofilament gillnets 36- to 50-meshes deep have been the preferred net type in Ontario waters since the 1970s. Beginning in 1982, Ontario required the use of gillnets with a minimum stretched-mesh size of 89 mm as a condition of licence for targeting walleye. This mesh size was selective for the most-marketable-sized walleye (406-533 mm, total length). In 1984, individual quotas were imposed, with allocations for each fisher based on their harvest during the 1970s (Cowan and Paine 1997). In 1985, the OMNR implemented an individual transferable quota (ITQ) system allowing commercial fishers to transfer their quota to other licensees (Cowan and Paine 1997). In 1986, the OMNR established "no-harvest" spawning sanctuaries that included the major spawning grounds in the western and central basins, and also prohibited the use of suspended gillnets during July through August to reduce conflict between recreational boaters and commercial fishers. The measures employed to constrain the fisheries appear to have been sufficient as the overall TAC has not been exceeded in most years during 1980-2006 (Fig. 5).

Fig. 5. Commercial and recreational fishery harvests and estimated total allowable catches (TACs) for walleye in western Lake Erie (SDs 1-3; see Fig. 1), 1980-2006.



Walleye fisheries thrived in western Lake Erie during the late 1980s (Fig. 5) due to the large biomass of age-2+ walleye that had accumulated during the 1970s (Walleye Task Group 2008). Recreational harvest decreased during the 1990s as fishing effort decreased in response to declining walleye abundance, whereas commercial harvest increased as fishers sought to meet their quotas by increasing gillnet effort (Fig. 6; Walleye Task Group 2008). Although total harvest remained within the recommended TACs, the CAGEAN model in use at the time is now believed to have overestimated walleye abundance. For example, using the CAGEAN model, the WTG estimated that there would be 49.2 million walleyes in SDs 1-3 in 1997, and the 1997 TAC was set at 9.7 million walleyes (Walleye Task Group 1997). However, based on the current and assumed more-accurate SCAA population model and ADMB software (SCAA/ADMB), the re-estimated abundance of walleye in 1997 was only 17.7 million (Walleye Task Group 2008). Inflated estimates of abundance during the 1990s using CAGEAN led to high TACs that only the commercial fishery could achieve (Fig. 5) (Walleye Task Group 2008). Population modeling methods advanced with the availability of more-flexible programming software and the incorporation of survey data into the models (Walleye Task Group 2000; Myers and Bence 2001). Although the reasons leading to the disparity between the CAGEAN and SCAA/ADMB model abundance estimates have not be identified, the WTG suspected that the SCAA/ADMB more accurately estimates abundance because it does not assume a terminal fishing rate as does the CAGEN model, and it is capable of incorporating fishery-independent survey data.

Fig. 6. Recreational fishing effort (angler hours) and commercial fishing effort (km of gillnet) for walleye fisheries in western Lake Erie, 1975-2006 (SDs 1-3; see Fig. 1).



The declining walleye abundance and increased commercial harvest of age-2+ walleye in the western basin during the mid- and late 1990s prompted the LEC to implement in 2000 the Coordinated Percid Management Strategy (CPMS), which included adopting a highly conservative harvest policy during 2001-2003 and improving the methodology used for estimating walleye abundance (Lake Erie Committee 2004). It was during this time that the potential for underestimating abundance using the CAGEAN model was realized and, after numerous SCAA models were tested, the current SCAA/ADMB model was adopted. The primary objective of the CPMS was to halt the decline in walleye abundance and restore abundance to levels approaching those achieved in the 1980s (Lake Erie Committee 2004). The LEC set interim TACs for 2001-2003 at 3.4 million fish, the lowest since 1980 (Fig. 5), in an effort to maintain abundance at the level estimated for 2000 (Lake Erie Committee 2004). To stay within the recommended TAC, Ontario's commercial fishery was constrained by ITQs, and each LEC agency made their sport-fishing regulations more restrictive in various ways, including spring closures and reduced creel limits (Lake Erie Committee 2004). The lower TACs and increased constraints on fisheries helped protect a moderately strong 1999 year-class. The 1999 year-class made up most of the spawning population in the spring of 2003 and, aided by favorable climatic and biotic conditions, produced the exceptionally strong 2003 year-class. Favorable climatic and biotic conditions are only inferred because strong year-classes were produced by several other species in the western basin, including yellow perch, lake whitefish (*Coregonus clupeaformis*), white bass, rainbow smelt, and white perch.

The LEC had difficulty reaching a consensus on the 2004 TAC, partially because of the exceptional 2003 year-class that would recruit to the fishery in 2005. The 2004 TAC was set at 2.4 million fish with the aid of a GLFC-mediated arbitration process (Ayles and Conlin 2004; Gaden 2007). Because of the lower walleye TACs during 2001-2004, fisheries in the western basin and west-central basin focused on other species (e.g., yellow perch, white perch, white bass, and lake whitefish).

In 2004, Ohio and Michigan increased restrictions on their walleye recreational fisheries. Ohio established a minimum size limit of 381 mm and Michigan increased the minimum size limit from 330 mm to 381 mm. This action was taken to reduce the harvest of yearling (age-1) walleye because this harvest was not accounted for in the TACs. Minimum size limits were not enacted in Ontario waters because the recreational harvest was assumed to be low. As a result of the increased minimum size limits, walleye release rates in the Ohio recreational fishery increased in 2004 and 2005, so minimum size limits likely reduced harvest, especially of yearling walleye (Ohio Department of Natural Resources 2007). Yearling walleye are caught as bycatch in the Ontario commercial yellow perch gillnet fishery, but this bycatch has not been quantified (Ontario Ministry of Natural Resources 2005; Walleye Task Group 2005). The increased release of walleye caught in the recreational fishery has prompted a concern regarding hooking mortality of released fish, but hooking mortality has not been quantified. Walleye hooking mortality reported from other waters ranged from 0 to 23% (Casselman 2005; Reeves and Bruesewitz 2007; Standing Technical Committee 2007).

The LEC, with assistance from Michigan State University, developed a walleye management plan during 2004 that was adopted in 2005 (Locke et al. 2005). A key feature of the plan was determination of TACs based on target fishing rates that were dependent on four thresholds of estimated walleye abundance (crisis, <15 million; rehabilitation, 15-20 million; maintenance, 20-40 million; and high quality, >40 million). The recommended instantaneous fishing rates (F) for these population thresholds were crisis, $F = 0.10$; rehabilitation, $F = 0.10$-0.20; maintenance, $F = 0.20$-0.35; and high quality, $F = 0.35$. As an example, recruitment of the strong 2003 year-class in 2005 resulted in abundance estimates in the high-quality range and in TACs that were much higher in 2005-2006 than in 2001-2004 (Fig. 5).

The management actions initiated in recent years appear to have reduced fishing mortality sufficiently as annual survival estimates (assuming a constant natural mortality rate of 0.32) for western-basin walleye have exceeded 60% since 2000. These high survival rates have been corroborated by tag returns from an interagency walleye tagging program (R. Haas, unpublished data). Largely due to these high survival rates and contribution from the strong 2003 year-class, the estimated biomass of spawning fish (age 3+) during 2006-2008 is expected to be high relative to the levels observed earlier in the decade (Walleye Task Group 2008), which is important in light of the weak to moderate year-classes produced after 2003 (Fig. 3).

The recreational harvest of walleye in SD 1-3, assessed annually in Ohio and Michigan waters but only sporadically in Ontario waters, contributes most of the recreational walleye harvest from the whole lake. The recreational walleye harvest in Ohio was 83% of the total recreational harvest in U.S. waters during 1996-2007, followed by Michigan (11%), Pennsylvania (4%), and New York (2%). Over 75% of walleye harvested in Michigan and Ohio waters are taken by private anglers with the remainder harvested by charterboats.

The western-basin walleye population is an economically important resource for all stakeholders, but the allocation of this resource has been controversial due to the competing interests of commercial and recreational fisheries. Commercial interests in Ontario favor more-liberal harvest approaches as compared to those preferred by recreational interests in all jurisdictions. The economic prosperity of the commercial fishery is dependent upon the TAC and the prices, whereas recreational-fishery economics depend mostly on population abundance and the ensuing high catch rates, which fuel greater angler participation. The proliferation of marinas, bait and tackle shops, charterboat operations, and fish-cleaning houses on the U.S. south shore is an indicator of the economic importance of the walleye recreational fishery. Although the recreational fishery is economically important in some Ontario waters, Ontario lacks the human-population density, natural harbors, and favorable prevailing winds thought necessary to support a comparable-sized recreational fishery. As of 2006, the sustainability of walleye fisheries in the western basin was improved due to better assessment and allocation methodology, conservative fishing regulations, and multi-jurisdictional management agreements (Great Lakes Fishery Commission 2007).

Future Management Considerations

Currently, walleye TACs for western-basin stocks are based on an exploitation policy utilizing predetermined fishing rates for defined population thresholds. The population model currently used to estimate population abundance is influenced heavily by fishery-dependent data (annual harvest and effort by the recreational and commercial fisheries), fishery-independent data (agency assessment surveys), and assumptions concerning the natural mortality rate, model structure, and proper weighting of data sources. In 2004, the LEC requested from the GLFC an independent evaluation of the efficacy, precision, and accuracy of the current techniques used to assess recreational and commercial percid harvest (Lester et al. 2005). The evaluation revealed that the techniques used by each agency were appropriate from a biological and statistical perspective but that some deficiencies existed. The LEC has addressed several of the recommendations relating to these deficiencies by making an effort to account for unreported harvest by "secondary" or minor recreational fisheries occurring at sites not normally assessed, by continuing the use of otoliths and bony structures rather than scales for age determination (Erickson 1983; Vandergoot et al. 2008), and by reporting the number of released fish in the recreational fishery. The post-release mortality of walleye in the recreational and commercial fisheries and the periodic testing of assumptions associated with different fishery-independent surveys are yet to be addressed (Lester et al. 2005).

Although year-class strength at age 2 is adequately estimated, the mechanisms driving recruitment in the western-basin walleye population remain poorly understood. Madenjian et al. (1996) suggested that walleye recruitment to age 2 was positively related to gizzard shad abundance the previous fall, spring warming rate, and the abundance of spawning walleye. However, since 1996, abundance of gizzard shad has declined, and the methodology used to estimate spawner abundance has changed with the switch from CAGEAN to SCAA/ADMB, making the relationship between these variables and recruitment of age-2 walleye no longer significant (CSV, unpublished data). Recent research suggests that year-class strength is related to winter severity prior to egg deposition (Fedor 2008), meteorological conditions such as high-wind events and water warming rates during the larval life stage (Roseman 2000; Crane 2007), and zooplankton size and spatial distribution (Crane 2007). As well, the effect of maternal characteristics on spawning success across different walleye stocks is currently being investigated.

Efforts are under way by the LEC agencies to verify or improve the accuracy of parameters used to estimate abundance of walleye in Lake Erie. Estimates of exploitation and mortality in recent years have been based on interagency jaw-tag return data (Locke et al. 2005). In 2005, an interagency passive integrated transponder (PIT) tagging program was initiated to estimate jaw-tag loss so that estimates of exploitation and mortality could be corrected for tag loss. The PIT tag program is costly because it relies on agency personnel to recover the tags rather than voluntary returns from fisheries. However, these costs may be justified if PIT tags provide more-robust estimates of mortality.

The non-reporting of jaw-tagged fish has also affected the estimates of exploitation and mortality. Non-reporting rates have been determined for both the sport and commercial fisheries via a high-reward tagging study (Pollock et al. 2001), but these rates have not yet been incorporated into mortality rate estimates. Preliminary analysis of the high-reward tagging study suggests that jaw-tag non-reporting rates appear to be higher for the commercial fishery than for the sport fishery (R. Haas, unpublished data).

Although genetic and microchemical markers have been successfully used for stock discrimination in other waters (Coutant 1990; Guy et al. 1996), there use has met limited success in Lake Erie. Strange and Stepien (2007) used genetic markers to distinguish between eastern- and western-basin walleye, but they were unable to distinguish between individual spawning stocks within the western-basin population. Recent studies using otolith microchemistry suggest that this technique may prove useful for walleye stock discrimination in Lake Erie (Hedges et al. 2002; Ludsin et al. 2006; Thresher 1999). Preliminary studies suggest that differentiation of tributary-spawning stocks using otolith microchemistry may be possible due to differing tributary water chemistries (Hedges et al. 2002; Ludsin et al. 2006; Bigrigg 2008). However, considerable effort would be required to fully evaluate these preliminary findings and to determine the utility of this technique for identifying the stock composition of the fishery harvest and the fishery-independent samples. The effort to improve stock-discrimination techniques supports the Lake Erie walleye fish-community objective of a sustainable western-basin walleye harvest via the guiding principles defined by Ryan et al. (2003). These principles recognize that, although walleye are currently managed as an aggregate population, discrete spawning stocks are the basic unit of management, and the resilience of the population depends on maintaining them. Results from the PIT-tagging and stock-discrimination studies should be forthcoming and may aid in identifying individual stocks. The ability to identify individual stocks should lead to new insights concerning stock-specific natural mortality, survival, and migration, which should result in better-informed management decisions in the future.

Despite many problems (changing habitat, variable recruitment, and balancing the interests of recreational and commercial fisheries), maintaining a sustainable walleye population in western Lake Erie is a common desire of agency managers and fishery participants. The biggest challenge to successful management is accurately estimating population abundance and determining TACs, given the large fluctuations typical in walleye recruitment. Management of recreational fisheries in response to fluctuating TACs may require frequent changes to creel and length limits These limit changes can confuse anglers and may also affect participation because of the trade-off between the expected harvest and the expenditures associated with achieving this harvest. For commercial fisheries, frequent changes in ITQs may affect market stability and demand.

The current management plan for western-basin walleye, calculating TACs using abundance-based fishing rates (Locke et al. 2005), is designed to stabilize the walleye population to near-desirable levels by reducing the duration of low TACs. Over the long term, the use of variable fishing rates to determine TACs results generally in greater population stability than use of constant fishing rates (J. Bence, personal communication).

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AN EMERGING VIEW OF THE MIXED-STOCK STRUCTURE OF LAKE ERIE'S EASTERN-BASIN WALLEYE POPULATION

Donald W. Einhouse[1] **and Thomas M. MacDougall**

Abstract

Lake Erie's eastern-basin walleye (*Sander vitreus*) populations have previously been viewed as discrete from the immense and productive walleye populations inhabiting the lake's western and central basins. However, several recent investigations support an alternative view that eastern-basin fisheries harvest immigrants from the western basin as well as resident eastern-basin fish. Comprehensive tagging studies, genetic investigations, and analysis of harvest patterns show that contributions from western-basin populations to individual eastern-basin fisheries vary geospatially and seasonally and comprise an important part of the harvest in the eastern basin. This new interpretation of walleye distribution and movement in Lake Erie has become a foundation for emerging efforts to develop interagency assessments and multi-jurisdictional management of eastern-basin walleye populations.

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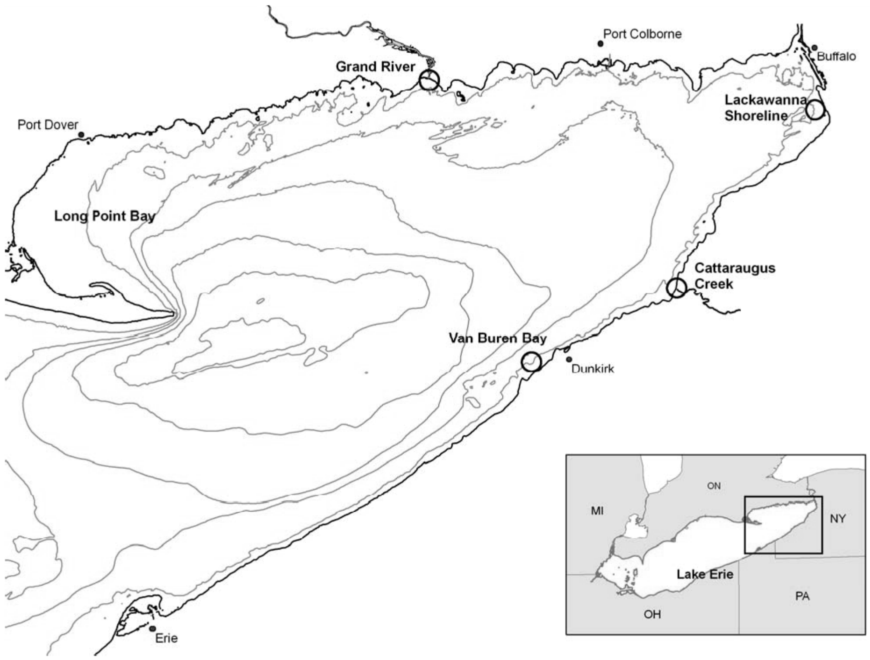
Introduction

The walleye (*Sander vitreus*) population of eastern Lake Erie (Fig. 1) has long been considered distinct from the immense and productive walleye populations of the western and central basins (Nepszy et al. 1991). Several early investigations distinguished eastern- from western-basin populations through differences in age composition and growth (Wolfert 1977), fecundity (Wolfert 1969), and spatial distribution (Wolfert and Van Meter 1978; Einhouse and Shepherd 1988). Walleye populations of the eastern basin have historically been much less abundant than those of the western basin, and they did not suffer the sharp declines that decimated western-basin populations in the 1950s and 1960s (Ryan et al. 2003b). The eastern basin is the least productive of Lake Erie's three basins and is typically a less-optimal environment for percid communities (Ryder and Kerr 1978). Nevertheless, since the 1960s, the eastern basin has continuously supported important walleye fisheries. Walleye are currently the most-sought species among eastern-basin sport fisheries in both Canada and the U.S. and are also a prominent target of commercial fisheries in Canadian waters. The historical view was that walleye inhabiting the eastern and western basins were essentially discrete, isolated populations. However, recent investigations support an alternative view that eastern-basin walleye fisheries are supported by a mixture of populations, including a major contribution from populations that spawn in the western basin. The objective of this paper is to synthesize published studies and ongoing assessments to confirm that walleye supporting eastern-basin fisheries originate from multiple, and often very distant, source populations. We also offer a new perspective on management by consensus for eastern-basin walleye that contrasts with the previous unilateral management by bordering jurisdictions (Nepszy et al. 1991).

Fig. 1. Map of the eastern basin of Lake Erie, including reference population centers (solid dots), and known walleye spawning locations (open circles). Basin depths are indicated with 10-m contour lines.



Historical Perspective of Walleye Inhabiting Eastern Lake Erie

Archaeological evidence from the eastern-basin's north shore indicates that walleye comprised an important portion of the fish consumed by local peoples prior to European settlement (MacDougall et al. 2007). Biological surveys prior to the 1950s did encounter walleye in eastern-basin waters; however, these investigations suggested that walleye were subordinate in abundance to the closely related blue pike. Commercial fishing reports prior to 1956 only list walleye as an incidental species in landings from the eastern basin during a period when blue pike (*Stizostedion vitreum glaucum*) were abundant (Wolfert 1981). However, beginning in the 1960s, commercial production of walleye expanded coincident with the collapse of the blue pike and lake whitefish (*Coregonus clupeaformis*) fisheries. Prominent walleye fisheries have continued since the 1960s, but walleye abundance in eastern Lake Erie prior to their emergence in fisheries remains unclear.

An initial tagging study conducted from 1968 to 1971 in New York waters concluded that walleye in the U.S. waters of eastern Lake Erie were geographically separate from those of the western basin (Wolfert and Van Meter 1978), and these findings were supported by a second New York tagging study conducted from 1977 to 1987 (Einhouse and Shepherd 1988). Similarly, an early tagging study in the western basin suggested that the movement of western-basin walleye eastward was negligible (Wolfert 1963), infrequent, and likely unidirectional (Regier et al. 1969). Colby and Nepszy (1981) propose that reduced abundance of western-basin walleye during the 1950s may have contributed to the geographic isolation of the eastern-basin populations. The notion of isolation of eastern-basin populations no doubt influenced early conclusions regarding their distinctness. Presumed to be geographically separated with exposure to different environmental and selection pressures, these populations were shown to exhibit differences in growth, maturity, and fecundity. Nepszy et al. (1991) suggested that differences in fecundity had a genetic basis and represented evolutionary divergence after isolation.

This view of isolation of eastern-basin walleye became the basis for pursuing independent management of these populations through the 1980s. The perceived lack of movement, even between jurisdictions within the eastern basin, was used to argue against multi-jurisdictional consensus-based management, implying that eastern-basin walleye were not truly a resource shared among all fishery-management agencies on the lake (Nepszy et al. 1991). As such, its management would not need to be negotiated within the Lake Erie Committee (LEC), which operates under the aegis of the Great Lakes Fishery Commission.

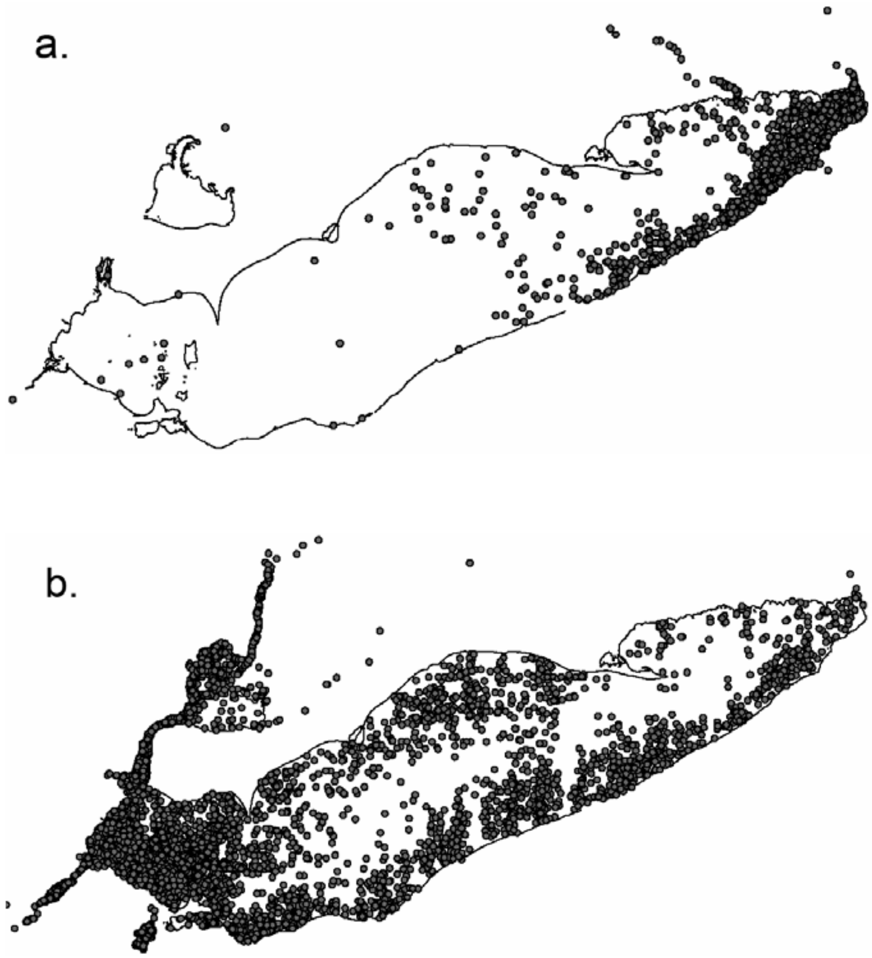
An Emerging View of Eastern-Basin Walleye Populations

Differential Movements

The results of a comprehensive, lakewide, multi-year, interagency tagging study, launched in 1990 by the LEC's Walleye Task Group (WTG), together with the results of other recent investigations, led to the emergence of a more-complex view of walleye movements and distribution throughout the lake. Wang et al. (2007) found that eastern-basin spring-tagged walleye tended to remain within the basin, while western-basin spring-tagged walleye were prone to migrate through the central and eastern basins in the summer months. Furthermore, western-basin tagged walleye recaptured in the eastern basin were generally larger than those recaptured in the western basin. Wang et al. (2007) hypothesized that cooler temperatures and more-abundant soft-rayed prey fishes produced energetically favorable foraging conditions that attracted large walleye eastward during summer. This view was supported by Kershner et al. (1999), who used bioenergetics modeling simulations to demonstrate that western-basin walleye, which migrate eastward seasonally to the central basin, should experience more-favorable temperatures for growth. Regardless of the impetus for these long summer migrations, it is generally accepted that walleye usually home to the location of origin for spawning. (Crowe 1962; Olson and Scidmore 1962; Olson et al. 1978; Einhouse and Haas 1995; Stepien and Faber 1998; Gatt et al. 2003).

The ongoing long-term tagging study by the WTG shows that western-basin walleye spawning populations produce a lakewide distribution of tag recoveries from fisheries, while tag recoveries from eastern-basin spawning populations show that these groups remain more confined to the eastern half of Lake Erie (Fig. 2). As such, the tagging study supports the notion that the large walleye population exploited in the western and central basins of Lake Erie originated from western-basin spawning aggregations. Conversely, the much smaller eastern-basin walleye populations include individuals that originated from the western and eastern basins of Lake Erie. Interagency walleye tagging also indicated that individuals from western-basin spawning populations contributing to eastern-basin fisheries were disproportionately large females. Wang et al. (2007) demonstrated that large walleye are recaptured further from their tagging location than smaller walleye, and that western-basin tagged walleye were recovered during summer at greater distances from tagging locations than eastern-basin tagged walleye.

Fig. 2. The distribution of tag recoveries from walleye tagged at (a) eastern- and (b) western-basin spawning sites from 1986 to 2008 (modified and updated from Haas et al. (2003)).



Population estimates of walleye spawning aggregations in the eastern basin, when contrasted with eastern-basin harvests, indicate that the fishable stock likely comprised walleye from outside the basin. Sufficient recaptures were obtained in eastern waters to make estimates of population abundance for two south-shore populations and a north-shore population. A very low tag-recapture probability from within the immense western-basin population precludes a similar analysis. Zhao (2005) estimated mean annual abundance of male spawners at two prominent New York spawning sites (Lackawanna Shoreline and Van Buren Bay) (Fig. 1) of approximately 1,500 and 11,000 fish, respectively, during 1992-2001. In contrast, New York's walleye harvest averaged approximately 31,000 fish annually over this same period. Similarly, the estimated 14,000 walleyes (both sexes) in the most-prominent north-shore population (Grand River) (Fig.1) in 2005 (MacDougall et al. 2007) is small in comparison to the 2005 Ontario commercial harvest of 17,000 walleyes. Also, average total reported annual harvest from all eastern-basin jurisdictions ranged from 107,000 to 206,000 walleyes from 1998 to 2001 (Walleye Task Group 2008). The degree to which western walleye contribute to individual fisheries appears to vary geospatially and seasonally. Whereas south-shore sport fisheries may receive large contributions from western populations, a snapshot afforded by 28 tag returns from one Long Point Bay (Fig. 1) commercial fishery in 2007 showed a predominate contribution (71%) from eastern tagging sites (Grand River, 4; Cattaraugus Creek, 5; Van Buren Bay, 11) (Fig 1) (Lake Erie Committee Walleye Task Group, unpublished data).

Genetic Discrimination

Genetic investigations have described varying degrees of stock structure in Lake Erie walleye both among and within the eastern and western basins (Stepien and Faber 1998; MacParland et al. 1999; Gatt et al. 2003; C. Wilson, OMNR, personal communication, 2003; Strange and Stepian 2007). Discrepancies between studies can be attributed to variation in study design or in methods of analysis, as well as in inherent fuzziness in stock structure due to differential straying among spawning sites. A within-basin examination using fuzzy cluster analysis indicated that eastern-basin spawning aggregations are not completely discrete, cohesive populations, suggesting that some straying occurs (Schaefer and Wilson 2002). Despite this finding, straying is limited enough that the two main eastern-basin aggregations (Grand River and Van Buren Bay) (Fig. 1) are readily discernable from each other, as well as from western-basin aggregations.

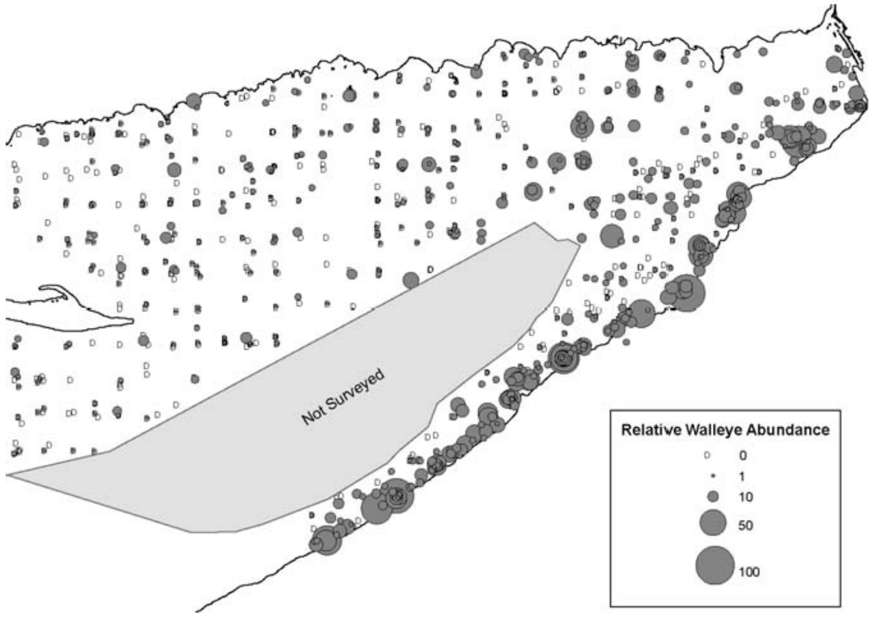
This separation contrasts with western-basin aggregations that are much more similar to each other genetically (Stepien and Faber 1998; Wilson 2003; Strange and Stepian 2007). Accordingly, attempts to genetically source individuals to their specific spawning locations were much less successful than sourcing to sub-basin or, most successfully, to basin (Johnson et al.2005).

Consequently, these two main categories of origin (east and west) have been used to describe relative contributions to the mixed summer walleye fisheries of the eastern basin. The relative proportion of western-origin walleye in the eastern-basin sport harvest was estimated at 73% in 1995-96 (Gatt et al. 2003) and 21-35% in 1999-2000 (Wilson 2003). In contrast, contributions to the commercial fishery remained similar between the two time periods (23% and 18-27%, respectively). The differences in these studies may reflect both spatial and temporal differences in western-basin walleye movements.

Sex, Age, Growth, and Fecundity Characteristics

Walleye tagged in the western basin and captured during summer in eastern-basin fisheries comprised disproportionately high numbers of large and/or female fish (Wang et al. 2007). This observation is consistent with attributes of eastern-basin walleye fisheries, which traditionally achieve peak yields in mid- to late summer and harvest predominately larger, older fish. From 1993 to 2003, sport-caught walleye checked at fish-cleaning stations in New York during peak summertime fishing periods were 80% female (Einhouse and Haas 1995). In addition, on a lakewide scale, the mean age of harvested walleye characteristically increases from west to east and is highest in eastern-basin waters (Walleye Task Group 2008). Taken together, these observations from eastern-basin fisheries are consistent with tagging results and underscore important contributions from larger, older, female, western-origin walleye. Examination of catch rates from standardized gillnetting across the eastern basin suggests that abundance of walleye is highest in New York waters, next highest along the northeastern shore, and lowest along the northwestern shore (Fig. 3). This unequal distribution may be attributable to a disproportionate contribution from western migrants, which may follow the southern shoreline rather than traverse the deeper waters in the middle of the basin.

Fig. 3. Spatial distribution of juvenile and older walleye collected in gillnets from eastern Lake Erie in standard agency surveys from 1998-2004 (modified and updated from Ontario Ministry of Natural Resources (2006)).



This new understanding of differential movement (by basin of origin, size, sex, and season) confounds some previous comparisons of "eastern" and "western" walleye. Those comparing characteristics, such as fecundity or juvenile growth (when sampled fish were presumably captured close to where they originated), are probably valid. However, those based on measurements of walleye captured during summer may simply describe heterogeneous mixtures of eastern- and western-origin fish, depending on the basin of capture. For example, Wolfert (1977) examined commercial summer catches and described growth during the first two years of life as being higher for western-basin walleye than for eastern-basin walleye. Differences diminished with increased age (earlier for males), and, at advanced ages, lengths and weights became similar (males) or were shown to be greater for eastern-basin (female) walleye. These growth differences are consistent with a current understanding of differential migrations and, therefore, may not represent innate characteristics of "eastern" and "western" populations, as proposed by Nepszy et al. (1991). Comparisons of early growth (based on a presumably non-migratory stage) likely make for valid eastern-western comparisons. Conversely, a random sample of the eastern-basin summer fishery would likely contain larger and older western migrants, making for invalid descriptions of a "resident" eastern population.

Differences in fecundity (lower in eastern-basin walleye), previously attributed to eastern-western differences in food availability and density of adult walleye (Nepszy et al. 1991) may reflect genetic differences between the populations, particularly if both the eastern-basin and migratory western-basin fish are utilizing the same summer forage base and thermal environment. Similarly, mean egg size (inversely related to fecundity) has been shown to be significantly larger (after factoring in maternal size) for at least one eastern-basin population of walleye (Grand River, Ontario) relative to western-basin populations (T. Johnston, unpublished data). Relevant to early (pre-migration) life history, this difference may reflect a local adaptation to the lower productivity of the eastern-basin nursery habitat; however, Johnston and Leggett (2002) point out that it may simply reflect plasticity in response to differing environments.

A recent examination of early growth of known-origin walleye, based on back-calculation of scale annuli, showed higher first-year growth for eastern-basin walleye originating in the Grand River and Van Buren Bay relative to western-basin walleye (Zhao 2005). This difference was attributed to more-favorable growth conditions in the eastern basin, as measured by a thermal suitability index, but this difference may have an inherited component, too.

Regardless of the cause (nature vs. nurture), these age, growth, and fecundity differences among walleye of eastern and western origins may offer another way to distinguish individuals caught within the mixed-stock fishery of the eastern basin. Understanding the relative contributions of western- and eastern-basin walleye spawning populations to eastern-basin fisheries is an important consideration for management of the eastern-basin populations.

Management Considerations

In contrast to the findings of Nepszy et al. (1991), contributions by western-basin walleye spawning stocks to eastern-basin fisheries are important, and the contribution comprises principally larger, older females. The emerging consensus that the eastern-basin walleye resource is not a closed population has ramifications for assessment and management. One of the fundamental assumptions typical of catch-at-age stock assessment models is that data inputs apply to closed populations. Walleye migrating seasonally from the west-central quota management area represent a trivial fraction of the population remaining within the western and central basins; however, this trivial fraction is large in relation to the resident population inhabiting the eastern basin.

Knowledge of walleye movements and stock contributions within Lake Erie is important for walleye management in that it can identify the components of spawning populations that contribute to fisheries in distant parts of the lake. One management objective is to provide sustainable harvests for all areas of the lake (Ryan et al. 2003a; Locke et al. 2005). Achievement of this objective will require maintenance of a threshold density of larger, older walleye, which are more prone to migrate and, thus, can provide fishing opportunities in areas like the eastern basin that otherwise have only modest-sized populations. The degree to which western emigrants contribute to individual fisheries varies spatially and temporally and needs to be more-precisely determined so that management actions can be taken to either protect or bolster the smaller, discrete eastern-basin populations. The recently developed walleye management plan for Lake Erie (Locke et al. 2005) acknowledges the differential movement of walleye populations as outlined here and emphasizes the need for multi-jurisdictional management of eastern-basin populations.

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THE STATUS OF WALLEYE IN LAKE ONTARIO, 1988-2006

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Abstract

Following a resurgence that began in the late 1970s and that continued through the early 1990s, the abundance of walleye (*Sander vitreus)* in eastern Lake Ontario, including the Bay of Quinte, declined sharply. This decline was associated with a 75% drop in the abundance of young-of-the-year walleye that occurred after establishment of dreissenids. Potential hypotheses explaining the decline in walleye abundance include decreased suitable spawning habitat, increased levels of predation and/or competition linked to dreissenid-induced clearing of the water column, or reduced food supply/availability linked to dreissenid-induced increases in macrophytes. Despite the decline in abundance, the walleye population in eastern Lake Ontario retains a broad age structure and supports an angling fishery with harvest rates close to 0.2 fish per angler-hour. Beginning in about 2000, walleye growth increased by about 10% while age at maturity of both male and female walleye declined by about one year. The summer diet of walleye in the Bay of Quinte has shifted from one

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dominated by alewife (*Alosa pseudoharengus)* to one, including a greater diversity of fishes, including the round goby (*Neogobius melanostomus)*, a recent invader.

Introduction

Walleye (*Sander vitreus*) support important commercial, angling, and aboriginal fisheries in Lake Ontario and provide top-down structuring of the nearshore ecosystem (Christie 1973; Hurley 1986a; Bowlby et al. 1991). The largest stocks of walleye in Lake Ontario are found in eastern waters and in the Bay of Quinte (Bowlby et al. 1991; Wilson and Gatt 2001; Wilson and Mathers 2003). Smaller stocks of walleye in eastern Lake Ontario are associated with other embayments and rivers, such as Wellers Bay, West Lake, East Lake, and tributaries of New York's eastern basin, including the Black River and Kents Creek. Bowlby et al. (1991) described the status of walleye stocks in eastern Lake Ontario and the Bay of Quinte prior to 1988. In this paper, we provide information on the status and trends of walleye stocks and fisheries in eastern Lake Ontario and the Bay of Quinte from 1988 through 2006.

Adult walleye in the study area are highly migratory. Walleye spawn during April, primarily along the shoreline and in the major rivers of the Bay of Quinte. During May, adult walleye migrate to eastern Lake Ontario where they stay throughout the summer (Payne 1963; Bowlby et al. 1991). In the fall, they migrate back to the Bay of Quinte where they overwinter and then spawn the following spring. Walleye eggs hatch during May and young-of-the-year are caught in bottom trawls fished in the Bay of Quinte during August at depths of 4-20 m. Juvenile walleye inhabit the Bay of Quinte throughout the year (Payne 1963; Hurley 1986a).

Walleye are piscivorous and the most-abundant top predator in the fish community of the Bay of Quinte and nearshore areas of eastern Lake Ontario. In past diet surveys in the Bay of Quinte, walleye ate alewife (*Alosa pseudoharengus*), gizzard shad (*Dorosoma cepedianum*), yellow perch (*Perca flavescens*), and white perch (*Morone americana*), all contributing notably at times (Hurley 1986b; Bowlby et al. 1991).

Walleye abundance in the Bay of Quinte declined in the 1960s due primarily to cultural eutrophication (Hurley and Christie 1977). Major phosphorous reductions in the Bay of Quinte started in 1977 following implementation of the Great Lakes Water Quality Agreement, and habitat for many aquatic organisms improved (Johnson and Hurley 1986; Mills et al. 2003). Winterkills of alewife in 1977 and white perch in 1978 (Hurley 1986a) may have released young walleye from competition or predation with both species. A resurgence of walleye in the Bay of Quinte began with a sizeable 1977 year-class and a modern-record 1978 year-class, which dominated the stock for a number of years (Bowlby et al. 1991). Walleye predation prevented both alewife and white perch from reaching their former levels of abundance in the Bay of Quinte (Hurley 1986a; Ridgway et al. 1990; Bowlby et al. 1991).

Dreissenid mussels (*Dreissena* spp.) invaded Lake Ontario in the early 1990s, impacting fish habitat soon thereafter (Mills et al. 2003). By 1993, they became abundant in eastern Lake Ontario (Dermott 2001; Hoyle et al. 2003), and their effects on water quality were measured that same year (Johannsson et al. 1998). Reductions in chlorophyll and phytoplankton were apparent by 1994 (Nichols 2001). In the Bay of Quinte, dreissenids began to proliferate in 1994 and impacted water quality the following year (Bailey et al. 1999; Dermott 2001; Hoyle et al. 2003). Increased water clarity resulted in an expanded distribution of aquatic vegetation in the Bay of Quinte (Leisti et al. 2006) and a subsequent increase in the 1990s in the distribution and abundance of fishes that prefer this habitat: bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), and largemouth bass (*Micropterus salmoides*) (Hoyle et al. 2007).

Our objective was to update longstanding abundance indices for gillnetting and bottom trawling conducted by the Ontario Ministry of Natural Resources (OMNR) in the Bay of Quinte and eastern Lake Ontario and for gillnetting conducted by the New York State Department of Environmental Conservation (DEC) in eastern Lake Ontario to determine the status of walleye in these waters. We especially looked for the effects that the dreissenid invasion had on walleye, i.e., the status of walleye before and after 1994 in eastern Lake Ontario and before and after 1995 in the Bay of Quinte.

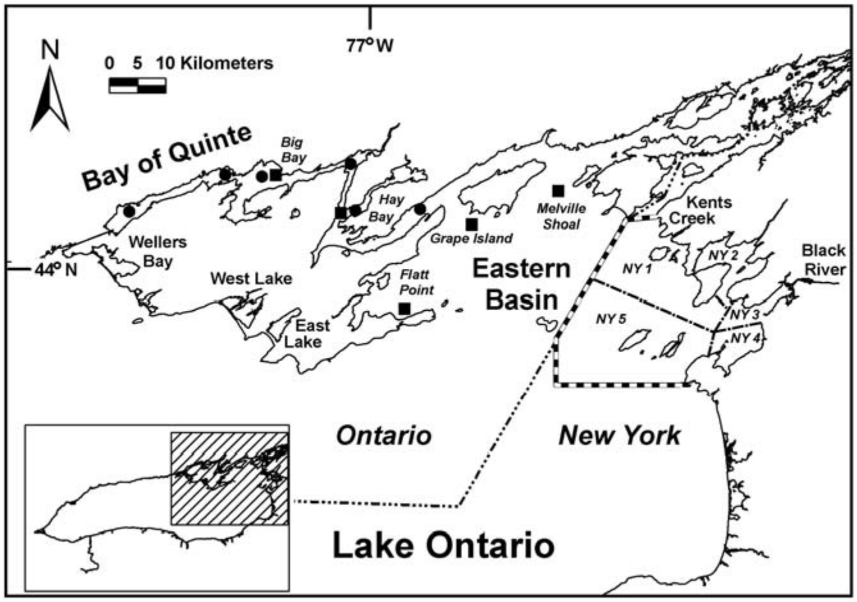
Methods

Detailed methodologies for the collection of gillnetting and bottom-trawling data are referenced in Table 1 and summarized here. Standardized gangs of gillnets were set on the bottom for approximately 24 hr. The number of gillnet panels (see below) and survey designs differed between agencies: the OMNR used fixed sites in the Bay of Quinte and eastern basin, and the DEC used randomly chosen sites within depths and regions in the eastern basin (Fig. 1).

Table 1. Major data sources and references for walleye in Lake Ontario.

Source program	Agency	Years in this study	References
Ontario:			
Bay of Quinte trawling	OMNR	1972-1988, 1990-2006	Hurley 1986a; Bowlby et al. 1991; Casselman et al. 1999; Casselman et al. 2002; Casselman and Scott 2003; Hoyle et al. 2008
Bay of Quinte gillnetting	OMNR	1958-2006	Hurley 1986a; Bowlby et al. 1991; Casselman et al. 2002; Casselman and Scott 2003; Hoyle et al. 2007; Hoyle et al. 2008
Ontario eastern basin gillnetting	OMNR	1978-2006	Bowlby et al. 1991; Casselman et al. 2002; Casselman and Scott 2003; Hoyle et al. 2008
Bay of Quinte angling surveys	OMNR	1957-2006	Bowlby et al. 1991; Hoyle et al. 2008
New York:			
New York eastern basin gillnetting	DEC	1976-2006	Eckert 1986; Bowlby et al. 1991; Eckert 1998; Casselman et al. 2002; Lantry et al. 2002; Eckert 2006; Hoyle et al. 2007; Lantry 2007

Fig. 1. The location of OMNR trawling (●) and gillnetting (■) sites and of DEC gillnet regions (NY 1-5) in eastern Lake Ontario.



Walleye age 1 and older were sampled June through September in OMNR gillnets in the Bay of Quinte from 1958 to 2006 and in the eastern basin from 1977 to 2006 (Hurley 1986a; Casselman et al. 1999; Casselman et al. 2002; Casselman and Scott 2003). No gillnetting was done in 1966. A standard gang of gillnets comprised nine 15.2-m panels with stretched-mesh sizes ranging from 38.1-152.4 mm in 12.5-mm increments. Multifilament gillnets were replaced with monofilament in 1991 (Bay of Quinte) and 1992 (eastern basin). Gear comparisons based on 42 paired sets resulted in a correction factor of 2.0 (JAH, unpublished data). Gillnet data for the eastern basin were from two depth strata (5-10 m, 10-15 m) at up to three fixed index sites: Melville Shoal, Grape Island, and Flatt Point (Fig. 1). During 1977-1985, gillnets in the eastern basin were set only at Melville Shoal and Flatt Point at a depth of 10 m. Two fixed index sites were used in the Bay of Quinte: Big Bay (1972-2006) and Hay Bay (1958-2006) (Fig. 1). Bay of Quinte sites were used to determine the abundance of juvenile walleye (age 1-4), and eastern-basin sites were used to determine the abundance of adult walleye (mostly age 5+). We estimated the overall catch-per-unit effort

(CPUE) as an unweighted marginal mean for each year, because, in some years, all sites and depths were not sampled.

Walleye age 1 and older were sampled in gillnets set by the DEC in the eastern basin of Lake Ontario from 1976 to 2006 (Eckert 1986; Eckert 1998; Casselman et al. 2002; Lantry et al. 2002; Eckert 2006; Lantry 2007). Gillnets comprised eight 15.2-m panels with stretched-mesh sizes ranging from 50.8-152.4 mm in 12.5-mm increments and were set parallel to depth contours. Netting locations were selected randomly within three depth strata (4-9, 10-15, 16-31 m) and five geographic regions (Fig. 1). Regions were drawn to ensure that the 4-9-m and 10-15-m depth strata were sampled in proportion to their surface areas. The regions were combined for the 16-31-m depth stratum. Sampling was usually scheduled for the first two weeks of August but began as early as July 29 and ended as late as August 25. During the first three years of the survey (1976-1979), the length of gillnet panels were twice as long, netting sites were not selected randomly within depth strata, and only two regions were fished (Eckert 1986). The CPUEs for 1976-1979 were adjusted to be consistent with effort in later years (Eckert 1986). Multifilament gillnets were replaced with monofilament in 1993 (Eckert 1998). All multifilament CPUEs were multiplied by a factor of 1.5. This factor was calculated from 34 paired mono/multifilament nets set in 1990-1993 (DEC, file data).

Age-0 walleye were sampled at up to six sites in the Bay of Quinte with bottom trawls (¾-Western bottom trawl with 19-m footrope and 12.7-mm cod mesh) from 1972 to 2006 (no trawling was done in 1989) (Hurley 1986a; Casselman et al. 1999; Casselman et al. 2002; Casselman and Scott 2003). The CPUE was standardized as the total catch in a single 6-min tow that covered 402.3 m of lakebed. All trawling occurred during August-September when age-0 walleye were about four months of age. Water depths at these sites ranged from 4 to 21 m. We estimated the overall CPUE as an unweighted marginal mean for each year, because, in some years, all sites were not sampled.

Second-order polynomial regressions of age-0 CPUE in the Bay of Quinte on adult (parental) CPUE in the Ontario waters of the eastern basin were used to test whether the stock-recruitment relationship changed in response to the invasion of dreissenids. These regressions were combined in a general linear model and the first-order term in the polynomial was allowed to vary over the pre- (1979-1995) and post-dreissenid (1996-2006) periods, while the second-order term was held constant over both periods. The interaction between the first-order term and time period was tested using Statistica 8.0 (StatSoft, Inc. 2007). The 1978 year-class was excluded, because earlier analyses determined this point was an extreme outlier (Studentized deleted residual = 6.24).

Walleye harvest statistics for all commercial gear (none in New York waters) were summarized from Baldwin et al. (1979) for 1957-1977 and from OMNR records (JAH, unpublished data) for 1978-2006. The Bay of Quinte open-water (May-November) angling fishery was monitored sporadically prior to 1979 (in 1957-1962, 1974, 1976). The fishery was surveyed annually from 1979-2006 (except for 1983) using a roving stratified sampling methodology that included boat counts and angler interviews (Lester and Trippel 1985) to estimate angling effort, harvest, and harvest-per-unit effort. Sampling was stratified by area, season (opening weekend and month), and day-types (weekend days and weekdays) (Hoyle 2005); and data were analyzed using Fishnet software (Lester et al. 1996). In some years, seasons with low effort were not surveyed; the missing data were estimated based on the seasonal pattern of angling effort and harvest from prior years. In this manner, all results were expanded to represent the open-water fishing season from the opening weekend in early May to November 30.

Growth (sexes combined) was based on fork length of age-3-5 walleye caught in gillnets in midsummer in the Bay of Quinte and in Ontario's waters of the eastern basin from 1992 to 2006. Age was estimated using otoliths sectioned through the origin. Maturity was determined during September-November from the ratio of gonad to total body weight for females and by visual inspection for males. All walleye assessed for maturity were gillneted during 1997-1998 and trapnetted during 1999-2003 in the Bay of Quinte. The indicated ages were corrected (i.e., 1 yr added) to represent age at spawning in the following spring.

Walleye diet in the Bay of Quinte was based on percent frequency of occurrence of each prey type and was based on pooled samples from gillnets and trawls during 1992-2006. Roughly similar numbers of walleye were sampled from the two gears. Diet in the eastern basin was based on gillnet samples collected in Ontario's waters during 1992-2006 and in New York's waters during 1998-2006.

Results and Discussion

Abundance

Walleye CPUE in the Bay of Quinte declined from 16.7±1.9 (mean±SD) per gang during 1958-1965 to 1.0±0.2 during 1972-1977, a drop of 94% (Fig. 2). The CPUE increased dramatically in 1978 and remained high through 1996 (mean = 18.2±1.6). After 1996, CPUE declined once more until stabilizing at moderate levels (mean = 6.4±0.4) during 1997-2006. When gillnetting began in the eastern basin in 1976-1977, the CPUEs were low just like they were in the Bay of Quinte, and they remained low through 1986 in Ontario (2.3±0.5) and New York (0.2±0.05) waters. The CPUE in the Ontario waters of the eastern basin began an increase in 1987 and peaked at 22.1±1.2 during 1989-1991. The CPUE then declined rather regularly through the 1990s until stabilizing at moderate levels during 2000-2006 (4.1±0.4). The increase in CPUE in Ontario waters, which began in 1987, occurred 9 yr after the increase in CPUE in the Bay of Quinte. The ups and downs of CPUE in New York waters of the eastern basin have not been as dramatic as those in Ontario waters (Fig. 2). In New York waters, CPUE increased modestly in concert with the sharper increase in Ontario waters, and, except for a few peaks over 1993-1996, has been relatively constant from 1988 to 2006 (mean = 1.8±0.2). The 9-yr lag in the rise of CPUE in the eastern basin (begun in 1987) as compared to the Bay of Quinte (begun in 1978) may be due in part to the differences in age composition between the two sampling areas. Juveniles and young adults (≤age 5) comprise 95% of the gillnet catch in the Bay of Quinte, whereas walleye >age 5 comprise 92% of the catch in Ontario waters of the eastern basin (Fig. 3). The declines in walleye CPUE in both the Bay of Quinte and in Ontario waters of the eastern basin began before dreissenids impacted water quality (Fig. 2), suggesting that factors other than dreissenids were responsible for the initial declines in walleye abundance. Perhaps, the dramatic increase in walleye abundance in the 1980s was an overshoot of carrying capacity resulting in an inevitable decline in stock size.

Fig. 2. Number of walleye per gang of multiple-mesh gillnets (CPUE) fished in the Bay of Quinte (BQ) during 1958-2006, Ontario waters of eastern Lake Ontario during 1977-2006 (OEB), and in New York waters of eastern Lake Ontario during 1976-2006 (NYEB). Results for BQ and OEB are on the left axis, and the results for NYEB are on the right.

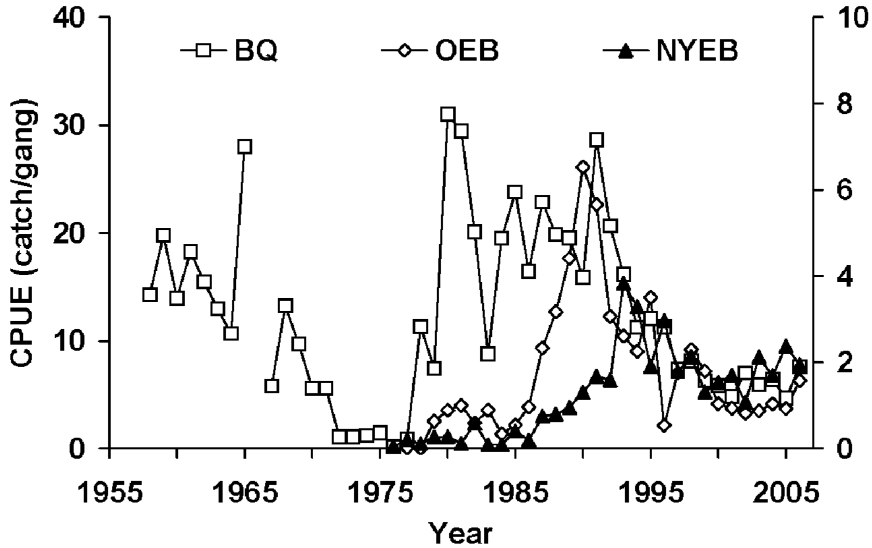
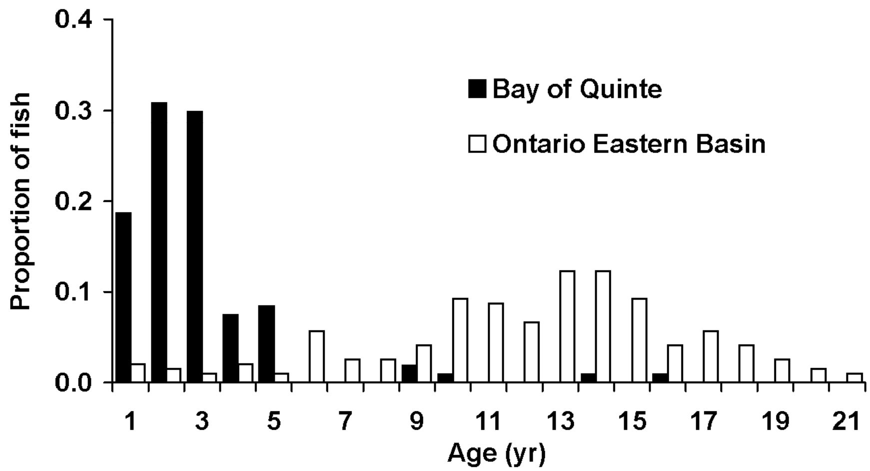
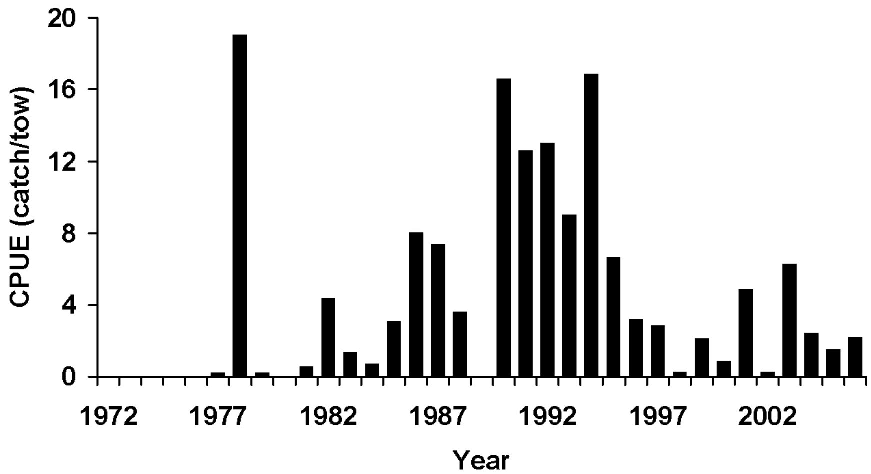


Fig. 3. Age distribution of walleye taken in gillnets in the Bay of Quinte and in Ontario waters of the eastern basin of Lake Ontario, 2004-2005.



Age-0 walleye were not caught in the Bay of Quinte until 1977, five years after trawling started (Fig. 4). Record numbers (19.0 fish/tow) of age-0 walleye were caught in 1978, but the next sizable year-class was not seen until 1982. Thereafter, CPUE generally increased, reaching consistently high levels (9.6±1.6) from 1985 to 1995. The CPUE varied over a lower range during 1996-2006 with mean CPUE (2.5±0.6) amounting to one-quarter of the 1985-1995 mean (Fig. 4).

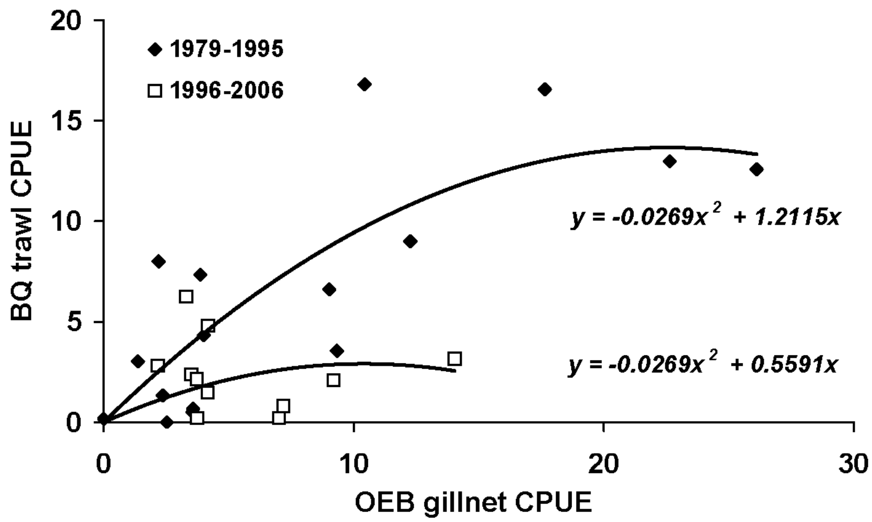
Fig. 4. Catch per 6-min tow (CPUE) of age-0 walleye in Bay of Quinte bottom trawls fished in late summer, 1972-2006 (no trawling in 1989).



Our stock-recruitment model comprising second-order polynomials (Fig. 5) of age-0 walleye abundance (trawl CPUE in the Bay of Quinte) (Fig. 4) regressed on the abundance of parents (gillnet CPUE in the Ontario eastern basin) (Fig. 2) for the pre- (1979-1995) and post-dreissenid (1996-2006) periods was significant (R^2 = 0.824, p < 0.000). Recruitment of age-0 walleye was significantly lower (p = 0.002) for a given parental abundance in the post-dreissenid period. For instance, at moderate levels of parental abundance (CPUE $\simeq$10.0) (Fig. 5), the dreissenid "effect" appears to have resulted in more than a 50% loss in abundance of age-0 walleye.

The cause of this decreased recruitment is unclear, but potential hypotheses pointing at a decreased survival of walleye eggs or larvae in the Bay of Quinte are worth discussing. First, when dreissenids proliferated, a major anticipated effect was increased water clarity due to their filter feeding. Aquatic vegetation, stimulated by a clearing of the water column, in the Bay of Quinte (Leisti et al. 2006) may have encroached on walleye spawning habitat, reducing it in quality or quantity.

Fig. 5. Scatter plot of CPUE of age-0 walleye in the Bay of Quinte (BQ) on adult CPUE in Ontario waters of the eastern basin (OEB) in the preceding year for the pre- (▲) and post- (□) dreissenid periods. The fitted lines are second-order polynomials forced through the origin. Data are from Figs. 2, 4.



Second, proliferating aquatic vegetation would make the bay more favorable for the predators and competitors of walleye, as hypothesized by Bowlby et al. (1991). Abundance of centrarchids and yellow perch increased as a result of clearer water and more aquatic vegetation (Hoyle et al. 2007), and these species have the potential to increase predation on and/or competition with young walleye. Hoxmeier et al. (2006), in a study of 15 Illinois reservoirs, found the density of both invertebrate and fish prey positively affected juvenile walleye survival, and the density of juvenile centrarchids had a negative effect on the survival of larval walleye, presumably mediated by predation. Quist et al. (2003) demonstrated that, in Kansas reservoirs, recruitment of walleye can be reduced by centrarchid predation on larval walleye, but they also found that water clarity had no direct effect on recruitment.

Growth and Maturity

The mean fork lengths of age-3-5 walleye in the Bay of Quinte were relatively invariable from 1992 to 1998 but were about 10% higher during 2000-2006 (Fig. 6). This finding is consistent with observations of a decline in age at maturity from 1997-1999 to 2000-2003 (Fig. 7). Male and female walleye matured about one year earlier in 2000-2003 (~age 3 for males and age 4 for females) than in 1997-1999 (age 4 for males and age 5 for females).

Fig. 6. Fork length at age 3-5 (sexes combined) for walleye caught during summer in Bay of Quinte gillnets, 1992-2006.

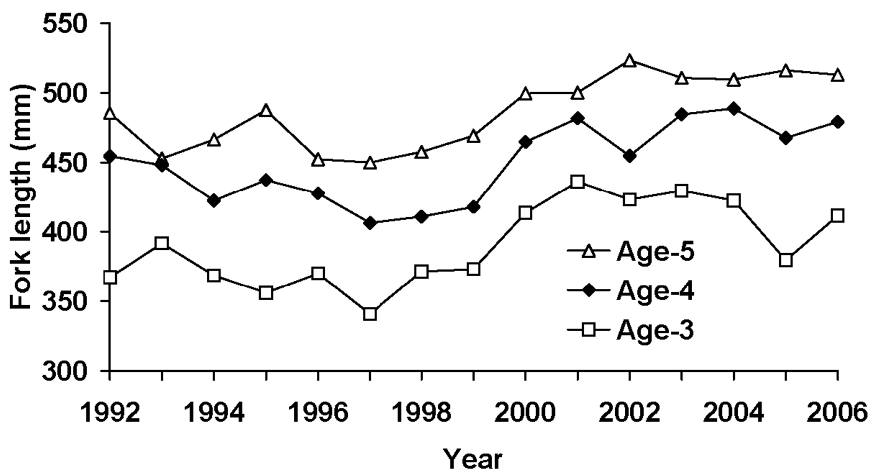
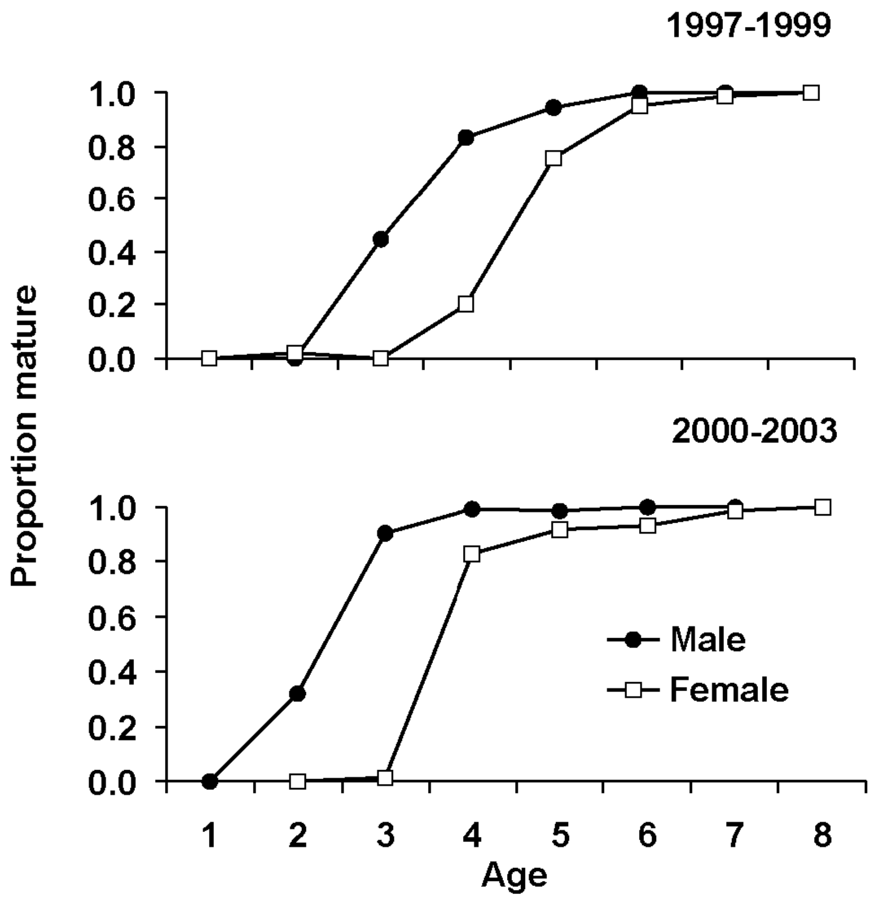


Fig. 7. Age-specific proportion of mature male and female walleye at the time of spawning for 1997-1999 (top panel) and 2000-2003 (bottom panel). Data for 1997-1999 are based on gillnets fished in the fall in the Bay of Quinte, and data for 2000-2003 are based on trapnets fished in the Bay of Quinte and in Ontario waters of Lake Ontario.



Potential causes for the increase in growth and associated decline in the age of maturity of walleye, which began in 2000, are not well understood, although these changes are generally consistent with lower walleye abundance. The diet of walleye and other top predators like lake trout (*Salvelinus namaycush)* also shifted after 2000 towards a greater diversity of prey items, including more yellow perch, white perch, and round goby (*Neogobius melanostomus*), a species that invaded the eastern Lake Ontario region in 1999 (Dietrich et al. 2006). The fish community in eastern Lake Ontario changed after the dreissenid invasion (Casselman and Scott 2003) and is expected to change even more with the ongoing establishment of the round goby.

Diet

Major prey types consumed by walleye in the Bay of Quinte during 1992-2006 included alewife (58% frequency of occurrence), yellow perch (17%), and white perch (10%) (Table 2). The occurrence of alewife in walleye stomachs declined from a peak of 95% in 1993 to a low of 28% in 2005. The occurrence of yellow perch increased during the 1990s and averaged 24% during 1998-2006. The occurrence of white perch was highly variable and reached peaks of 25% and 46% in 2000 and 2004, respectively. Round goby entered the diet of walleye in 2003, and the frequency of occurrence averaged 17% during 2003-2006. In contrast, alewife was the only major prey type in the eastern basin, with 99% occurrence in Ontario waters in 1992-2006 and 84% occurrence in New York waters in 1998-2006 (Table 2).

Table 2. Percent frequency of occurrence of prey types consumed by walleye in summer, based on pooled samples from gillnets and bottom trawls in the Bay of Quinte and on gillnets fished in Ontario and New York waters of the eastern basin of Lake Ontario, 1992-2006. The number of stomachs is indicated in parentheses and does not include empty stomachs or stomachs containing only unidentified fish. Species grouped as "Other fish" were less than 1% occurrence for the whole time period.

Prey type	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Mean
Bay of Quinte																
Alewife	82	95	64	70	48	66	66	49	72	42	52	47	32	28	56	58
Yellow perch	3	1	13	2	15	6	31	40	3	50	24	26	0	22	22	17
White perch	1	1	7	0	15	18	0	7	25	0	6	7	46	9	13	10
Round goby	0	0	0	0	0	0	0	0	0	0	0	9	24	25	13	5
Johnny darter (*Etheostoma nigrum*)	1	3	4	0	12	10	7	0	0	0	0	7	0	0	0	3
Gizzard shad	8	2	3	0	3	0	0	5	0	0	6	0	0	0	0	2
Other fish	7	7	13	19	9	9	7	9	0	8	13	4	8	19	0	9
Invertebrates	13	1	4	9	9	4	7	2	0	0	0	5	0	0	0	4
Number of stomachs	(88)	(99)	(67	47)	(70)	(51)	(34)	(48)	(17)	(9)	(17)	(24)	(20)	(18)	(24)	(42)

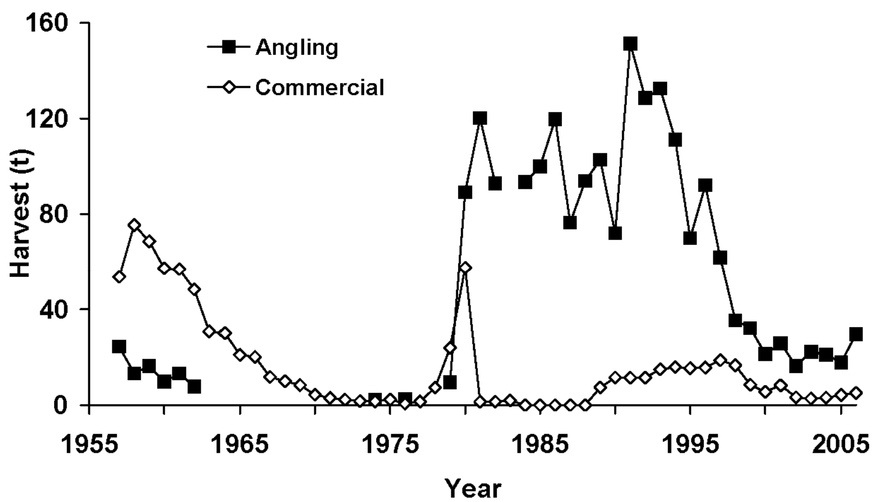
Table 2, continued.

Prey type	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Mean
Ontario eastern basin																
Alewife	100	98	100	98	93	96	100	93	100	100	100	100	100	100	100	99
Other fish	0	2	0	2	7	2	0	5	0	0	2	0	0	0	0	1
Invertebrates	0	1	0	0	0	2	0	2	0	0	0	0	0	0	0	0
Number of stomachs	(107)	(107)	(49)	(42)	(15)	(47)	(51)	(42)	(15)	(29)	(41)	(20)	(25)	(27)	(58)	(45)
New York eastern basin																
Alewife							100	100	50	100	71	100	75	100	56	84
Other fish							0	0	50	0	29	0	25	0	11	13
Invertebrates							0	0	0	0	0	0	0	0	33	4
Number of stomachs							(6)	(6)	(2)	(16)	(7)	(17)	(8)	(2)	(9)	(8)

Fisheries

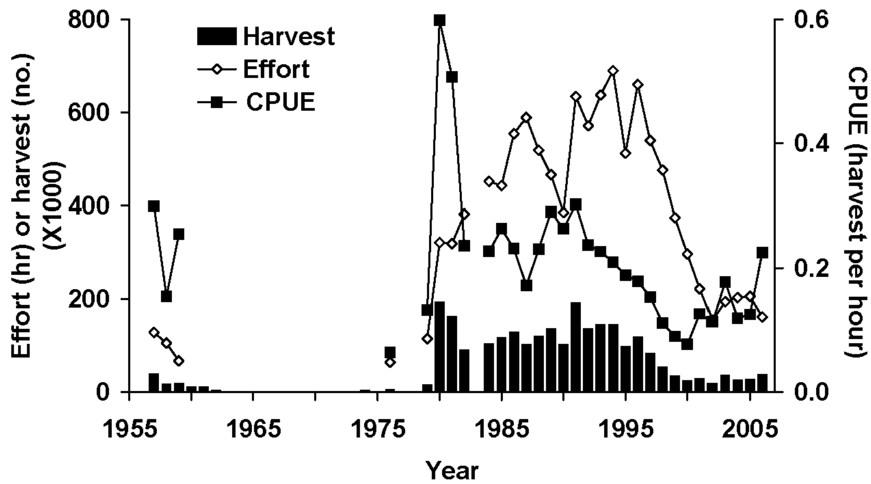
Commercial harvest of walleye in Ontario waters of Lake Ontario averaged 60 metric tonnes (t) annually from 1957-1962, declined to negligible levels during the 1970s, and increased sharply in 1979, reaching 58 t in 1980, after which the fishery was closed to allow the population to recover further (Fig. 8). The commercial fishery was reopened in 1989, and the harvest increased gradually, reaching 19 t by 1997. Thereafter, the harvest declined (<5 t per year after 2001) in response to quotas set as a percentage of lake whitefish quotas, which were decreasing (Hoyle et al. 2009).

Fig. 8. Weight (t, metric tonnes) of walleye harvested by commercial and open-water angling fisheries for the Bay of Quinte and Ontario waters of Lake Ontario, combined, 1957-2006. Angling surveys were conduced sporadically until 1978.



The angling harvest of walleye in the Bay of Quinte averaged 14 t annually from 1957 to 1962 and was lower than the commercial harvest during this period (Fig. 8). Regularly scheduled angling surveys were largely discontinued from 1963 to 1978, creating a sizeable gap in the record, although isolated surveys in 1974 and 1976 indicated that harvest remained low through 1976 (2 t annually). When regularly scheduled surveys resumed in 1979, the harvest had reached nearly 10 t (15 000 fish) (Fig. 9). The walleye harvest increased sharply the next year, reaching nearly 90 t (192,000 fish), and high harvests averaging 100 t were maintained through 1997. From 1998 to 2006, the angler harvest declined and remained relatively consistent and low, averaging 25 t per year. In brief, harvest during 1980-1997 was four times greater than during 1998-2006. As would be expected, angler effort increased in 1980 in response to the first year of high walleye abundance and remained high even as CPUE declined during the last years of high catch in the mid-1990s (Fig. 9). To simplify, the trend in angler effort can be divided into three stanzas: an early period (1957-1979), where effort averaged <130,000 hours per year; a middle period (1980-1997), where effort averaged ~600,000 hours; and a recent period (1998-2006), where effort averaged ≃200,000 hours.

Fig. 9. Walleye angling effort (hours), number harvested, and harvest per angler-hour (CPUE) for the Bay of Quinte, 1957-2006. Effort not available for 1960-1975, 1977-1978, and 1983, and number-harvested data not available for 1963-1973, 1975, 1977-1978, and 1983.



All of the fisheries responded to the changes in walleye abundance, each fishery in its own way. Once the eastern Lake Ontario walleye population recovered in the 1980s (Bowlby et al. 1991), a large angling fishery developed (Fig. 9), and, for a time, it displaced the commercial fishery, which, having been closed in 1981, was not allocated a quota for walleye until 1989 (Hoyle et al. 2009). In 1992, an incidental catch allowance was established for the expanding lake whitefish gillnet fishery. Walleye are also harvested in the Bay of Quinte and its tributaries with spears and gillnets by First Nations (Mohawks of Tyendinaga). In the late 1990s, the spear harvest was roughly the same size as the licensed commercial harvest (Stewart et al. 2002). A gillnet fishery by First Nations is also ongoing, has not been formally monitored, and may have harvested enough walleye in the late 1990s to warrant its inclusion in an analysis of stock dynamics (Stewart et al. 2002).

The dreissenid-induced clearing of the water column in the Bay of Quinte likely resulted in changes in walleye behavior and distribution that affected the fisheries and assessment. Mills et al. (2003) suggested that, with clearing, the distribution of walleye generally "moved" down to the lower bay and eastern Lake Ontario. This suggested change in distribution may have occurred as walleye density increased and as alewife, its preferred prey, became depleted in the upper bay during the late 1980s (Ridgeway et al. 1990) and in the lower bay during the early 1990s (Casselman and Scott

2003). There is no indication that the altered walleye distribution within the Bay of Quinte resulted in a major change in walleye migration, first described by Payne (1963). Immature walleye still reside in the Bay of Quinte, and mature walleye, having spent the summer months in eastern Lake Ontario, return to the Bay of Quinte to overwinter and spawn.

In conclusion, during the past two decades, walleye abundance in eastern Lake Ontario and the Bay of Quinte declined in association with dramatic ecosystem changes following the invasion of dreissenids. Population indicators suggest that the current abundance is stable. Moreover, the current abundance is unlikely to increase to pre-dreissenid levels. Ecosystem change in the Great Lakes is likely to be ongoing and to cause further impacts on walleye. Fishery management will need to be responsive to changes in walleye status and to public expectations.

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STATUS AND DELINEATION OF WALLEYE (*Sander vitreus*) GENETIC STOCK STRUCTURE ACROSS THE GREAT LAKES

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Abstract

Many Great Lakes stocks of walleye (*Sander vitreus*) had crashed by the mid-twentieth century, and, although some have since recovered, others were lost. Identifying the genetic composition and distinctiveness of the remaining spawning aggregations is essential for present and future fishery management. Here we test for genetic stock structure among 781 walleyes comprising 20 spawning aggregations from across all five Great Lakes using allelic variation at 10 nuclear microsatellite DNA loci. In addition to analyzing broad-scale patterns, we test for fine-scale differences among closely spaced spawning aggregations in Lake Erie, Lake St. Clair, and Georgian Bay of Lake Huron. Our results show that similar levels of genetic diversity characterize most spawning aggregations of walleye, which diverge significantly in genetic composition from each other with little allelic exchange among lakes. The most-distinct genetic separations among geographical groups of stocks, in order of importance, were Lake Superior, western Lake Erie reefs, Lake Ontario, Georgian Bay, eastern Lake Erie rivers, and Lake St. Clair. Within lakes, several spawning aggregations in close proximity were separable genetically despite apparent ready

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opportunities for gene flow; these sites included the Moon and Musquash Rivers in Georgian Bay, individual eastern Lake Erie rivers, and some of the reefs in western Lake Erie. Intralake gene flow among some walleye spawning aggregations was evident along the south shore of western and central Lake Erie. These broad- and fine-scale patterns reflect the signatures of long-ago stock differentiation in two or more separate glacial refugia, as well as contemporary maintenance through spawning-site fidelity. Despite some migration from lake to lake during summer months, most walleye, we believe, return to their natal sites to spawn. Although some of the pre-settlement genetic variation in walleye likely disappeared due to anthropogenic activities, many distinct native stocks remain and, thus, should be conserved.

Introduction

Some of the most-pressing issues in fisheries management today center on delineating genetically meaningful population units, i.e., stocks, as well as interpreting their linkages. Fishery stocks are population subunits that interbreed freely in given geographic locations, share a common gene pool, and differ significantly from other subunits (Hallerman et al. 2003). Stocks often possess novel genetic, physiological, and/or ecological variations that reflect local adaptations. These characteristics may enable them to withstand environmental perturbations, including fishing pressure, habitat degradation, and competition from exotic species. Preserving the genetic variation within and among stocks is believed to be fundamental for enabling a species to adapt to changing and existing environments (summarized by Allendorf and Luikart 2007) and, thus, constitutes a key goal for conservation management.

The Great Lakes house large numbers of walleye (*Sander vitreus*) that migrate each spring to historically used spawning grounds in river or reef localities (Scott and Crossman 1973; Goodyear et al. 1982; Colby et al. 1994). Past studies have found that geographic regions and spawning localities often contain genetically divergent groups of walleye (Billington and Hebert 1988; Todd and Haas 1993; Jennings et al. 1996; Stepien and Faber 1998; McParland et al. 1999; Stepien et al. 2004; Strange and Stepien 2007). Jennings et al. (1996) provided support for natal homing by tracking the spawning returns of laboratory-reared walleye after release, indicating that it is a genetically based response to environmental cues.

Tagging studies showed that walleye move readily among the Great Lakes during the summer months (Ferguson and Derksen 1971; Nepszy et al. 1991), including between Lakes St. Clair and Erie (Todd and Haas 1993), as well as among the basins of Lake Erie (Wolfert 1963; Wolfert and Van Meter 1978; Wang et al. 2007). However, mitochondrial (mt) and nuclear DNA (microsatellite) studies indicated that most spawning aggregations in Lakes St. Clair and Erie were significantly divergent, showing little genetic mixing (Stepien and Faber 1998; Strange and Stepien 2007). In those studies, significant genetic differences were found among walleye spawning in eastern Lake Erie rivers, whose divergences were more pronounced than those among most western Lake Erie spawning aggregations (Stepien et al. 2004, 2009; Strange and Stepien 2007).

Walleye habitats in the Great Lakes and their tributaries have undergone extensive changes over the past century, including loss of wetlands, channelization of major streams, construction of dams, oxygen depletion, shoreline modification, siltation of spawning areas, nutrient enrichment, water-quality deterioration, sand and gravel extraction, and invasive species introductions (Trautman 1981; Bolsenga and Herdendorf 1993; Fielder 2002a, 2002b; Ryan et al. 2003). The numbers of Lake Erie walleye declined throughout the 1960s and early 1970s (Regier and Hartman 1973). Reduced exploitation resulting from international management, coupled with improved environmental conditions, produced a strong recovery of stocks during the 1980s (Knight 1997). However, in the past several years, both the sport and commercial fisheries have reported that walleye became increasingly difficult to catch, and their numbers have declined by about 60% from the 1990s (Locke et al. 2005; Great Lakes Fishery Commission 2009a, 2009b). Agency surveys have indicated that there are fewer older walleye in Lake Erie, harvests are depending more on younger fish, fish are growing at slower rates, and stocks are retreating to the western basin of the lake (Locke et al. 2005). Understanding and maintaining walleye stock structure, thus, are designated as critically important fisheries-management goals by the Great Lakes Fishery Commission (Great Lakes Fishery Commission 2009a, 2009b).

Our study objective is to identify native stocks of Great Lakes walleye using a high-resolution nuclear DNA microsatellite database. We analyze genetic variation at 10 nuclear microsatellite loci for 781 walleyes from 20 historically used spawning sites across the Great Lakes, including individuals from stocks that have rebounded from anthropogenic disturbances (Fig. 1; Table 1). We attempt, where possible, to avoid areas stocked with fish from other regions and focus on spawning aggregations of natural origin; however, some of our sites, such as the St. Louis River in Lake Superior and Saginaw Bay in Lake Huron, have been supplemented for many years (Hile 1937; Kampa and Jennings 1998; Fielder 2002a, 2002b; Great Lakes Fishery Commission 2009b). Accordingly, we examine, where possible, whether stocking likely obscured the genetic distinctiveness of such spawning aggregations. Additionally, we test for the degree of gene flow between geographically distant versus more closely spaced spawning aggregations within Georgian Bay of Lake Huron, Lake St. Clair, and Lake Erie.

Fig. 1. Sampling sites of walleye spawning aggregations in the Laurentian Great Lakes (latitude and longitude are given in Table 1). Bars denote 10 primary genetic divisions delineating groups of spawning stocks using the Manni et al. (2004a, 2004b) Barrier approach, which are ranked in magnitude from greatest (I) to less pronounced (X).

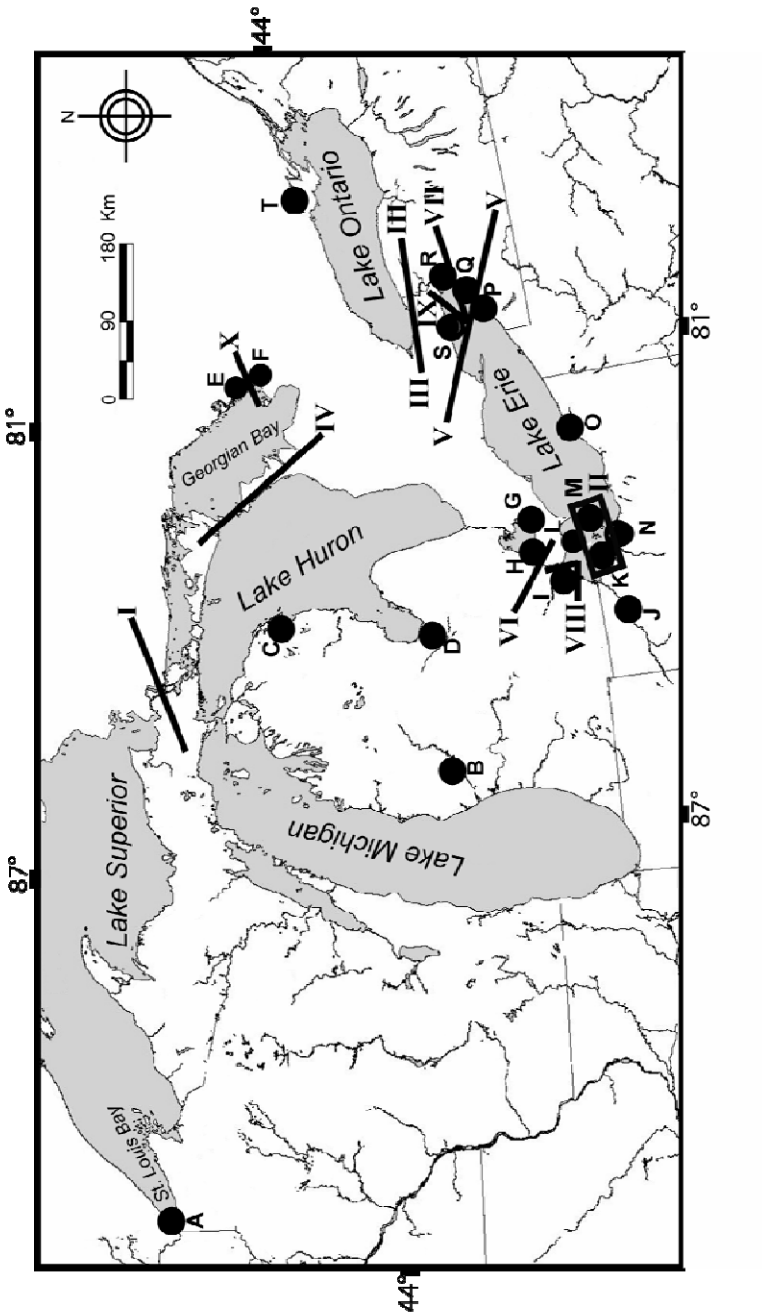

Lake Superior
St. Louis Bay
Lake Michigan
Lake Huron
Georgian Bay
Lake Erie
Lake Ontario
0
90
180 Km
N
44°
81°
87°

Table 1. Walleye spawning aggregations and summary genetic statistics based on nine microsatellite loci (Note: *Svi*L8 was excluded due to deviations from Hardy-Weinberg equilibrium resulting from null alleles; see Results). N = sample size (number of individual fish), H_O = observed heterozygosity, H_E = expected heterozygosity, F_{IS} (as measured by θ_{IS}) = deviation from Hardy-Weinberg (H-W) proportions with positive values indicating heterozygote deficiency and negative values denoting heterozygote excess (Weir and Cockerham 1984), N_A = number of alleles, N_{PA} = number of private alleles, P_{PA} = proportion of private alleles (Note: those for bodies of water are sometimes greater than for the individual sites due to sharing of private alleles among sites).

Locality	**Lat °N**	**Long °W**	N	H_O	H_E	F_{IS}	N_A	N_{PA}	P_{PA}
Lake Superior:									
A. St. Louis River, MN	46.73	92.13	28	0.69	0.75	0.09	70	2	0.03
Lake Michigan:									
B. Muskegon River, MI	43.48	85.83	50	0.72	0.77	0.06	71	0	0.00
Lake Huron:			**125**	**0.71**	**0.75**	**0.06**	**96**	**2**	**0.02**
C. Alpena, MI	45.02	83.43	40	0.70	0.72	0.02	72	1	0.01
Saginaw Bay:									
D. Flint River, MI	43.33	84.05	50	0.73	0.75	0.02	79	1	0.01
Georgian Bay:									
E. Moon River, ON	44.85	79.80	21	0.73	0.70	-0.04	59	0	0.00
F. Musquash River, ON	44.84	79.77	14	0.62	0.72	0.14	54	0	0.00
Lake St. Clair:			**78**	**0.73**	**0.76**	**0.04**	**101**	**4**	**0.04**
G. Thames River, ON	42.32	82.45	38	0.73	0.74	0.01	80	0	0.00
H. Detroit River, MI	42.33	82.91	40	0.74	0.75	0.02	70	4	0.06
Lake Erie:			**450**	**0.70**	**0.78**	**0.10**	**124**	**13**	**0.11**

Table 1, continued.

Locality	Lat ^{0}N	Long ^{0}W	N	H_O	H_E	F_{IS}	N_A	N_{PA}	P_{PA}
Western Basin:			**238**	**0.69**	**0.77**	**0.10**	**117**	**3**	**0.03**
I. Huron River, MI	42.09	83.29	20	0.76	0.75	-0.01	74	0	0.00
J. Maumee River, OH	41.56	83.65	76	0.70	0.74	0.06	90	2	0.02
K. Western reefs, OH	41.63	83.02	20	0.69	0.67	-0.03	61	0	0.00
L. Hen Island Reef, ON	41.81	82.79	82	0.67	0.74	0.10	88	0	0.00
M. Chickenolee Reef, ON	41.72	82.61	20	0.65	0.69	0.05	59	0	0.00
N. Sandusky River, OH	41.46	82.89	20	0.78	0.78	0.01	70	0	0.00
Central Basin:									
O. Grand River, OH	41.78	81.25	30	0.69	0.76	0.09	74	0	0.00
Eastern Basin:			**182**	**0.72**	**0.80**	**0.10**	**115**	**3**	**0.03**
P. Van Buren Bay, NY	42.46	79.41	77	0.74	0.76	0.03	80	1	0.01
Q. Cattaraugus Creek, NY	42.57	79.13	50	0.73	0.75	0.02	85	1	0.00
R. Smokes Creek, NY	42.81	78.86	20	0.78	0.78	0.01	73	0	0.00
S. Grand River, ON	42.86	79.58	35	0.69	0.77	0.10*	74	1	0.01
Lake Ontario:									
T. Bay of Quinte, ON	44.16	77.37	50	0.70	0.74	0.06	77	0	0.00
All Sites:			**781**	**0.71**	**0.79**		**134**		

The product of our study is a baseline data set for resolving stock-structure and genetic-diversity levels of walleye across the Great Lakes. We compare our results with other studies of Great Lakes walleye stocks that used less-variable genetic markers, e.g., allozymes (Ward et al. 1989; Fulton et al. 1992; Todd and Haas 1993, 1995; McParland et al. 1999), whole mtDNA restriction fragment length polymorphisms (RFLP) (Billington and Hebert 1988; Ward et al. 1989; Merker and Woodruff 1996; McParland et al. 1999; Gatt et al. 2002), and mtDNA control region sequences (Stepien and Faber 1998; Stepien et al. 2004). Comparisons also are made with previous microsatellite data studies of walleye (Wilson et al. 2007; Strange and Stepien 2007; Stepien et al. 2009). Our results provide a foundation towards understanding how to best conserve the genetic diversity and variability of Great Lakes walleye.

Methods

Sample Sites and Preparation

We analyzed genetic variation at 10 nuclear microsatellite loci for 781 walleyes from 20 historically used spawning sites across the Great Lakes, including individuals from stocks that have rebounded from anthropogenic disturbances (Fig. 1; Table 1). To test fine-scale variation in Lake Erie, we included 450 individuals from 11 primary spawning sites in 2003, augmenting our earlier study of walleye spawning groups (reported by Strange and Stepien 2007) by 40 individuals from two additional reef sites in the western basin.

Most of our samples were collected by fishery-agency personnel, who clipped a small portion (~1-2 cm^2) of a pectoral fin from adult fish at known spawning sites during the spawning season. The fish were measured, often tagged, and then released. The clip was placed directly in 95% ethanol and archived at room temperature. We analyzed samples from the 2003 and 2004 spawning years, adding samples from 2006 from the Detroit River (Lake St. Clair, Michigan, for which earlier samples were not available). Sex data for eight spawning groups (Muskegon River, Huron River, Sandusky River, Grand River (Ohio), Van Buren Bay, Cattaraugus Creek, Smokes Creek, and Grand River (Ontario)) allowed us to test for possible differences in allelic distributions between males and females.

Microsatellite Loci Procedure

Genomic DNA was extracted and purified from the ethanol-fixed tissues with a DNeasy Qiaquick kit (Qiagen, Inc., Valencia, CA), then frozen and archived. The polymerase chain reaction (PCR) was used to amplify allelic length variants from 10 microsatellite loci developed by other investigators for walleye, including:

- Borer et al. (1999): *Svi*4, *Svi*6, *Svi*17, *Svi*18, *Svi*33
- Wirth et al. (1999): *Svi*L6, *Svi*L7, *Svi*L8
- Eldridge et al. (2002): *Svi*2 and *Svi*7

Our PCR reaction profiles and determination of microsatellite alleles followed Strange and Stepien (2007) and were determined using an ABI 3130XL Genetic Analyzer (Applied Biosystems Inc., Fullerton, CA) and

GeneMapper 3.7 software. We also manually checked all output profiles to confirm allelic size variants.

Data Analyses

Population samples were tested for conformance to Hardy-Weinberg (H-W) equilibrium expectations at each locus, and the Markov chain Monte Carlo (MCMC) method and 1,000 randomization procedures were used to estimate their significance in Genepop v. 4.0 (Raymond and Rousset 1995; Rousset 2008). Deviations were tested for heterozygosity deficiency or excess, each locus was tested for linkage disequilibrium, and results were adjusted using Bonferroni corrections (Sokal and Rohlf 1995). Possible occurrence of null (non-amplified) alleles was assessed following van Oosterhout et al. (2004, 2006), using the program Micro-checker v. 2.2.3 (http://www.microchecker.hull.ac.uk).

Two sets of analyses tested for genetic differences among pairs of samples. Unbiased θ estimates of F-statistics (Weir and Cockerham 1984) and their associated levels of significance were used to test for genetic heterogeneity between spawning sites with the programs *F*stat v. 2.9.3.2 (Goudet 2002) and Genepop. Additional pairwise tests were conducted using the exact nonparametric procedure method of Goudet et al. (1996) and MCMC probabilities in Genepop, a procedure that is not affected by sample size or dependent on a normal distribution (Raymond and Rousset 1995; Rousset 2008). Probability levels for both tests were adjusted using the sequential Bonferroni method (Rice 1989) to minimize type-I errors.

The hypothesis of whether genetic isolation among spawning aggregations ($F_{ST}/1\text{-}F_{ST}$) corresponds to their geographic distance separation (measured as the shortest waterway distances between pairs of spawning sites, km) was tested in Genepop with 1,000 permutations (Mantel 1967). To further examine the relationships among spawning aggregations, Cavalli-Sforza and Edwards' (1967) chord distances (*Dc*) were calculated from the allelic frequency data with the Gendist program and used to construct neighbor-joining trees (Saitou and Nei 1987) in Phylip v. 3.68 (Felsenstein 2008). Relative support values for the nodes of the trees were estimated using 2,000 bootstrap pseudoreplicates (Felsenstein 1985) in Phylip.

The relative magnitude of genetic structure among walleye spawning aggregations was further investigated using an analytical computational geometry approach in Barrier v. 2.2 by Manni et al. (2004a, 2004b), which identified geographically continuous and discontinuous assemblages of samples, independent from *a priori* knowledge of their geographic population structure. Pairwise estimates of F_{ST} were mapped onto a matrix of their geographic coordinates (latitude and longitude). The spatial organization of the spawning aggregations was modeled by Voronoi tessellation, and a Monmonier (1973) maximum-difference algorithm identified which of the borders between neighboring aggregations exhibited the highest levels of genetic differences. A second analysis calculated single-locus F_{ST} values, which were used to evaluate how many loci supported each barrier. Relative support and rankings for the barriers were further evaluated with a bootstrap analysis of the multilocus F_{ST} matrix with 2,000 iterations in Geneland v. 2.3.41 (Guillot et al. 2005a, 2005b, 2008), which was based on the *R* statistical analysis software suite v. 2.8.1 (R Development Core Team 2008). Barriers with bootstrap values higher than 50% and supported by more than 50% of the loci are reported.

To further evaluate distinctive population groups, we employed a Bayesian clustering algorithm that was independent of assumptions about mutation processes using the program Structure v. 2.2.3 (Pritchard et al. 2000; Pritchard and Wen 2004). This analysis identified groups with distinctive allelic frequencies without prior knowledge of their true spawning aggregation identity. We analyzed correspondence to spawning aggregations by specifying number of groups (K) in independent runs of the algorithm ranging from $K = 1$ (thus testing the null hypothesis of panmixia) to $K = 20$ (the total N of spawning aggregations sampled). The program assigned individual walleye to one or more groups, with their relative frequency of predicted membership in groups totaling 1.00. We used 10 independent runs for each K, with pre-sampling iterations of 100,000 followed by 500,000 generations. We then examined the consistency among runs, the comparative probabilities of individuals assigning to one or more groups, the log likelihood and posterior probability values from each run, and the respective grouping patterns. Results from the Structure analyses were evaluated using the posterior probability procedure of Pritchard et al. (2000) and the ΔK method of Evanno et al. (2005), the latter being based on the rate of change in the log probability values between successive Ks. We graphed the magnitude of ΔK versus K for the mean of 10 replicate runs for each K, whose peak values designated the most-probable K. Results of the Structure analyses were then compared with population relationships derived from genetic divergences, neighbor-joining trees, and Barrier analyses.

Results

Genetic Variation within Spawning Aggregations

The mean number of alleles per microsatellite locus among all walleye sampled across the Great Lakes was 15.1 (Table 2), ranging from 8 (*Svi*18) to 24 (*Svi*L7). The frequency of the most-abundant allele-per-locus ranged from 19% (*Svi*33) to 52% (*Svi*17). Summation frequencies for the three most-common alleles combined ranged from 47% (*Svi*33) to 94% (*Svi*17). Based on mean F_{ST} variation, *Svi*18 was the most-informative locus, and *Svi*4, *Svi*17, and *Svi*33, respectively, were next in importance (Table 2).

Table 2. Summary of allelic variation within 10 microsatellite loci for Great Lakes walleye (N = 781 individuals). N_A = number of alleles in Great Lakes walleye at that locus. Size of alleles = length in bp. F_{IS} = mean genetic differentiation within a spawning aggregation (range: 0-1), F_{IT} = deviation in the total sample, F_{ST} = mean genetic divergence between pairs of spawning aggregations.

			Frequency of most-abundant alleles					
Locus	N_A	**Allele size range**	**First**	**Second**	**Third**	F_{IS}	F_{IT}	F_{ST}
*Svi*2	14	188-222	0.40 (192)	0.15 (190)	0.13 (202)	0.034	0.063	0.029
*Svi*4	10	104-122	0.32 (116)	0.24 (114)	0.12 (118)	0.047	0.100	0.055
*Svi*6	21	126-188	0.49 (140)	0.10 (146)	0.07 (148)	0.016	0.040	0.024
*Svi*7	16	140-190	0.41 (162)	0.23 (156)	0.14 (164)	0.078	0.117	0.042
*Svi*17	9	102-120	0.52 (104)	0.23 (112)	0.19 (110)	0.012	0.055	0.044
*Svi*18	8	116-130	0.25 (122)	0.24 (124)	0.18 (128)	0.113	0.260	0.166
*Svi*33	13	82-106	0.19 (94)	0.15 (96)	0.13 (86)	0.011	0.054	0.044
*Svi*L6	17	106-138	0.46 (110)	0.12 (108)	0.11 (124)	0.019	0.032	0.013
*Svi*L7	24	160-234	0.24 (200)	0.15 (198)	0.09 (196)	0.068	0.091	0.025
*Svi*L8	19	106-150	0.28 (128)	0.13 (130)	0.12 (136)	0.274	0.296	0.029
Mean	15.1					0.070	0.114	0.048

Tests for conformance to H-W equilibrium expectations revealed significant departures at the *Svi*L8 locus, which occurred at nine sampling sites. Micro-checker determined that these deviations at the *Svi*L8 locus were due to the presence of null (non-amplified) alleles. Thus, locus *Svi*L8 was eliminated from further analyses, after which all samples except one (Grand River, (Ontario) in eastern Lake Erie) were in H-W equilibrium (Table 1). Because 20 spawning aggregations of walleye were tested overall and because we set $\alpha = 0.05$, this single deviation was attributed to chance.

Overall observed heterozygosity values for all spawning aggregations averaged 71% (Table 1), ranging from 62% (for the Musquash River in Georgian Bay of Lake Huron) to 78% (for the Sandusky River in western Lake Erie and for Smokes Creek in eastern Lake Erie). Lakes Superior, Huron, St. Clair, and Erie each housed "private" alleles, i.e., those found only at specific sampling sites. Walleye in Lakes St. Clair and Erie had the greatest proportions of private alleles (4% and 11%, respectively; Table 1).

No significant differences in allelic distributions occurred between males and females collected from the same locality within the eight samples for which sex information was available (Muskegon River, Huron River, Sandusky River, Grand River (Ohio), Van Buren Bay, Cattaraugus Creek, Smokes Creek, and Grand River (Ontario). Males and females at spawning sites thus appeared to have very similar genetic composition and site fidelity.

Genetic Divergence among Spawning Aggregations

Pairwise estimates of genetic divergence revealed that most walleye spawning aggregations differed significantly in allelic composition (Table 3, below the diagonal). Walleye populations that were most divergent included those from the St. Louis River in western Lake Superior (average F_{ST} = 0.069 from all other sites), the Bay of Quinte in Lake Ontario (0.056), the Grand River (Ontario) in eastern Lake Erie (0.058), and the Moon and Musquash Rivers in Georgian Bay of Lake Huron (0.063 and 0.089, respectively). Pairwise F_{ST} estimates between walleye spawning aggregations ranged from 0.128 between the Musquash River in Georgian Bay of Lake Huron and the western reef system in Lake Erie, to only 0.001 between sites in the Sandusky and Maumee Rivers, which are adjacent in western Lake Erie. Spawning aggregations that were most similar genetically to others nearby occurred along the southern shores of the western and central basins of Lake Erie (Table 3). Notably, high gene flow linked the walleye spawning aggregation in the Maumee River with those in the Sandusky River, Grand River (Ohio), and Van Buren Bay.

Table 3. Pairwise estimates of genetic divergence (χ^2 above diagonal, Goudet et al. 1996) and F_{ST} analog values (below diagonal, Weir and Cockerham 1984) between spawning aggregations of Great Lakes walleye. Inf = χ^2 denoted as infinite by Genepop, NS = not significant, * = significant at $p < 0.05$ (prior to Bonferroni correction), ** = remaining significant following sequential Bonferroni correction (Rice 1989) for 190 pairwise comparisons ($p < 0.00026$).

Location	A	B	C	D	E	F	G
A. St. Louis R., Lake Superior	—	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
B. Muskegon R., Lake Michigan	0.050 **	—	Inf **	Inf **	Inf **	120.71 **	Inf **
C. Alpena, Lake Huron	0.069 **	0.028 **	—	58.40 **	Inf **	Inf **	Inf **
D. Flint R., Lake Huron	0.058 **	0.010 *	0.010 *	—	Inf **	Inf **	Inf **
E. Moon R., Lake Huron	0.087 **	0.051 **	0.057 **	0.041 **	—	55.58 **	Inf **
F. Musquash R., Lake Huron	0.102 **	0.057 **	0.097 **	0.069 **	0.034 **	—	Inf **
G. Thames R., Lake St. Clair	0.051 **	0.032 **	0.025 **	0.013 **	0.029 **	0.069 **	—
H. Detroit R.. Lake St. Clair	0.062 **	0.033 **	0.022 **	0.017 **	0.043 **	0.081 **	0.013 *
I. Huron R., Lake Erie	0.059 **	0.044 **	0.071 **	0.040 **	0.057 **	0.062 **	0.045 **
J. Maumee R., Lake Erie	0.083 **	0.072 **	0.080 **	0.057 **	0.089 **	0.113 **	0.060 **
K. Western Reefs, Lake Erie	0.093 **	0.069 **	0.059 **	0.037 **	0.067 **	0.128 **	0.014 *
L. Hen Island, Lake Erie	0.069 **	0.066 **	0.075 **	0.052 **	0.083 **	0.108 **	0.056 **
M. Chickenolee Reef, Lake Erie	0.075 **	0.049 **	0.034 **	0.024 **	0.045 **	0.106 **	0.012 *
N. Sandusky R., Lake Erie	0.073 **	0.068 **	0.081 **	0.055 **	0.087 **	0.108 **	0.059 **
O. Grand R., OH, Lake Erie	0.073 **	0.059 **	0.068 **	0.050 **	0.078 **	0.100 **	0.050 **
P. Van Buren Bay, Lake Erie	0.077 **	0.072 **	0.081 **	0.059 **	0.089 **	0.110 **	0.064 **
Q. Cattaraugus Creek, Lake Erie	0.051 **	0.042 **	0.039 **	0.023 **	0.032 **	0.071 **	0.003 NS
R. Smokes Creek, Lake Erie	0.055 **	0.039 **	0.063 **	0.030 **	0.075 **	0.080 **	0.047 **
S. Grand R., ON, Lake Erie	0.054 **	0.060 **	0.076 **	0.056 **	0.087 **	0.108 **	0.044 **
T. Bay of Quinte, Lake Ontario	0.061 **	0.039 **	0.039 **	0.028 **	0.063 **	0.093 **	0.026 **

Table 3, continued.

Location	H	I	J	K	L	M	N
A. St. Louis R., Lake Superior	Inf **	Inf **	Inf **	131.17 **	Inf **	Inf **	Inf **
B. Muskegon R., Lake Michigan	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
C. Alpena, Lake Huron	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
D. Flint R., Lake Huron	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
E. Moon R., Lake Huron	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
F. Musquash R., Lake Huron	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
G. Thames R., Lake St. Clair	Inf **	Inf **	Inf **	38.37 *	Inf **	39.35 *	Inf **
H. Detroit R.. Lake St. Clair	—	Inf **	Inf **	70.15 **	Inf **	63.24 **	Inf **
I. Huron R., Lake Erie	0.053 **	—	Inf **	Inf **	Inf **	Inf **	Inf **
J. Maumee R., Lake Erie	0.061 **	0.041 **	—	Inf **	52.50 **	Inf **	16.31 NS
K. Western Reefs, Lake Erie	0.036 **	0.063 **	0.063 **	—	Inf **	53.26 **	Inf **
L. Hen Island, Lake Erie	0.057 **	0.035 **	0.005 *	0.065 **	—	Inf **	34.56 *
M. Chickenolee Reef, Lake Erie	0.021 **	0.054 **	0.060 **	0.020 *	0.052 **	—	Inf **
N. Sandusky R., Lake Erie	0.062 **	0.048 **	0.001 NS	0.064 **	0.005 NS	0.062 **	—
O. Grand R., OH, Lake Erie	0.044 **	0.034 **	0.002 NS	0.059 **	0.002 NS	0.046 **	0.003 NS
P. Van Buren Bay, Lake Erie	0.067 **	0.048 **	0.002 NS	0.067 **	0.012 **	0.063 **	0.003 NS
Q. Cattaraugus Creek, Lake Erie	0.021 **	0.038 **	0.057 **	0.017 *	0.055 **	0.016 *	0.055 **
R. Smokes Creek, Lake Erie	0.056 **	0.003 NS	0.037 **	0.057 **	0.033 **	0.056 **	0.032 **
S. Grand R., ON, Lake Erie	0.060 **	0.059 **	0.060 **	0.063 **	0.049 **	0.051 **	0.050 **
T. Bay of Quinte, Lake Ontario	0.038 **	0.079 **	0.072 **	0.049 **	0.073 **	0.037 **	0.073 **

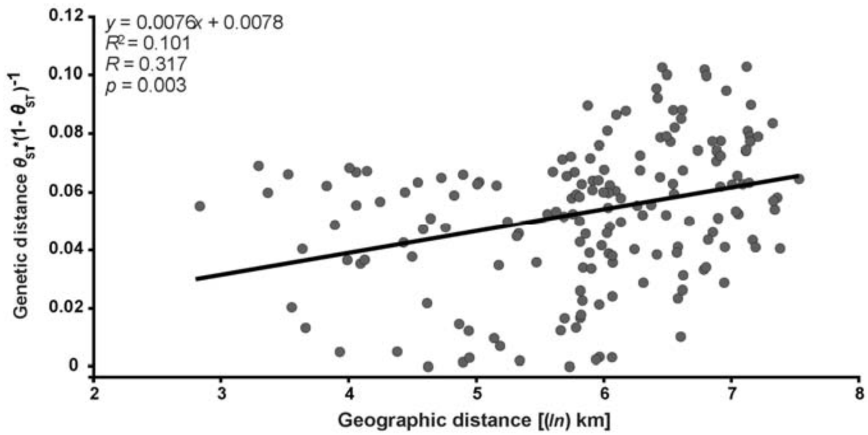
Table 3, continued.

Location	O	P	Q	R	S	T
A. St. Louis R., Lake Superior	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
B. Muskegon R., Lake Michigan	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
C. Alpena, Lake Huron	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
D. Flint R., Lake Huron	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
E. Moon R., Lake Huron	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
F. Musquash R., Lake Huron	Inf **	Inf **	Inf **	Inf **	Inf **	Inf **
G. Thames R., Lake St. Clair	Inf **	Inf **	29.03 *	Inf **	Inf **	Inf **
H. Detroit R.. Lake St. Clair	Inf **	Inf **	89.55 **	Inf **	Inf **	Inf **
I. Huron R., Lake Erie	Inf **	Inf **	Inf **	23.54 NS	Inf **	Inf **
J. Maumee R., Lake Erie	37.14 *	38.61 *	Inf **	Inf **	Inf **	Inf **
K. Western Reefs, Lake Erie	Inf **	Inf **	52.40 **	Inf **	Inf **	99.44 **
L. Hen Island, Lake Erie	49.80 **	Inf **	Inf **	Inf **	Inf **	Inf **
M. Chickenolee Reef, Lake Erie	Inf **	Inf **	51.84 **	Inf **	117.91 **	88.56 **
N. Sandusky R., Lake Erie	33.95 *	24.91 NS	Inf **	Inf **	Inf **	Inf **
O. Grand R., OH, Lake Erie	—	68.26 **	Inf **	Inf **	Inf **	Inf **
P. Van Buren Bay, Lake Erie	0.007 *	—	Inf **	Inf **	Inf **	Inf **
Q. Cattaraugus Creek, Lake Erie	0.043 **	0.056 **	—	Inf **	Inf **	Inf **
R. Smokes Creek, Lake Erie	0.034 **	0.034 **	0.039 **	—	108.99 **	Inf **
S. Grand R., ON, Lake Erie	0.047 **	0.058 **	0.046 **	0.035 **	—	Inf **
T. Bay of Quinte, Lake Ontario	0.063 **	0.082 **	0.041 **	0.062 **	0.044 **	—

In contrast, spawning aggregations located in close proximity in the Moon and Musquash Rivers of Lake Huron's Georgian Bay had significantly different genetic compositions (θ_{ST} = 0.034; Table 3). Among 190 pairwise θ_{ST} comparisons (Table 3, below the diagonal), nine, amounting to 4.7% of all comparisons, were not significant at the p = 0.05 level (4.7%) and 10 additional comparisons were not significant following sequential Bonferroni correction, totaling 10.0% of the overall comparisons. Thus, significant population divergence was found for 90% of the pairwise comparisons and can be considered the "norm" for walleye spawning aggregations in the Great Lakes.

The nonparametric method for discerning population differentiation indicated that only three pairwise comparisons (1.6% of the total) were not significant prior to Bonferroni correction (Table 3, above the diagonal), and these included both the Lake Erie walleye spawning aggregations in the Maumee and Sandusky Rivers and between both of these aggregations and Van Buren Bay. Following Bonferroni correction, seven additional comparisons were not significant, totaling 5.3% of the overall comparisons. These comparisons involved gene flow among spawning aggregations located along the southern shore of Lake Erie (the Maumee River, Sandusky River, and Grand River (Ohio)), and among aggregations in the Thames River (Lake St. Clair) and some Lake Erie sites (western reefs, Chickenolee Reef, and Cattaraugus Creek). In summary, most walleye spawning aggregations across the Great Lakes were genetically differentiated. Our Mantel test supported the hypothesis of genetic isolation by geographic distance across the Great Lakes, but the relationship was relatively weak (R^2 = 0.101, Fig. 2).

Fig. 2. Mantel test of the relationship between genetic divergence and geographic distance for 20 walleye spawning aggregations across the Great Lakes (190 pairwise comparisons), expressed as $F_{ST} \bullet (1\text{-}F_{ST})^{-1}$ versus the natural logarithm of their nearest water pathway in kilometers (km). The equation is $y = 0.0076x + 0.0078$, $R^2 = 0.1006$, $R = 0.3171$, $p = 0.0025$.



Analysis of genetic divisions among Great Lakes walleye spawning stocks using barriers identified 10 primary separations (Fig. 1), which delineated population groups (groups of stocks) with greater genetic distinctiveness than would be expected from their geographic connectivity. The foremost separation (numbered I on Fig. 1) delineated walleye from western Lake Superior from other sites (59% bootstrap support and support from 8/9 loci). Other genetic separations defined walleye spawning aggregations from selected reefs in western Lake Erie (Western and Chickenolee Reefs, Barrier II; 56% bootstrap, 8/9 loci), Lake Ontario (III; 50%, 7/9 loci), Lake Huron's Georgian Bay (IV; 52%, 9/9 loci), eastern Lake Erie rivers (V; 50%, 8/9 loci), and the upper from the lower Great Lakes below Lake St. Clair (VI; 57%, 7/9 loci). Within Lake Erie, genetic separations distinguished the following Lake Erie tributary spawning aggregations: Cattaraugus Creek from nearby Smokes Creek (VII; 50%, 4/9 loci), the Huron River (VIII; 60%, 6/9 loci), and Grand River (Ontario) (IX; 51%, 6/9 loci). The final barrier of importance separated walleye spawning aggregations in the Moon and Musquash Rivers (Georgian Bay, Lake Huron) (X; 53%, 5/9 loci).

Our neighbor-joining tree (Fig. 3) found similar relationships among walleye spawning stocks, as resolved from the Barrier analysis (above and Fig. 1) and the Structure analysis (below and Fig. 4). The tree depicted the aggregation spawning in the St. Louis River in Lake Superior as basal and closest to the sauger (*S. canadensis*), the sister species of walleye (Faber and Stepien 1998). Spawning stocks in Lake Huron and Lake Michigan appeared more closely related to each other, with those from Georgian Bay diverging more (shown by its horizontal branch length). Aggregations spawning in the Moon and Musquash Rivers of Georgian Bay were linked by 99% bootstrap support, with their branch lengths reflecting significant genetic separation from each other. Most walleye spawning aggregations in Lake Erie clustered together on the tree (with 76% bootstrap support), within which a clade grouped the spawning aggregations from the Grand River (Ohio), Hen Island Reef, Maumee River, Sandusky River, and Van Buren Bay (64% bootstrap support). The latter three aggregations formed an additional internal clade (76% bootstrap support), denoting a region of high gene flow also identified in the pairwise analyses (Table 3). Three other Lake Erie spawning aggregations, the western reefs, Chickenolee Reef, and Cattaraugus Creek, grouped separately on the tree (with low bootstrap support), and appeared linked to the aggregation from Lake St. Clair (Fig. 3). The relative magnitudes of relationships among these sites were also seen in the pairwise analyses (Table 3).

Fig. 3. Neighbor-joining tree (Saitou and Nei 1987; constructed in Phylip) showing relationships among walleye spawning aggregations based on Cavalli-Sforza and Edwards' (1967) chord distances. Values at nodes denote relative percent support from 2,000 bootstrap iterations. Bar indicates chord distance.

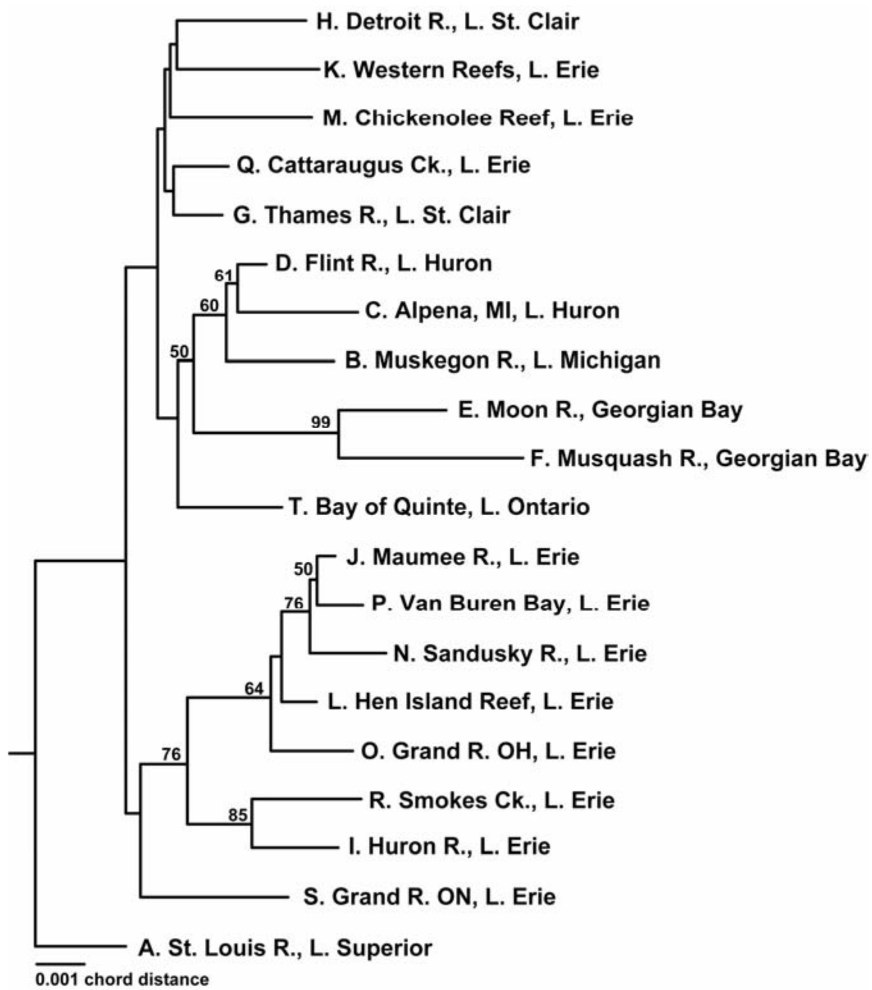
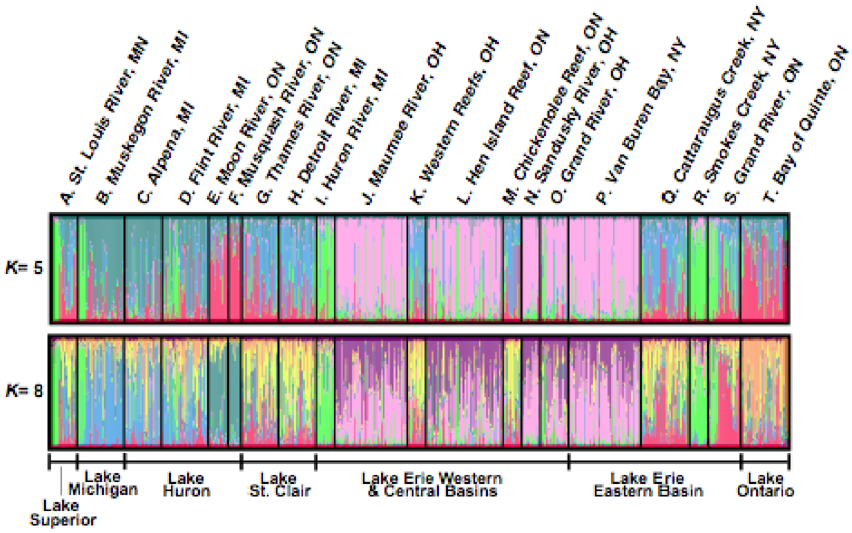

H. Detroit R., L. St. Clair
K. Western Reefs, L. Erie
M. Chickenolee Reef, L. Erie
Q. Cattaraugus Ck., L. Erie
G. Thames R., L. St. Clair
D. Flint R., L. Huron
61
C. Alpena, MI, L. Huron
60
B. Muskegon R., L. Michigan
50
E. Moon R., Georgian Bay
99
F. Musquash R., Georgian Bay
T. Bay of Quinte, L. Ontario
J. Maumee R., L. Erie
50
P. Van Buren Bay, L. Erie
76
N. Sandusky R., L. Erie
64
L. Hen Island Reef, L. Erie
O. Grand R. OH, L. Erie
76
R. Smokes Ck., L. Erie
85
I. Huron R., L. Erie
S. Grand R. ON, L. Erie
A. St. Louis R., L. Superior
0.001 chord distance

Fig. 4. Estimated population composition from Bayesian Structure analysis for $K = 5$ and 8 population groups, with each graph constituting the highest probability run among 10 separate runs at that K. Black lines separate different spawning sites. Walleye groups that originally emerge at lower values of K are the most differentiated. $K = 8$ had the greatest mean likelihood and posterior probability (0.999) values and, thus, represents the best estimate of the true number of population groups, according to this method (Pritchard et al. 2000); whereas $K = 5$ and $K = 8$ were both supported by the ΔK method (Evanno et al. 2005).



Bayesian Structure analyses to determine the number of genetic clusters of walleye across the Great Lakes revealed the greatest mean log likelihood and posterior probability values at $K = 8$ clusters (posterior probability = 0.999), and supported both $K = 5$ and $K = 8$ using the ΔK criterion (Fig. 4). These results thus showed similar groupings to those found with the other analyses, including Barrier (Fig. 1), pairwise divergence (Table 3), and the neighbor-joining tree (Fig. 3). Fig. 4 indicates Structure results from the highest posterior probability run at each of the two Ks, grouping samples into their membership in putative genetic groups by color. The predominant genetic groups emerged at the lowest K runs (visible in $K = 5$), with finer-scale patterns evident at $K = 8$.

Structure analyses (Fig. 4) thus showed the distinctiveness of spawning stocks in Georgian Bay from all others (colored blue green in K = 8, representing 67% of individuals from the Moon River spawning aggregation and 82% from the Musquash River), a relationship shown also in Barrier (Fig. 1), the neighbor-joining tree (Fig. 3), and pairwise analyses (Table 3). Also supported in the Structure and other analyses are closer relationships between the other Lake Huron and Lake Michigan spawning aggregations (light blue), divergence of the stock spawning in Lake Ontario (orange), and linkage among the Lake Erie spawning aggregations in the Maumee River, Hen Island, Sandusky River, Grand River (Ohio), and Van Buren Bay (purple). In summary, results from all analyses were congruent in defining groups of divergent Great Lakes walleye spawning stocks.

Discussion

Genetic Diversity and Divergence Patterns of Great Lakes Walleye

Overall heterozygosity levels per sampling site were relatively high (averaging 0.71) and consistent (ranging from 0.62 to 0.78), indicating appreciable genetic diversity in walleye spawning aggregations across the Great Lakes. Our findings also demonstrate considerable genetic divergences among most spawning aggregations across the Great Lakes, reflecting both broad- and fine-scale patterns of stock relationships. All analyses reveal that the greatest genetic distinctiveness occurred among walleye spawning stocks from Lake Superior, some western Lake Erie reefs, Lake Ontario, Georgian Bay of Lake Huron, and eastern Lake Erie rivers. Although relationships among walleye spawning stocks across the Great Lakes typically followed a broad-scale pattern of genetic isolation by geographic distance, relationships among spawning aggregations within individual lakes did not reflect geographic distance. Notably, relatively large genetic separations delineated some proximate spawning aggregations: the Moon from the Musquash Rivers in Lake Huron, the Grand River (Ontario) from other Lake Erie sites, and the riverine sites in eastern Lake Erie from other Lake Erie sites.

Relation of Walleye Genetic Patterns to the History of the Great Lakes

Patterns of genetic divergences among walleye stocks likely reflect differential contributions originating from refugia in the early Great Lakes, which were subsequently modified by drainage connections and basin isolation (Bailey and Smith 1981; Mandrak and Crossman 2001). Walleye from Lake Superior have been linked to a Missourian glacial refugium ancestry, whereas those from Lakes Huron, Michigan, St. Clair, and western Lake Erie are hypothesized to be largely descendent from a Mississippian glacial refugium (Ward et al. 1989). Walleye in Lake Ontario are believed to have descended from an Atlantic refugium (Billington and Hebert 1988; Ward et al. 1989), and mtDNA data indicated they are historically linked to those spawning in eastern Lake Erie (Stepien and Faber 1998).

The Lake Superior region was long covered in ice, except for glacial Lake Duluth in the west until ~9-8.5 thousand years ago (kya), thus isolating its walleye gene pool. The genetic relationship between walleye spawning in Lake Michigan and Lake Huron proper (including Saginaw Bay) likely reflects their former connection as glacial Lake Algonquin ~12-10.6 kya, which drained west to the Mississippi River system (Bailey and Smith 1981). Lake Huron walleye stocks diverged ~11.5 kya when Georgian Bay (the former glacial Lake Hough) was isolated from the main basin population (the former glacial Lake Stanley) (Lewis et al. 1994). Lake Erie's formation dates to glacial Lake Maumee (~14 kya), which then drained west via the Ohio River to the Mississippi, changing outlets during several lake stages, to its current outlet east into Lake Ontario (~10 kya) (Underhill 1986). Lake Erie walleye stocks today appear geographically isolated and genetically differentiated from most other Great Lakes stocks. Lake Erie is physically separated from Lake Ontario by Niagara Falls and from the upper Great Lakes by the narrow and short Detroit River, which drains Lake St. Clair. Our results, however, reflect some limited genetic exchange between the Thames River aggregation of Lake St. Clair and the aggregations spawning on Lake Erie reefs, which are on opposite sides of barrier VI (Fig. 1).

Genetic separations similar to those described here for walleye have been discerned among spawning stocks of other Great Lakes fishes, including brown bullhead (*Ameiurus nebulosus)* (Murdoch and Hebert 1997), smallmouth bass (*Micropterus dolomieu)* (Stepien et al. 2007), and yellow perch (*Perca flavescens*) (Sepulveda-Villet et al. 2009). These similarities reveal a general population pattern that originated with recolonization from glacial refugia, was modified by changes in connections and drainages, and has been maintained by reproductive site philopatry from generation through generation.

Fine-Scale Patterns Distinguishing Walleye Spawning Groups

In contrast to their broad-scale variation patterns across the Great Lakes, fine-scale variation among walleye spawning groups across Lake Erie does not follow a genetic isolation by geographic distance pattern (p = 0.827; also reported in Strange and Stepien 2007). This finding is due to high genetic differentiation between some closely located spawning aggregations: between the Huron and the Maumee Rivers in western Lake Erie; between Hen Island and Chickenolee Reef in western Lake Erie; and among Van Buren Bay, Cattaraugus Creek, Smokes Creek, and the Grand River (Ontario) in eastern Lake Erie.

Some closely located walleye spawning aggregations in Lake Erie were genetically distinct from each other, implying high site fidelity; these sites include all those in the eastern basin (riverine spawning sites), most of those near the western-basin reefs, and those nearest the Huron River, which is the most westerly location in the lake. Appreciable genetic differentiation among eastern Lake Erie basin spawning aggregations is also evident in other fishes, including smallmouth bass (Borden and Stepien 2006; Stepien et al. 2007) and yellow perch (Ford and Stepien 2004; Sepulveda-Villet et al. 2009).

Conversely, walleye spawning aggregations along the southern shore in the western and central Lake Erie basins, which are the largest in numbers, are linked by higher connectivity and gene flow (discussed in detail by Strange and Stepien 2007). This connectivity also was described by other researchers using a variety of genetic techniques (Merker and Woodruff 1996; Stepien and Faber 1998; Strange and Stepien 2007). A study by McParland et al. (1999) using mtDNA RFLPs and allozymes found no differentiation between walleye spawning at Chickenolee Reef and the Huron River in western Lake Erie, but this comparison differed significantly in our study using higher-resolution microsatellites.

Our investigation shows that both male and female walleye have analogous genetic patterns at given spawning sites, and thus appear to have similar site fidelity. Similar conclusions were drawn from a study of mtDNA variation

(Stepien and Faber 1998). Although the mechanism for homing behavior is unknown, a study by Gerlach et al. (2001) suggested that Eurasian yellow perch (*Perca fluviatilis*) may recognize kin through olfactory cues. Thus, it is possible that walleye returning to their natal sites are guided by olfactory information imprinted during early stages of their life history. If so, it may be the primary mechanism for maintaining divergence among spawning aggregations, but this idea remains to be tested.

Relation of Genetic Data to Restoration of Native Walleye Stocks

During the mid-20th century, walleye stocks in Lake Superior declined due to exploitation, river damming, pollution, and habitat loss and degradation (Hoff 2003), which are common factors that led to their decrease in most regions across the Great Lakes. In contrast, the size of the native St. Louis River stock has increased due to river cleanup (MacCallum and Selgeby 1987), and it now constitutes the majority of walleye spawning in western Lake Superior (Schram et al. 1992). MacCallum and Selgeby (1987) hypothesized that an appreciable number of older individuals (reaching age 20) survived in the St. Louis River through the 1980s, a contention supported by diversity and divergence levels found two decades later in our study. The Great Lakes Fishery Stocking Database (Great Lakes Fishery Commission 2009b) indicates that the St. Louis River and bay area were stocked with walleye from the river throughout the 1990s to the present. Elsewhere on Lake Superior, a microsatellite study by Wilson et al. (2007) inferred natural reproduction of transferred stocks to Nipigon and Black Bays and suggested possible retention of native stocks, whose natural populations declined severely in the mid-1960s (Ryder 1968; MacCallum and Selgeby 1987). Our findings for the St. Louis River also support retention.

The Flint River spawning aggregation in Lake Huron's Saginaw Bay shows appreciable genetic diversity and divergence from other spawning aggregations. Its genetic relationship appears closer to yet divergent from walleye spawning in Lake Michigan's Muskegon River and in Lake Huron at Alpena. Saginaw Bay once housed the second-largest walleye fishery in the Great Lakes (Schneider and Leach 1977; Fielder 2002a, 2002b), which collapsed in the 1940s, owing to spawning-habitat degradation and overfishing (Jude and Leach 1999). Commercial walleye fishing was banned in Saginaw Bay in 1969, and a sport fishery supported by stocking came into prominence in the 1980s (Fielder 2002a, 2002b; Great Lakes Fishery

Commission 2009b). The Flint River aggregation does not resemble those in western Lake Erie, despite stocking inputs of fry from that source in the past (Fielder 2002a, 2002b) and seasonal immigration (Haas et al. 1988; Fielder 2002a, 2002b). Todd and Haas (1995), using allozymes, showed that Saginaw Bay's Tittabawassee River (like the Flint River, a tributary of the Saginaw River) runs of walleye differed from the cultured pond stocks transferred there from Lake Michigan's Muskegon River and appeared to be dominated by native genotypes. Moreover, their results, like ours, showed differences between walleye spawning in Saginaw Bay tributaries and those spawning in the Muskegon River, suggesting that diverged native genotypes likely predominate in Saginaw Bay today.

Among walleye stocks in Lake Huron's Georgian Bay, the Moon River aggregation showed the greatest potential for recovery during the 1970s, despite several year-class failures (Colby and Nepszy 1981). Our results indicate that the Moon River stock, which had been supplemented (Great Lakes Fishery Commission 2009b), has relatively high genetic diversity and diverges from the nearby stock spawning in the Musquash River. In contrast, a study of mtDNA RFLPs by Gatt et al. (2002) found low genetic variability and little genetic divergence among walleye spawning groups in Georgian Bay, a discrepancy that appears attributable to our use of higher-resolution markers. Our results thus support appreciable broad- and fine-scale population structure of walleye in Lake Huron, and our data will be valuable for monitoring these native stocks.

Walleye aggregations spawning in the Thames and Detroit Rivers of Lake St. Clair have slightly higher-than-average levels of genetic diversity and differ somewhat from each other, indicating some genetic exchange with aggregations spawning in Lake Erie. The walleye spawning aggregation in the Thames River was large, and, although individuals from it often migrate to Lake Huron and western Lake Erie to feed during summer months (Colby and Nepszy 1981), our data indicate that most return to spawn. The Lake St. Clair fishery was closed due to mercury contamination in the early 1970s (Colby and Nepszy 1981), and, by the 1980s, the Thames River stock had recovered (Nepszy et al. 1991), but it declined in the 1990s apparently owing to dramatic changes caused by non-indigenous species (Belore et al. 2010). Our study found that the present-day Detroit River aggregation has some unique alleles that may have been retained despite these population fluctuations.

The genetic diversity of Lake Erie walleye spawning aggregations is relatively high, and some aggregations are genetically differentiated, despite pronounced anthropogenic habitat alterations in the western and central basins and associated tributaries and decreased size of spawning stocks (Trautman 1981; Bolsenga and Herdendorf 1993). Western-basin stocks declined markedly during the 1950s and 1960s due to overexploitation, interactions with introduced species, and nutrient loading (Schneider and Leach 1977). They then rebounded in the 1970s following harvest restrictions and increased to historical abundance levels during the 1990s (Knight 1997). The Lake Erie Walleye Task Group of the Lake Erie Committee, which operates under the Great Lakes Fishery Commission, estimated that western-basin walleye now number 30-40 million spawning individuals (Thomas et al. 2005).

In contrast, walleye stocks in the eastern basin of Lake Erie have historically been much smaller than those of the west and have not declined markedly (Wolfert and Van Meter 1978). Our data reveal more site-specific differentiation in the eastern basin, especially for riverine stocks. Eastern-basin spawning stocks were recently estimated at 0.5-2 million individuals (Thomas et al. 2005). Our sampling sites did not have a known recent history of supplementation from other sources, excepting Cattaraugus Creek and Smokes Creek, New York, which were stocked with Maumee River walleye. They are no longer being stocked, and the stockings were considered unsuccessful (D. Einhouse, New York Department of Environmental Conservation, personal communication, 2008). The brief stocking history at Cattaraugus Creek and Smokes Creek did not appear to genetically affect the native mtDNA genotypes (Stepien et al. 2004), although our microsatellite data indicate a possible western basin influence.

Our results show considerable genetic diversity of walleye spawning stocks across Lake Erie with some unique alleles in the Maumee River, Van Buren Bay, and Grand River (Ontario) aggregations. Spawning aggregations in the Huron River, Smokes Creek, and Grand River (Ontario) are the most divergent from other sites. Gene flow links aggregations along the south shore, extending from the western basin to Van Buren Bay in the eastern basin (Strange and Stepien 2007). However, the degree and location of this gene flow appears to differ among years and may have been particularly pronounced in 2003, which was the largest spawning run in two decades (R. Knight, Ohio Division of Wildlife, personal communications, 2006-2010). More walleye may have strayed to spawn in other sites in 2003 due to habitat crowding, an idea that merits further study.

Our study indicates that the spawning aggregation in Lake Ontario's Bay of Quinte is characterized by average genetic diversity and high genetic divergence from spawning stocks in other lakes. Although walleye stocks in Lake Ontario rebounded in the 1990s following declines during the 1960s that were linked to high phosphorous levels and alterations of spawning habitats (Jude and Leach 1999), appreciable genetic variability is now evidenced. A previous genetic study of the Bay of Quinte and New York walleye by Wilson and Mathers (2002) found no differences among sites, but their collections did not involve spawning groups and were made during August, when walleye stocks mix while feeding. We suggest that future investigations should expand our database to include other Lake Ontario spawning aggregations.

In conclusion, our results offer a valuable comparative database for defining stock structure of walleye spawning populations across the Great Lakes. The native spawning stocks we examined appear to have retained appreciable genetic diversity and to have diverged from other stocks, both nearby and distant, despite anthropogenic influences. Accordingly, we recommend conserving their genetic composition and stock differentiation pattern by maintaining and restoring spawning habitats.

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