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Fish Assemblage Shifts and Population Dynamics of Smallmouth Bass (Micropterus dolomieu) in the Beaver Archipelago, Northern Lake Michigan: A Comparison Between Historical and Recent Time Periods Amidst Ecosystem Changes.

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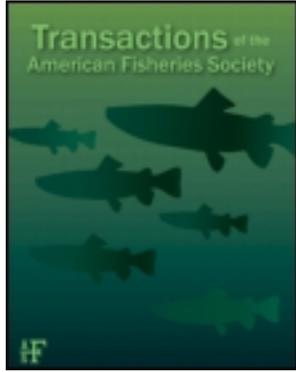
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Abstract

The ecological and economic importance of Great Lakes nearshore areas and the paucity of information on nearshore Lake Michigan fish assemblages prompted us to document changes that occurred from a historical time period (1969–1972, 1975, 1977, and 1984) to a recent period (2005–2008) in a nearshore northern Lake Michigan (Beaver Archipelago) fish assemblage, with an emphasis on smallmouth bass *Micropterus dolomieu*. From historical to recent periods, the Beaver Archipelago fish assemblage shifted from predominantly brown bullheads *Ameiurus nebulosus* to predominantly smallmouth bass. Relative abundance of brown bullheads and white suckers *Catostomus commersonii* declined from historical to recent time periods, as did overall species richness. The relative abundance, recruitment variability, and mortality rates of smallmouth bass have not significantly changed since the historical time period, whereas both condition (ages 5–7) and growth (ages 2–7) of this species have significantly increased. Our results suggest that the smallmouth bass population in the Beaver Archipelago area has not been negatively affected by recent ecological changes (i.e., declining primary productivity, increasing benthic invertebrate densities, increasing numbers of double-crested cormorants *Phalacrocorax auritus*, and increasing introductions of nonnative species). The smallmouth bass is currently the dominant nearshore species and remains a critical component of the nearshore fish assemblage in northern Lake Michigan.

The spread of nonnative species, regulation changes, and other anthropogenic perturbations (both intentional and unintentional) have contributed to the alteration of all aquatic ecosystems (Vitousek et al. 1997; Kolar and Lodge 2001; Rahel 2002). Effects on native species may be negative (Miller et al. 1989; Krueger and May 1991; Marsh and Douglas 1997; French and Jude 2001; Janssen and Jude 2001; Balshine et al. 2005) or positive (Jude et al. 1995; Skubinna et al. 1995; MacIsaac 1996;

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Ricciardi et al. 1997), but it is often difficult to identify any long-term effects these disturbances impose, primarily because of the limited availability of long-term data (Turner et al. 2001). Increased understanding of these relationships and effects can improve our chances for conserving native species and maintaining biodiversity within these ecosystems (Allan and Flecker 1993; Dudgeon et al. 2006).

Since the 1970s, the Lake Michigan ecosystem has undergone many substantial changes, which are well documented in offshore areas (depth > 30 m) of Lake Michigan (see Madenjian et al. 2002). Phosphorus loadings have decreased since the 1970s (Madenjian et al. 2002; Bunnell et al. 2006; Mida et al. 2010); recently, native amphipods *Diporeia* spp., once the dominant offshore macroinvertebrates, were replaced by the nonnative quagga mussel *Dreissena bugensis* (Nalepa et al. 2009). The crustacean zooplankton community has also changed; decreases in several cladoceran species and lower species richness were observed after the invasion of the predatory cladocerans *Bythotrephes* spp. in the 1980s (Barbiero and Tuchman 2004). Dynamics in offshore fish assemblages have also been altered, including (1) reduced population numbers of alewives *Alosa pseudoharengus* due to predation by introduced salmonines; and (2) reduced energy density of large alewives due to the reduction in *Diporeia* spp. via negative interactions with nonnative mussels (Madenjian et al. 2002, 2006, 2008; Bunnell et al. 2006). A reduction in alewife numbers may have led to the rehabilitation of burbot *Lota lota*, deepwater sculpin *Myoxocephalus thompsonii*, and yellow perch *Perca flavescens* populations during the 1970s and 1980s (Madenjian et al. 2002, 2008).

Substantial changes have also occurred in nearshore areas (depth < 30 m) of Lake Michigan since the 1970s, especially for lower trophic levels; however, these nearshore areas are not as well studied as offshore areas (see Vadeboncoeur et al. 2011). These changes include a decline in total phosphorus concentrations and phytoplankton densities (Madenjian et al. 2002; Mida et al. 2010). Crustacean zooplankton abundance in southern Lake Michigan was also higher during the 1970s compared with the 1980s and 1990s (Hawkins and Evans 1979; Evans 1990; Dettmers et al. 2003); however, very little change was observed in *Daphnia* spp. community structure between these periods (Evans and Jude 1986). Major benthic macroinvertebrate densities (i.e., *Diporeia* spp., Oligochaeta, and Sphaeriidae) in the nearshore areas of Lake Michigan declined from 1980 to 1993 (Nalepa et al. 1998; Madenjian et al. 2002), but localized areas with high densities of zebra mussels *Dreissena polymorpha* produced increased densities of other benthic macroinvertebrates due to increased food availability provided by zebra mussel biodeposits (Wisenden and Bailey 1995; Ricciardi et al. 1997). Much of the change to lower-trophic-level dynamics in the nearshore areas of Lake Michigan can be attributed to anthropogenic effects (i.e., reduced nutrient loadings) and introduction of nonnative invertebrate species.

Introduction of nonnative fish species and increases in avian predators also have the potential to influence ecosystem function in nearshore areas of Lake Michigan. Round goby *Neogobius melanostomus* have become established in northern Lake Michigan since the late 1990s (Clapp et al. 2001) and contribute to decreases in macroinvertebrates through direct predation (Lederer et al. 2006). Major declines in populations of the mottled sculpin *Cottus bairdii* and johnny darter *Etheostoma nigrum* have also been attributed to competitive interactions with round goby in Lake Michigan (Janssen and Jude 2001; Lauer et al. 2004). Round goby also provide an additional prey resource for yellow perch (Truemper and Lauer 2005) and probably for smallmouth bass *Micropterus dolomieu* (Steinhart et al. 2004) in Lake Michigan. This added prey resource could result in faster growth rates and improved condition for smallmouth bass and other nearshore piscivorous fishes in Lake Michigan. Population numbers of double-crested cormorants *Phalacrocorax auritus* have steadily increased in northern Lake Michigan since the 1970s (Seefelt and Gillingham 2005), probably facilitated by the invasion and expansion of alewife prey over this same time period (Weseloh et al. 1995; Seefelt and Gillingham 2008). Direct predation effects of double-crested cormorants on fish populations have been noted in the Great Lakes in recent years as cormorant numbers have increased (Maruca 1997); however, their overall effect on fish population dynamics remains unclear (Diana et al. 2006; Fielder 2008; Diana 2010).

Although several documented changes have occurred at multiple trophic levels in Lake Michigan's nearshore areas since the 1970s, very little attention has been given to changes observed in the nearshore fish assemblage of Lake Michigan (but see Bunnell et al. 2006). In particular, there is little information on the effect of these disturbances on recreationally and economically important species that typically inhabit depths less than 10 m (e.g., smallmouth bass, rock bass *Ambloplites rupestris*, and brown bullhead *Ameiurus nebulosus*). Rock bass and brown bullheads are important components of the nearshore fish assemblage and provide a potential forage source for nearshore piscivorous fishes. Smallmouth bass are of considerable interest as they are a top predator and provide important recreational angling opportunities in the nearshore areas of Lake Michigan.

In addition to ecosystem changes in Lake Michigan, management of smallmouth bass has also changed since the 1970s, especially for the smallmouth bass population in the Beaver Archipelago area of northern Lake Michigan. Recreational angling has the potential to affect population size structure and result in growth overfishing of the targeted species (Goedde and Coble 1981; Webb and Ott 1991; Muoneke 1994; Maceina et al. 1998). During the early 1970s, the minimum length limit was 254 mm for smallmouth bass in Lake Michigan. The minimum length limit was increased to 305 mm total length (TL) in 1976 and to 356 mm TL in 1995 (i.e., the current length limit; Bremigan et al. 2008). A limit of five smallmouth bass has remained in effect since the 1970s. The smallmouth bass season on Lake Michigan begins on the Saturday preceding Memorial Day in late May and closes on December 31; however, starting in 2001, a special closed season lasting until July 1 was implemented for

the Beaver Archipelago smallmouth bass fishery (i.e., within 0.8 km of Beaver, Garden, Hog, or High Island).

Given the changes (i.e., ecological and management) that have transpired since the 1970s and the paucity of information on nearshore Lake Michigan fish assemblages during this time period, we sought to characterize fish assemblage and population dynamics changes that have occurred in the Beaver Archipelago area from a historical time period (1969–1972, 1975, 1977, and 1984) to a recent period (2005–2008), with emphasis on the smallmouth bass population. We examined differences between recent and historical time periods in fish assemblage composition (proportion of fish species in survey catches), species richness, and relative abundance (trap-net catch per unit effort [CPUE]) of important nearshore fish species. The mortality rates, recruitment variability, growth, and condition of smallmouth bass were also compared between recent and historical time periods. Where differences were detected between historical and recent population dynamics of smallmouth bass and other fish populations in the Beaver Archipelago, we related these changes (by using other published studies) to other documented ecosystem perturbations that have occurred in the nearshore areas of Lake Michigan. The results of our study contribute to a more comprehensive understanding of how disturbances have affected Great Lakes nearshore fish populations.

METHODS

Study site.—The Beaver Archipelago is located in northeastern Lake Michigan, approximately 25–30 km from both the Lower and Upper Peninsulas of Michigan (Figure 1). Beaver Island is the largest island (145 km^2) within the archipelago. The Beaver Archipelago includes several other large islands (i.e., Garden, High, Hog, Squaw, Trout, and Whiskey islands). A few smaller islands (Gull, Hat, and Pismire islands) are important breeding grounds for several species of water birds,

TABLE 1. Bays (and associated islands) in the Beaver Archipelago, northern Lake Michigan, that were sampled with trap nets (indicated by X) during historical (1969–1972, 1975, 1977, and 1984) and recent (2005–2008) time periods.

Bay	Island	Time period	
		Historical	Recent
St. James Bay	Beaver	X	2005 only
Garden Harbor	Garden	X	X
Indian Harbor	Garden	X	X
Manitou Bay	Garden	X	X
Northcut Bay	Garden		X
Sturgeon Bay	Garden	X	X
Fisherman's Bay	Hog		X

including double-crested cormorants (Seefelt 2005). Fishes were sampled in bays associated with Beaver, Garden, and Hog islands (Table 1; Figure 1).

Fish sampling.—Fish were captured via trap nets (frame dimensions: 1.5 m wide × 2.5 m long × 0.9 m deep; 4-cm stretched mesh). Depending on bottom gradient, a 20- or 40-m lead was set perpendicular to shore at depths of 1–2 m. In total, six trap nets were distributed within the bays around Garden and Hog islands, and no more than two nets were set per bay during each sampling event. Each net was fished daily for 5–10 d in June and August of 2005–2008. Fish were sampled with similar methods during the historical period, except that sampling occurred only in August. All fish were identified, enumerated, and returned to the lake. For smallmouth bass only, the TL (mm) and weight (nearest 10 g) of each captured individual were recorded. Scales of each smallmouth bass were removed from below the lateral line in the area distal to the pectoral fin when it is pressed against the body (Everhart 1950). Each smallmouth
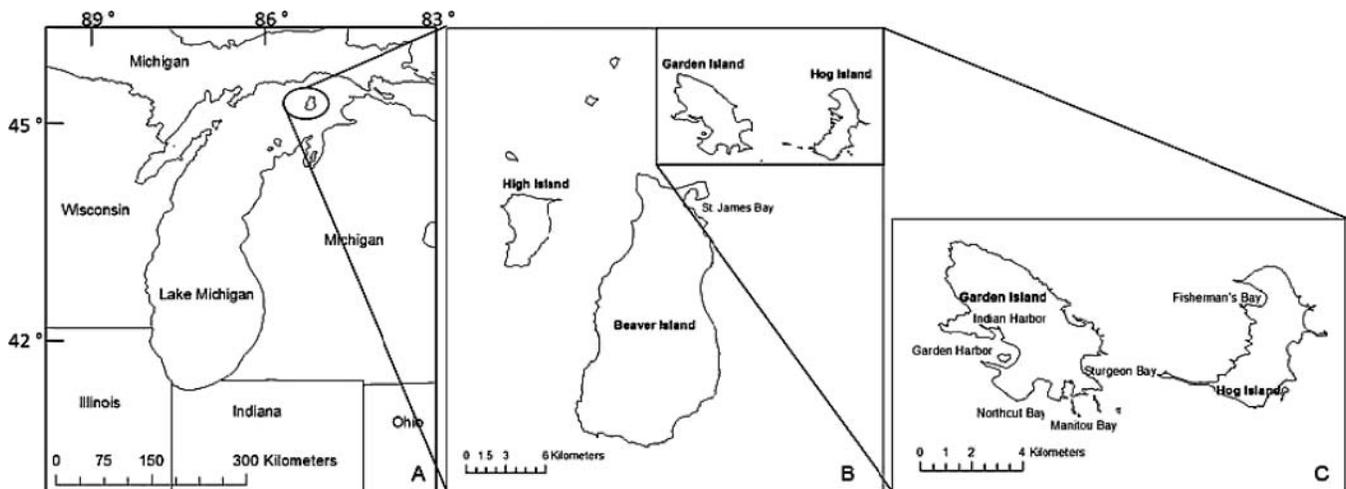

FIGURE 1. Locations of (**A**) the Beaver Island Archipelago, northern Lake Michigan; (**B**) major islands within the archipelago; and (**C**) bays adjacent to Garden and Hog islands, where fish population sampling occurred during historical and recent time periods.

bass (>80 mm TL) was given a different fin clip each year (i.e., dorsal, pelvic, or caudal fin) to identify recaptures. Smallmouth bass smaller than 80 mm TL did not receive a fin clip owing to fast growth at the juvenile stage, which typically rendered the mark unidentifiable by the next year.

Age determination.—Smallmouth bass scales collected in the recent time period were placed between acetate slides, and impressions were made with a scale press (Ann Arbor roller press, Wildlife Supply Co.). A minimum of 3 scale impressions/individual was imaged with a Nikon SMZ800 compound microscope and Image-Pro PLUS version 5.1 (Media Cybernetics). Each fish was aged by counting where circuli crossed over to form an annulus. Annuli were marked and measured from the scale focus by using Image-Pro PLUS. Aging was done primarily by two experienced readers; a third reader was used to resolve discrepancies only. If all three readers failed to reach agreement on age (12%) but disagreed by only 1 year regardless of age (4%), an average age was assigned. Samples in which all readers failed to reach agreement (as described, 8%) were omitted from analysis. Scales collected in the historical time period were aged by using the same methods except that a microfiche reader was used instead of image analysis software.

The likely outcome of these aging techniques for both recent and historical time periods was that ages for smallmouth bass older than age 7 were probably underestimated owing to annuli crowding and that reader agreement was probably low for these older fish (<60%; Maceina and Sammons 2006). Fish with age estimates greater than age 7 were therefore omitted from further analyses. Fish with assigned ages of 7 years or less for both periods were included in all analyses, as these ages typically show higher agreement among readers for smallmouth bass (Maceina and Sammons 2006).

Data analyses.—To minimize potential effects of temporal variability, only the data collected during August sampling events were used for comparisons between historical and recent periods. For each species, trap-net CPUE during each year sampled was calculated as

$$\text{CPUE} = \frac{\text{number of fish captured}}{\text{unit effort}},$$

where unit effort is hours fished; final values were standardized to 24 h. A repeated-measures (RM) analysis of variance (ANOVA) was used to compare the relative abundances (CPUE; fish/net-night) of smallmouth bass, rock bass, white suckers *Catostomus commersonii*, and brown bullheads between historical and recent time periods. A mixed model was used due to the nonconstant variability in dependent variables (MIXED procedure in the Statistical Analysis System [SAS]; SAS Institute 2003). The maximum likelihood method was implemented because it allowed for unbalanced designs (e.g., more data for one time period; Littell et al. 1996). Each year was treated as the experimental unit, and time period was a fixed effect in all models; an α value of 0.05 was used to determine significance

for all analyses. Species richness (i.e., total number of species captured) and fish assemblage composition (percentage of trap-net catch contributed by the various species) were reported for each time period.

For smallmouth bass, the proportional size distribution (PSD) and the relative size distributions of preferred-length fish (RSD-P) and memorable-length fish (RSD-M) in each year were calculated. Size categories were as defined by the five-cell model of Gabelhouse (1984; i.e., stock-, quality-, preferred-, memorable-, and trophy-length fish) but were adjusted by increasing each length-group by 5 mm TL (i.e., stock size = 185 mm; quality size = 285 mm; preferred size = 355 mm; memorable size = 435 mm) because the historical length distributions were recorded in this fashion (i.e., 5-mm length-groups). Analyses did not include trophy-length smallmouth bass owing to underrepresentation of fish in this size-class during both time periods. Fulton's condition factor (K) for each age-class was calculated as

$$K = (W/L^3) \times 100{,}000,$$

where W is the weight (g) and L is the TL (mm) of an individual fish. Fulton's K was used to determine whether changes in condition for smallmouth bass of ages 2–7 had occurred between time periods. Mean length at age was also calculated for each age-class (ages 2–7) and each year sampled to compare growth between time periods.

The RM-ANOVA was used to compare smallmouth bass size structure (PSD, RSD-P, and RSD-M), condition (Fulton's K), and growth (length at age) between historical and recent periods. A mixed model (MIXED procedure in SAS) that implemented the maximum likelihood method was also used to analyze these variables (year = the experimental unit) for the same reasons as described above for CPUEs.

Smallmouth bass mortality rates were compared between historical and recent periods by using catch curves. The catch curves were created by pooling age frequency data for 1970–1972 and likewise for 2005–2008 to minimize the effects of unequal recruitment among years (Miranda and Bettoli 2007). Other years from the historical period were omitted from this analysis because specific age frequency data were not available for some years (i.e., 1969, 1975, 1977, and 1984); the selected years 1970–1972 provided the longest continuous data set, thereby yielding a more robust estimate of mortality. Age frequencies were $\log_e$ transformed before instantaneous total mortality rates (Z) were estimated. The slopes of the regression lines were compared between time periods by using an F-test for homogeneity of slopes (ANOVA; GLM procedure in SAS). Ninety-five percent confidence intervals (CIs) around Z were also estimated for each time period by using the following formula:

$$95\% \, \text{CI}(Z) = Z \pm t_{0.05, \, (n-2)}\text{SE}_Z,$$

where Z is the instantaneous rate of mortality calculated by estimating the slope of the regression line, t is the Student's t-distribution at an α of 0.05 for $n - 2$ (n = number of age-groups represented in the sample), and SE_Z is the standard error estimated from the slope of the regression line. Smallmouth bass of ages 3–7 were used in this analysis, as ages 1 and 2 were not fully recruited to the gear.

Recruitment variability was compared between time periods by using the absolute value of the residuals generated from the catch curves from each time period described above (Maceina 2004). A two-sample t-test (TTEST procedure in SAS) was used to evaluate differences in mean residual estimates between time periods. Thus, differences in mean residual estimates would imply that one time period has greater recruitment variability than the other period.

RESULTS

Fish Assemblage Shifts

Differences in fish assemblages were detected between recent and historical time periods; the brown bullhead was the most abundant species during the historical period, whereas the small-mouth bass was the most abundant species during the recent time period. Brown bullheads comprised 59.6% of the total trap-net catch (number of fish caught) during the historical time period (Figure 2). Other species captured during the historical period included the smallmouth bass (14.0%), rock bass (14.0%), white sucker (7.3%), alewife (2.9%), and northern pike *Esox lucius* (1.2%). Additional species (yellow perch, trout-perch *Percopsis omiscomaycus*, common carp *Cyprinus carpio*, pumpkinseed *Lepomis gibbosus*, channel catfish *Ictalurus punctatus*, bluegill *Lepomis macrochirus*, largemouth bass *Micropterus salmoides*, coho salmon *Oncorhynchus kisutch*, bowfin *Amia calva*, rain-bow smelt *Osmerus mordax*, and round whitefish *Prosopium*

cylindraceum) constituted approximately 1% of the total catch during the historical period.

During the recent time period, 93.3% of the fish assemblage was composed of smallmouth bass (Figure 2). The remainder of the catch included channel catfish (2.2%) and the following species (<1% each): the rock bass, walleye *Sander vitreus*, white sucker, freshwater drum *Aplodinotus grunniens*, northern pike, bowfin, brown bullhead, common carp, longnose gar *Lepisos-teus osseus*, yellow perch, pumpkinseed, largemouth bass, and black bullhead *Ameiurus melas*. The CPUEs of brown bullheads and white suckers decreased significantly between time periods (RM-ANOVA, brown bullhead: $F_{1,5} = 9.99$, $P = 0.03$; white sucker: $F_{1,5} = 12.03$, $P = 0.02$; Figure 3). While the CPUE of rock bass decreased markedly from historical to recent time periods, the change was not significant (RM-ANOVA: $F_{1,5} = 5.84$, $P = 0.06$; Figure 3). Species richness also declined from
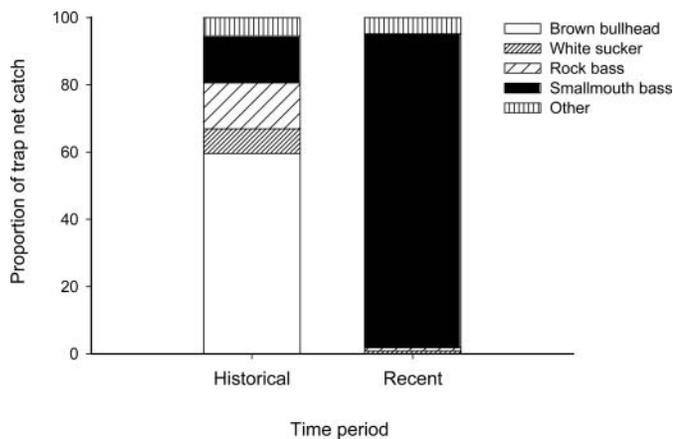

FIGURE 2. Percentages of smallmouth bass, rock bass, white suckers, brown bullheads, and other species (listed in Results) in August trap-net catches (num-ber of fish) from the Beaver Archipelago during historical (1970–1972, 1984) and recent (2005–2008) time periods.
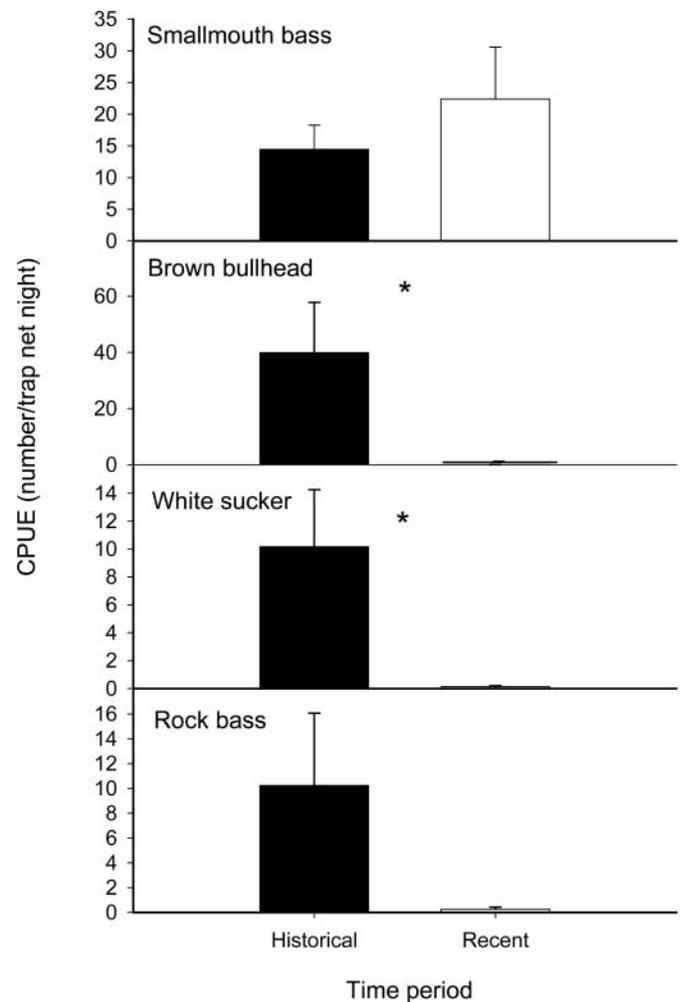

FIGURE 3. Mean (+ SE) trap-net catch per unit effort (CPUE) for small-mouth bass, brown bullheads, white suckers, and rock bass sampled in August during historical (1970–1972, 1984) and recent (2005–2008) time periods in the Beaver Archipelago. Note the different y-axis for each species; asterisks denote significant differences in CPUE between time periods ($P < 0.05$).

the historical time period ($N = 17$ species) to the recent period ($N = 15$ species).

Smallmouth Bass Abundance, Mortality, and Recruitment

Smallmouth bass relative abundance did not differ between historical and recent time periods (RM-ANOVA: $F_{1,6} = 1.04$, $P = 0.35$; Figure 3), and mortality rates were not different between the historical time period ($Z = 0.43$; 95% CI $= 0.25$–0.56) and the recent time period ($Z = 0.31$; 95% CI $= 0.09$–0.47; ANOVA: $F_{1,1} = 2.71$, $P = 0.15$). In addition, smallmouth bass recruitment variability in the Beaver Archipelago was similar across time periods (historical recruitment variability $= 0.20$, 95% CI $= 0.08$–0.32; recent recruitment variability $= 0.19$, 95% CI $= 0.05$–0.32; t-test: $t_{1,8} = -0.23$, $P = 0.82$).

Smallmouth Bass Size Structure, Condition, and Length at Age

Size structure indices significantly increased during the recent time period in comparison with the historical time period, as indexed by PSD (RM-ANOVA, $F_{1,5} = 25.85$, $P < 0.01$), RSD-P ($F_{1,5} = 11.34$, $P = 0.02$), and RSD-M ($F_{1,5} = 20.60$, $P < 0.01$; Figure 4). Condition (Fulton's K) of smallmouth bass in the Beaver Archipelago area did not differ between time periods for fish of age 2 (RM-ANOVA, $F_{1,7} = 0.19$, $P = 0.67$), age 3 ($F_{1,9} = 0.06$, $P = 0.81$), or age 4 ($F_{1,9} = 3.90$, $P = 0.08$); however, smallmouth bass were in better condition during the recent time period for age 5 (RM-ANOVA, $F_{1,9} = 10.92$, $P < 0.01$), age 6 ($F_{1,9} = 13.31$, $P < 0.01$), and age 7 ($F_{1,8} = 29.68$, $P < 0.001$; Figure 5). Additionally, length at age of smallmouth bass increased from the historical period to the recent period for all ages (RM-ANOVA, age 2: $F_{1,7} = 157.29$, $P < 0.0001$; age 3: $F_{1,8} = 152.55$, $P < 0.0001$; age 4: $F_{1,8} = 408.11$, $P = 0.0001$; age 5: $F_{1,8} = 523.58$, $P < 0.0001$; age 6: $F_{1,8} = 200.11$, $P < 0.0001$; age 7: $F_{1,8} = 297.94$, $P < 0.0001$; Figure 5).

DISCUSSION

Fish assemblage composition within the nearshore area of the Beaver Archipelago has shifted from an assemblage dominated by brown bullheads in the 1970s and 1980s to a more recent assemblage dominated by smallmouth bass. Relative abundances of brown bullheads and white suckers significantly declined from the historical period to the recent period, most likely due to habitat alterations that have occurred in Lake Michigan from the 1970s to the present. Invasive mussels (i.e., zebra mussel and quagga mussel) have enhanced water clarity (Kerfoot et al. 2010) and altered habitat via large aggregations on benthic substrate (Stewart and Haynes 1994; Kuhns and Berg 1999), potentially affecting populations of brown bullheads and white suckers. Very few brown bullheads have been captured recently in other regions of Lake Michigan or in the other Great Lakes, which implies a more widespread decline in population numbers (Jude and Pappas 1992; Schneeberger 2000; Ludsin et al. 2001). Optimal brown bullhead habitat typically consists of turbid water and soft benthic substrate (e.g., muck; Becker
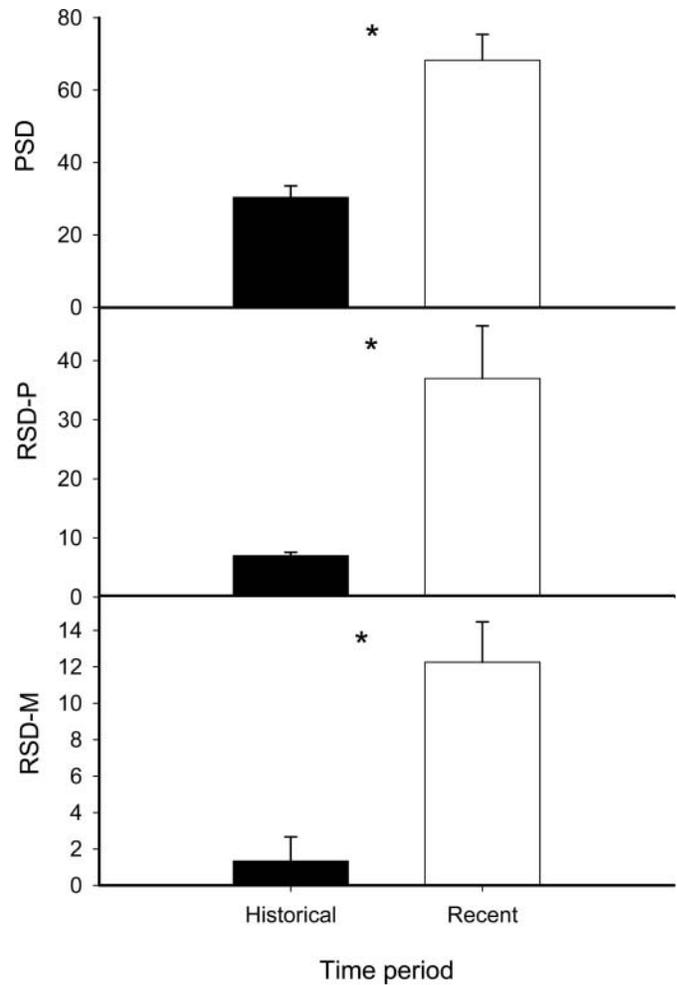

FIGURE 4. Mean (+ SE) size-structure indices describing smallmouth bass in August trap-net catches during historical (1970–1972) and recent (2005–2008) time periods in the Beaver Archipelago (PSD = proportional size distribution; RSD-P = relative size distribution of preferred-length fish; RSD-M = relative size distribution of memorable-length fish; stock length = 185 mm, quality length = 285 mm, preferred length = 355 mm, memorable length = 435 mm). See Methods for a more detailed description of size-structure indices. Asterisks denote significant differences in an index between time periods ($P < 0.05$).

1983); this type of habitat may be diminishing within Lake Michigan as a result of declining productivity facilitated by invasive mussels. Similarly, white suckers are quite tolerant of turbid water and are typically found in rocky habitats (Becker 1983), which are now primarily colonized by invasive mussels in many of the nearshore areas of Lake Michigan (Nalepa et al. 2009). Bunnell et al. (2006) noted a decline in white sucker abundance in Lake Michigan since 2001 and also documented a concurrent decrease in overall species richness (as was observed in this study). A decline in species richness could be a result of habitat alterations, such as a decline in nutrients over these time periods in Lake Michigan (Bunnell et al. 2006). Limited information exists on specific causes for the declines
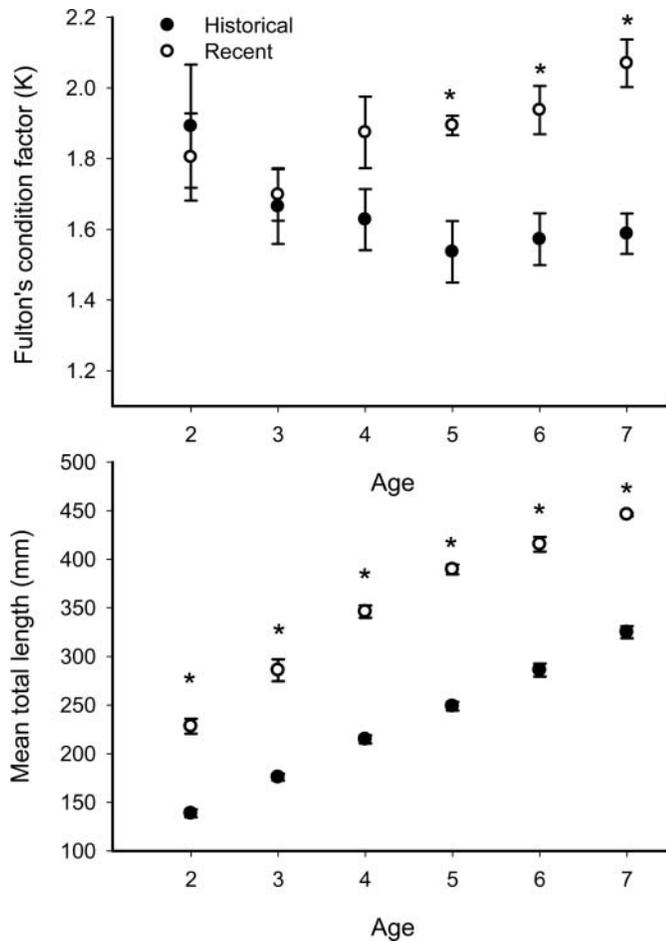
FIGURE 5. Mean ($\pm$ SE) Fulton's condition factor (K; upper panel) and length at age (lower panel) of smallmouth bass (ages 2–7) captured with trap nets in August during historical (1969–1972, 1975, 1977, 1984) and recent (2005–2008) time periods in the Beaver Archipelago. Asterisks denote significant differences in K or length at age between time periods ($P < 0.05$).

in brown bullhead and white sucker populations and in overall species richness, and therefore future research is warranted.

The nearshore fish assemblage in the Beaver Archipelago region is currently dominated by smallmouth bass, and relative abundance estimates for this species appear to have increased by about 60% between the historical and recent time periods. However, our statistical test revealed no significant differences between historical and recent estimates of smallmouth bass relative abundance. Our decision to avoid pseudoreplication by treating each year as the experimental unit may have decreased our ability to detect a significant difference in relative abundance between time periods. Of considerable interest is whether double-crested cormorants have substantially influenced the smallmouth bass population in the Beaver Archipelago (see, for example, USDA 2010). Since the late 1970s, double-crested cormorant numbers within the Beaver Archipelago have increased (Seefelt and Gillingham 2005). Double-crested cormorants often forage in nearshore habitats in close proximity to fish spawn-

ing areas, primarily preying on local fish communities (Birt et al. 1987). This foraging pattern could result in high mortality of juvenile smallmouth bass via direct predation. However, empirical evidence from this area indicates that the primary diet item of double-crested cormorants within the Beaver Archipelago area is the alewife rather than the smallmouth bass (Seefelt and Gillingham 2008). Furthermore, double-crested cormorants typically foraged approximately 2.5 km away from any islands within the Beaver Archipelago, and their foraging areas were not typical juvenile smallmouth bass habitat (Seefelt and Gillingham 2006). If double-crested cormorants were foraging heavily on juvenile smallmouth bass, we would expect lower relative abundance estimates in recent years and possibly a change in recruitment variability (missing year-classes) between the historical and recent time periods; however, this was not empirically supported. In recent years, both strong and weak year-classes were present in the smallmouth bass population, but there were no missing year-classes (Kaemingk 2008). Smallmouth bass nesting success was also very high (80%) during 2008 (Kaemingk et al. 2011a). Double-crested cormorants do forage on juvenile smallmouth bass within the Beaver Archipelago region (Seefelt and Gillingham 2008), but they apparently do not exert a severe effect on overall recruitment. Collectively, these results do not support the hypothesis that double-crested cormorants are having a measurable negative effect on the smallmouth bass population of the Beaver Archipelago.

Although recent relative abundance of smallmouth bass has remained similar to historical estimates, size-structure indices have significantly increased. More smallmouth bass currently are reaching preferred and memorable sizes, whereas these size-classes were mostly absent during the 1970s and 1980s. Minimum harvest length limits were increased from 254 to 305 mm in 1976 and were raised to 356 mm in 1995 (Bremigan et al. 2008). Potentially elevated angling pressure and a smaller minimum size limit during the 1970s may have caused increased harvest of larger fish (i.e., size-structure reduction or growth overfishing; Goedde and Coble 1981; Webb and Ott 1991; Muoneke 1994; Maceina et al. 1998). This phenomenon, in combination with an abundance of smaller fish, would have reduced the modal size of the smallmouth bass population (Johnson and Anderson 1974). Until 2001, smallmouth bass angling and retention were permitted during the spawning season (i.e., June) within the Beaver Archipelago. This more liberal open season would also have increased the harvest of larger male smallmouth bass, which are more vulnerable to angling as they are guarding their nests (Suski and Philipp 2004). While specific information on regulation effects are not available, the 4 years between the implementation of regulations and the commencement of the current study would have been enough time for the population to have responded as observed.

In addition to an increase in size-structure indices, condition for smallmouth bass of ages 5–7 has also improved in recent years and lengths at all ages examined have significantly increased in comparison with historical estimates. The current

lengths at age for smallmouth bass rank in the upper 75th percentile for all age-classes among smallmouth bass populations across North America (Beamesderfer and North 1995). The recent increase in both condition and length at age compared with historical estimates could be explained in part by the ecological disturbances that have affected Lake Michigan over the past 30 years. The first of these disturbances was the invasion of zebra mussels, which became established in southern Lake Michigan in 1993 (Nalepa et al. 1998). The benthic community was probably restructured by zebra mussels after colonization (Stewart and Haynes 1994). Benthic invertebrate densities in nearshore areas have increased substantially within the Great Lakes owing to increased food availability provided by zebra mussel biodeposits and to additional habitat in the form of increased interstitial spaces in large aggregate zebra mussel colonies (Wisenden and Bailey 1995; Ricciardi et al. 1997). Increased densities of macroinvertebrates within nearshore areas could provide additional food for smallmouth bass. The more recent (2006) invasion of the round goby into the Beaver Archipelago region could also provide an additional forage source for smallmouth bass (Steinhart et al. 2004). There is also evidence that some crayfish populations, including nonnative rusty crayfish *Orconectes rusticus* (Gunderson 2008), have increased since the zebra mussel's invasion of the Great Lakes (Martin and Corkum 1994; Stewart and Haynes 1994); rusty crayfish are now abundant in nearshore areas of northern Lake Michigan (Jonas et al. 2005). These increases may be direct effects of zebra mussels, which can provide an additional forage source where food is scarce (Perry et al. 1997), or indirect effects via biodeposits that increase food (e.g., macroinvertebrates) availability for crayfish (Martin and Corkum 1994; Momot 1995). Adult smallmouth bass typically forage on crayfish, which in some cases are the primary dietary item (Weidel et al. 2000). In total, the combined indirect and direct effects of aquatic invaders in Lake Michigan probably enhanced the forage base for smallmouth bass in the Beaver Archipelago area, resulting in greater length at age and improved condition of smallmouth bass relative to historical estimates.

Long-term, fishery-independent surveys can be vital to assessing predator abundance, prey production, and other aspects of fish population dynamics, and these kinds of surveys are critical to the application of more integrated and comprehensive management strategies (Christie et al. 1987; Kline 1996). Long-term surveys permit appropriate hypothesis testing in community ecology, allow accumulation of data over time periods that are sufficient for measuring variance in relevant parameters, and serve as the basis for building synthetic generalizations that lead to new, strong theory (Tinkle 1979). Our historical comparison highlights the importance of long-term assessments in elucidating ecosystem effects in large systems. By combining standard survey collections from a period of more than 40 years with focused evaluations of mechanisms, behavior, and system ecology (e.g., Nalepa et al. 1998; Kaemingk 2008; Seefelt and Gillingham 2008; Kaemingk et al. 2011b), we were able to evaluate the positive and negative effects of significant ecosystem changes (e.g., expanding avian populations and multiple introductions of nonnative species) on an ecologically and economically important fish community. These effects included diminished nearshore fish species richness, enhanced predator growth and condition, and relative stability in predator abundance and recruitment. Our results and conclusions rendered could have been strengthened if annual samples had been taken between 1969 and 2008, but our study still provides a long-term perspective on changes that have occurred within the nearshore fish assemblage in northern Lake Michigan. The information collected is important to current Great Lakes management efforts (e.g., Holey and Trudeau 2005; Clapp and Horns 2008; USDA 2010). Given the regular introduction of new ecosystem perturbations, continuation of long-term monitoring and mechanistic evaluations in this system should be of high priority.

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