2011

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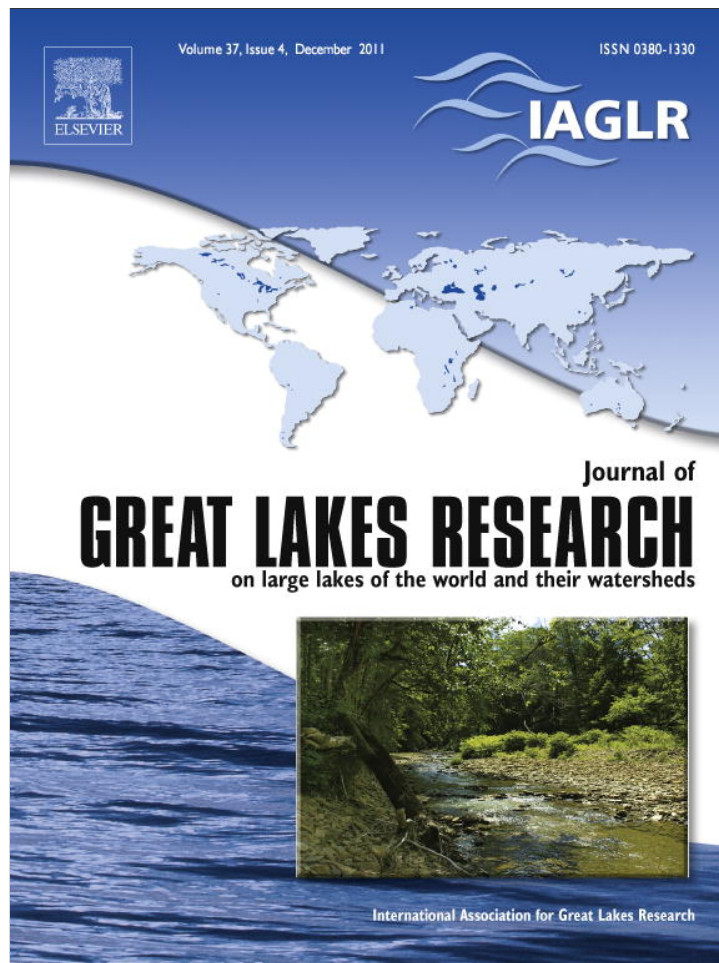
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Volume 37, Issue 4, December 2011   ISSN 0380-1330

IAGLR

Journal of
GREAT LAKES RESEARCH
on large lakes of the world and their watersheds

International Association for Great Lakes Research

Movement of smallmouth bass within the Beaver Island Archipelago, northern Lake Michigan

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ARTICLE INFO

ABSTRACT

Fish movement may vary across a wide array of aquatic ecosystems and may be related to the overall size of the system inhabited. We investigated movement of smallmouth bass in Lake Michigan because this information is lacking for larger systems. A total of 16 smallmouth bass were surgically implanted with ultrasonic transmitters within the Beaver Archipelago, northern Lake Michigan. During 2007–2008, a maximum of one location per individual was recorded daily during three specific tracking periods – pre-spawn, spawning, and post-spawn – to determine diurnal movement patterns. Movement was evaluated as site fidelity, minimum displacement rate, maximum excursion rate, and distance from shore. Smallmouth bass exhibited greater maximum excursion rates during the spawn period compared to pre-spawn. Movement rates did not differ between tracking periods; however, movement rates were greater during the spawn period in 2007 than 2008. Both sexes moved further offshore to deeper water during post-spawn, but females were located further offshore than males during this period. Annual site fidelity was more evident during post-spawn than during spawning for both sexes. Two smallmouth bass emigrated outside of the Archipelago, suggesting this population may be more "open" in terms of individuals moving throughout northern Lake Michigan than previously thought. These results indicate smallmouth bass may move greater distances in larger aquatic systems and therefore larger management units (in terms of total area) should be established in Lake Michigan to account for these greater excursion distances.

Published by Elsevier B.V. on behalf of International Association for Great Lakes Research.

Introduction

Smallmouth bass (*Micropterus dolomieu*) movement has been studied in many aquatic ecosystems. Smallmouth bass within lotic systems appear to be relatively sedentary, except during spawning and prior to moving to overwintering habitats (Bunt et al., 2002; Lyons and Kanehl, 2002; Todd and Rabeni, 1989). Earlier work (Funk, 1955) suggested that two types of smallmouth bass – sedentary and mobile – might exist within lotic populations. Similar to lotic populations, smallmouth bass in smaller lentic habitats exhibit restricted movement and homing tendencies (Forney, 1961; Kraai et al., 1991; Pflug and Pauley, 1983; Ridgway and Shuter, 1996). Nest site fidelity among male smallmouth bass has also been shown to exist in lentic populations as a majority of males will nest within 100 m of their spawning site from a previous year (Ridgway et al., 1991). Although previous studies have documented some similarities between lentic and lotic smallmouth bass populations in relation to movement, most of these studies were conducted in systems that are much smaller and energetically more stable relative to the Great Lakes (Bunt et al., 2002; Kraai et al., 1991; Lyons and Kanehl, 2002; Pflug and Pauley, 1983; Ridgway and Shuter, 1996; Todd and Rabeni, 1989).

Although similarities can exist between movement of smallmouth bass populations in small diverse aquatic habitats (e.g., lotic vs. lentic), some differences have been observed that can be related to specific characteristics (e.g., temperature regimes, size, bathymetry, structure type, productivity) of the study system (Gerber and Haynes, 1988). For example, movement can vary seasonally within a system (Gerber and Haynes, 1988; Lyons and Kanehl, 2002). Movement has also been linked to depth and light intensity; smallmouth bass seek shelter or cover within highly illuminated streams and may remain less active in these shallow systems than in deeper lentic habitats (Gerber and Haynes, 1988; Haines and Butler, 1969; Reynolds and Casterlin, 1976). Due to differential movement of smallmouth bass in contrasting aquatic systems (i.e., smallmouth bass may move at different rates or greater distances depending on system size), a more thorough understanding of smallmouth bass movement is needed in large, understudied lentic systems.

The Great Lakes, and Lake Michigan specifically, differ significantly from other smaller bodies of water in which smallmouth bass

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movement has been evaluated. The different temperature regimes (Gorham and Boyce, 1989; Plattner et al., 2006), current patterns (Beletsky et al., 1999), and habitat complexity experienced by smallmouth bass in Great Lakes systems likely have a strong influence on movement patterns. Great Lakes habitat can generally be characterized as diverse, with deep, oligotrophic areas found adjacent to mid-lake reefs, shallow bays, and fringing wetlands. Submerged aquatic vegetation is mostly sparse to non-existent (except in a few unique coastal areas; e.g., Green Bay), water clarity and light penetration is generally greater than in most inland systems, and large woody cover used by smallmouth bass in inland systems is largely lacking, replaced instead by cobbles, boulders, and other rock and reef structures. Because the Great Lakes are high energy systems (i.e., strongly influenced by wind, waves, and currents), habitat is constantly changing. Water levels in the Great Lakes can also fluctuate dramatically (Lenters, 2001; Quinn and Selliger, 2006), leading to seasonal and interannual changes in habitat structure and availability (Webb, 2008). The differences seen between these system characteristics and those of inland systems make a study of Great Lakes smallmouth bass movement important to an improved understanding of the ecology and population dynamics of this species.

In addition to examining differences between movements of smallmouth bass among lentic aquatic systems, important information on movement of smallmouth bass in the Great Lakes could be obtained and incorporated into future management decisions. For example, the Beaver Archipelago (northern Lake Michigan) smallmouth bass population is managed under different regulations (i.e., extended spawning closure compared to adjacent Lake Michigan and inland populations) because it is considered a separate or isolated population from the rest of northern Lake Michigan. Evaluation of this assumption could aid in identifying whether this population should continue to be managed as a separate population or alternatively as an "open population" if movement occurs outside the Archipelago (> 5 km away from Archipelago). In addition, identifying movement patterns of smallmouth bass in the Beaver Archipelago will also allow managers to identify important areas (e.g., nearshore, offshore) during pre-spawn, spawn, and post-spawn, that should be protected from future anthropogenic disturbances.

We investigated, via acoustic telemetry, several aspects of movement within the Beaver Archipelago population to provide managers with information (e.g.; site use, emigration) that is essential for effectively managing Great Lakes smallmouth bass. The specific objectives of this study were to: 1) identify the maximum extent of movement (within the Beaver Island Archipelago as well as emigration from the Archipelago) by individuals within this population, 2) determine if between-year site fidelity was exhibited for areas used during spawn and post-spawn tracking periods, and 3) determine movements from nearshore to offshore and daily movement rates during three specific tracking periods: pre-spawn, spawn, and post-spawn. We hypothesized differential movement for smallmouth bass between Lake Michigan and other lotic and smaller lentic systems because larger systems may be inherently different in terms of system stability and productivity. Our goal was to better elucidate movement tendencies of smallmouth bass within a large lentic system to further our understanding of population structure and spatiotemporal distribution, important components of population dynamics. In addition, understanding movement is vital to appropriate conservation and management (e.g., regulation, predator control, habitat protection) of smallmouth bass in Great Lakes systems.

Methods

Study site

The Beaver Island Archipelago is located in northeastern Lake Michigan approximately 25–30 km from both the Lower and Upper Peninsulas of Michigan (Fig. 1). Beaver Island is the largest island

(144 km^2) within the Archipelago. The Archipelago includes fifteen additional islands (depending on Great Lakes water levels); the largest of these are Garden, High, and Hog Islands.

The Beaver Island Archipelago exhibits a wide variety of habitat types: many diverse bays (in relation to bathymetry; e.g., shoals, reefs), substrate complexity, and aquatic vegetation. For example, Indian Harbor (Fig. 1) is relatively shallow with a moderate density of submergent and emergent aquatic macrophytes and substrate composed of organic material, whereas Northcut Bay is deeper and contains fewer macrophytes and a much rockier substrate. In addition, this Archipelago system is relatively isolated from the mainland, providing ample opportunities for smallmouth bass to move large distances in open water.

Fish tagging

Sixteen smallmouth bass were implanted with temperature-telemetry transmitters (Sonotronics, model CTT-83-3-E, 62×16 mm, 10.0 g in H_2O) in early May 2007. Eight of the smallmouth bass tagged were from Indian Harbor and eight were from Sturgeon Bay (Fig. 1). Our sample size was limited by the expense of transmitter costs and logistics of tracking large numbers of individuals in such a large system. Garden Island bays were selected because historical sampling indicated higher abundances of smallmouth bass near this island compared to other islands within the Archipelago and represent important nesting sites (Kaemingk et al., 2011). The smallmouth bass selected were representative of the population according to their movement patterns as movement between bays was often observed in a mark-recapture study from 2005 to 2008, where within a 7 day sampling period 30% of smallmouth bass recaptured (45/148) were captured in a different bay than previously caught (Kaemingk, Central Michigan University, 15 September 2008, unpublished data). This further suggests mixing is common among bays within the Archipelago and that a point sample is an accurate representation of the population. Acoustic transmitters were chosen for this study because large smallmouth bass (>406 mm) have been observed to inhabit deep water (>8 m) during late summer (Cole and Moring, 1997). To minimize the effects of the transmitters on the behavior of the fish, transmitters did not exceed 2% of the fish's total weight (Winter, 1996). The life expectancy of each transmitter was 36 months.

Smallmouth bass were captured in trap nets (1.5 m width × 0.9 m depth frame; 2.5 m long pot with 4 cm mesh, stretched). Weight (g), total length (mm), and sex were recorded for each transmittered smallmouth bass (Table 1). Each smallmouth bass captured was placed into a tank of water containing MS-222 (85 mg L^{-1}) until loss of equilibrium occurred. Each fish was then placed on an operating platform capable of holding the fish stationary during surgery. While the fish was undergoing surgery, a continual flow of anesthetic (MS-222, 30 mg L^{-1}) was irrigated over the fish's gills until the surgery was completed (Adams et al., 1998). All transmitters and surgical instruments were sterilized with a 4% Chlorhexidine Gluconate solution and rinsed with sterile water prior to conducting the surgeries. A small incision (approximately 20 mm long) was made slightly above the fish's ventral midline to insert the transmitter. Once the incision was made, the transmitter was gently placed within the body cavity of the fish. Single interrupted sutures were made with a round needle through the integument and musculature using monofilament absorbable suture to close the incision. Each fish was held in a holding cage positioned in the bay of capture until it exhibited normal swimming behavior before being released back into the lake. Transmittered smallmouth bass were also marked with two jaw tags and an upper caudal fin clip in case of transmitter failure, which allowed identification of the specific fish if recaptured. Incisions of transmittered smallmouth bass recaptured during a mark-recapture study appeared to have healed, as evident from a small scar where the incision was made.
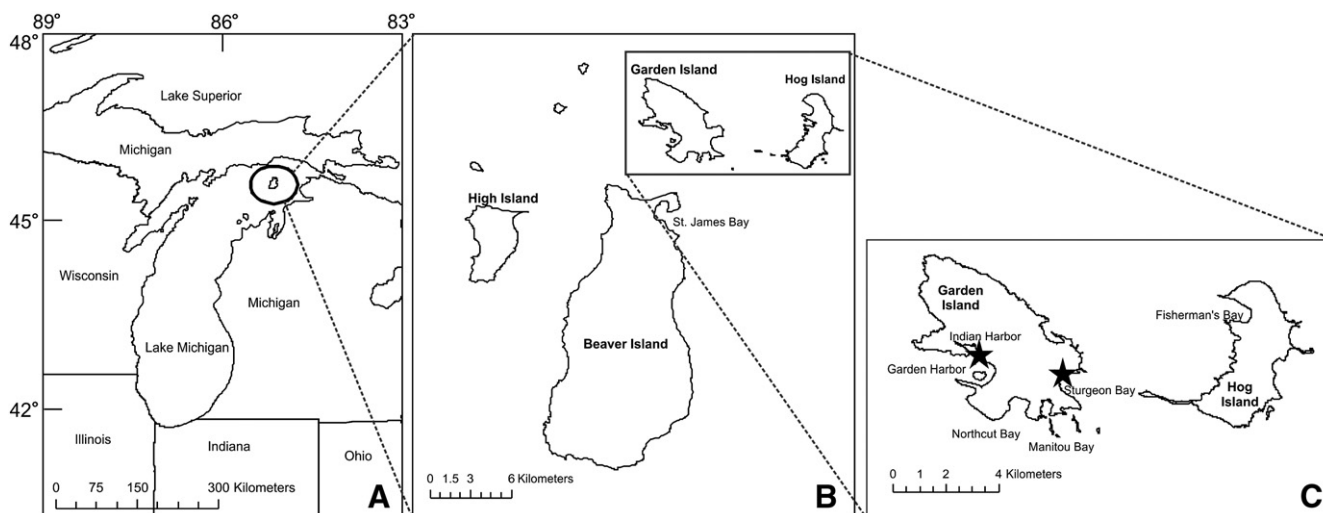
Fig. 1. Michigan (A), Beaver Island Archipelago (B), Garden and Hog Islands and associated bays, with stars indicating tagging locations (C).

Fish tracking

Smallmouth bass were tracked using a boat and directional hydrophone (Sonotronics, model DH-4) attached to a receiver (Sonotronics, model USR-96). Some locations were recorded from shore to minimize time taken between identifying successive waypoints used to triangulate the location of the fish. Locations were not recorded until a week had elapsed after the surgery, since fish may exhibit erratic movement patterns during this time (Mesing and Wicker, 1986). An attempt was made to locate each fish daily, between 0700 and 1900 h, from May to August in 2007 and 2008. Each fish was located at different hours each day (by varying direction of search), which allowed for an unbiased estimate of diurnal movement patterns. Because smallmouth bass remain somewhat inactive during nocturnal hours and due to the difficulty of boating around islands at night, no tracking was done from 1900 to 0700 h. Spatial autocorrelation among consecutive locations was appropriately accounted for by treating the fish as the experimental unit in all analyses (Kenward, 1992; Rogers and White, 2007).

Three tracking periods (pre-spawn, spawn, post-spawn) were established for all smallmouth bass. Each period was determined by visually inspecting near-shore habitats for nesting smallmouth bass each week during May and June each year. The pre-spawn period (18 May–28 May, 2007; 8 May–23 May, 2008) was defined by locations of transmittered smallmouth bass observed prior to the construction of the first nest by an individual male bass within the study area. Locations recorded between the initial and last sightings of a male guarding a nest were considered spawning locations (29 May–25 June, 2007; 24 May–July 1, 2008). Any locations recorded after the sighting of the last nesting activity were assigned to the post-spawn tracking period (26 June–22 Aug, 2007; 2 July–8 Aug 2008).

A grid system (500 m × 350 m) was used to locate each fish, because it was difficult to obtain an exact location due to water clarity (i.e., boat was highly visible and fish appeared to avoid the boat; Secchi disk measurements >13.4 m, Galarowicz, Central Michigan University, 15 August 2010, unpublished data), high mobility of fish, and the many shallow water locations occupied early in the season. For analyses, all locations were assigned to the centroid (i.e., the exact center) of each grid where the fish was located. Triangulation from visual landmarks was used to assign each individual to its respective grid. For locations where visual landmarks were unidentifiable (i.e., farther away from shore/greater depths), positions and grid assignments were determined by triangulating from GPS coordinates on the water (e.g., minimum of three GPS coordinates and bearings for each fish location). The accuracy of these methods was assessed during spawning by first determining in which grid a fish location was perceived, followed by a visual location of the fish (i.e., males on the nest). For analysis purposes, significant differences in movement rates where means differed by less than 250 m (i.e., distance from midpoint of grid to outside edge of grid) may not fully represent true differences, but rather are reflective of the level of precision associated with using a grid-based system.

Movement pattern analysis

Movement was evaluated as site fidelity, minimum displacement rate, maximum excursion rate, and distance from shore. A multiple response permutation procedure (MRPP) was implemented to evaluate site fidelity for the spawn and post-spawn tracking periods between 2007 and 2008 using the program BLOSSOM (Slauson et al., 1994). The MRPP uses mean pairwise Euclidian distances to compare within-group distances (e.g., locations within a year) to between-group distances (e.g., locations compared between years) when groups

Table 1
Length (mm), sex, and total number of locations by year within tracking periods for the 16 smallmouth bass surgically implanted with transmitters. Total search days for the respective period are listed below each tracking period. Location describes the bay (see Fig. 1) in which the bass were initially captured (IH = Indian Harbor, SB = Sturgeon Bay) and Fish ID is an individual letter given to each bass for identification purposes.

Fish				2007			2008		
ID	Location	Length (mm)	Sex	Pre (7)	Spawn (18)	Post (30)	Pre (12)	Spawn (26)	Post (21)
A	IH	495	F	4	8	9	11	16	6
B	IH	445	F	2	2	4	4	1	0
C	SB	470	F	3	9	16	7	19	14
D	IH	440	F	4	12	4	3	13	3
E	IH	388	M	3	16	8	11	19	14
F	IH	453	M	3	15	8	4	14	9
G	IH	473	F	3	15	22	12	16	17
H	SB	415	F	2	15	0	0	0	0
I	SB	445	F	3	3	5	8	11	8
J	SB	458	F	3	8	3	8	18	1
K	IH	500	F	1	9	11	3	14	16
L	IH	424	F	0	0	7	8	3	4
M	SB	403	F	0	15	19	6	7	16
N	SB	398	M	3	15	16	0	13	16
O	SB	461	F	0	0	0	0	0	0
P	SB	473	F	1	2	7	4	9	10
Total				35	144	139	89	173	134

are ignored (Garrot and White, 1990). The null hypothesis states that there is no difference in utilization distributions between 2007 and 2008 (i.e., site fidelity was exhibited). Only smallmouth bass with a minimum of five locations per tracking period per year were used in this analysis (N = 10 fish), thereby reducing the effects of a single location on the overall results. Limited 2007 pre-spawn period locations precluded us from using this analysis to determine pre-spawn site fidelity.

Location distance from shore (m) was used to determine the extent of movement away from shore for a specific tracking period (pre-spawn, spawn, post-spawn) for each individual fish. Each location distance from shore was measured using the spatial analyst extension in ArcView (version 3.3). A mean location distance from shore was calculated for each fish for each tracking period.

Mean minimum displacement rate (m·day^{-1}) describes distance traveled per day for each fish tracked throughout all three tracking periods. Straight-line distances between successive locations were calculated to estimate minimum displacement (ArcMap version 9.2). A significant positive correlation existed between days at large and distance moved for all tracking periods except during pre-spawn in 2007. Therefore, distance between successive locations was divided by the number of days at large to estimate mean minimum displacement. The largest straight line distance moved per day by each fish for each tracking period was considered its maximum excursion rate (m·day^{-1}) for the specified tracking period.

A repeated measures (with the individual fish as the repeated measure and experimental unit; Rogers and White, 2007) analysis of variance (RMANOVA) was used to assess differences between tracking periods, years, and sexes for the following dependent variables: location distance from shore (m), maximum excursion rate (m·day^{-1}), and mean minimum displacement rate (m·day^{-1}). Due to the non-constant variability in the dependent variables, a mixed model was used (PROC MIXED; SAS Institute Inc., 2003). Fixed effects in the model included sex, tracking period, and year (Rogers and White, 2007). The random effect was the individual fish, allowing inferences to be made about the population as a whole rather than only the fish sampled (Rogers and White, 2007). The maximum likelihood method was used because it allowed for unbalanced designs (e.g., data missing for an individual fish for specific tracking periods; Littell et al., 1996). Data from males and females were pooled for further analyses if no differences existed between sexes. Tukey's pairwise comparison test was used where multiple comparisons were made. Dependent variables were transformed using $\log_{10}\times$(distance from shore) or $\log_{10}x+1$ (maximum excursion, mean minimum displacement) to achieve normality. Alpha was set at 0.05 for all statistical tests.

Results

Fifteen of the 16 smallmouth bass were located at least once during the course of this study (Table 1). Seven smallmouth bass were located a minimum of three times per tracking period for all three tracking periods both years. Smallmouth bass "O" was never located after being released in Sturgeon Bay. More locations were identified during spawning in 2007 and 2008 than in periods before and after spawning (Table 1).

Smallmouth bass moved between bays adjacent to individual islands and among islands within the Archipelago during all three tracking periods in 2007 and 2008. Two of the individuals tagged during this study were caught by anglers outside of the Archipelago at mainland locations near Epoufette Island, MI (33 km to the northeast), and Manistique, MI (59 km to the northwest). One of these smallmouth bass could not be assigned to its specific identification because the angler did not record the jaw tag numbers; however, a total length was recorded and it fit the description of one of the two other smallmouth bass that was not located during that time period. Some females (4/7) and none of the males (0/3) exhibited annual site

fidelity during spawning (MRPP test, $P<0.05$); however, a majority of males (2/3) and females (7/7) did exhibit site fidelity during post-spawn (MRPP test, $P>0.05$; a limited number of locations precluded us from performing this analysis on all individuals for each period).

Distance from shore did not differ between sexes for pre-spawn (RMANOVA, $F_{1,\,8}=0.23$, $P=0.64$) and spawn (RMANOVA, $F_{1,\,11}=0.00$, $P=0.94$) tracking periods; however, females were further offshore than males during post-spawn across years (RMANOVA, $F_{1,\,12}=5.48$, $P=0.04$; Fig. 2). Males were further offshore during post-spawn compared to the remaining two tracking periods during 2007 (RMANOVA, $F_{2,\,4}=18.99$, $P<0.01$), but there was no difference between tracking periods with respect to distance from shore during 2008 (RMANOVA, $F_{2,\,3}=1.99$, $P=0.28$; Fig. 2). Females remained further offshore during post-spawn than pre-spawn and spawning for both 2007 (RMANOVA, $F_{2,\,12}=27.68$, $P<0.0001$) and 2008 (RMANOVA, $F_{2,\,17}=31.32$, $P<0.0001$; Fig. 2). Male distance from shore did not differ between years during pre-spawn (RMANOVA, $F_{1,\,1}=10.32$, $P=0.19$) and spawn (RMANOVA, $F_{1,\,2}=0.65$, $P=0.50$), but males were further offshore in 2007 than in 2008 (RMANOVA, $F_{1,\,2}=26.95$, $P<0.05$; Fig. 2) during the post-spawn period. Female distance from shore did not differ between years for pre-spawn (RMANOVA, $F_{1,\,5}=1.67$, $P=0.25$), spawn (RMANOVA, $F_{1,\,7}=1.63$, $P=0.24$), and post-spawn (RMANOVA, $F_{1,\,8}=0.84$, $P=0.38$; Fig. 2).

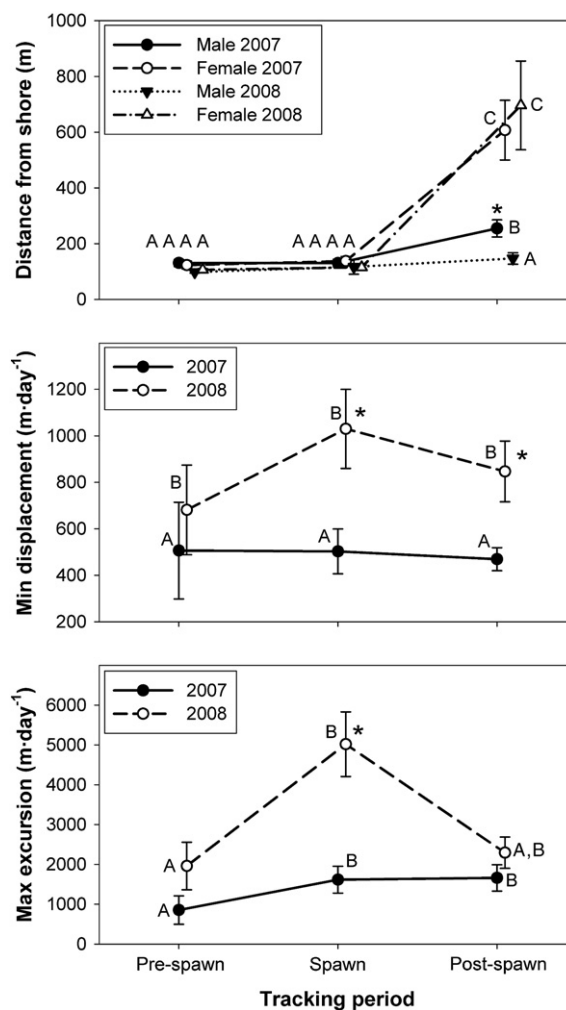**Fig. 2.** Mean male and female distance from shore (m) (top), mean minimum displacement (m·day^{-1}) (middle), and mean maximum excursion (m·day^{-1}) (bottom) during pre-spawn, spawn, and post-spawn periods for 2007 and 2008. Asterisks (*) indicate significant differences between years within tracking periods and letters indicate significant differences across tracking periods within years/sex. Vertical bars are ±1SE.

Males and females did not differ with respect to minimum displacement ($m \cdot day^{-1}$) during pre-spawn (RMANOVA, $F_{1, 8} = 0.11, P = 0.74$), spawn ($F_{1, 11} = 3.12, P = 0.10$), and post-spawn ($F_{1, 12} = 0.69, P = 0.42$); data for both sexes are combined for subsequent analysis. Displacements were similar across all three tracking periods for 2007 (RMANOVA, $F_{2, 18} = 1.99, P = 0.16$) and 2008 (RMANOVA, $F_{2, 22} = 3.02, P = 0.06$; Fig. 2). Smallmouth bass exhibited greater movement rates during spawn (RMANOVA, $F_{1, 10} = 9.38, P < 0.05$) and post-spawn (RMANOVA, $F_{1, 11} = 8.54, P < 0.05$) in 2008 compared to 2007, but there was no difference in movement rates between years during pre-spawn (RMANOVA, $F_{1, 7} = 1.84, P = 0.21$) (Fig. 2).

Maximum excursion rates ($m \cdot day^{-1}$) did not differ between sexes during pre-spawn (RMANOVA, $F_{1, 8} = 0.30, P = 0.60$), spawn ($F_{1, 11} = 0.20, P = 0.66$), and post-spawn ($F_{1, 12} = 0.29, P = 0.60$) periods. In 2007, smallmouth bass exhibited greater maximum excursion rates during the spawn and post-spawn period in comparison to the pre-spawn (RMANOVA, $F_{2, 18} = 6.0, P = 0.01$) period (Fig. 2). In 2008, bass exhibited greater maximum excursion rates during spawn in comparison to pre-spawn (RMANOVA Tukey's post hoc, $t_{22} = -3.57, P < 0.01$), but no difference existed between post-spawn and pre-spawn periods (RMANOVA Tukey's post hoc, $t_{22} = -1.46, P = 0.15$). Maximum excursion rate did not differ between years during pre-spawn (RMANOVA, $F_{1, 7} = 3.94, P = 0.08$) or post-spawn (RMANOVA, $F_{1, 11} = 3.83, P = 0.07$); however, maximum excursion rates during the spawn period were greater in 2008 than in 2007 (RMANOVA, $F_{1, 10} = 29.30, P = <0.001$; Fig. 2).

Discussion

These results support other studies conducted in lentic and lotic habitats where smallmouth bass movement is more restricted during summer months (Hubert and Lackey, 1980; Pflug and Pauley, 1983; Savitz et al., 1993). In our study, it appeared that most (13 of 15 individuals tagged) smallmouth bass remained within the Archipelago (<5 km away from Archipelago), as each of these were located on multiple occasions throughout most tracking periods; however, some individuals may have left the Archipelago and returned. While smallmouth bass in many populations exhibit restricted movements, some individuals have been seen to move upwards of 89 km (Bunt et al., 2002; Langhurst and Schoenike, 1990) in riverine systems. Our study also documented more extensive movement, with known instances where female smallmouth bass moved 33 km and 59 km outside the Archipelago. This study supports the idea that two different individual movement types may exist among smallmouth bass, with some smallmouth bass exhibiting restricted movements and others more extensive movements. A majority of smallmouth bass in most studies exhibit the former pattern rather than the latter; this was also seen in the current study.

While evidence from this study indicates two types of smallmouth bass may exist (restricted vs. extensive movement) in the Archipelago, it also suggests that migration rates may be higher than previously thought, with several individuals dispersing out of the Archipelago. A Lake Erie smallmouth bass genetics study showed that migration rates may be higher in lake-spawning, as opposed to lotic-spawning, smallmouth bass (Stepien et al., 2007). Findings from this study and other evidence from Lake Erie (Stepien et al., 2007) may indicate that this population is more "open", with some individuals leaving the Archipelago. Therefore, northern Lake Michigan may need to be considered one management unit for smallmouth bass.

Extensive movement is typically observed during the fall or spring when bass are relocating to overwintering grounds or spawning sites (Langhurst and Schoenike, 1990; Montgomery et al., 1980), but increased maximum excursion rates in this study were also observed during the spawn and post-spawn periods, especially during the spawn period in 2008. Greater movement distances during these tracking periods could be due to the size of smallmouth bass tagged

in this study; more extensive movements have been recorded for bass greater than 400 mm in length (Cole and Moring, 1997). Larger smallmouth bass may be more mobile than smaller conspecifics and more likely to move greater distances (Beam, 1990; Cole and Moring, 1997). Increased daily food requirements for larger bass as opposed to smaller conspecifics may cause larger bass to search larger areas to meet these higher energy demands (Beam, 1990; Ridgway and Shuter, 1996).

Daily movement rates during 2007 (mean = 493 m day^{-1}) were similar to those reported from a study conducted in a deep oligo- to mesotrophic lake in Maine (Cole and Moring, 1997; Table 2). Our 2008 minimum displacement rates (mean = 853 m day^{-1}) were more similar to a study conducted in Lake Ontario, another Great Lakes system comparable in size to Lake Michigan; however, some of the Lake Ontario fish were experimentally displaced, and data from these fish may not truly reflect normal daily movement patterns (Gerber and Haynes, 1988). Our results, in combination with Gerber and Haynes (1988), suggest that daily movement may not be related to the size of the system inhabited but rather a function of prey availability or some abiotic factor such as temperature. In terms of bioenergetics and system productivity, fish in larger systems (i.e., those that are less productive) may be required to travel greater distances to meet daily energy requirements.

No differences were observed for minimum displacement rates between tracking periods within a given year for smallmouth bass in this study. Other studies have found differences in movement in relation to light intensity, with smallmouth bass in more illuminated systems exhibiting less activity than those located in deeper lentic habitats (Gerber and Haynes, 1988; Haines and Butler, 1969; Reynolds and Casterlin, 1976). Water clarity was high during all tracking periods during both years of sampling, and thus movement rates may not have been affected by differences in turbidity across tracking periods. However, movement rates could differ in more eutrophic systems that experience a much wider range of turbidity across seasons.

Although no differences in movement rates were observed between tracking periods within a given year, there were differences in movement rates between years during the spawn and post-spawn tracking periods. Differences in movement rates during these periods in 2007 and 2008 may be related to seiches or upwellings as found in another smallmouth bass movement study in Lake Michigan (M. Carter, personal communication). Seiches and wind-driven upwelling events can cause dramatic short-term temperature fluctuations (Plattner et al., 2006), and the magnitude or number of these occurrences may have differed between years.

Table 2

Smallmouth bass greatest maximum distance traveled (Max) and minimum displacement per day (Min/day) for various sizes of lakes (shown in ascending order with corresponding data source) in comparison to this study (n.a. = data not available). Studies where smallmouth bass were experimentally displaced by humans (Gerber and Haynes, 1988) were not included in this table because movement by these smallmouth bass may not reflect natural movement.

Location	Size (ha.)	Max (km)	Min/day (m)	Study
Green Lake, Maine	1209	2.4	590	Cole and Moring, 1997
Lake Sammamish, Washington	2000	4.8	n.a.	Pflug and Pauley, 1983
Melton Hill Reservoir, Tennessee	2270	3.5	1,925	Bevelhimer, 1995
Lake Opeongo, Ontario	5860	9.1	n.a.	Ridgway and Shuter, 1996
Meredith Reservoir, Texas	6447	6.5	n.a.	Kraai et al., 1991
Lake Michigan	5,780,000	148.1	n.a.	Latta, 1963
Lake Michigan	5,780,000	59.0	658	This study (2007 & 2008)

A majority of smallmouth bass were found further offshore during post-spawn compared to the two remaining tracking periods, similar to smallmouth bass in other lentic habitats (Cole and Moring, 1997; Hubert and Lackey, 1980). During both years, females remained further offshore than males during the post-spawn tracking period; however, we caution that these differences may not reflect differences at the population level as our sample size was limited for males. Sex-related differences in movement have been found in other centrarchid species (Paukert and Willis, 2002) but not specifically in smallmouth bass. Sex-related differences in movement could coincide with differential energy demands in which male smallmouth bass need to forage more in near-shore areas because large amounts of energy are expended during nest guarding (Gillooly and Baylis, 1999; Hinch and Collins, 1991), especially in the presence of nest predators (Steinhart et al., 2004). Further studies are needed to elucidate the importance of differential movement patterns between sexes among smallmouth bass.

Movement into deeper water observed during post-spawn could also be attributed to changing thermal regimes (Suski and Ridgway, 2009) such as the formation of a deep thermocline layer (Gorham and Boyce, 1989); in these situations, smallmouth bass may move into deeper water as a result of thermal preference. Cole and Moring (1997) suggested smallmouth bass may be integrated into the offshore food web in a deep oligo-mesotrophic lake in Maine and may compete with offshore fishes for available resources to some extent. The offshore movement observed in the current study averaged 1000 m offshore (mean = 4.5 m in depth), which is still considered near shore in Lake Michigan due to its wide ranges of depth. As a result, smallmouth bass are most likely not competing with offshore fishes (e.g., Pacific salmon) for available food resources or fully integrated in the Lake Michigan offshore food web.

Based on other studies (Barthel et al., 2008; Ridgway et al., 1991), we expected all the males to return to within 1200 m of previous nest sites. During the spawn period, all males failed to exhibit site fidelity. The closest a male returned to the 2007 spawning site was 6.3 km. However, approximately half of the females did exhibit annual site fidelity in 2007 and 2008 with many located within the same grid as found in the previous year. All males occupied different nesting sites within different bays in 2008 compared with 2007. These males could have been reproductively unsuccessful and abandoned their nest during 2007 and as a result nested in a different location the following year. Females in this study that did exhibit spawning site fidelity could be selecting larger males not tracked in our study who do exhibit spawning site fidelity.

Post-spawn site fidelity may be more important than site fidelity during the spawn period, as indicated by the number of individuals exhibiting post-spawn site fidelity. A majority of both males and females were located in the same location during post-spawn in 2007 vs. 2008. Smallmouth bass during post-spawn are likely recovering from high energy losses due to spawning and preparing for overwintering by consuming large amounts of food. Post-spawn foraging success in previous years may result in the return to these sites each year since individuals are more likely to stay in an area that will maximize their fitness and alternatively abandon sites that will decrease their fitness (Railsback et al., 1999). Smallmouth bass within this system may be achieving increased fitness each year due to the tendency for these individuals to exhibit post-spawn site fidelity.

This study suggests that large smallmouth bass may move greater distances in larger aquatic systems but may have similar daily movement rates compared to smaller aquatic systems (Cole and Moring, 1997). Daily movement rates appear more variable among the various lake sizes (Table 2); however, a positive relationship exists between lake size and maximum distance traveled (Fig. 3). Because Lake Michigan is three times as large as any other lentic system investigated, it may have undue influence in the correlation analysis; however, a significant relationship remains between lake size and maximum
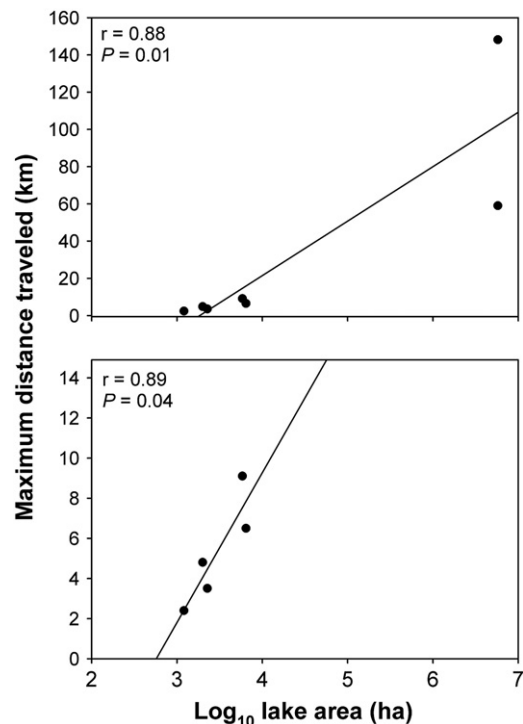

Fig. 3. Relationship between lake size ($\log_{10}$ transformed, ha) and maximum distance traveled (km) by smallmouth bass for both large (>50,000 ha; N = 2) and small lakes (<50,000 ha; N = 5) (top) and for only small lakes (<50,000 ha; N = 5) (bottom). Data are from studies cited in Table 2 and this study.

distance moved on smaller lentic systems (Fig. 3). Smallmouth bass movement may be system-specific to some extent, with maximum excursion distances only limited by the size of the lake occupied. For example, a smallmouth bass in a small lake may travel the same distance per day on average as a smallmouth bass found in a larger lake, but the latter has the ability to travel much farther due to a more expansive habitat from which to select.

In summary, the results of this study provide information regarding smallmouth bass daily movement patterns, site fidelity across two different seasons, and maximum distance traveled in a smallmouth bass population in northern Lake Michigan where this information is lacking. Information gained via this study will allow biologists to make more informed decisions concerning management of this and other Great Lakes populations; for example, deciding on the appropriate scale for management actions targeting Great Lakes smallmouth bass. In addition, by estimating daily movement patterns and site fidelity tendencies, specific areas can be identified for management as important smallmouth bass habitat. These results also reflect the need to study movement patterns and site fidelity of smallmouth bass in multiple systems as these patterns may differ across habitat type and the size of aquatic system inhabited.

Acknowledgements

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