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Frequency, composition and stability of associations among individual largemouth bass (*Micropterus salmoides*) at diel, daily and seasonal scales

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Abstract – A whole-lake acoustic telemetry observatory situated in eastern Ontario was used to continuously monitor the three-dimensional position of 20 largemouth bass (*Micropterus salmoides*) over a 120-h period during the winter and a separate 120-h period during the early spring. These data were used to evaluate the frequency and stability of associations among fish to provide an understanding of seasonal aggregations and the sociobiology of largemouth bass. The temporal and spatial proximity of each fish relative to the other 19 individuals was assessed and, based on our definition of spatial/temporal proximity (i.e., two fish having an average hourly position <2 m apart), associations were shown to vary among fish, as well as diurnally, daily and seasonally. Associations during the winter were found to be more stable and involved fewer fish than associations during the spring. Of those fish that formed pair aggregations during the winter and spring study periods, male–female pairs occurred more often than male–male and female–female pairs. Our analysis also demonstrated that associations occurred primarily during daylight hours, suggesting that fish may use visual cues to form these aggregations.

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Key words: largemouth bass; winter; associations; acoustic telemetry; sociobiology

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Introduction

The largemouth bass (*Micropterus salmoides*, Lacepède) is a popular target species for anglers (Economic and Policy Analysis Directorate 2003). Despite this popularity, there is a paucity in the scientific literature on the sociobiology of largemouth bass and the winter habits of bass (Suski & Ridgway in review). Anecdotal and laboratory studies have suggested that during the winter largemouth bass exhibit reduced activity and swimming capability (Lemons & Crawshaw 1985; Kolok 1992; Tschantz et al. 2002) and form aggregations (Carlson 1992; Raibley et al. 1997; Karchesky & Bennett 2004; Suski & Ridgway in review). Similar winter aggregations have also been observed for other centrarchid fishes (e.g., Breder & Nigrelli 1935). Some anecdotal evidence suggests that aggregations occur primarily during the day, with aggregated individuals dispersing at night (Breder & Nigrelli 1935). Recent studies of winter aggregations of largemouth bass and other centrarchids in the wild; however, have been limited to few position measurements acquired during manual telemetry studies, or have been dependent on observations and samples from anglers (Greenbank 1956; Carlson 1992; Karchesky & Bennett 2004).

While the phenomenon of winter aggregation among largemouth bass has been documented (Greenbank 1956; Carlson 1992; Karchesky & Bennett 2004), to our knowledge, no study has demonstrated that aggregations form outside the winter period. A radio telemetry study by Essington & Kitchell (1999) demonstrated that multiple largemouth bass frequent particular locations and thus could have the opportunity to aggregate. Unfortunately, their sample points were taken at coarse spatial and temporal scales and lacked the resolution to assess the presence of meaningful aggregations. Moreover, the study by Essington & Kitchell (1999) did not encompass the spawning period when aggregations between at least a single male and female pair must occur. Males will attract females to their nest for spawning bouts, though the time scale over which these bouts occur is on the order of minutes to hours and would likely not be recorded in most telemetry studies.

Here, we quantify the occurrence of largemouth bass aggregations in both the winter and the spring using spatial/temporal data from acoustically tagged individuals, within a fixed, code division multiple access (CDMA) telemetry array (Niezgoda et al. 2002). More specifically, we asked two main questions: (i) Do individual largemouth bass form winter and/or spring associations and with whom? And if they do, (ii) What are the temporal and spatial characteristics of these associations?

Materials and methods

Study site and telemetry observatory

Warner Lake is a freshwater lake in eastern Ontario that is located entirely within the property of the Queen's University Biological Station (QUBS; 44°31′N, 76°22′W). Warner Lake has a surface area of 8.3 ha and is composed of two basins; a smaller shallow basin that defines the north section of the lake (maximum depth of 3 m) and a larger deep basin (maximum depth of 7 m) that defines the southern section of the lake. The lake is a closed system with inflows and outflows that are mainly subterranean and not large enough for the movement of fish. Details on the plant and fish community of Warner Lake can be found in Cooke et al. (2005) and Hanson et al. (in press). In 2003, a fixed, submerged acoustic telemetry array consisting of a CDMA-based telemetry system (Lotek MAP 600, Lotek Wireless Inc., Newmarket, Canada; Niezgoda et al. 2002; Cooke et al. 2005) and 13 hydrophones was installed in the lake. The moored hydrophones, placed 2 m below the water surface, were connected to two receivers located on shore through cabling. To enable operation during winter periods and seasonal transitions, hydrophone cabling running to the receiver on shore was routed through insulated Acrylonitrile-Butadiene-Styrene (ABS) piping at the water's surface for protection from surface ice. Collected data were exported to personal computers for processing via flash storage cards. Positions are triangulated when three or more hydrophones are within acoustic range of a ping from a transmitter and the positions have been found to have sub-metre accuracy (further detail on the operation and accuracy of the system can be found in Cooke et al. 2005).

Study animals

Fish capture occurred between 14 October and 16 October 2003. Twelve male and eight female largemouth bass were captured by angling, and sex was determined by visual inspection and confirmed by internal visual inspection during subsequent surgeries. CDMA temperature–pressure sensing acoustic transmitters (Lotek CTP-M11-55, 11 × 55 mm, burst rate 15 s, life expectancy of 270 ± 30 days, depth resolution ±0.7 m, temperature resolution ±0.5 °C) were implanted intraperitoneally by a single trained surgeon using the techniques described in detail by Cooke et al. (2005) and Hanson et al. (in press).

Data processing and analysis

Raw data obtained from the observatory receivers were filtered to remove erroneous position solutions (caused by echos, interference, multipath, etc.), resulting in approximately 75% of position solutions being included (realised sampling rate of 20 s; Cooke et al. 2005). Filtered tables were then queried to determine the mean position for each fish during each hour over a 5-day (120 h) sample period starting at midnight 1 January 2004 and ending at midnight 6 January 2004. These days defined our winter study period and were chosen as representative of days with stable water temperature during ice cover on the lake (Hanson et al. in press). The period starting at midnight on 9 April 2004 and ending at midnight on 14 April 2004 was also assessed in an identical manner, and defined our spring study period. These days were chosen as representative of other post-ice off period during the spring and were prior to the start of the spring spawn when many fish move outside the footprint of the array and positioning of tagged fish less reliable. For this study, an 'association' between two largemouth bass was deemed to have occurred when their mean hourly X, Y and Z positions were within 2 m of each other for a minimum duration of 60 min. This definition was chosen in response to a food reward study with largemouth bass where it was determined that fish could distinguish different fishing lines at distances

<2 m, but could not differentiate fishing lines at distances >2 m, suggesting a decrease in visual acuity at distances beyond 2 m (Miller & Janzow 1979). To assess the temporal characteristics of any associations, sunrise and sunset times for Warner Lake on the sampled days were found at http://www.sunrisesunset.com (accessed 3 April 2006; Eastern Standard Time Zone), allowing the timing of each association to be categorised as 'day' or 'night.' Processed data were exported to ARCGIS 9 (ARCMAP V9.1; ESRI, Redland, CA, USA) for association analysis. It should be noted that during both of the 5-day periods all fish had calculable average hourly positions and contributed equally to the analysis.

Statistical methods

To analyse the data, we compared the number of associations per individual occurring in the winter study period to the number of associations per individual occurring in the spring study period using repeated measures ANOVA. A significant difference would imply a difference in the number of associations per individual occurring across study periods. To compare each individual and the amount of time spent associating during each study period, the number of associations per day by each fish was assessed for both the winter and the spring study period using repeated measures ANOVA. A significant difference within each study period would indicate differences among individuals and the number of associations they participate in. All statistical analyses were performed using JMP 6.0.2 (SAS Institute Inc., Cary, NC, USA) and at a confidence level of 95%.

Sex of associating fish was tested against a uniform distribution using a chi-squared test for the winter study period. Observed values were the number of male–male, male–female and female–female associations, and the expected values were found by dividing the total number of associations by 3 (the number of categories). All chi-squared tests and frequency distributions were performed using the Data Analysis Tool pack in Microsoft Excel 2003 (Zar 1984).

In addition, McQuitty linkage analysis was conducted for each tagged largemouth bass with three or more associations over the 5-day study periods (McQuitty 1966). McQuitty linkage analysis examines the number of pairwise links between fish and identifies 'core' reciprocal pairs that are most often linked to each other. All other fish are then assigned to the fish to which they are most linked. Typically, this analysis partition individuals into several groups surrounding the cores. To include only 'core' largemouth bass we used three associations between a pair of fish as the minimum limit for inclusion in the McQuitty linkage analysis because when the number of associations was plotted per individual there was a clear natural break in the data set at 3 (data not shown).

Once all associations in the two study periods had been quantified, associations were investigated spatially by calculating kernel density estimations (95% and 50%; $h = 25$) using the Hawth's tool in ARCGIS 9 (ARCMAP V9.1; ESRI; Beyer 2004) to identify the location of the majority of associations. Associations were also assessed to determine any temporal patterns in the dates and times of associations compared with sunrise and sunset times using chi-squared analysis.

Results

Quantitative and qualitative description of associations

During the winter study period tagged largemouth bass remained in the large deep basin, whereas during the spring period most tagged fish were located in the

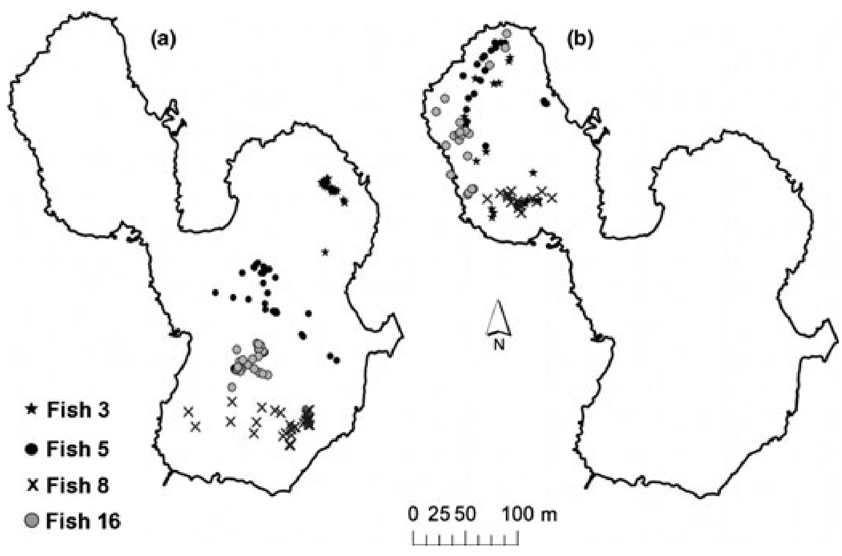

Fig. 1. Hourly positions for four largemouth bass [fish 3 (solid, black star), 5 (solid, black circle), 8 (solid, black cross) and 16 (solid, grey circle with black outline)] for 1 January 2004 (a, winter) and 1 April 2004 (b, spring) as obtained from a code division multiple access equipped submerged acoustic hydrophone array. Each unique symbol represents one average hourly position for each fish.

small shallow basin (Fig. 1). When fish were associating during the winter, there were 3.4 ± 0.2 individuals participating each hour and the association period (the number of hours between when the first associations occurred and when the last associations occurred) lasted 9.4 ± 1.5 h (Fig. 2). When fish were associating during the spring, there were 5.6 ± 0.6 individuals participating each hour and the association period lasted at 3.6 ± 1.9 h. Statistically, in the winter there were fewer individuals per hour, but the associating period for the day was longer (*t*-test; $t_{13.26} = -3.53$; $P = 0.004$; *t*-test; $t_{7.50} = 2.40$; $P = 0.045$; Fig. 2). The number of associations per individual during the winter study period did not differ significantly from the spring study period (RMANOVA; $F_{1,30} = 0.0013$; $P = 0.97$; Fig. 3).

During the winter study period, 16 of the 20 largemouth bass exhibited associations, often with multiple other fish (Figs 3a and 4). On average, each largemouth bass had 8.0 associations, although this varied among individual from 0 to 29 ($n = 160$, SD = 8.6). No fish were found to associate significantly more or less than other tagged fish (RMANOVA; $F_{19,80} = 1.27$; $P = 0.23$). Of the 24 different pairs associating, seven were between pairs of males, 14 were between one male and one female, and three were between pairs of females. Male–female associations occurred more frequently than expected, while the female–female associations were less common than expected (uniform, $\chi^2 = 7.75$, d.f. = 2, $P = 0.02$). The male–male associations were similar to what would be expected (uniform, $\chi^2 = 7.75$, d.f. = 2, $P = 0.02$).

During the spring study period, 14 of the 20 bass exhibited associations with other fish (Fig. 3b). On average, a tagged largemouth bass had 7.8 associations during this period, although this was also variable, ranging from 0 to 34 ($n = 156$, SD = 8.6). No fish were found to associate significantly more or less than the other tagged fish (RMANOVA; $F_{19,80} = 1.66$; $P = 0.06$). Of the 41 different pairs associating, 11 were between pairs of males, 24 were between one male and one female, and six were between pairs of

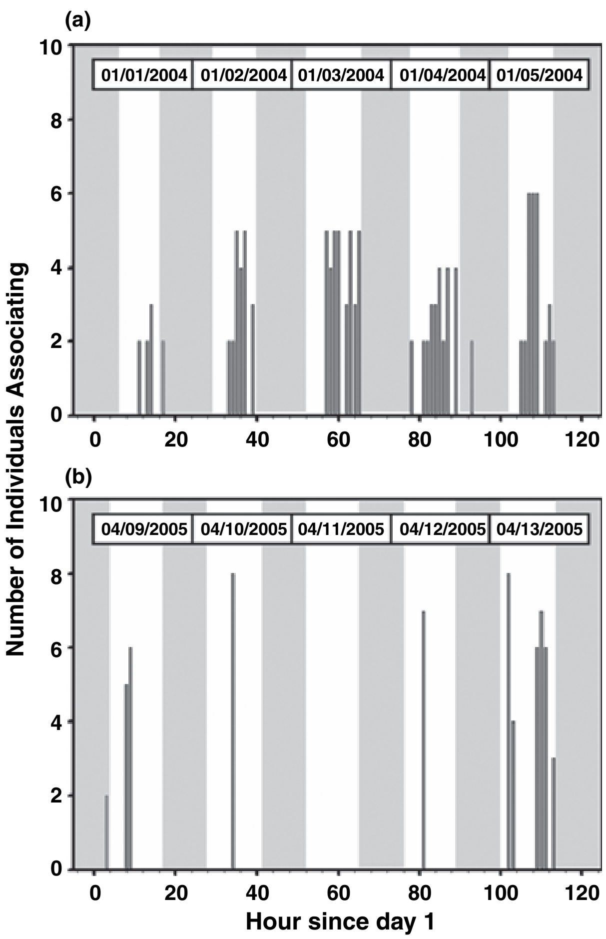

Fig. 2. Total number of acoustically tagged largemouth bass associating with other acoustically tagged largemouth bass ($n = 20$) each hour during the winter study period (a) and the spring study period (b). Periods of night are shaded grey, while periods of daylight are not shaded.

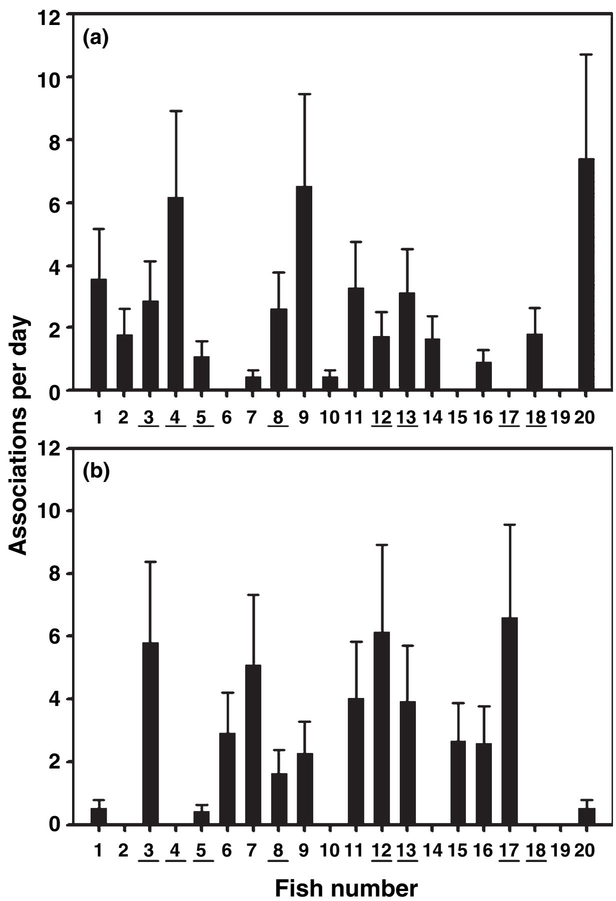

Fig. 3. Mean number of associations per day for each of the 20 acoustically tagged largemouth bass over a 5-day winter (January) study period (a) and a 5-day spring (April) study period (b). Standard error bars are included and underlined fish numbers indicate the fish is female.

females. Male–female associations occurred more frequently, while the female–female associations were less common than expected (uniform, $\chi^2 = 12.63$, d.f. = 2, $P = 0.002$). The male–male associations occurred as often as expected (uniform, $\chi^2 = 12.63$, d.f. = 2, $P = 0.002$).

McQuitty linkage analysis of the winter study period revealed that there were three groups of major linkages among tagged largemouth bass: Group 1 = fish 1 (♂) and 13 (♀); Group 2 = fish 2 (♂), 3 (♀), 8 (♀), 11 (♂) and 18 (♀); and Group 3 = fish 4 (♀), 9 (♂), 11 (♂), 14 (♂) and 20 (♂) (Fig. 4). The third group was the most coherent with most of the group members, with the exception of fish 14, associating with the entire group. The second group was less connected, although fish 2, 3, 11 and 18 associated with other fish in the group. In addition, fish 11 was the only fish that associated with two groups. Because spring associations were more sporadic and most did not last for more than an hour, a McQuitty linkage analysis was not performed.

Temporal and spatial characteristics of associations

Although the mean number of daily associations was 16.0 ± 9.4 ($n = 5$) for the winter study period and 16.8 ± 17.4 ($n = 5$) for the spring study period, the number of associations varied among days (Table 1). During the spring study period, over half of the associations occurred on one day (13 April 2004), with one day (11 April 2004) contributing zero associations. In both seasons, associations occurred significantly more often during daylight hours (Winter Study Period: RMANOVA; $F_{1,38} = 18.32$; $P = 0.0001$; Spring Study Period: RMANOVA; $F_{1,38} = 13.56$; $P = 0.0007$; Fig. 2).

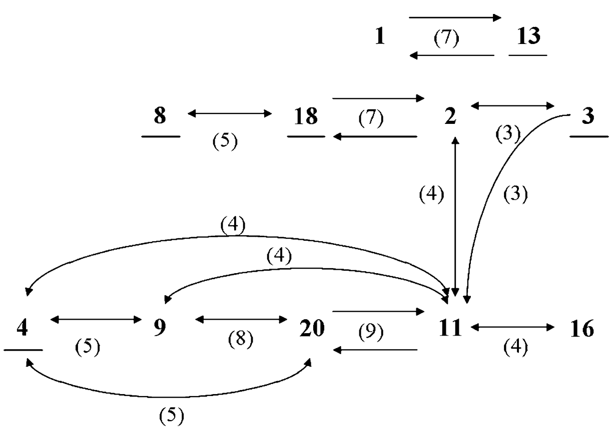

Fig. 4. McQuitty linkage analysis for associations between 20 acoustically tagged largemouth bass with three or greater associations over the 5-day winter (January) period. Numbers in bold are fish IDs, numbers in parentheses are the number of associations between two fish and underlined numbers indicate a female. Double arrows represent reciprocal pairs of fish that are most linked to each other and form the core of each group.

Table 1. The number of associations between 18 largemouth bass outfitted with acoustic tags and monitored using a code division multiple access equipped submerged acoustic hydrophone array during 5 days in January and April 2004.

Winter date	Number of associations	Spring date	Number of associations
1 January 2004	5	9 April 2004	19
2 January 2004	15	10 April 2004	7
3 January 2004	32	11 April 2004	0
4 January 2004	13	12 April 2004	12
5 January 2004	15	13 April 2004	40
Total	80	Total	78

For both study periods, the associations among individual fish demonstrated a spatial concentration (Figs 2 and 5). A kernel density estimate (95% and 50%; $h = 10$) showed that 50% of all winter study period associations were located in two small sections of the lake; the middles of the southern and northern portion of the deep basin. Ninety-five percent of the winter study period associations were found in one of five locations within the deep basin (Fig. 5). In contrast, the spring study period associations were all found to be located only in the southern portion of the shallow basin (Fig. 5).

Discussion

Our study demonstrates that largemouth bass form multi-individual associations during both the winter and the spring as evidenced by multiple incidences of

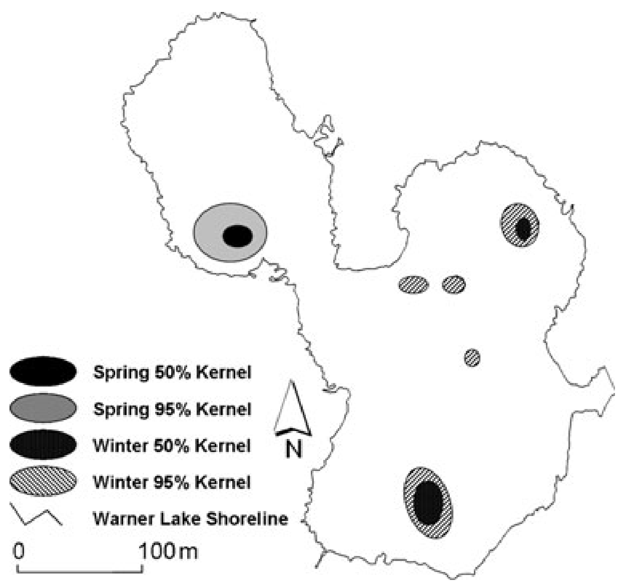

Fig. 5. Kernel density estimation coverage for 20 acoustically tagged largemouth bass during a 5-day study in spring and winter. Kernel densities were calculated from the mean values of the location for each association. The black area represents the location of 50% of all the associations, while the hatched areas represent the locations of 95% of all associations.

fish being within 2 m of each other for 1-h periods. We found no difference between the number of associations per individual between the winter and the spring, though there were differences between the characteristics of associations between the two seasons. Associations during the winter, although involving fewer individuals per hour, were more stable throughout the day as evident by the association period being longer in the winter than in the spring. Moreover, the number of individuals associating and the number of associations per day were less variable during the winter, suggesting more sporadic association formation during the spring. These findings suggest that largemouth bass are spending considerable time in close proximity to conspecifics (i.e., within 2 m of each other) and that winter aggregations are more stable than spring aggregations. Because we did not tag all the fish in the lake, fish with low number of associations in our sample group may in fact be involved in aggregations, but with untagged conspecifics. Even though we tagged a relatively small proportion of the largemouth bass in our population, spatial, temporal and sex-specific differences in aggregations were obvious, suggesting that aggregations are extremely prominent for overwintering largemouth bass.

In nature, aggregations between individuals have been shown to form at beneficial habitats (Breder & Nigrelli 1935; Carlson 1992), be useful for protection against predators (Godin & Morgan 1985) and be indicative of genetic relatedness between group members (Fraser et al. 2005). Indeed, centrarchid species such as smallmouth bass (*M. dolomieu*, Lacepède), largemouth bass and redbreast sunfish (*Lepomis auritus*, Linnaeus) have been shown to form multi-individual aggregations during the winter (Townsend 1916; Breder & Nigrelli 1935; Carlson 1992). Reasons for forming aggregations during the winter include crowding caused by reduced lake area and fewer areas of suitable habitat with respect to temperature and dissolved oxygen (Breder & Nigrelli 1935; Carlson 1992). For largemouth bass, Carlson (1992) found that 59% of the estimated largemouth bass population in the Hudson River Estuary aggregate at five winter refugia, but that study was only able to determine fish positions following ice-out. Our study is the first to quantify largemouth bass aggregations in the winter at fine spatial and temporal scales, and also show that those aggregations are not stable throughout the winter. Moreover, we were able to demonstrate through our McQuitty linkage analysis that there are multiple aggregations and the membership in those aggregations varies.

Though we found no statistical difference between individuals and associations between the winter and spring study period, we did find that the spring associations were more sporadic and more variable. The associations formed during the spring study period were typically short-term, often only lasting 1 h, whereas several winter associations lasted up to 6 h (data not shown). We suggest that there are three possible reasons for the characteristics of the association between tagged largemouth bass observed during the spring study period. First, as water temperature rises in the spring, largemouth bass become more active (Kolok 1992; Hanson et al. in press) and feed more to promote gamete formation (Mackereth et al. 1999). Because largemouth are active cruising predators, fish would likely only be in areas for short periods of time to feed and then would move on, thus associations did not last long. Secondly, during the spring, if a male bass attempts to spawn, he builds a solitary nest in the near-shore environment (Breder & Rosen 1966). Thus, male largemouth bass are more likely to be alone in the shallows for a greater portion of the day rather than in aggregations during our spring study period as they begin the process of searching for suitable nest sites (Waters & Noble 2004). Lending credence to this idea, three of the tagged male bass in our study spawned immediately after our spring study period, and were observed not to be associating with other tagged fish during that time.

Associations between sexes of largemouth bass occurred frequently in this study. In our data, based on the sex ratio of tagged individuals, we observed significantly more male–female associations during both the winter and the spring and significantly fewer female–female associations compared with an expected uniform distribution. Male–female associations were observed to occur four times more often than female–female associations, while the proportion of male–male associations during the winter did not occur more frequently than would be expected if associations were uniform. The increased frequency of male–female associations during the winter and spring may be attributed to prespawning activity (Breder & Rosen 1966) and 20 years of observations of largemouth bass spawning has produced numerous observations of tagged individual females spawning with different males (and the reverse) both within a single season, and among years (D. P. Philipp, Illinois Natural History Survey, personal communication). Indeed, it may be important for largemouth bass to associate with the opposite sex prespawn to determine pair-bonds for siring young.

Our data also demonstrated that associations between tagged largemouth bass exhibited a pronounced diel component, with over 97 times more associations occurring during the day than at night. Previous research on centrarchid aggregations indicated that although they are present over long periods of time (i.e., throughout the season), on a daily basis individuals disperse nightly and reform aggregations during the day (Breder & Nigrelli 1935). Based on the results of controlled laboratory studies, Breder & Nigrelli (1935) suggested that visual cues were needed for the formation of aggregations, and, therefore, aggregations dissolve at night when vision is limited. Our field-based results demonstrated that aggregations rarely formed outside of daylight hours in both the winter and the spring study period, which is consistent with the results found by Breder & Nigrelli (1935). Considering the apparent long-term stability of these aggregations, it is interesting that the members of the associations and the number of associations varied across the 5-day study period. Previous field and laboratory studies have suggested largemouth bass are dormant during the winter (Crawshaw 1984; Demers et al. 1996; Cooke et al. 2003). Because we found aggregations forming and dispersing daily and the individuals in the aggregations varied daily, it can be implied fish are moving considerably and are not dormant (also see Hanson et al. in press). Although we did not measure light levels under ice in the winter, ice and snow cover (ice depth was approximately 1 m and snow cover was approximately 0.2 m; F. J. S. Phelan, Queen's University Biology Station, personal communication) were unlikely to be sufficiently thick to have obscured all light.

Our kernel density coverage indicated there was also a spatial component to associations between tagged largemouth bass, as evidenced by the fact that 95% of our observed associations were restricted to only a few, relatively small areas. Formation of aggregations, and presumably associations among specific individuals, may indicate fish are optimising their habitat choices, possibly seeking to inhabit areas with optimal temperature, dissolved oxygen and/or presence of food and macrophyte beds (Breder & Nigrelli 1935; Beamish 1970; Carlson 1992; Raibley et al. 1997; Karchesky & Bennett 2004). Many aggregations are believed to occur during the winter periods because decreases in the number of areas with suitable environmental conditions tend to concentrate fish (Carlson 1992). Ice cover in the littoral zone coupled with decreases in temperature and dissolved oxygen content can lead to loss of suitable fish habitat (Breder & Nigrelli 1935; Greenbank 1956; Carlson 1992; Karchesky & Bennett 2004). Both Breder & Nigrelli (1935) and Karchesky & Bennett (2004) found that as temperature decreased during the fall–winter interface, aggregations among centrarchid fish increased, and the aggregations were stable until temperature decreased to fatal levels or significant warming occurred. Karchesky & Bennett (2004) suggest largemouth bass will seek out the warmest locations in a water body. During the spring, the lake has more available suitable habitat because the water is warmer, dissolved oxygen levels are 'normal' (i.e., normoxic), and there is more area of the lake available for fish to disperse to. Having more suitable habitat available may decrease the likelihood of fish aggregating (Breder & Nigrelli 1935).

Because associations were found to occur at particular locations throughout the lake we must explore the possibility that concentrations in fish were due to desirable environmental conditions. Because fish were found to be mobile and associations varied spatially, temporally and within individuals, the paradigm that largemouth bass are quiescent in the winter can be questioned. Future research on this topic should include: (i) an examination of environmental variables that may affect associations; (ii) a genetic investigation of the kin relationships among associating and nonassociating fish and (iii) a long-term study on winter aggregation using an entire winter season. Collectively, this information should provide a greater understanding of the mechanisms responsible for the formation of winter aggregations and the factors which influence individual sociality.

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