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FISH TELEMETRY

Assessment of largemouth bass (*Micropterus salmoides*) behaviour and activity at multiple spatial and temporal scales utilizing a whole-lake telemetry array

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Abstract A whole-lake acoustic telemetry array was utilized to monitor the three-dimensional position of 20 largemouth bass (*Micropterus salmoides*). Code division multiple access (CDMA) technology enabled the simultaneous monitoring of the 20 transmitters (equipped with pressure and temperature sensors) at 15 s intervals with sub-meter accuracy. Fish were monitored between November 2003 and April 2004 to evaluate the behaviour of fish across different temporal and spatial scales. The distance moved by largemouth bass, assessed both on a daily and hourly basis, varied by season and was positively correlated with water temperature. For example, daily movement rates were 2.69 ± 1.45 km/day in mid November (average daily water temperature 5.9°C), 2.24 ± 0.73 km/day in early January (5.1°C), and 7.28 ± 2.62 km/day in mid April (7.7°C). Interestingly, daily movement rates varied by as much as 25 fold among individual fish. Visualization of fish swimming paths revealed that whereas some fish occupied discrete areas and made only localized movements, other individuals made lengthier journeys covering much of

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Developments in Fish Telemetry

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the lake in periods of as little as one day. Analysis of fish behaviour at a finer temporal scale revealed that during the winter, fish spend more than 95% of their time swimming at speeds less than 0.1 m/s (0.07 ± 0.24 m/s). During late fall, and especially in spring, swimming speeds were higher with mean swimming speeds of 0.11 ± 0.27 m/s and 0.19 ± 0.29 m/s, respectively. When the telemetry dataset was queried to simulate 24 h manual tracking intervals, it was clear that manual tracking data would not have been representative of actual daily movement rates, underestimating daily movement and swimming speeds by at least 75 fold. This study identifies the importance of evaluating fish activity at multiple spatial (whole lake to sub-meter position) and temporal (seasonal to seconds) scales and illustrates the potential of CDMA telemetry to yield such data.

Keywords Biotelemetry · Behaviour · Scale · Winter biology · Activity

Introduction

Studies of fish movement and activity have increased in both number and importance in recent years (Lucas & Baras, 2000), reflecting the need to understand the spatial ecology of fish when developing effective management and conservation strategies. Underlying the explosion of studies evaluating movement and activity have been major advances in research techniques for monitoring the behaviour of fish in the wild. The advent of telemetry techniques has enabled researchers to obtain detailed activity and movement data remotely across different temporal and spatial scales (Lucas & Baras, 2000; Cooke et al., 2004a, b). Rarely, however, have multiple scales been considered within a single study. Although mobile tracking of telemetered individuals has become a standard technique in fisheries science, it still fails to provide researchers with fine scale activity data, and if fish are to be tracked continuously, it requires large investments in labour (Cooke et al., 2004a, b). To overcome those deficiencies, researchers have turned to either fixed telemetry stations to continuously monitor movements (e.g., Cooke et al., 2001a; Cote et al., 2002) or physiological telemetry devices to assess fine scale patterns of swimming activity (e.g., Cooke et al., 2004a, b). Fixed monitoring stations can provide information on the two- and three-dimensional position and movement of fish continuously and in a manner that is independent of the presence of a researcher. With sub-meter accuracy, an array of fixed stations also has the potential to provide detailed information on fish swimming speeds and energetics, data previously limited to physiological telemetry systems. Fixed stations have become even more robust when coupled with code division multiple access (CDMA) technology, enabling numerous animals to be tracked simultaneously in a confined area without the signal collision problems evident in previous deployments of fixed telemetry stations (see Niezgoda et al., 2002; Cooke et al., 2005). Niezgoda et al. (2002) utilized such an acoustic CDMA system to continuously monitor the movements of blue crab (*Callinectes sapidus*) in a salt marsh pond for several weeks. For the first time, we use a whole-lake three-dimensional CDMA acoustic telemetry observatory to assess fish behaviour and activity at multiple spatial and temporal scales.

The use of a remote, three dimensional positioning system allows us to generate a continuous and detailed dataset of fish behaviour for the entire life of each transmitter, a period that can span multiple seasons. Such a complete dataset is one of the first of its kind. In their review of biotelemetry, Cooke et al. (2004a) noted that desirable characteristics of remotely monitored telemetry studies included the partnering of physiology with field data, individual based focus, continuous monitoring over multiple scales, and ability to work with unrestrained animals. This study incorporated all of those characteristics. This initial exploratory analysis is intended to provide an assessment of system capabilities and to identify future detailed research questions that are possible to address using this dataset.

Using largemouth bass (*Micropterus salmoides*) as the test organism, we investigated fish behaviour and activity at multiple spatial and temporal scales using a three dimensional CDMA acoustic whole-lake telemetry array in an eastern

Ontario lake. Experiments focused on largemouth bass as a model species for several reasons. First, a long-term population ecology study of largemouth bass in the study lake (i.e., Warner Lake) provided baseline information (see Suski, 2000). In addition, because largemouth bass exhibit different seasonal movement patterns, with some individuals occupying discrete home ranges, while others being more transient, it provides the opportunity to assess the level of individual variation (Demers et al., 1996). Largemouth bass are also thought to vary their activity among seasons, being active in the warmer seasons and quiescent in the winter (Demers et al., 1996; Cooke et al., 2003b). Finally, largemouth bass are a heavily managed species owing in part to their popularity as a recreational sport fish (Pullis & Laughland, 1999), thereby providing much opportunity for applied research.

Methods

Study site

In 2003 a freshwater lake (Warner Lake, Queen's University Biological Station [QUBS]) was instrumented with a CDMA acoustic telemetry system as the backbone of an aquatic "ecological observatory". The observatory extends traditional telemetry studies involving manual triangulation of a few representative animals to a fully automated all-season community and species-interactive multi-dimensional view. Warner Lake is a private research reserve located in eastern Ontario (44°31′ N, 76°22′ W) that is wholly enclosed on QUBS property, enabling the deployment and field testing of equipment in an undisturbed setting. The small lake (18.2 hectare surface area) is composed of two basins; a smaller shallow basin (max depth = 2 m) and a slightly larger deeper basin (max depth = 7 m). The entire shallow basin and the near shore regions of the deeper basin have extensive littoral zone characterized by emergent and submergent vegetation. The deeper areas have dense weed beds with the majority of the lake bottom covered by *Chara* spp. The entire shoreline has substantial amounts of fallen timber. Warner Lake is a closed system for fish and has been the focus of a long-term ecological study on the reproductive dynamics of largemouth bass (see Suski, 2000). Beginning in 1996, researchers have conducted underwater nesting surveys of largemouth bass and have implanted nesting males with passive integrated transponders (PITs) to monitor the growth, survival, and reproductive activity of individual fish over time, providing ample background data for this current research activity. Other documented species include white sucker (*Catostomus commersonii*), pumpkinseed (*Lepomis gibbosus*), yellow perch (*Perca flavescens*), brown bullhead (*Ameiurus nebulosus*) and golden shiner (*Notemigonus crysoleucas*).

Telemetry array

The underwater acoustic telemetry array was installed in Warner Lake during November 2003 (Detailed description of the equipment, configuration, and system performance is provided in Cooke et al., 2005). To meet the acoustic telemetry requirements of the observatory, a CDMA-based telemetry system (MAP_600, Lotek Wireless, Newmarket, ON) was installed at the observatory. The telemetry equipment consists of two multi-port MAP_600 receivers monitoring a total of 13 hydrophones distributed in such geometry as to provide coverage of the entire lake, including the littoral zones. Equipment was configured to monitor eight hydrophones (large basin) on one receiver, with the remaining five hydrophones (small basin) on the other receiver. A CDMA temperature-pressure sensing tag (burst rate 15 s) was also placed at each moored hydrophone location. Cabling (i.e., connecting hydrophones to shore-based receiving equipment) was routed along the bottom of the lake to one point on the shoreline and brought out of the water through conduit. Hydrophones were moored from fixed posts (steel piping driven into the lake bottom) at an approximate depth of 2 m from the water surface to ensure that lake ice conditions would not damage or move the hydrophones. To facilitate sub-meter positioning of instrumented fish, all hydrophones were surveyed using differential GPS (±0.2 m). Data were transferred from each receiver to a personal computer for further processing by use of flash storage cards.

Study animals

Largemouth bass were collected by angling between October 14 and October 16, 2003. We attempted to target individuals that had previously been implanted with PITs. These PIT tagged fish were part of a long-term study of the reproductive ecology of largemouth bass in the lake and provided information on reproductive history, sex, age, and capture history. In total, we implanted 14 males and 8 females with CDMA temperature-pressure sensing acoustic transmitters (Lotek CTP-M11-55, 11 mm × 55 mm, burst rate 15 s, life expectancy of one year). After surgery, two telemetered individuals either died or suffered from transmitter failure. These individuals were removed from all analyses in this study. The burst rate of the tags was selected to ensure transmitter longevity through the fall-winter and winter-spring transitions. Depth and temperature resolution for the fish tags was ±0.7 m and ±0.5°C, respectively.

To implant fish, they were first anesthetized in a 60 ppm induction bath of clove oil solution (emulsified in ETOH, clove oil:ETOH, 1:9; Anderson et al., 1997). When fish lost equilibrium, they were measured (total length in mm) and weighed (mass in g). Fish were then placed on a foam surgery table with a recirculating supply of water containing a maintenance dose of anesthetic (20 ppm clove oil solution) irrigating the gills. An initial laparotomy incision of 12 mm was made slightly off center from the ventral midline behind the pelvic girdle of each fish (Cooke et al., 2003a). Cleaned transmitters (ETOH and betadine) were inserted into the body cavity, and the incision was closed with two simple interrupted sutures (3/0 PDS II, absorbable monofilament sutures; Ethicon Inc.). All surgeries were conducted by the same experienced individual to eliminate variance associated with multiple surgeons (Cooke et al., 2003a). Fish were then placed in coolers containing lake water and allowed to recover from anesthesia. Equilibrium was usually regained within 5 min, and the fish were then released in the lake at one central location.

Data processing and analysis

Raw data were loaded into the BioMAP program (v. 2.1.12.1, Lotek Wireless, Newmarket, ON), where temperature information was retrieved to compute sound speed on a day-to-day basis to enable hyperbolic position determination. Raw position solutions were generated after running flash card files through the two-dimensional positioning engine within the BioMAP program. Depth information (i.e., the 3rd dimension) was determined from the pressure information relayed by each tag. To remove outliers, a series of filtering processes within BioMAP were applied to the data. At the time a position solution is recorded, the array assigns a reliability number (RN) and condition number (CN) to assess the numerical stability of the position (Niezgoda et al., 2002). If these numbers showed that a point may have been an outlier, it was filtered out of the data set (RN > 0.75 , CN < 10). Remaining position solutions that did not fall within sub-meter degree of precision (GDOP) were filtered out of the dataset as well. Lastly, impossible position solutions, defined as areas the fish could not possibly access (i.e., land) as well as movements that were not physically possible (large distance movements in impossibly short periods of time; i.e., swim speeds that exceeded 6 body/lengths per second) were also filtered out. Overall, more than 75% of solutions were deemed valid locations.

This paper sought to assess the behaviour of largemouth bass on varying scales across seasons. As such, we first plotted the seasonal trends of the data (on a weekly basis) and then selected one representative day within each season to analyze movements in detail (fall, November 11, 2003; winter, January 1, 2004; spring, April 13, 2004). Fully filtered data were then queried to generate tables of information for each fish on each particular day. To determine daily distance traveled for the seasonal trend line, position estimates were averaged hourly, and then the difference was found between successive X, Y positions assuming that the fish maintained the same elevation (Z) between positions. For the representative days in each season, distance traveled was determined as the distance between each X, *Y* position recorded. The Pythagorean Theorem was then utilized to determine linear distance between the points. Daily distances were measured as the sum of all distances moved across a day for each individual. Hourly distances were measured as the sum of all distances moved across a single hour of a day by each fish. Swim speeds were determined by dividing each instantaneous distance moved by the time required to move that distance (represented by the time between signal transmissions). To simulate manual tracking, a daily distance was determined by the above procedure, but only the first and last points of the data set were utilized (i.e., the closest point to 00:00 h and almost 24 h later (i.e., closest signal to 00:00 h the following day). Statistical analysis was performed in JMP IN v. 4.0. All values presented represent means ± SD unless otherwise noted.

Results

Seasonal trends

At the broadest scale, we observed trends across the fall and winter seasons. Activity, measured as daily distance swam, decreased from November 2003 to early December 2003, corresponding to a drop in water temperature (Fig. 1) and a period when fish were observed in deep water. As temperature steadied from December 2003 to early March 2004, activity level and average depth utilization remained relatively constant (Fig. 1). In spring, however, fish were found shallower in the water column, and activity estimates declined dramatically (Fig. 1). Both depth and activity seemed to be correlated with water temperature, though this was not quantified. We used these general trends to identify representative days for further in depth analysis.

Daily movements

Focusing our efforts on three representative 24 h periods, we observed that daily swimming activity varied among the three seasonal periods examined. Overall, mean total daily swimming activity across all individuals was lowest in winter, but was 1.2 fold higher in fall and 3.25 fold higher in spring (Table 1, Fig. 2). This range of daily swimming activity seemed to be positively correlated with water temperature (fall: November 11, 2003 = 5.9 ± 0.32°C, winter: January 1, 2004 = 5.1 ± 0.62°C, spring: April 13, 2004 = 7.7 ± 0.82°C), but this was not quantified statistically. Although individual activity levels were generally consistent with this pattern, there were instances in which certain individuals swam more during periods of cooler temperatures, revealing individual variation in behaviour.

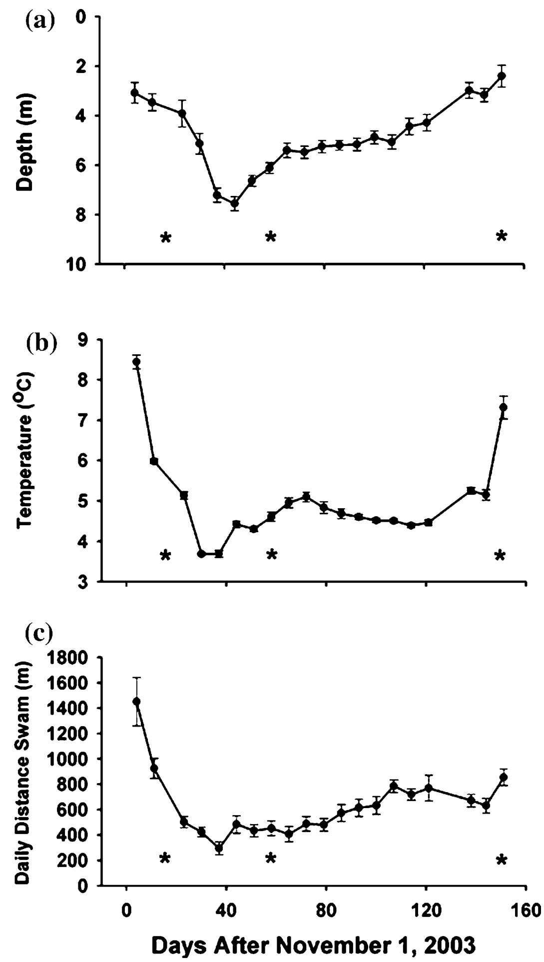

Fig. 1 Seasonal patterns of activity, depth, and water temperature of largemouth bass. (**a**) details the mean depth utilized by all individuals weekly across the seasons. (**b**) details the mean temperature utilized by all individuals weekly across the seasons. (**c**) details the mean daily distance swam by all individuals weekly across the seasons. Error bars represent ±1 SD. Asterisks indicate representative 24 h periods analyzed

Table 1 Mean total daily swimming distances for all 20 telemetered largemouth bass in Warner Lake over the three representative dates. All numbers are shown mean ± SD, with minimum and maximum values in parentheses below

Date	Daily water temperature (°C)	Total daily swimming distance, array tracking (m)	Total daily swimming distance, manual tracking (m)
11/11/3	5.9 ± 0.3	2,700 ± 1,500 (920/6,800)	76 ± 59 (1.5/200)
1/1/4	5.1 ± 0.6	2,200 ± 730 (1,040/3,400)	68 ± 71 (2.4/202)
4/13/4	7.7 ± 0.8	7,300 ± 2,600 (450/11,000)	61 ± 93 (0.7/320)

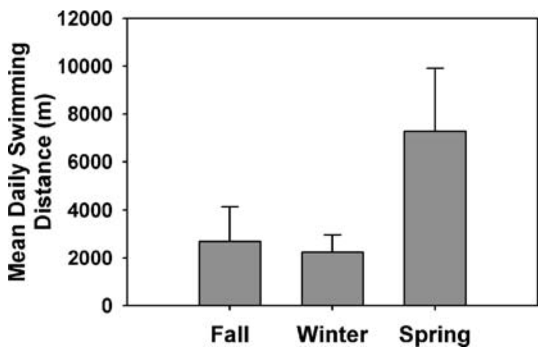

Fig. 2 Mean daily distance traveled (mean ± SD) as recorded by the hydrophone array for the three representative dates. Statistical quantification of between-date differences were not performed, as discussed in the text

Individual fish also varied extensively in daily swimming activity within a seasonal period, in some cases with differences exceeding 25 fold. For example, on April 13, LMB #*2* moved less than 1 km in 24 h whereas, LMB #*7* moved more than 11 km (Figs. 2, 3). Indeed, when daily movement traces were plotted for these two individuals, distinct differences in behaviour were evident. LMB #*2* occupied a very specific site and conducted only localized movement compared to LMB #*7* that made extensive movements within the lake, transiting numerous habitat types.

Hourly movements

For an intermediate time scale, mean hourly movement of all individuals was examined across all three seasonal periods. Hourly movement was also positively correlated with water temperature. Fish moved the longest distances during any hour in spring (150 ± 47 m/h), followed by winter (82 ± 10 m/h), and finally by fall (75 ± 9 m/h) (Fig. 4). The larger standard deviation around the

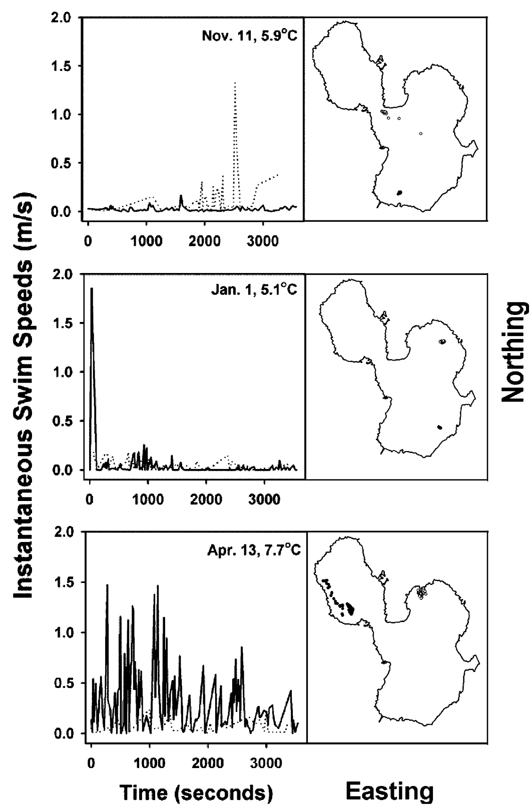

Fig. 3 Individual variation in behaviour and activity as determined by movement pattern and swim speed utilization over the three representative dates. The left panels show the instantaneous swim speed (m/s) utilized over time (s) across a one hour period of each date. The solid line represents individual LMB #*7*, and the dashed line represents individual LMB #*2*. The right panels show the two-dimensional position solutions within the lake that were used to determine the above mentioned instantaneous swim speeds. Individual LMB #*7* is represented by dark colored dots, while individual LMB #*2* is represented by light colored dots

mean hourly movement value for spring reflects the fact that fish were more active during daylight hours than at night (Fig. 4). In contrast, activity

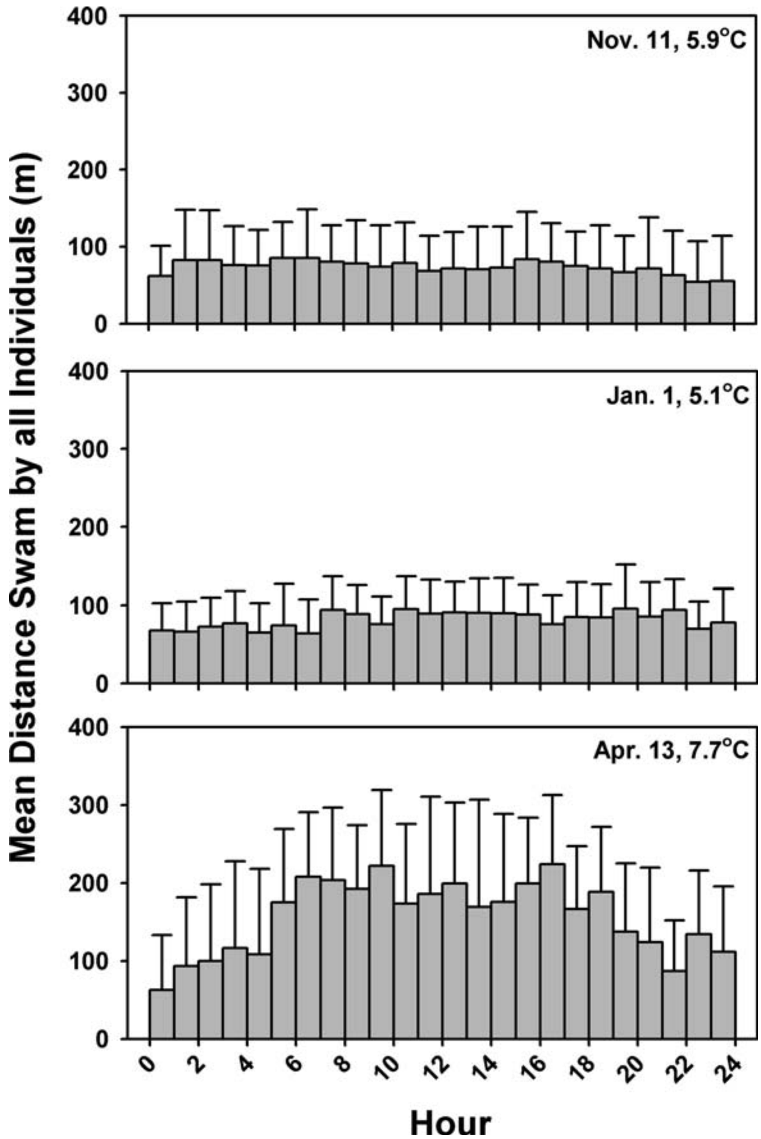

Fig. 4 Mean hourly daily distances swum, as recorded by the hydrophone array, for the three representative dates by each fish. Error bars represent ±1 SD

levels remained at a fairly consistent level during the day in both fall and winter (Fig. 4).

Instantaneous swim speeds

The final temporal scale investigated was that of instantaneous swim speeds. Again, a positive correlation was found between temperature and the frequency of faster swim speeds in both body lengths per second and meters per second. In fall, fish spent over 80% of the time swimming at a rate of 0.30 body lengths per second or less (between 0 and 0.12 m/s). The winter mean swimming speed was the lowest, with the fall and spring mean swimming speeds being 1.78 and 3.18 fold higher, respectively (Table 2, Fig. 5). In winter, fish exhibited swim speeds of 0.30 body lengths per second or less (between 0 and 0.12 m/s) over 90% of the time indicating that fish were moving much slower most of the time. During spring fish were much more active and moved faster. Approximately 55% of the observations of swimming speeds were in the 0–0.30 body lengths per second class (between 0 and 0.12 m/s) and speeds between 0.30 and 1.2 (between 0.12 and 0.60 m/s) body lengths per second accounted for

Table 2 Array tracking and manual tracking simulation instantaneous swim speeds for all 20 telemetered largemouth bass over three representative dates. All numbers are shown mean ± SD, with minimum and maximum values in parentheses below

Date	Daily water temperature (°C)	Array swim speed (m/s)	Manual mean swim speed (m/s)	Array mean swim speed (body length/s)	Manual mean swim speed (body length/s)
11/11/3	5.9 ± 0.32	0.107 ± 0.267 (0/2.67)	0.0009 ± 0.0007 (0.000017/0.0022)	0.262 ± 0.645 (0/5.99)	0.0023 ± 0.0017 (0.000042/0.0056)
1/1/4	5.1 ± 0.62	0.060 ± 0.237 (0/2.60)	0.0008 ± 0.0008 (0.000028/0.0027)	0.121 ± 0.402 (0/5.99)	0.0020 ± 0.0021 (0.000063/0.0064)
4/13/4	7.7 ± 0.82	0.191 ± 0.291 (0/2.50)	0.0008 ± 0.0011 (0.0000083/0.0041)	0.472 ± 0.715 (0/5.99)	0.0019 ± 0.0029 (0.000024/0.010)

40% of the other swim speeds. This result indicates that fish were more active during spring, a period that also had the highest water temperatures. During spring fish swam at higher speeds at least 20% more than they did during the fall and winter time periods.

Array versus manual tracking simulations

Daily swimming activity estimates were influenced dramatically by tracking interval. As described above, mean distances traveled by all individuals when tracked by the array were on the order of several km/day. When manual tracking simulations were conducted from the same empirical data set, however, daily swimming activity estimates plummeted for all seasons, in all cases to less than 0.5 km/day. These values represent a 3.5 fold decrease in estimated daily swimming activity for fall, a 3.3 fold decrease for winter, and a 12 fold decrease for spring. In addition, the positive correlation between water temperature and daily swimming activity that was present in the array tracking data was lost in the manual tracking simulation. This is not surprising considering that there was no correlation between daily swimming distance estimates generated from both techniques (Fig. 6). Mean instantaneous swimming speeds generated from manual tracking simulations were significantly lower than those empirical values from the array data in all seasons (fall, 122 fold lower; winter, 75 fold lower; and spring, 238 fold lower; Table 2, Fig. 6). Again, the positive correlation between water temperature and mean instantaneous swimming speed noted for the array tracking data was lost in the simulated manual tracking data.

Discussion

For the first time, we provide preliminary information with sub-meter accuracy on the simultaneous movement and activity of teleost fish within an entire lake. Our analyses focused on evaluating fish activity and movement at different spatial and temporal scales to yield new insights into largemouth bass behaviour as well as to assess the capabilities of the telemetry array. Hydrophone arrays that enable the real-time 3-dimensional positioning of numerous fish for extended durations, while remotely recording data on a fine scale, have enormous potential for answering biological questions (Cooke et al., 2005). Data derived from this research were incorporated into databases that can be used to form individual-based studies that continuously monitor unrestrained animals over multiple scales (Cooke et al., 2004a; Cooke et al., 2005).

Our analyses of fish movement began at a broad temporal scale, covering several seasons and eventually focused on instantaneous swimming speeds using intervals on the order of seconds. A consistent pattern was observed; i.e., there was a positive correlation between activity level of largemouth bass and water temperature at various temporal scales all derived from the same CDMA acoustic telemetry dataset. The fact that largemouth bass behaviour is influenced by temperature is not surprising and is supported by a large body of literature on largemouth bass thermal ecology (e.g., Beamish, 1970; Kolok, 1992), as well as general relationships between metabolic rate and temperature (Fry, 1971; Brett & Groves, 1979). That said, some of our findings are inconsistent with the notion that during winter, most

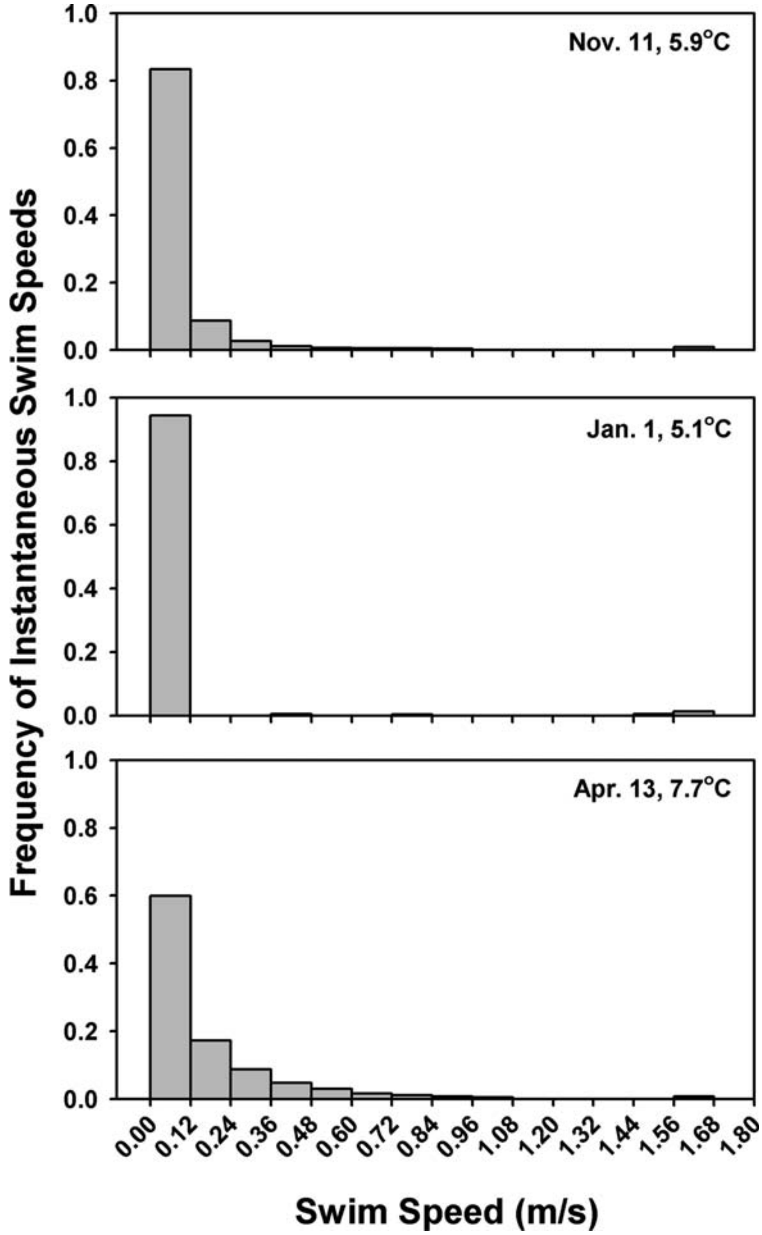

Fig. 5 Frequency histogram of instantaneous swim speeds (m/s) of 20 telemetered largemouth bass as recorded by a hydrophone array across three seasons

largemouth bass are sedentary, as has been a long standing paradigm (e.g., Heidinger, 1975). Our under-ice telemetry observations during the winter reveal that although the spatial distribution of largemouth bass is rather confined relative to the entire lake, fish still undertake significant localized movements, at times swimming at speeds up to 1.6 m/s. The majority (over 95%) of time, however, is spent swimming at speeds between zero (i.e., holding position) and 0.1 m/s. Due to the possibility of a winter energy deficit (Sullivan, 1985), coupled with thermal constraints on metabolism (Cooke et al., 2003b), when water temperatures decrease, bass may minimize energy usage by localizing movements. Restricted winter movements may also reflect environmental conditions

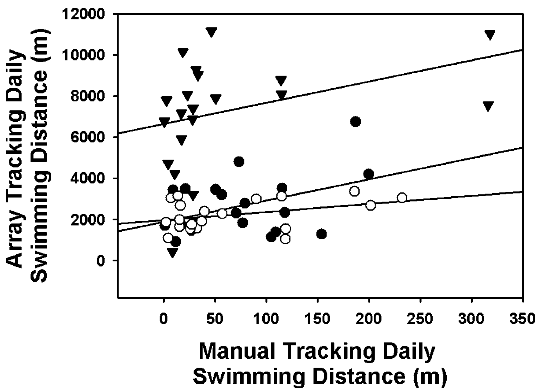

Fig. 6 Regression of array tracking vs. manual tracking daily distances swum over the three representative dates. Filled circles represent data from November 11, 2003, open circles represent data from January 1, 2004, and filled triangles represent data from April 13, 2003

that may limit distribution in a waterbody (e.g., hypoxia or anoxia). Localized movements may reflect subtle attempts to behaviourally thermoregulate (Crawshaw, 1984) or to seek or avoid other environmental conditions (Cunjak, 1996; Raibley et al., 1997). Behavioural paradigms of both warmwater fish in general and largemouth bass in particular propose that fish become quiescent in winter (Heidinger, 1975; Crawshaw, 1984). This study shows that although largemouth bass may significantly decrease activity levels during winter months, they certainly do not become completely dormant or sedentary.

In the fall, and especially in the spring, fish spent more time swimming at speeds that were between 0.2 and 1.0 m/s. Higher swim speeds during these times were positively correlated with higher water temperatures on these days. Also, fish moved up to 10.7 times farther on a daily basis in spring than winter, and up to 6.5 times farther in fall than winter. These movement patterns were also positively correlated with water temperature. Fish may show increased activity levels during fall in an attempt to obtain additional food and increase overwinter energy reserves (Miranda & Hubbard, 1994; Mackereth et al., 1999) and/or to locate overwintering regions with suitable water quality conditions (e.g., Raibley et al., 1997). Increased activity in spring may be in preparation for reproductive activities. Fish seek out food and warmer water temperatures to acquire food and enable gonad development needed for spawning. When water temperatures approach 15°C, male largemouth bass construct nests, court females, spawn, and then assume active parental care of up to one month depending on fry development (Kramer & Smith, 1962). During this season spawning and active parental care occurred during the second week of May and lasted until early June (Hanson, unpublished data). The spring date (April 13) that was analyzed in this study may have detected fish movements in preparation for spawning.

Across the three periods examined, largemouth bass activity (daily distance swam) varied considerably, and this variation may be partly due to competition and prey density. During warmer months, patches of vegetation attract both prey species seeking to avoid being consumed (Crowder & Cooper, 1979), as well as largemouth bass involved in ambush predation (Savino & Stein, 1982; Valley & Bremigan, 2002). Largemouth bass may therefore seek out areas of intermediate structural complexity that increase prey density as well as improve the probability of encountering a prey item (Crowder & Cooper, 1979). Due to the fact that vegetation growth in lakes is partly influenced by light penetration into water, many vegetated areas occur in the shallow reaches of the water column (Barko & Smart, 1981; Sheldon & Boyle, 1977) and are limited during the winter when the lake is covered by ice. In the spring, when vegetation has just begun to emerge, largemouth bass may be quite active as they search for ideal areas in which to forage. When vegetated areas are fully grown in, largemouth bass activity may decline as fish remain in localized areas while foraging. Therefore, the seasonal variation in swimming activity observed in largemouth bass may be partly driven by habitat complexity, competition, and prey behavior. Future studies to document vegetation dynamics will be needed to elucidate its potential role in mediating activity associated with competition and foraging.

Individual variation in daily distances traveled was greatest during spring, correlating with the highest water temperatures. Differences of up to 25 fold were seen between individuals on the April sampling day. In November, differences as great as 7.4 fold were seen. The lowest amount of variation occurred in January (up to 3.2 fold). This same variation occurred with hourly movements as well, indicating that individual fish behave much more similarly during winter than during either fall or spring. This finding is consistent with other work (Carlson, 1992; Karchesky & Bennett, 2004) that points to the fact that largemouth bass enter large aggregations and make localized movements during winter. In addition to variation among individuals and across seasons, diel differences were also noted. Interestingly, these differences were only apparent in the spring and were characterized as elevated activity during the day, with slightly higher peaks at dawn and dusk. Previous laboratory research has revealed that largemouth bass exhibit crepuscular activity peaks at warm water temperatures (Reynolds & Casterlin, 1978).

Data analysis on multiple scales can be used to develop energetic models of free-swimming fish, but of particular relevance are the data generated from the instantaneous swimming speeds (Lucas et al., 1993; Cooke et al., 2004b). Profiles of fish swimming speeds are typically generated by manually tracking telemetered fish to determine rates of movement (Lucas & Baras, 2000) or using physiological telemetry to assess muscle activity or tail beats (Demers et al., 1996; Cooke et al., 2004b). Our data on swim speeds represent one of the first long-term tracks of fish swimming activity at this whole-lake scale for multiple individuals. As discussed above, we noted that fish spent little time swimming faster than 1 m/s, even in the spring. This is not surprising considering both the swimming capability of bass as well as the sampling limitations associated with the transmitters that we used. Based upon laboratory swim tunnel work, field acclimated juvenile largemouth bass are believed to have maximum critical swimming speeds (i.e., the speed at which fish switch from aerobic to anaerobic activity) of 2.22 body lengths per second at 5°C (Kolok, 1992). Although we monitored fish in three seasons, the water temperature was always reasonably low. In fact, much of the current dogma on largemouth bass is that they are quiescent below about 8°C (our highest temperature analyzed here was 7.7°C), reflecting the fact that under laboratory conditions bass often fail to swim at low water temperatures (Cooke et al., 2001b). It is somewhat remarkable, therefore, that we observed the level of activity that we did. A second reason why we detected so little high speed swimming may be because the "instantaneous" speeds we generated are actually average speeds over a 15 s or greater period. Using transmitters with more frequent burst rates would greatly improve our ability to generate detailed information on swimming dynamics and energetics. Furthermore, because fish rarely swim in a straight line, more frequent pulses would also reduce underestimates of activity costs. That said, the dataset that we present is truly unique and unprecedented in its level of detail.

When the same dataset was subjected to simulated manual tracking, fish activity estimates were greatly underestimated. Multiple studies have indicated that telemetry investigations that utilize large time intervals between position solutions may in fact miss the vast majority of daily movements by fish. For example, experiments described in Demers et al. (1996) using EMG telemetry revealed that the majority of largemouth bass activity on daily basis may occur at spatial and temporal scales that are too small to be detected by current telemetry techniques that rely upon generating position solutions using manual tracking. Løkkeberg et al. (2002) showed that when artificially increasing the interval between signal transmissions, estimates of swimming speeds of cod (*Gadus morhua*) were decreased by 30–70%. Ovidio et al. (2000) also found a drastic reduction in accuracy of home range estimates of brown trout (*Salmo trutta*) when utilizing subsamples of a dataset with longer intervals between radio tracking position fixes. Our findings also indicate that manual tracking with larger intervals between position solutions may be particularly prone to underestimating movement and activity levels for fish that are highly mobile, but on a localized basis (or, in this case, during seasons when fish show increases in activity and mobility). Underestimation of fish movements seemed to be at the lowest during periods when the fish were most sedentary. During these time periods, although fish are least active and occupy the most discrete areas, longer intervals between position solutions are less likely to miss gross movements. In addition, we observed dramatic differences in daily activity estimates depending upon how these activity estimates were generated. For example, to evaluate seasonal trends at weekly intervals, we calculated distances using mean hourly position (Fig. 1). Conversely, to evaluate more fine scale activity, we summed the distances between every valid position solution (Figs. 2–5). Not surprisingly, using average hourly position solutions generated lower activity estimates than when all data points were essentially connected and summed. These findings have profound ramifications for the field of energetics modeling based upon field data, as discussed by Cooke et al. (2001a). Due to the differences between activity estimates based upon time interval between position solutions and on how data are analyzed, much of the current energetics modeling efforts likely incorporates activity estimates that are underestimations of actual fish activity. Not only is this relevant to understanding variation among studies, it is also important when considering variation and in selecting data analysis techniques within a single study or dataset.

This paper, based upon work collected during a trial period for the whole lake array, is intended to help focus future research efforts. Indeed, to refine our energetic estimates and develop seasonal sex-specific energetics models, transmitters with more frequent burst rates should be utilized (recognizing the tradeoffs between burst rate, battery life, and transmitter size). A study by Rand & Hinch (1998) determined that averaging over periods even as short as 5 s can underestimate the true costs of activity for migratory salmonids. Furthermore, this technology shows much promise for being able to detect the frequency with which fish burst at speeds that require anaerobic metabolism. Integrating this CDMA technology with other sensors such as EMG could provide information on fish energetics during periods when fish are stationary in terms of an *X–Y* coordinate but are turning continuously, such as those activities that occur when male largemouth bass are engaged in parental care. Future research efforts will focus on more detailed analyses of distribution, movements, depth use, habitat relationships and the factors associated with individual variation. Novel analytical software and filtering techniques currently under development will enable us to process and analyze data for the entire study period, providing power for statistical tests and enabling hypothesis driven research.

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