

Intersexual variation in the seasonal behaviour and depth distribution of a freshwater temperate fish, the largemouth bass

K.C. Hanson, C.T. Hasler, S.J. Cooke, C.D. Suski, and D.P. Philipp

Abstract: Because fish are poikilothermic, water temperature is regarded as a primary factor influencing their activity and behaviour. Rarely have field studies been conducted with the spatiotemporal resolution to enable rigorous quantitative assessments of that relationship. Furthermore, there have been few studies that have considered the influence of sex on the seasonal behaviour of fish. Twenty largemouth bass (*Micropterus salmoides* (Lacepède, 1802)) were implanted with coded acoustic telemetry transmitters and remotely tracked in near real time in a small lake in Ontario, Canada, via a whole-lake hydrophone array between 1 November 2004 and 30 September 2005. Fish inhabited the deepest waters and were least active during the winter months under ice. During the warmest months, fish were most active and inhabited the littoral zone. Sex-specific differences were noted year-round. Reproductive males were less active and inhabited shallower depths during the spawning and post-reproductive periods. Reproductive males inhabited the deepest depths during winter and fall, with nonreproductive males at the shallowest depths. Throughout the year, the behaviour of nonreproductive males and females was similar. While differences in behaviour of bass are primarily driven by water temperature, sex and reproductive status play important roles year-round, especially during and after the reproductive period.

Résumé : Parce que les poissons sont des poikilothermes, la température de l'eau est considérée comme un des facteurs principaux qui influencent leur activité et leur comportement. De rares études ont été menées à une échelle spatio-temporelle assez fine pour permettre des évaluations quantitatives rigoureuses de cette relation. De plus, peu d'études ont pris en considération l'influence du sexe sur le comportement saisonnier des poissons. Nous avons muni 20 achigans à grande bouche (*Micropterus salmoides* (Lacepède, 1802)) d'émetteurs acoustiques codés de télémétrie et nous les avons suivis en temps quasi réel dans un petit lac de l'Ontario, Canada, à l'aide d'un réseau d'hydrophones répartis sur l'ensemble du lac entre le 1^{er} novembre 2004 et le 30 septembre 2005. Les poissons se retrouvent dans les eaux les plus profondes et sont le moins actifs durant les mois d'hiver sous la glace. Durant les mois les plus chauds, les poissons sont le plus actifs et ils habitent la zone littorale. Il existe des différences spécifiques au sexe pendant toute l'année. Les mâles reproducteurs sont moins actifs et se retrouvent dans les eaux les moins profondes durant la fraye et la période qui suit la reproduction. Les mâles reproducteurs sont dans les profondeurs les plus grandes durant l'hiver et l'automne, alors que les mâles non reproducteurs se trouvent dans les sites moins profonds. Durant toute l'année, les comportements des mâles non reproducteurs et des femelles sont semblables. Bien que les différences de comportement des achigans s'expliquent principalement par la température de l'eau, le sexe et le statut reproducteur jouent un rôle important pendant toute l'année, mais particulièrement durant et après la période de reproduction.

[Traduit par la Rédaction]

Introduction

A number of abiotic factors can influence the behaviour, activity, and depth utilization of teleost fishes (Hoar and Randall 1971). These factors include dissolved oxygen concentrations (Domenici et al. 2000; Burlinson et al. 2001),

atmospheric conditions (Popiel et al. 1996), and light intensity (Beers and Culp 1990; Kolok 1991). However, water temperature has been regarded as the primary determinant of many aspects of the biology of fishes and has been referred to as "the master" environmental factor (Beamish 1970; Brett 1971; Hazel 1993). Water temperature affects

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metabolism (Fry 1971; Brett and Groves 1979; Cooke et al. 2003b) and growth (Nunn et al. 2003; Gabillard et al. 2005) as well as initiation of spawning (Kramer and Smith 1962), migration (Bjornn 1971; Jonsson et al. 1990), and winter dormancy (Crawshaw 1984), underscoring its importance on overall function, activity, and spatial distribution of fish.

The current body of literature argues that, in general, fishes from temperate latitudes should behave differently during winter relative to other seasons, with these changes in behaviour being due to decreases in water temperatures. As water temperature decreases, fish should reduce their activity (Todd and Rabeni 1989), lower their rate of movement (Kolok 1991; Cote et al. 2003), and utilize deeper water (Lewis and Flickinger 1967; Raibley et al. 1997; Karchesky and Bennett 2004). Fish in cold water also show reduced swimming performance relative to fish in warmer water when tested in a controlled laboratory environment (Larimore and Duever 1968; Berry and Pimentel 1985). Individual species vary with respect to the degree to which their activity is reduced during winter, but many species are believed to enter a state of extended torpor during the winter season, especially under the cover of ice (Crawshaw 1984; Cunjak 1996).

In addition to the regulating impacts of abiotic factors on behaviour, the behaviour of teleost fishes is also influenced through a complex interplay of multiple biotic factors. Temperate fish behaviour has been shown to vary significantly within species with respect to life history strategies (Gross 1979), ontogeny (Lenormand et al. 2004; Georgalas et al. 2007), and size (Bradford and Higgins 2001; Bystrom et al. 2003; Magnhagen 2006; Potthoff and Christman 2006). Furthermore, sex-specific differences in behaviour are increasingly being documented for a number of temperate freshwater fish species (Magurran and Garcia 2000; reviewed in Hanson et al. 2008). Sex-specific differences in behaviour have been noted not only in relation to the spawning period proper but also relative to feeding (Davies 1991; Temming and Hammer 1994; Oxenford and Hunte 1999), predator avoidance (Giles and Huntingford 1984; Andersson 1994), aggression (Johnsson and Akerman 1998), and migratory behaviour and swimming activity (Jonsson et al. 1990; MacNutt et al. 2006). However, there is currently a general lack of information describing gross-scale behavioural differences between the sexes outside the reproductive period.

In this study, we used telemetered largemouth bass (*Micropterus salmoides* (Lacepède, 1802)) monitored by a whole-lake acoustic hydrophone array in eastern Ontario, Canada, as a model to investigate the effects of sex and water temperature on the depth utilization and activity across a complete annual cycle. Largemouth bass are a widely distributed temperate freshwater fish native to eastern North America where they tend to occupy lentic waters. There is a wide body of literature based on laboratory studies of largemouth bass that suggests that they are quiescent when water temperatures are low, as would be experienced by bass during the winter in the northern parts of their distribution including eastern Ontario (Crawshaw 1984). As such, we predicted that water temperature was the primary cue that would influence changes in behaviour by individuals throughout the year. Specifically, we predicted that decreasing water temperatures throughout the fall would

trigger individuals to limit movements (realized as a decrease in daily distance traveled) and begin to utilize deeper waters. When water temperatures increased after ice melt in the spring, we predicted that fish would begin to expand both their range of activity and their range of depths utilized. Additionally, other abiotic factors such as wind speed and rainfall were included in analysis to determine to what extent, if any, local weather patterns affected bass behaviour. We also predicted that sex-specific cues related to spawning would influence behaviour during the reproductive period in spring because reproductive-aged largemouth bass exhibit sexual dimorphism in terms of behaviour during the reproductive period. Further, because of the energetic costs of parental care to the individual (Mackereth et al. 1999; Cooke et al. 2002), we predicted that sex-specific differences would occur in multiple seasons outside the reproductive period.

Methods

Study site

This study was carried out from 1 November 2004 through 30 September 2005 in Warner Lake, eastern Ontario, Canada (44°31'N, 76°20'W), and is wholly enclosed on Queen's University Biological Station property, thereby enabling the monitoring of individual fish implanted with transmitters without disturbance from unauthorized personnel. Further details on the lake structure and community can be found in Suski (2000) and Hanson et al. (2007). Briefly, Warner Lake is a small lake (8.3 ha surface area) comprising a shallow basin (maximum depth 2 m) and a deep basin (maximum depth 7 m). The lake is characterized by homogenous habitat consisting of extensive littoral zone featuring both emergent and submergent macrophytes as well as large amounts of fallen timber. Other documented fish species include white sucker (*Catostomus commersonii* (Lacepède, 1803)), pumpkinseed (*Lepomis gibbosus* (L., 1758)), yellow perch (*Perca flavescens* (Mitchill, 1814)), brown bullhead (*Ameiurus nebulosus* (Lesueur, 1819)), and golden shiner (*Notemigonus crysoleucas* (Mitchill, 1814)).

Study animals

Largemouth bass were collected by angling between 14 and 18 October 2004. In total, 11 males and 9 females (mean \pm SD: males, 948 \pm 220 g; females, 925 \pm 210 g) were implanted with code division multiple access temperature-pressure sensing acoustic transmitters (Lotek CTP-M11-25, 11 mm \times 25 mm, signal transmission rate 15 s, depth resolution \pm 0.7 m, temperature resolution \pm 0.5 °C, life expectancy of 1 year, weight 10.0 g in air; Lotek Wireless, Inc., Newmarket, Ontario) following methods described in Cooke et al. (2003a) and Hanson et al. (2007). Prior to surgery, individual fish were anesthetized in an induction bath of clove oil (0.6 mL/L (60 ppm) emulsified in ethanol, clove oil-ethanol, 1:9) and ethanol (Anderson et al. 1997). Following loss of equilibrium, fish were measured (total length to the nearest millimetre) and weighed (mass to the nearest gram). During surgery, a recirculating maintenance dose of anesthetic (20 ppm clove oil) in lake water was used to irrigate the gills. The sex of individuals was determined during transmitter implantation via inspection of

Table 1. Environmental and intrinsic biological variables of largemouth bass (*Micropterus salmoides*) measured at Warner Lake.

	Instrument	Units measured
Environmental variable		
Water temperature	Temperature sensor on internally implanted transmitter	°C
Depth	Pressure sensor on internally implanted transmitter	m
Wind speed	Anemometer at Queen's University Biological Station	km/h
Rainfall	Rain gauge at Queen's University Biological Station	mm
Barometric pressure	Environment Canada weather archive	kPa
Intrinsic biological variable		
Sex	Determined visually during transmitter implantation	Male or female
Male reproductive status	Determined if male spawned during the study	Nonreproductive or reproductive

internal anatomy. Two simple interrupted sutures (3/0 PDS II, absorbable monofilament sutures; Ethicon, Inc.) were used to close the incision. Additionally, all individuals were marked with a passive integrated transponder to allow for future identification. All surgeries were conducted by the same experienced individual to eliminate variance associated with multiple surgeons (Cooke et al. 2003a). Following surgery, fish recovered in coolers containing lake water until equilibrium was regained (usually within 5 min) and were released in the lake at a central location.

Telemetry array

Fish movements were recorded by a fixed-station acoustic telemetry array installed in Warner Lake in November of 2003. The array consists of two multiport MAP_600 receivers monitoring 13 hydrophones configured in an optimal geometry to provide coverage throughout the entire lake. Details on system performance and accuracy can be found in Niezgodá et al. (2002) and Hanson et al. (2007). Briefly, the system relies upon code division multiple access technology that encodes transmissions from each telemetered individual, thereby eliminating issues associated with signal collision and data loss associated with monitoring multiple transmitters on the same frequency in a discrete area. Positions calculated by triangulation with as little as four hydrophones have submetre precision within the footprint of the array and precision greater than 1 m outside the footprint of the array. Submetre positioning of instrumented fish results from the geometry of the implemented hydrophone array, which was surveyed by differential GPS (± 0.2 m) (Niezgodá et al. 2002). Error decreases significantly as more hydrophones receive the transmissions and are added to triangulation calculations (Niezgodá et al. 2002). All received data were logged on flash storage cards and routinely transferred to a personal computer for subsequent processing.

Data processing and analysis

Data processing details may be found in Niezgodá et al. (2002) and Hanson et al. (2007). Raw data were loaded into the software program BioMAP (version 2.1.12.1; Lotek Wireless Inc.) and then subjected to a two-dimensional positioning engine to form raw position solutions (depth was determined using a pressure sensor). To remove outliers, multiple filtering procedures within BioMAP, as detailed in Niezgodá et al. (2002), were applied to the data. These filters assessed the numerical stability of each transmission event, removing nonstable positions. Additionally, any trans-

mission events that did not exhibit a submetre geometric dilution of precision were removed.

To quantify activity over approximately one calendar year, every day across the time period of 1 November 2004 through 30 September 2005 was included in the analyses, and information tables for each individual were gathered from fully filtered data. For analytical purposes, a day was defined as starting with the closest point to 00:00 and ending with the closest signal to 23:59:59. Mean daily depth was determined by summing all depth information transmitted by an individual across the course of a day and then dividing by the number of depth transmission events. Mean daily temperature was determined by summing all temperature information transmitted by an individual across a single day and then dividing by the number of temperature transmission events. Activity was quantified by calculating the daily distance traveled, which, therefore, corresponded to the total linear distance covered by the fish (i.e., the distance between each successive X,Y position was calculated assuming that the fish maintained the same elevation (Z) between positions and summed across an entire day). Although the linear distance traveled served as a good indicator of daily activity throughout the year, we realize that the telemetry system may not be able to detect linear movements when an individual is conducting movements below the resolving power of the array (>1 m).

Environmental data and intrinsic biological measures

All environmental data (with the exception of water temperature and barometric pressure) were measured at Queen's University Biological Station using a monitored weather station approximately 10 km east of Warner Lake (Table 1). Wind speed was recorded in kilometres per hour with a Met One model 013A heavy duty wind speed sensor (by Met One Instruments, Inc., Oregon), while rainfall was measured in millimetres with a model RG2501 Sierra tipping bucket rain gauge (Sierra-Misco, Inc.). Measurements were taken every 5 s and later pooled to generate daily mean values. Water temperature was recorded every 30 s by the transmitters implanted into the fish with a resolution of ± 0.5 °C. Daily mean barometric pressures (kilopascals) for the nearest major city (Ottawa, Ontario, ~ 125 km) were obtained from the Environment Canada weather archive (climate.weatheroffice.ec.gc.ca/climateData). As mentioned above, these temperature readings were averaged across all fish to determine mean daily water temperatures. Subsequent reproductive status as males, defined as either reproductive

(spawning) or nonreproductive (not spawning), was determined by daily snorkeling surveys in the littoral zone during the spring nesting period and examination of telemetry data. Subsequently, nesting male bass were angled from the nest and scanned for passive integrated transponder tag presence. Of the 11 male bass telemetered, 3 fish (mean \pm SD: reproductive males, 1098 ± 240 g; nonreproductive males, 922 ± 206) constructed nests and successfully received eggs. All three were successful at raising their broods to the point where the offspring became independent of male parental care. We were unable to determine the reproductive status of female fish because direct observation of spawning events was not possible.

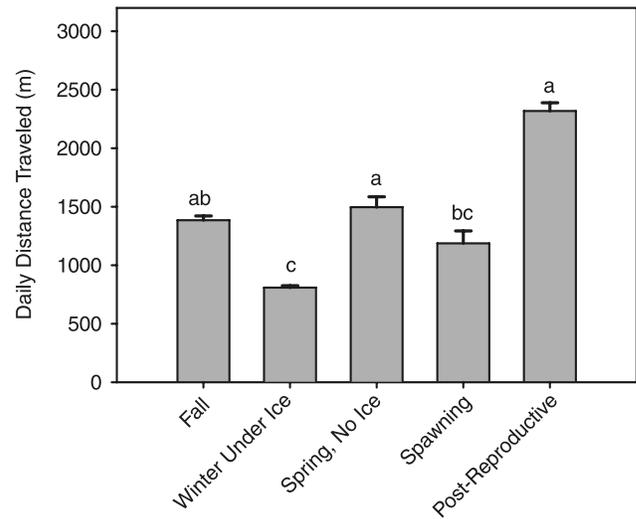
For further analysis, data were divided into five ecologically relevant time periods that correspond to key seasonal periods in the annual cycle or key life history periods for largemouth bass. The winter under ice period was defined as the time from which the entire lake was covered by ice (3 December 2004) until the lake was ice free in the spring (11 April 2005). The spring no-ice period was defined as the time between when the lake was ice free (12 April 2005) and when snorkeling surveys found the first newly spawned bass nest with eggs (9 May 2005). The spawning period was determined by visual observation of male nesting activity and was defined as the time period between when the first nest received eggs (9 May 2005) until the last nest was vacated by the attending male at the cessation of the parental care period (1 June 2005). The post-reproductive period extended from the cessation of the spawning period (2 June 2005) until water temperatures decreased to 20°C (from this point on in the year, water temperatures steadily decreased until ice formed on the lake) (31 August 2005). Lastly, the fall period was defined as the days preceding ice cover on the lake in 2004 (1 November–3 December 2004) as well as the time after the post-reproductive period until transmitters stopped functioning because of battery drain in 2005 (1–30 September 2005).

Statistical analysis

A repeated-measures (with individual as the repeated variable) analysis of variance (ANOVA) was employed to determine differences in both behaviour and depth utilization between the sexes and across the five ecologically relevant time periods (Day and Quinn 1989; Zar 1999). The type IV sum of squares method was selected because of unequal sample sizes between sexes ($n_{\text{females}} = 9$, $n_{\text{nonreproductive males}} = 8$, $n_{\text{reproductive males}} = 3$). The repeated-measures ANOVAs and subsequent post hoc tests were performed using SPSS version 14.0 (SPSS, Inc., Chicago, Illinois). One-way ANOVAs followed by a Tukey HSD post hoc test were employed to test for sex-specific differences in activity and depth utilization within ecologically relevant time periods using the statistical package JMP IN version 4.0 (SAS Institute, Inc. Cary, North Carolina). If the homogeneity-of-variances assumption was violated (assessed using the Levene test; Zar 1999), a Welch ANOVA was utilized.

Two different forward-loading stepwise multiple regression (using JMP IN version 4.0) were utilized to determine the factors most influencing behaviour throughout the year (Cohen et al. 2003). The first model had activity rate (de-

Fig. 1. Mean daily distance traveled for 20 largemouth bass (*Micropterus salmoides*) outfitted with acoustic tags during ecologically relevant time periods. Letter groups denote between-season significant differences ($P < 0.05$).



finer as daily distance traveled in metres) as the dependant variable, while the second had average daily depth in metres below the surface as the dependant variable. The independent variables for all regressions were activity (daily distance traveled), daily mean depth, daily mean water temperature, daily mean wind speed, daily total rainfall, daily mean barometric pressure, sex, and reproductive status of male fish. Parameter effects and measures of significance were determined by running the final model through the standard least squares method regression tool. The level of significance for all tests (α) was assessed at 0.05 (Zar 1999). All values presented represent means \pm SE unless otherwise noted.

Results

Year-round activity and depth utilization

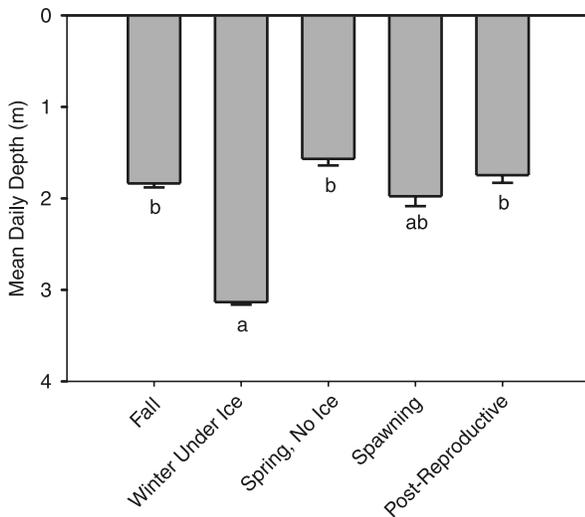
Variations in both activity and depth utilization were noted between ecologically relevant time periods. Specifically, largemouth bass traveled the least during two periods (Fig. 1): winter (when ice covered the lake) and during spawning period (when males were guarding nests). Coinciding with the decreases in movement, largemouth bass selected deeper positions in the water column during the winter period (Fig. 2). Following the melting of ice in the spring, mean daily distance swum increased approximately twofold relative to winter distances swam, and fish also inhabited shallower water (usually <2 m deep; distance traveled repeated-measures ANOVA: $F_{[4,60]} = 8.41$, $P < 0.001$; depth utilization repeated-measures ANOVA: $F_{[4,64]} = 7.17$, $P < 0.001$ (Table 2; Figs. 1 and 2). Daily distance traveled by largemouth bass was highest during the post-reproductive period, which also corresponded to the warmest months of the year (Fig. 1). There were no significant effects of sex on either activity or depth utilization between time periods, indicating that all the sexes had similar patterns in depth utilized and daily distances swum when measured at a gross scale across all ecologically relevant time periods (distance traveled repeated-measures ANOVA: $F_{[8,60]} = 0.67$, $P = 0.72$;

Table 2. One-way analysis of variance for differences in largemouth bass (*Micropterus salmoides*) activity and depth utilization within ecologically relevant time periods and separated by reproductive status in Warner Lake.

Time period and dependent variable	Source	df	F	P
Fall activity	Reproductive status	2, 153	0.34	0.72
Fall depth	Reproductive status	2, 380.56	31.93	<0.0001†
Winter ice activity	Reproductive status	2, 312	0.48	0.62
Winter ice depth	Reproductive status	2, 312	4.77	0.009
Spring no-ice activity	Reproductive status	2, 54	0.32	0.73
Spring no-ice depth	Reproductive status	2, 126.07	1.15	0.32†
Spawning activity	Reproductive status	2, 236.81	21.69	<0.0001†
Spawning depth	Reproductive status	2, 191.5	19.55	<0.0001†
Post reproductive activity	Reproductive status	2, 290.54	6.27	0.002†
Post reproductive depth	Reproductive status	2, 252.36	11.66	<0.0001†

Note: *Italicized* statistical output indicates a significant difference at $\alpha = 0.05$. If variances were heterogeneous, Welch’s ANOVA was utilized (denoted by a dagger).

Fig. 2. Mean daily depth utilized of all fish across ecologically relevant time periods for largemouth bass (*Micropterus salmoides*) in Warner Lake. Letter groups denote between-season significant differences (Bonferroni-adjusted multiple comparisons); $n = 20$ for each time period.



depth utilization repeated-measures ANOVA: $F_{[8,64]} = 0.54$, $P = 0.83$) (Figs. 1 and 2).

Multiple regression analyses revealed that the average daily water temperature inhabited by largemouth bass was the best indicator of both activity and depth utilization across the entire year of the study (Table 3). Of all of the environmental factors measured, water temperature explained the greatest amount of variance associated with both the activity model (sequential $R^2 = 0.314$, Table 3) and the depth utilization model (sequential $R^2 = 0.327$, Table 3). As evidenced by the parameter estimates, average water temperature was positively correlated with both activity and the utilization of shallower depths throughout the seasons (Figs. 3–5). Other factors, such as male reproductive status, average daily depth, average wind speed, average daily barometric pressure, and average wind direction, were found to contribute significantly to daily activity and depth utilization but accounted for smaller proportions of the variance in the model (Table 3).

Sex-specific differences in seasonal activity and depth utilization

Sex-specific differences in both behavioural metrics (i.e., activity and depth utilization) were noted during multiple ecologically relevant time periods. More specifically, largemouth bass depth utilization was influenced by both sex and reproductive status in every time period except for the spring no-ice period. During under ice winter periods, reproductive male bass inhabited deeper water than nonreproductive male bass (Table 2; Fig. 6), although these differences did not persist into the spring ice-free period (Table 2; Figs. 6 and 7). Sex-specific differences in behaviour were most apparent during the spawning period (Figs. 6 and 7). During spawning, reproductive male daily distance traveled was 43% that of females and 37% that of nonreproductive males (Table 2; Figs. 6 and 7). Additionally, reproductive males also inhabited the shallowest mean depth (1.15 m) in the lake during spawning, followed by females (1.79 m) (Table 2; Figs. 6 and 7). Nonreproductive males selected the deepest mean depth (2.59 m) during the spawning season (Table 2; Figs. 6 and 7). Sex-specific differences in daily distance traveled and depth utilization persisted into the post reproductive period, as reproductive males were approximately 70% as active as other fish and inhabited 70% shallower water (Table 3; Figs. 6 and 7). Lastly, reproductive males inhabited the shallowest depths during the fall months when compared with females and nonreproductive males (Table 2; Fig. 6).

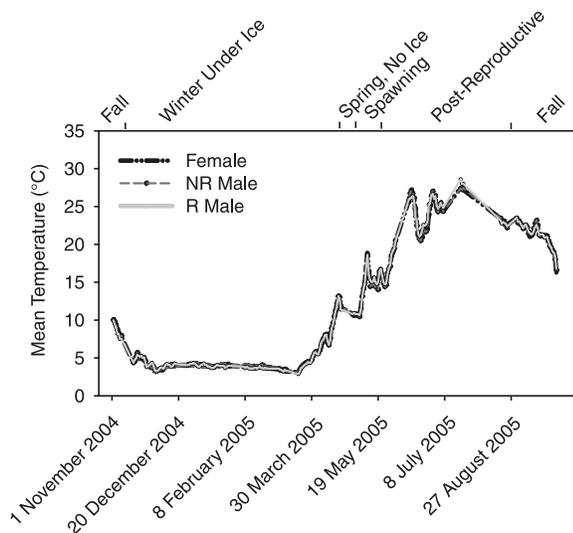
During the spawning period, sex, reproductive status and environmental factors were all significant indicators of activity and depth distribution (Table 3). Average daily depth explained the most variance associated with the activity model (sequential $R^2 = 0.37$, Table 3), followed by sex of the individual (Table 3). Female and nonreproductive male fish traveled the largest distances daily during the spawning period (Figs. 3 and 6). Depth distribution was strongly influenced by reproductive status (for males, Table 3) and the sex of the individual (Table 3). Reproductive male fish were located shallower in the water column, with nonreproductive males at intermediate depths and female fish in the deepest water (Figs. 4 and 7). Interestingly, average daily water temperature had little to no effect on activity and depth utilization during this period (Table 3).

Table 3. Results of forward-loading stepwise multiple regressions to determine the effects of various environmental cues, sex, and reproductive status on the activity and depth utilization of largemouth bass (*Micropterus salmoides*) outfitted with acoustic tags.

Model	Sources of variation	Sequential R^2 explanation (%)	F	P
Mean daily distance swum (m), entire year	Reproductive status	1.6		<i><0.001</i>
	Average Depth	3.8		<i><0.001</i>
	Average water temperature	31.4		<i><0.001</i>
	Average barometric pressure	<1		<i><0.001</i>
	Average wind speed	<1		0.25
	Whole model	37.8	81.49	<i><0.001</i>
Depth (m), entire year	Sex	<1		0.16
	Average water temperature	32.7		<i><0.001</i>
	Average barometric pressure	2.1		<i><0.001</i>
	Average wind speed	1.5		<i><0.001</i>
	Average distance traveled	3.7		<i><0.001</i>
	Whole model	40.2	90.39	<i><0.001</i>
Mean daily distance swum (m) during spawning period	Sex	5		0.01
	Average depth	37.5		<i><0.001</i>
	Average water temperature	5.3		0.02
	Average wind speed	1.3		0.19
	Whole model	46	16.15	<i><0.001</i>
	Depth (m) during spawning period	Sex	24.8	
Reproductive status		57.1		<i><0.001</i>
Average wind speed		<1		0.06
Rainfall		<1		0.03
Average distance traveled		1.4		0.01
Whole model		84	75.74	<i><0.001</i>

Note: *Italicized* statistical output indicates a significant difference at $\alpha = 0.05$. In the study, 20 fish were tagged, with 3 being reproductive males, 9 being females, and 9 being nonreproductive males.

Fig. 3. Plot of daily average water temperature within Warner Lake across 1 year beginning with 1 November 2004 and split by sex and reproductive status of male largemouth bass (*Micropterus salmoides*) (NR, nonreproductive; R, reproductive) with ecological time period on the top x -axis and date on the bottom x -axis.



Discussion

As poikilotherms, the metabolism of largemouth bass is governed by ambient temperature (Fry 1971; Brett and Groves 1979). Because of this temperature constraint, it is

understandable that largemouth bass would alter their behaviour in winter by reducing activity (Cooke et al. 2003b) that may force fish to enter into a quiescent state to conserve energy stores (Crawshaw 1984). In the current study, the activity level of telemetered largemouth bass in the winter was decreased by 60% compared with levels observed during warmer months. Fish may restrict winter movements to behaviourally thermoregulate (Crawshaw 1984) or to seek out other favourable environmental conditions (e.g., oxygen concentrations; Cunjak 1996). Low water temperatures can directly lower maximum swimming speeds by decreasing the efficiency of biochemical reactions resulting in increases in the amount of time required for muscle contraction, which also reduces tail beat frequency (Wardle 1980) as well as power output (Rome 1990). Additionally, low water temperatures reduce the scope of cardiac output (Kolok 1991) and may decrease the ability of a fish to uptake and transport oxygen (Pörtner 2002). Thus, the results from this study clearly demonstrate that largemouth bass experienced decreased activity levels during winter when water temperatures are lowest. Similarly, water temperature influenced the depth distribution of largemouth bass more than any other factor analyzed in this study. Many studies have shown that as water temperature decreases during the fall, centrarchid fishes move to overwintering habitat that is typically deeper than summer habitat (Langhurst and Schoenike 1990; Karchesky and Bennett 2004). The shift to deeper water observed in our study is likely a result of fish migrations to overwintering areas. Other than a correlation with depth of the lake, no abiotic information was obtained in the present

Fig. 4. Plot of daily average activity (distance traveled) of largemouth bass (*Micropterus salmoides*) in Warner lake across 1 year beginning with 1 November 2004 and split by sex and reproductive status of male fish (NR, nonreproductive; R, reproductive) with ecological time period on the top x-axis and date on the bottom x-axis.

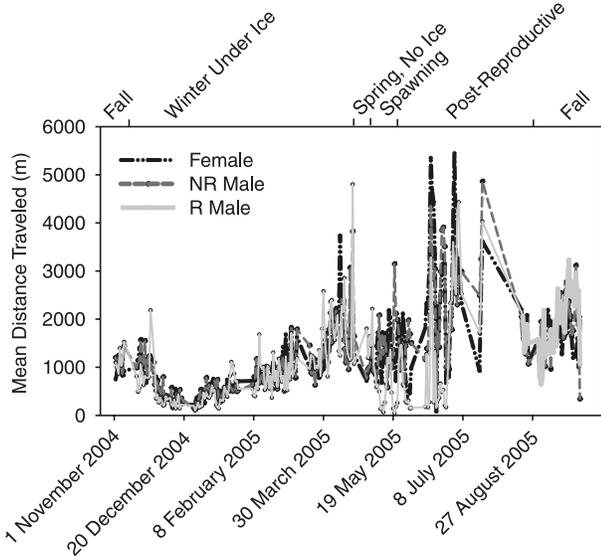
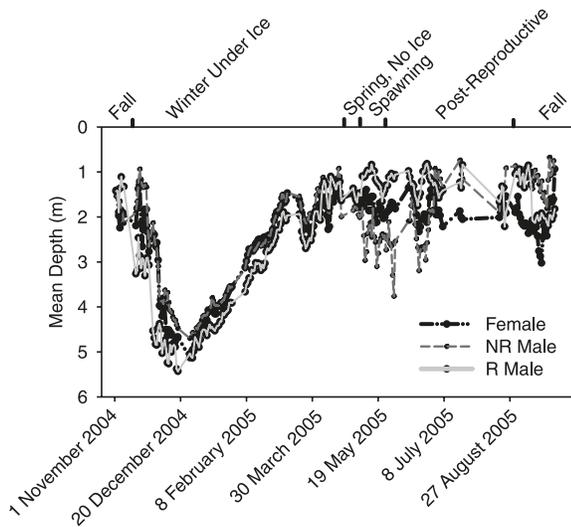


Fig. 5. Plot of daily depth utilization of largemouth bass (*Micropterus salmoides*) in Warner lake across 1 year beginning with 1 November 2004 and split by sex and reproductive status of male fish (NR, nonreproductive; R, reproductive) with ecological time period on the top x-axis and date on the bottom x-axis.



study to determine the causal factors for the movement to these portions of the lake.

While temperature plays a major role in dictating bass behaviour, sex-specific differences in behaviours were noted throughout the year. This was especially evident during the spawning period, as both sex and reproductive status influenced mean daily distance traveled and depth utilization. While initiated by ambient water temperature, male bass spawning behaviour is radically different during the parental care period. When water temperatures reach approximately

Fig. 6. Mean daily depth utilized across ecologically relevant time periods for telemetered largemouth bass (*Micropterus salmoides*) in Warner Lake separated by sex and reproductive status of male fish (NR, nonreproductive; R, reproductive). Number groups denote within-season significant differences (Tukey HSD post hoc test). Error bars represent ± 1 SE; $n_{\text{female}} = 9$, $n_{\text{nonreproductive male}} = 8$, $n_{\text{reproductive male}} = 3$.

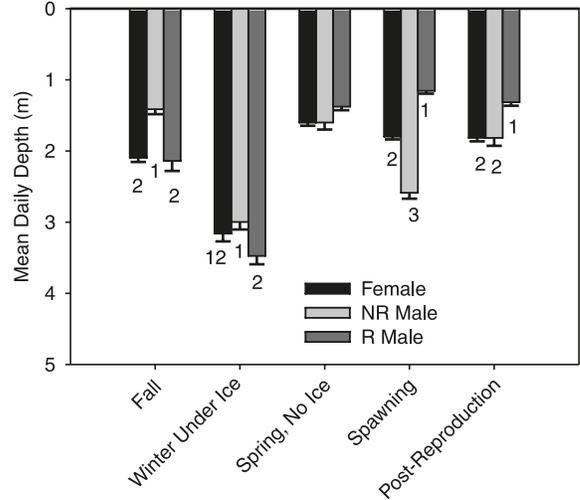
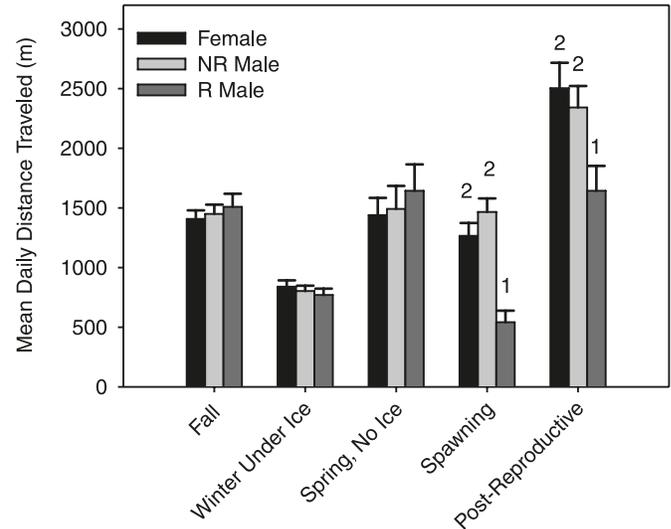


Fig. 7. Mean daily distance traveled across ecologically relevant time periods for telemetered largemouth bass (*Micropterus salmoides*) in Warner Lake separated by sex and reproductive status of male fish (NR, nonreproductive; R, reproductive). Number groups denote within-season significant differences (Tukey HSD post hoc test). Error bars represent ± 1 SE; $n_{\text{female}} = 9$, $n_{\text{nonreproductive male}} = 8$, $n_{\text{reproductive male}} = 3$.



14 °C, males move into the shallow littoral zones of a lake and construct saucerlike nests in the substrate to which they court females and attempt to spawn (Kramer and Smith 1962). If a male receives eggs, he will remain at the nest providing parental care (in the form of brood defense and maintenance) until the fry have hatched and become independent, a time period typically lasting up to a month (Kramer and Smith 1962). These parental care activities occur in the immediate vicinity of the brood, thereby confin-

ing the male to localized movements within visual range of the nest (Kramer and Smith 1962). These sex-specific behavioural alterations result in the male being confined to a localized area (realized as low daily distance traveled in this study) and inhabiting only shallow portions of the water column (realized as a shallow depth distribution during spawning).

While realized in the current study as a decline in daily distance traveled, nesting male bass are in actuality some of the most active bass in the population, as brood maintenance and guarding activities require constant movement characterized most often by "swimming in place" (Hinch and Collins 1991; Cooke et al. 2002). The acoustic telemetry array used in this study was unable to resolve the fine-scale, extremely localized movements and activity of nest-guarding male largemouth bass. During the reproductive period, largemouth bass engage in vigilant nest defense and maintenance activities that result in very little linear distance traveled (Hinch and Collins 1991). Reproductive males are constantly sculling and rotating in place defending the nest (Hinch and Collins 1991). Considering that the transmitter is located roughly in the centre of the body, a fish engaged in this activity could be quite active without the position of the transmitter ever moving in relation to the array. By measuring muscle contractions through the use of electromyogram telemetry, Cooke et al. (2002) estimated that males involved in nest-guarding behaviour traveled an average of 49 km daily as compared with their non-nest-guarding counterparts traveling 12 km daily. Because the array records spatial utilization data that were used to determine the activity levels associated with individual fish, a male largemouth bass that is guarding a nest and making discreet localized movements would be shown to be quite inactive. In reality, nest-guarding fish have been shown to be much more active than other individuals that are not involved in the same behaviour. Furthermore, sex-specific differences in behaviour continued after the spawning period, as reproductive male bass exhibited reduced levels of activity and shallower depth utilization during the post-reproductive period relative to female and nonreproductive male fish (Figs. 6 and 7), although the proximate causes for these shifts in behaviour are currently unknown.

Reproductive male bass also behaved differently relative to other fish during the winter prior to their reproductive bout. During winter, the daily distance traveled by fish that were going to spawn in several months was significantly less than at other periods of the year (with the exception of the spawning period), possibly an effort to conserve energetic stores. Spawning and parental care are extremely energetically demanding on the male bass (Hinch and Collins 1991; Mackereth et al. 1999; Cooke et al. 2002). Also, during this the reproductive period, male bass are only able to forage opportunistically and quite infrequently because they are required to stay with the brood at all times (Kramer and Smith 1962; Hinch and Collins 1991), resulting in decreased energy stores across the nest defense stage (Mackereth et al. 1999). Reduced activity levels during winter relative to other nonspawning periods (as indicated by significant reductions in mean daily distance swum) may be a behavioural modification that allows a male bass to conserve enough energy to enable spawning in the following spring.

While water temperature was determined to be the most important indicator of both activity and depth utilization, the multiple regression analyses presented in this paper rarely accounted for more than 50% of the variance associated with the models. Numerous studies on multiple taxa, including centrarchid fishes, have shown that both energy reserves and absolute metabolic rate increase with body mass (Calder 1984; Lindstedt and Boyce 1985; Murphy 1985; Shuter and Post 1990). As such, individual variation in size (which was minimal in the current study) may exert influence of both activity and depth utilization owing to the fact that larger individuals may have marked differences in energy stores and metabolic rates. Individual variation in behaviour, specifically swimming performance, may also be quite important (Kolok 1999). Hanson et al. (2007) noted that individuals in this system often exhibit vastly different movement patterns whereby some occupy discreet locations for extended time periods when others make lake-wide movements. Individual variation, such as the abovementioned, would contribute higher levels of error to the regression models. Lastly, the models in this study did not take seasonal habitat changes into account, as behaviour may change related to the presence or absence of key seasonal habitats such as large macrophyte beds present during summer. Vegetated areas both attract prey seeking to avoid predators (Crowder and Cooper 1979) and provide cover for largemouth bass involved in ambush predation (Savino and Stein 1982; Valley and Bremigan 2002). Largemouth bass may seek out areas of intermediate structural complexity that increase prey density and thereby maximize foraging efficiency (Crowder and Cooper 1979). The presence or absence of such areas could greatly affect the movement patterns of largemouth bass. Because of the fact that vegetation growth in lakes is determined by light penetration into water, many vegetated areas occur in the shallow reaches of the water column (Sheldon and Boylen 1977; Barko and Smart 1981). If largemouth bass preferentially chose these areas to forage within, they would also be selecting for the utilization of shallower water depths and movements in an area of the lake defined by the vegetation growth. Because of the small size of the lake and homogeneity of available habitat, we believe that habitat-specific differences in behaviour would be most prominent for between-season comparisons, as individuals would be restricted to similar habitats within each season.

While temperature is generally considered the "master" abiotic factor influencing the behaviour of temperate fish (Beamish 1970), other factors, particularly those of biotic origin, influence the behaviour of individuals throughout the year. As this study has shown, sex and reproductive status can have major implications for behaviour not only during spawning but also during the periods leading up to this activity and after reproduction has concluded. Given that male bass that reproduce provide sole parental care to their offspring, acquisition and conservation of energy reserves are critical to their lifetime fitness. As evidenced by the data in this study, apparently the decision to provide parental care by a male influences behaviour both before and after parental care, indicating that they may alter activity to maximize their limited energy resources. What is unknown is whether fish that have different reproductive systems

(e.g., no parental care or biparental care) exhibit differences in behaviour relative to sex or reproductive status.

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