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Effects of lunar cycles on the activity patterns and depth use of a temperate sport fish, the largemouth bass, *Micropterus salmoides*

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Abstract The behaviour of free-swimming, telemetered, adult largemouth bass, *Micropterus salmoides* (L.), was monitored using a whole lake, three-dimensional acoustic telemetry array to test the hypothesis that fish activity and depth distribution are influenced by lunar phase. The percent of lunar face shining and whether the moon was waxing or waning were significant determinants of swimming activity and depth distribution during most of the lunar cycles evaluated, although these patterns were not consistent across the year. In spring and summer, daily depth distribution followed a pattern in which the fish inhabited greater depths on the 26–50% and 51–75% waxing moon. Fish daily movement distances were five times greater during spring and summer than in winter, but no repeatable patterns were noted in relation to lunar periodicity. This

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research suggests that solunar tables frequently consulted by recreational anglers may have little predictive value for identifying peak fishing time.

KEYWORDS: behaviour, biotelemetry, largemouth bass, lunar cycle, sport fish.

Introduction

It has long been accepted that behaviour and activity patterns of individual animals are influenced by entrained endogenous rhythms associated with environmental cues (summarised in Koukkari & Sothern 2006), particularly in relation to the changing light conditions created by the differing lunar phases (Koukkari & Sothern 2006; Lang, Kalko, Romer, Bockholdt & Dechmann 2006). In marine environments, the lunar cycle is associated with both differing light conditions and tidal fluctuation, caused by the moon's varying magnetic pull on the earth at different positions throughout the lunar cycle (Gliwicz 1986). Multiple behaviours of various species (including predator avoidance, prey location, spawning behaviour, stratum migration and swimming activity) across a range of taxa (e.g. zooplankton, invertebrates, birds and fish) are altered by the lunar cycles (Gliwicz 1986; Leatherland, Farbridge & Boujard 1992; Srisurichan, Caputi & Cross 2005; Lang *et al.* 2006).

To date, most research on the impact of lunar cycles on fish has focused on elucidating how the lunar cycle and associated changing tides affect the reproductive synchrony, tidal migration, stratum migration and hormone dynamics of marine species (Chatterji, Vajayakumar & Parulekar 1992; Leatherland *et al.* 1992; Rahman, Takemura, Nakamura & Takano 2003). All of these studies were conducted near equatorial regions, which is advantageous for studying the effects of the lunar cycle because day length fluctuates to a lesser degree than at higher or lower latitudes. Furthermore, there tends to be less drastic change in seasonal temperature and weather in some tropical equatorial regions (Gliwicz 1986; Hernandez-Leon, Almeida, Yebra & Aristegui 2002; Lecchini 2006). Although studies in equatorial regions enable standardisation of some environmental factors to evaluate the direct influence of lunar cycles, these findings may not be relevant to non-equatorial locales, suggesting a need for research on the influence of lunar cycles on fishes, especially freshwater species, outside of equatorial regions.

Beyond the basic interest in understanding environmental influences on animal behaviour, the knowledge of lunar cycles is also of interest to anglers because these cycles are believed to influence catch rate in recreational fisheries. Numerous (anecdotal) fishing articles have been published in magazines and on the Internet that propose the ideal fishing times for certain species of fish based on lunar cycles, usually in tabular form. These articles are based on observations and belief that popular game fish species such as northern pike, *Esox lucius* L., walleye, *Sander vitreus* (Mitchell) and largemouth bass, *Micropterus salmoides* (L.), tend to feed and synchronise activity with the changing solar and lunar positions. Currently, however, there appears to be no conclusive scientific study to support the claims that temperate sport fish behaviour varies during certain times of the year in response to changing lunar periods in a manner that increases the likelihood of capturing fish via recreational angling.

The hypothesis that daily activity and depth distribution is influenced by lunar cycles was tested using largemouth bass as a model for a temperate freshwater lake-dwelling fish. The study took advantage of a whole lake acoustic telemetry array deployed in eastern Ontario, Canada, where there is a population of adult largemouth bass that are acoustically tagged and continuously monitored in three dimensions (see Hanson, Cooke, Suski, Niezgoda, Phelan, Tinline & Philipp 2007). This resource provides an opportunity to collect data simultaneously on many individual fish throughout all periods of the day, as well as throughout the year (including under ice) in their natural environment. Additionally, largemouth bass are one of the most popular sport fishes in North America (US Fish and Wildlife Service 2002).

Materials and methods

The study was carried out at the Warner Lake Ecological Observatory (WLEO) study site located in southeast Ontario from 1 November 2004 to 21 September 2005 (see Cooke, Niezgoda, Hanson, Suski, Phelan, Tinline & Philipp 2005; Hanson *et al.* 2007). Warner Lake has a surface area of 8.3 ha comprising a shallow basin (maximum depth 2 m) and a deep basin (maximum depth 7 m). Details on the habitat and fish community present within the lake can be found in Hanson *et al.* (2007). On 14 and 15 September 2004, 14 males and 8 females (mean length 403 ± 28 mm; mean weight 938 ± 210 g), collected using standard angling techniques, were implanted with CDMA temperature–pressure sensing acoustic transmitters (Lotek CTP-M11–55, 11 mm × 55 mm, weighing 29.3 g in air, burst rate of 15 s, life expectancy of 1 year). The burst rate of the tags was selected to ensure transmitter longevity through the autumn, winter, and winter–spring transitions. Depth and temperature resolution for the fish transmitters was ± 0.7 m and ± 0.5 °C, respectively. Surgical protocols followed Cooke, Graeb, Suski & Ostrand (2003) and involved the intraperitoneal implantation of transmitters on 14 September and 15 September 2004. Fish were first anesthetised in a 60 ppm induction bath of clove oil solution emulsified in ETOH (clove oil:ETOH, 1:9). Upon equilibrium loss, fish were measured for total length (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 anaesthetic 20 ppm clove oil solution) irrigating the gills. Initial incisions of 12 mm were made slightly off centre from the ventral midline behind the pelvic girdle of each fish (Cooke *et al.* 2003). Transmitters (sterilised in 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.). Surgeries were conducted by the same experienced individual to eliminate variance associated with multiple surgeons (Cooke *et al.* 2003). After surgery, fish were placed in coolers containing fresh lake water to recover from anaesthesia and then fish were released at one central location. Following surgery, two telemetered individuals (two males) either experienced delayed mortality or suffered from transmitter failure and were removed from subsequent analyses.

Warner Lake is the site of a fixed station telemetry array using code division multiple access (CDMA) technology consisting of two multi-port MAP_600 receivers (Lotek Wireless, Newmarket, ON, Canada) connected by cabling to 13 hydrophones that were distributed throughout the lake enabling coverage of the entire lake (Hanson *et al.* 2007). Hydrophones were moored on rods driven into the lake bottom and placed approximately 2 m below the water surface to prevent damage from ice during the winter (Hanson *et al.* 2007). Specific details on the telemetry equipment and array performance can be found in Cooke *et al.* (2005) and Hanson *et al.* (2007). For the purposes of this study, only data obtained from six full lunar cycles with relatively stable water temperatures, as measured by implanted transmitters (16 November to 15 December, mean water temperature 4.2 ± 0.5 °C; 28 December to 26 January, mean water temperature 4.0 ± 0.2 °C; 8 February to 9 March, mean water temperature 3.7 ± 0.1 °C; 10 March to 7 April, mean water temperature 5.6 ± 0.3 °C; 3 June to 28 June, mean water temperature 24.2 ± 0.7 °C; 22 August to 20 September, mean temperature 21.4 ± 0.6 °C) were incorporated into analyses.

Raw data were loaded into the BIOMAP program (v. 2.1.12.1, Lotek Wireless, Newmarket, ON, Canada) 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. To remove outliers, a series of filtering processes within BIOMAP were applied to the data as described in Niezgoda, Benfield, Sisak & Anson (2002) and Hanson *et al.* (2007). Briefly, at the time of signal acquisition, a reliability number (RN) and condition number (CN) to assess the numerical stability of each individual position were assigned by the array and points determined to be outliers were eliminated (RN > 0.75, CN < 10; Niezgoda *et al.* 2002). Additionally, any remaining position solutions that did not fall within sub-metre degree of precision (GDOP) were filtered out of the data set. Lastly, impossible position solutions, defined as any position where a fish was located in an inaccessible area (i.e. land) or movements that are not physically possible (swim speeds of over six body lengths per second) were also removed from the data set. To assess activity, mean distance swum per day (determined as the linear distance between subsequent XY coordinates) and mean depth were quantified for each individual. Swimming activity was assumed to be a composite measure of gross activity patterns. Depth information (i.e. the third dimension) was determined from the information relaid via the pressure sensor in each tag. Depth was also included in the analysis because the previous studies found that certain marine species change their diel vertical depth depending on lunar light levels (Gliwicz 1986; Leatherland *et al.* 1992; Hernandez-Leon *et al.* 2002). Mean daily distance and mean daily depth data were analysed for six periods where data were available for a complete lunar cycle (defined as the complete return of the moon to the original phase at which the data began being collected). Data on lunar cycles for the nearest major city (Ottawa, ON, ~125 km) were obtained from the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneYear.html; providing data on percentage of lunar face shining).

Mean daily swim distance and mean daily depth were partitioned into quarters according to the moon's visible illuminated disk percentage (0–25%, 26–50%, 51–75% and 76–100%) for both the waxing and waning periods, i.e. eight distinct lunar phases (Lang *et al.* 2006). For the purpose of this study, activity and depth were evaluated over 24-h periods (00:00 to 23:59) because lunar light levels were previously shown to influence diel activity periods and not just nocturnal activity of animals (Jetz, Steffen & Linsenmair 2003). To determine whether there was a general relationship between lunar phase and daily distance travelled and depth use operating on an annual scale, repeated measures ANOVAS, with individual nested within lunar period (with lunar quarter as the repeated variable) followed by Tukey's HSD *post hoc* tests were used (Zar 1999). Additionally, data were analysed based upon individual lunar cycles as multiples of other abiotic and biotic factors that vary seasonally can impede the ability to develop generalised annual trends in behaviour. ANOVAS with individual nested within lunar period were conducted to test for differences between lunar periods. Additionally, Spearman's rank order tests were conducted to determine if the patterns noted within each lunar cycle were repeatable in other lunar cycles (Zar 1999). All analyses were performed in the statistical package JMP IN V 4.0 (SAS Inc., Cary, NC, USA) with significance assessed at $\alpha = 0.05$, and because of multiple comparisons, simultaneous Bonferroni corrections were performed (Zar 1999). All values presented represent mean ± SD.

Results

No significant relationships were found between lunar phase and both daily distance travelled (RMANOVA, $F = 0.2088$, d.f. = 7, $P = 0.981$) and depth use (RMANOVA, F-ratio = 0.2310, d.f. = 7, $P = 0.975$) (Fig. 1). Finer scale analyses were conducted focusing on individual lunar cycles based on exploratory visualisation of data on a seasonal basis and a large body of literature supporting the idea that seasonal patterns in activity relative to lunar phase exist. Daily distance travelled and depth use varied significantly across an individual lunar cycle in all lunar cycles analysed (Table 1, Figs 2 & 3). The influence of lunar phase on activity and depth distribution, however, was not consistent across lunar cycles (Figs 2 & 3). During the autumn and winter months (lunar cycles 1–3: 16 November to 15 December; 28 December to 26 January; 8 February to 9 March), although statistically significant differences between lunar periods were noted, the activity level and the depth use showed non-repeatable patterns when compared with lunar periodicity (Fig. 2). Additionally, fish were twice as deep and were three times less active during autumn and winter than the summer and spring months (lunar cycles 4–6; 10 March to 7 April, 3 June to 28 June, 22 August to 20 September). The spring and summer months, however, were characterised by marked effects of lunar cycle on both activity and depth use (Fig. 3). Specifically, deeper depths were occupied by fish during the second (26–50% waxing moon face) and third (51–75% waxing moon face) lunar quarters, the waxing phase of the lunar cycle (Fig. 3). The correlations between these three periods (i.e. lunar cycles 4–6; 10 March to 7 April, 3 June to 28 June, 22 August to 20 September) were evaluated using Spearman's rank order test to determine the repeatability of this pattern. This relationship between lunar phase and bass depth use was repeated between the fourth and sixth lunar cycles (Spearman's $P = 0.81$,

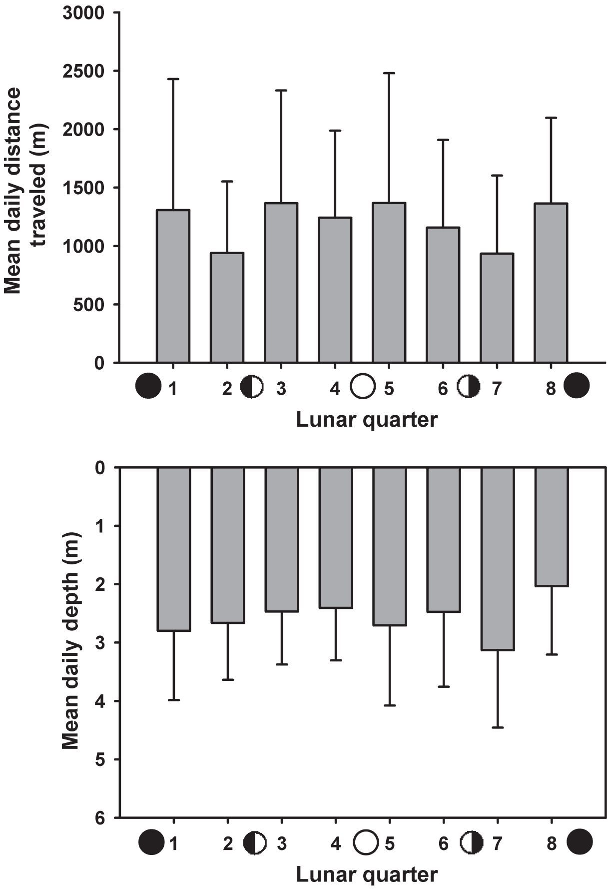

Figure 1. Effects of lunar periodicity on mean daily distance travelled and mean daily depth distribution of *Micropterus salmoides* in Warner Lake, southeast Ontario, Canada, for six lunar cycles across a single calendar year. Cartoons depict the lunar cycle. Daily distance travelled and depth distribution did not vary significantly across lunar phase (RMANOVA, $P > 0.05$). Error bars show ± 1 SD.

Table 1. Effects of lunar period on mean daily distance travelled and mean daily depth by *Micropterus salmoides* for 6 lunar cycles throughout the 2004–2005 calendar years as assessed by analysis of variance

Lunar cycle number	Date	Mean temperature (°C)	Variable	*F*-ratio	d.f.	*P*-value
1	16 November to 15 December	4.2 ± 0.5	Daily distance	1.80	161	< 0.0001
			Depth	5.74	161	< 0.0001
2	28 December to 26 January	4.0 ± 0.2	Daily distance	3.77	133	< 0.0001
			Depth	4.71	133	< 0.0001
3	8 Febuary to 9 March	3.7 ± 0.1	Daily distance	1.96	152	< 0.0001
			Depth	14.83	152	< 0.0001
4	10 March to 7 April	5.6 ± 0.3	Daily distance	1.33	152	< 0.0001
			Depth	17.17	152	< 0.0001
5	3 June to 28 June	24.2 ± 0.7	Daily distance	11.79	116	< 0.0001
			Depth	76.72	116	< 0.0001
6	22 August to 20 September	21.4 ± 0.6	Daily distance	6.53	126	< 0.0001
			Depth	29.26	126	< 0.0001

$P = 0.015$), and nearly significant between the fourth and fifth lunar cycles (Spearman's $\rho = 0.68$, $P = 0.094$) and fifth and sixth lunar cycles (Spearman's $\rho = 0.75$, $P = 0.052$; Fig. 3). No such consistent patterns were noted in the mean daily distance travelled data.

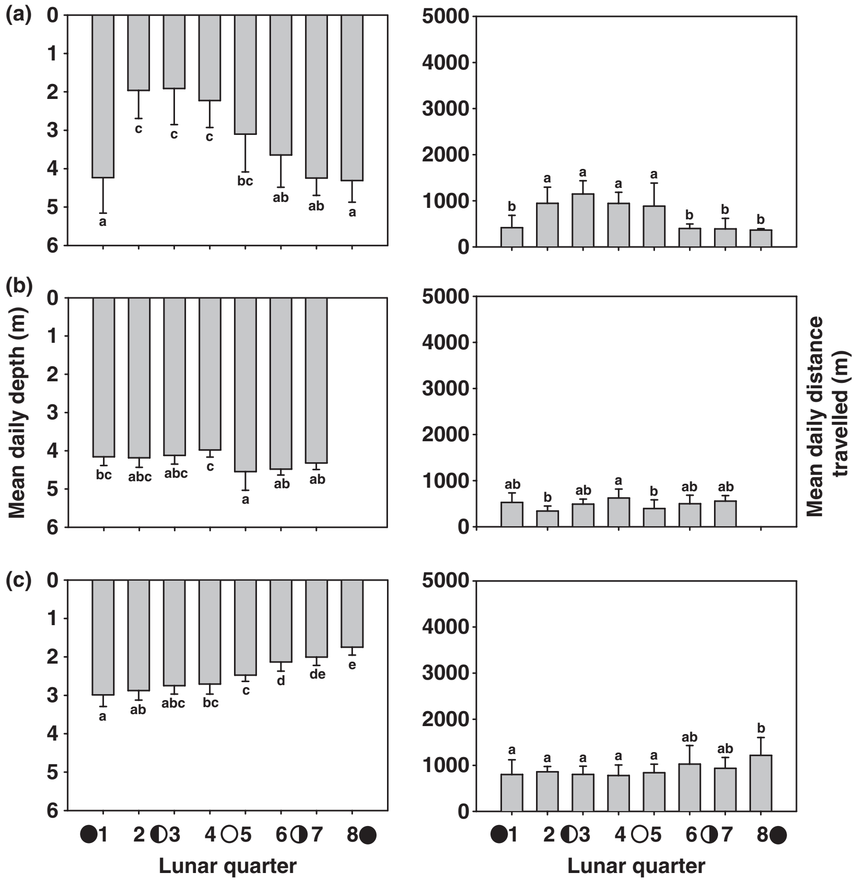

Figure 2. Effects of lunar periodicity on daily distance travelled and daily depth distribution of largemouth bass (*Micropterus salmoides*) in Warner Lake, southeast Ontario, Canada, for the autumn and winter lunar cycles of 2004–2005. Cartoons depict the lunar cycle. No consistent effect of lunar periodicity was noted for either response variable during these particular months (lunar cycles 1–3: (a) 16 November to 15 December; (b) 28 December to 26 January; (c) 8 February to 9 March). Error bars show ± 1 SD. Dissimilar letter groups denote significant differences between lunar periods ($P < 0.05$).

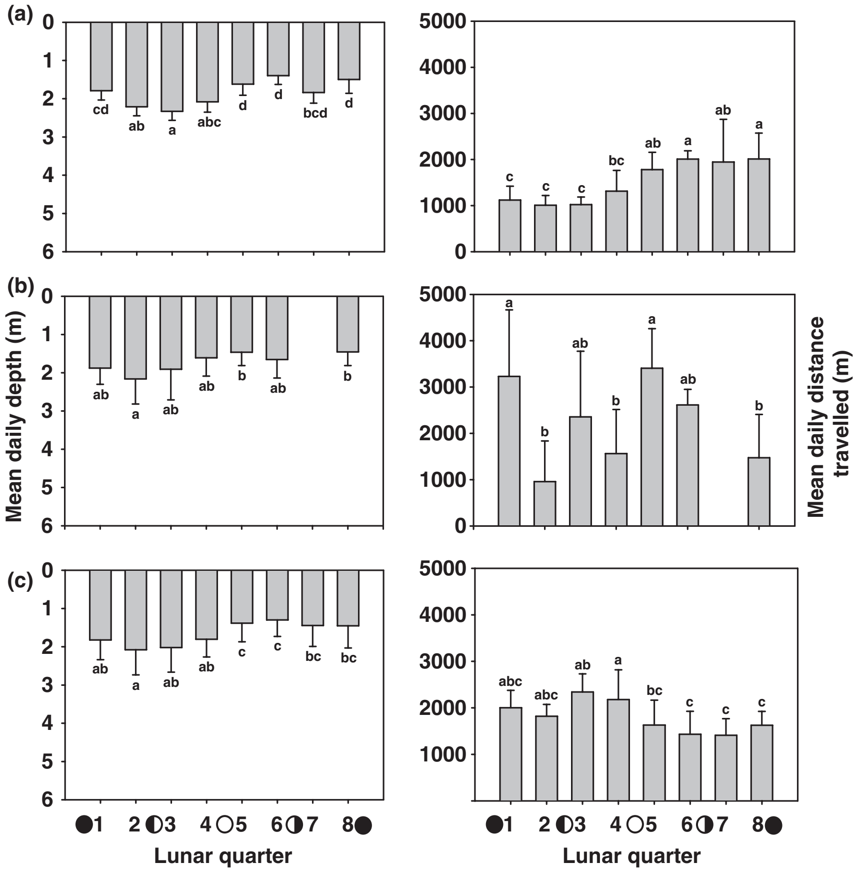

Figure 3. Effects of lunar periodicity on daily distance travelled and daily depth distribution of *Micropterus salmoides* in Warner Lake, southeast Ontario, Canada, for the spring and summer lunar cycles of 2004–2005 (lunar cycles 4–6: (a) 10 March to 7 April; (b) 3 June to 28 June; (c) 22 August to 22 September). Cartoons depict the lunar cycle. A repeated pattern in depth use emerges at this time in which fish are at the deepest depths during the 26–50% and 51–75% waxing moon phases. No consistent effect of lunar periodicity was noted for mean daily distance travelled. Error bars show ± 1 SD. Dissimilar letter groups denote significant differences between lunar periods ($P < 0.05$).

Discussion

The goal of the current study was to determine the effects, if any, of lunar periodicity on the activity and depth distribution of largemouth bass, a popular sport fish. Additionally, this study also provided insight into the solunar tables used by recreational anglers to determine peak fishing times. Lunar phase was found to be a significant determinant of activity and depth distribution, though rarely in a uniform and repeatable manner. Only depth distribution during the spring and summer months was affected by lunar phase in a repeatable and uniform manner (Fig. 3). During these months, deeper portions of the lake were used by fish during the 26–50% and 51–75% shining moon face during the waxing phase of the lunar cycle. This result corresponds to the idea that foraging largemouth bass could be pursuing prey species, which are in turn responding to shifts in zooplankton dispersal caused by ambient lunar light levels (Gliwicz 1986; McMahon & Holanov 1995). In general, nocturnal vertical migration can be controlled by ambient light present in the water column originating from the lunar cycle (Gliwicz 1986). Zooplankton and smaller fish were noted to move to deeper depths during times of high moonlight to avoid visually oriented predators (Gliwicz 1986; Manuel & O'Dor 1997; Tarling, Buchholz & Matthews 1999; Sponaugle, Fortuna, Grorud & Lee 2003). Subsequently, predatory fish species also migrate to depth following prey species (Manuel & O'Dor 1997; Tarling *et al.* 1999; Chiou, Cheng & Chen 2003). Additionally, it is believed that when the levels of lunar light increase, visually oriented predators can have prey capture benefits from extended periods of light (McCrimmon & Robbins 1981; Gjelland, Boehn, Knudsen & Amundsen 2004). Consistent with this idea, the nocturnal foraging efficiency of largemouth bass was shown to vary with environmental light levels, increasing with the amount of simulated moonlight (McMahon & Holanov 1995). As such, the literature is replete with reasons why largemouth bass activity and depth distribution should be influenced by lunar phase.

No clear patterns of lunar effects on activity or depth distribution emerged on an annual scale. As the activity and depth distribution were not affected in a repeatable or uniform manner throughout the other lunar cycles analysed, other abiotic factors may drive these responses for the rest of the year, particularly, decreasing in water temperature during the autumn and winter months. In general, water temperature has been called the abiotic master factor driving fish behaviour and activity because of its manifold effects on metabolism and ultimately, swimming performance (Fry 1971; Brett & Groves 1979; DeVries & Wainwright 2006). Currently, it is believed that largemouth bass become quiescent during the winter months, ceasing foraging and limiting movements to localised areas (Johnson & Charlton 1960; Cunjak 1996; Raibley, Irons, O'Hara, Blodgett & Sparks 1997). Additionally, any effects of lunar light during the winter months may be dampened by ice accumulation on the surface of lakes in northern climates (Steinhart & Wurtsbaugh 1999). Ice cover with subsequent snow accumulation lowers the amount of ambient light penetrating the water column (Steinhart & Wurtsbaugh 1999). As such, bass may not respond to lunar rhythms during the winter months because of metabolic constraints on behaviour and activity combined with the lack of penetration of lunar light caused by ice and snow cover on the surface of the lake.

As a result of the prevalence of information showing the lunar influence on fish behaviour, calendars basing peak fishing times on the lunar cycle have been created and widely used by anglers. These calendars are based on the premise that sport fish behaviour changes during certain lunar events making individuals of these species easier to capture via recreational angling, and hence suggesting optimal periods for angling. The current study found no evidence suggesting that activity levels of largemouth bass are affected by the lunar cycle in a repeatable manner throughout the year as suggested by solunar calendars. Although not directly related to catch rates, in other fish species, the activity levels have been shown to be positively correlated with feeding behaviour as well as negatively correlated with satiation post-feeding (Boisclair 1992; Asaeda, Priyadarshana & Manatunge 2001). Combining these beliefs with the findings of the current study suggests that lunar periodicity may not influence the feeding activity of largemouth bass in the predictable manner suggested by solunar calendars. However, the current study did demonstrate that there are repeatable patterns in depth use during the spring and summer months. Changes in depth distribution may relate to increased catch rates if individual fish move to depths where they are more susceptible to angling, lending some credence to the claims of solunar calendars. Additional research on this topic is needed to determine the validity of solunar tables for different fish species and systems.

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