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Seasonal pattern of depth selection in smallmouth bass

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Abstract

The current study used a stationary acoustic telemetry array to monitor the depth selection of adult smallmouth bass *Micropterus dolomieu* in a large, oligotrophic lake in Ontario, Canada. At an annual scale, smallmouth bass demonstrated regular, seasonal changes in inhabited depths: fish occupied shallow water during the summer (2–5 m depth) and descended to deeper water (12–15 m depth) during winter under ice. Smallmouth bass remained above the thermocline in the summer, seasonal depth patterns did not vary across fish size and movements to and from seasonal depths were closely linked to the development and degradation of the thermocline. At finer time scales, smallmouth bass exhibited diel vertical migrations in summer, with fish moving to <2 m at night, and then descending to 3–5 m during the day. This pattern remained constant during the summer period examined, and varied with size such that larger fish remained deeper than smaller fish. During winter, depth did not vary across the 3-month monitoring period (*c*. 14 m), but small (<2 m) changes in depth were observed periodically, suggesting limited movements were occurring. Results are further discussed in the context of climate change and reproductive success for this species.

Introduction

Choices animals make with respect to habitat selection are reflected in movement at different time scales, ranging from daily movements, often in response to predator–prey decisions (Hrabik *et al*., 2006), to seasonal movements following environmental cues signaling cycles in habitat productivity or breeding (Teo *et al*., 2007). In aquatic organisms, these two scales of movement can be found in daily and seasonal patterns of depth selection. Assumptions about individual choices that underpin population-level sampling often are based on trade-offs between growth and risk of predation, as predator and prey populations move over a range of depths at hourly or daily time steps (Clark & Levy, 1988). Such trade-offs have been studied in freshwater and marine ecosystems, particularly during diel vertical migration (DVM), which arguably represents the longest sustained interest in habitat selection, although the phenomenon has not always been placed in this context (Pearre Jr, 2003). Hypotheses concerning the adaptive significance of DVM have focused on fish species that cross temperature gradients, where bioenergetic efficiency and predator avoidance are reasonable alternative hypotheses. Over diel cycles, depth selection in fish occurs as an outcome of predator–prey behavior in juveniles (Clark & Levy, 1988; Scheuerell & Schindler, 2003) and adults (Stokesbury *et al*., 2005) or as a means of increasing bioenergetic efficiency for benthic (Sims *et al*., 2006) as well as pelagic foragers (Mehner, Kasprzak & Hölker, 2005).

In warm water fish and those that seasonally occupy the epilimnia of lakes, bioenergetic hypotheses regarding DVM do not seem to apply because temperature gradients are weak or absent, yet populations still undergo vertical movement even over relatively shallow depths (Piet & Guruge, 1997). Tracking individual depth selection in a warm water fish would help resolve this uncertainty.

Daily and seasonal depth selection of smallmouth bass *Micropterus dolomieu* are understood in outline based on population-level sampling and tracking of individuals. Individual male smallmouth bass show nest site fidelity (1–3 m depth) in the littoral zone in spring (Ridgway, MacLean, & MacLeod, 1991*a*) and home range fidelity in summer following breeding (Ridgway & Shuter, 1996; Ridgway *et al.*, 2002). Netting programs have shown movement from summer locations to deeper overwintering sites (Webster, 1954; Keast, 1968) with return movements in spring. Depth selection over diurnal cycles and seasons is largely unknown with one tracking study showing a positive correlation between size of smallmouth bass and depth occupied in the littoral zone (Cole & Moring, 1997).

The purpose of this study was to determine the presence and magnitude of depth selection among seasons, and across diurnal periods within seasons, in smallmouth bass. In particular, we were interested in testing hypotheses of DVMs and habitat selection in a warmwater fish, and consequently relating movement and activity patterns to habitat parameters.

Materials and methods

Study site

Data were collected from 7 August 2004 to 1 May 2006 from smallmouth bass in Lake Opeongo (45°42′N; 78°22′W), Ontario, Canada. Lake Opeongo is a large (area ≈ 5860 ha; mean depth ≈ 14.8 m) oligotrophic (Secchi disk reading ≈ 6 m) lake with a self-sustaining population of smallmouth bass that has been studied for decades (Martin & Fry, 1973).

Experimental animals

Smallmouth bass [$n = 28$; mean fork length = 367.5 mm, standard error (SE) = 6.6 mm, range = 317–451 mm] were collected by trap net or angling and transported by boat to the aquatic laboratory at the Harkness Laboratory of Fisheries Research on Lake Opeongo. Surgical procedures outlined in Ridgway & Shuter (1996) were used to implant an individually coded and calibrated acoustic tag outfitted with a pressure sensor (V13P Acoustic Coded Transmitter, Vemco Inc., Shad Bay, NS, Canada; 44 × 13 mm, weight = 6 g in water) into the body cavity. Tags were programmed to emit an identification signal at random intervals every 30–90 s, and the accuracy of depth measurements was ± 0.3 m.

Monitoring equipment

To monitor movements of tagged fish, five stationary omnidirectional receivers (VR2 Single Channel Monitoring Receiver, Vemco Inc.) were anchored at various locations around Lake Opeongo during 2004–2005, and an additional 10 receivers were added in mid-May of 2006; all receivers were placed at depths of *c.* 1–1.5 m. These receivers logged the date, time, identification number and depth of any acoustic tag entering their listening range (*c.* 300 m radius). Data from each receiver were downloaded to a personal computer at regular intervals, and receivers were periodically repositioned to maximize fish detections. Before analyses, the database was filtered to remove erroneous data points (i.e. simultaneous detections of an individual from multiple hydrophones) and data from fish that died (no change in depth). During the study, 944 818 data points were generated with < 10% needing to be omitted.

Water temperature was monitored from May to November of 2004, 2005 and 2006 with two strings of 10 temperature loggers (StowAway TidBiT, Onset Computer Corporation, Bourne, MA, USA) spaced *c.* 1.5 m apart to a depth of *c.* 20 m anchored at two locations within the study site. During the winter of 2005–2006 (November–May), seven temperature loggers were distributed around the study site at depths ranging from 4 to 21 m to allow for the determination of water temperature under ice.

Analyses

The entire database was queried to quantify the depths inhabited by individual smallmouth bass, as well as the range of depths covered (maximum–minimum). Depth and range were examined during five time periods: the entire 2-year study examined at 1-week intervals (a total of 99 intervals), a representative 92-day period during the summer (July–September), a representative 90-day period under ice during the winter (December–February) as well as a representative 21-day period in spring (April–May) and a representative 56-day period in fall (September–November) during the creation and degradation of thermal stratification within the lake. For all five study periods, individual data points were grouped by 1 week, day/night or 1-h intervals for analyses. Data were filtered to ensure that there were at least two depth readings used to generate a range value for each fish within a time interval. To assign depths to day/night categories, sunrise and sunset times using the latitude and longitude of Lake Opeongo were collected from the National Research Council of Canada Herzberg Institute of Astrophysics website (http://www.hia-iha.nrc-cnrc.gc.ca/sunrise_adv_e.html).

Differences in depth and range across time periods were quantified using a repeated-measures (mixed model) analysis of variance (RMANOVA) with time period and fish size entered as fixed treatment effects, and individual fish entered as a random effect (Sokal & Rohlf, 1998; SAS Institute Inc., 2005). All statistical analyses were performed using JMP 6.0.2 (SAS Institute Inc., Cary, NC, USA), and the level of significance (α) for all tests was 0.05. Data are reported as means ± SE where appropriate.

Results

Annual patterns in depth selection

When examined in 1-week intervals, smallmouth bass exhibited cyclical changes in depth selection that alternated between shallow depths in summer and deeper depths during winter (Fig. 1a; RMANOVA, $F_{98} = 43.2$, $P < 0.0001$). The size of fish did not have a significant influence on depth selection at an annual scale (RMANOVA, $F_1 = 0.8$, $P = 0.4$). The repeated pattern of seasonal depth selection over the course of 2 years in Fig. 1a can be

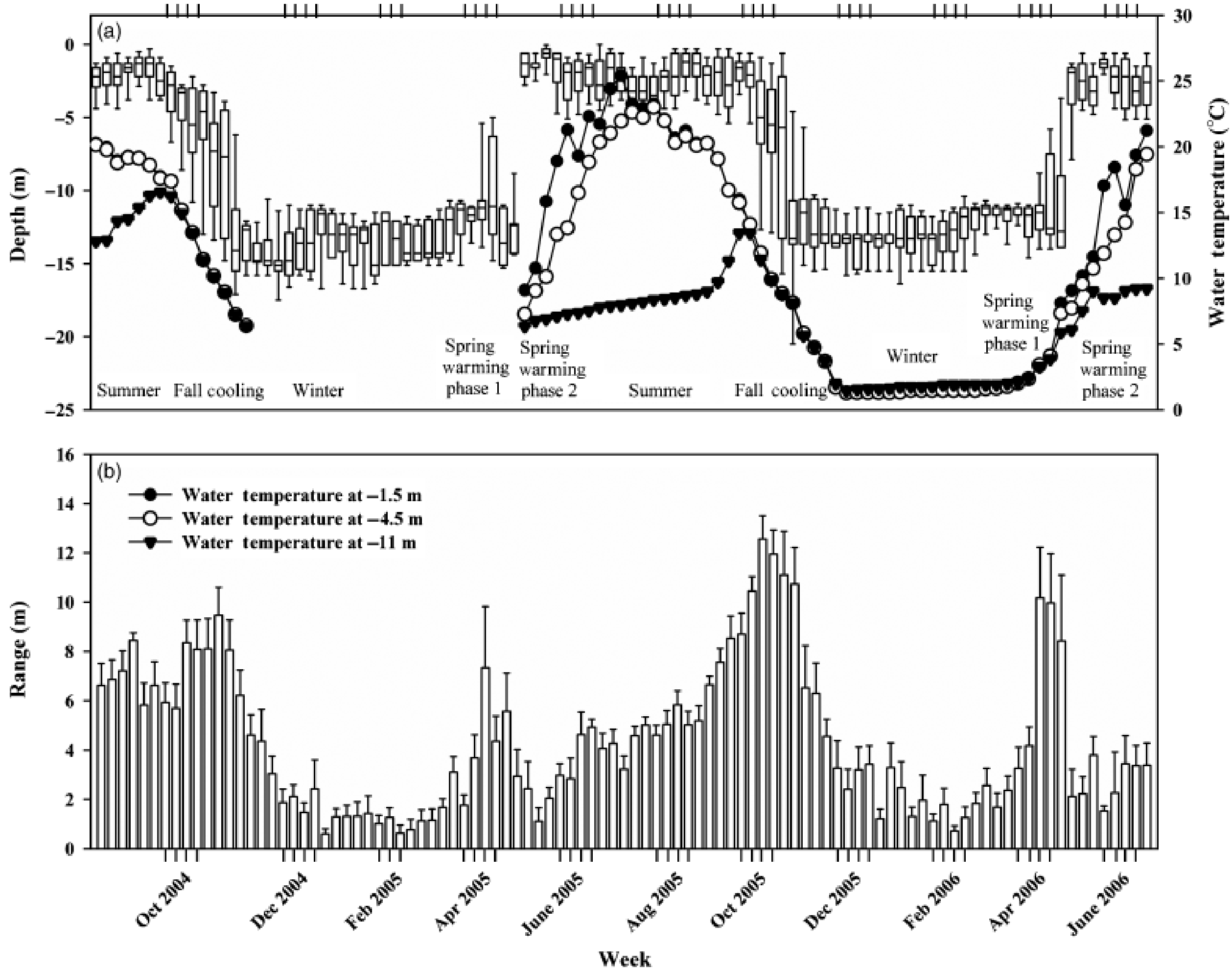

Figure 1 Weekly depth (a) and range (maximum depth–minimum depth) (b) of acoustically tagged smallmouth bass monitored over a 99-week period in an oligotrophic lake in Ontario, Canada. Each bar or box corresponds to 1 week of data pooled from 28 adult smallmouth bass *Micropterus dolomieu* monitored with a stationary acoustic telemetry array. Weekly water temperatures at three depths are shown by line graphs in (a). Seasonal activity patterns are denoted by labels in (a) and described in more detail in the text.

partitioned into distinct periods based on the mean depth, range in depth and annual temperature cycle.

During the summer of all 3 years examined, smallmouth bass remained at a mean depth of 2–4 m, a period of time that corresponded to the peak in lake temperatures (labeled as Summer in Fig. 1a). The range in depths occupied in summer was high compared with the mean depth and differed across years with a range of 6–8 m week^{-1} in summer 2004, and 4–6 m in summer 2005 and 2006 (Fig. 1b).

Following the peak in epilimnetic temperature in late summer, the depth of smallmouth bass decreased from 4 to 12 m, accompanied by an increase in range in October 2004 and 2005 (labeled as Fall Cooling in Fig. 1a). During this cooling phase, epilimnetic temperatures declined providing temperatures above 10 °C at depths previously below the thermocline for at least 1 month (Fig. 1a). At the start of isothermal conditions in the fall, the extent of weekly range increased resulting in the widest range of occupied depths (8–10 m in 2004; 10–12 m in 2005) (Fig. 1b).

The maximum depth occupied by smallmouth bass occurred when water temperature dropped below 10 °C at all depth strata (labeled as Winter in Fig. 1a). At this time, depth was *c.* 14 m with a range of 2 m or less for most of the winter period during ice cover. During both 2004 and 2005, smallmouth bass remained at this maximum depth for 24 weeks under isothermal conditions (Fig. 1a).

The sharpest rate of change in weekly depth of smallmouth bass occurred when lake temperatures began to increase in association with the separation of water temperatures from isothermal conditions (labeled as Spring Warming Phase 1 in Fig. 1a). Over a 3-week period, mean depth shifted from 10–12 m to 2 m in 2004 and 2005 and occurred during the period of spring equinox in 2005 and 2006 indicating an increase in bass activity under ice.

In the weeks following initiation of spring activity, smallmouth bass occupied the shallowest depths (< 2 m in 2005 and 2–3 m in 2006) with a range equivalent to that observed during winter (labeled Spring Warming Phase 2 in Fig. 1a).

In 2005, this period lasted 2 weeks, and in 2006, this period lasted 2–3 weeks.

Summer

During summer (June–August), depths inhabited by smallmouth bass showed significant variation across the 92 days examined (Fig. 2a; RMANOVA, $F_{91} = 2.4$, $P < 0.0001$) and also on a diel scale (Fig. 2a; RMANOVA, $F_1 = 7354.5$, $P < 0.0001$). Depths averaged 2–5 m during the day and varied between 1 and 3 m at night (Fig. 2a). Although this shift from day to night depths is relatively small, the consistency of the behavior resulted in a significant difference during the diel cycle. Fish size had a significant influence on depth inhabited during summer (RMANOVA, $F_1 = 19.8$, $P < 0.0001$) with larger fish remaining deeper in the water column than smaller individuals. Similarly, the range of water covered during summer showed significant variation both across days (Fig. 2b; RMANOVA, $F_{91} = 1.9$, $P = 0.0001$) and from day to night (Fig. 2b; RMANOVA, $F_1 = 413$, $P < 0.0001$) with ranges during the day significantly greater than at night (*c.* 3–6 m during the day as compared with 1–3 m at night).

When 6 days during the summer sampling period (7–12 August) were examined at fine scales, hourly depth among individuals did not vary across days (Fig. 3a; RMANOVA, $F_5 = 0.5$, $P = 0.8$), but depths varied across hours of the day (Fig. 3a; RMANOVA, $F_{23} = 54.3$, $P < 0.0001$). Specifically, smallmouth bass ascended to shallow depths soon after sunset with the shallowest depths inhabited (*c.* 1.5–2.5 m) between *c.* 23:00 and 03:00 h (Fig. 3a). Soon after sunrise, smallmouth bass descended to greater depths, and the deepest depths inhabited on a diel basis (between *c.* 4 and 5 m) were between 06:00 and 13:00 h. Intermediate depths were inhabited at all other times. The mean depth of smallmouth bass did not fall below the thermocline of the lake, despite the fact that the depth inhabited for some hours were > 5 m (Fig. 3a). Fish size had a significant impact on hourly depths during the summer (RMANOVA, $F_1 = 8$, $P = 0.007$) with larger fish remaining deeper in the water column than smaller individuals. Similar to depth, the ranges inhabited varied significantly across hour of the day during summer (Fig. 3b; RMANOVA, $F_{23} = 3.7$, $P < 0.0001$), but did not vary across the 6 days examined (RMANOVA, $F_5 = 1.1$, $P = 0.4$). Hourly ranges were greatest between *c.* 06:00 and 13:00 h,

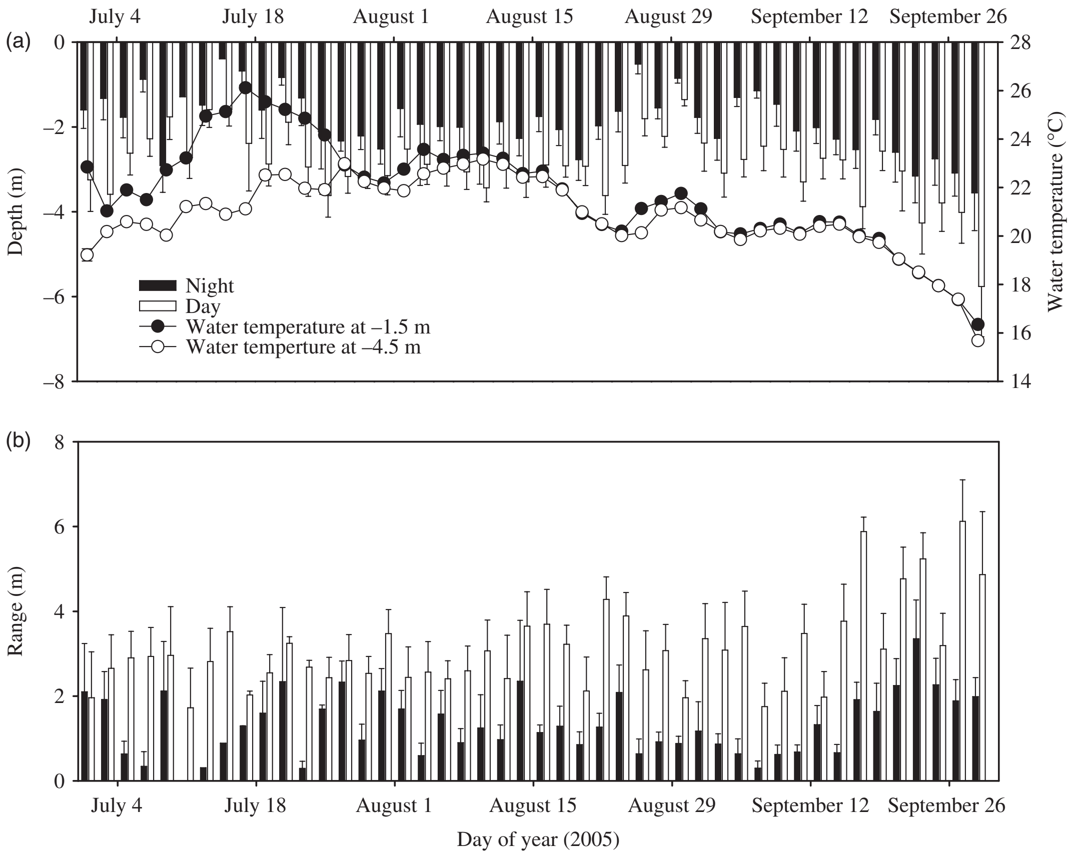

Figure 2 Daily depth (a) and range (maximum depth–minimum depth) (b) of acoustically tagged smallmouth bass *Micropterus dolomieu* monitored over a 92-day period in summer in an oligotrophic lake in Ontario, Canada. Data are divided such that depth/range during daylight hours are shown with open bars, and depth/range during night are shown by black bars. Bars are grouped by day, and, to aid with presentation of data, every second day has been omitted from the figure. Daily water temperatures at two different depths are shown by line graphs in (a).

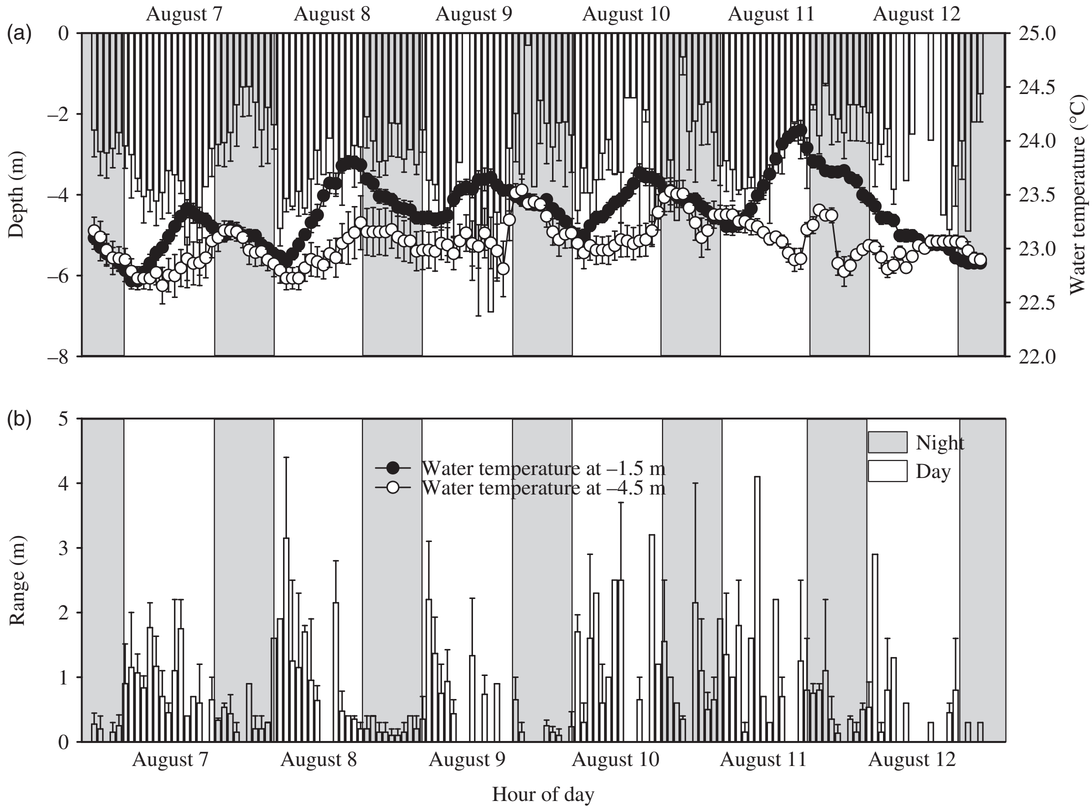

Figure 3 Hourly depth (a) and range (maximum depth–minimum depth) (b) of acoustically tagged smallmouth bass *Micropterus dolomieu* monitored over a 6-day period in summer in an oligotrophic lake in Ontario, Canada. Each bar represents depth or range for a single hour of the day. Night (after sunset) is indicated by shading, and daylight (between sunrise and sunset) is indicated by light areas. Hourly water temperatures at two different depths are shown by line graphs in (a).

ranging from 1 to 3 m. During all other hours, ranges were *c*. 0.75–2 m.

Fall Cooling

During the 56-day fall sampling period, water in Lake Opeongo cooled, thermal stratification within the lake degraded and the lake became isothermal (Fig. 4a). During this time, depths inhabited decreased from *c*. 4 m in late September to 14 m by mid-November (Fig. 4a; RMANOVA, $F_{55} = 14.9$, $P < 0.0001$). There was also a significant difference in diel depth at this time with fish remaining deeper during daylight compared with night (Fig. 4a; RMANOVA, $F_1 = 711$, $P < 0.0001$). In contrast to the patterns in summer, fish size had a significant impact on depths inhabited at this time with smaller fish remaining deeper in the water column than larger individuals (RMANOVA, $F_1 = 10.6$, $P = 0.001$). Similar to depth, smallmouth bass exhibited a significant decline in range during this sampling period, changing from *c*. 3–5 m in late September to 2–4 m in mid-November (Fig. 4b; RMANOVA, $F_{55} = 1.4$, $P = 0.04$).

Winter

During the winter months, smallmouth bass remained at *c*. 14 m depth across the entire 90 days examined and did not demonstrate significant changes in depth (Fig. 5a; RMA NOVA, $F_{89} = 0.5$, $P > 0.05$). Size had a significant influence on depth with larger fish remaining more shallow than smaller fish (RMANOVA, $F_1 = 4.6$, $P = 0.03$). The impact of size on winter depth was quite small, however, with depth differences between the largest and smallest fish being *c*. 0.5 m. Ranges during the winter sampling period varied significantly across days (Fig. 5b; RMANOVA, $F_{89} = 1.9$, $P < 0.0001$) exceeding 1.5 m in early December and decreasing to < 0.5 m by February (Fig. 5b). In addition, smallmouth bass exhibited a significant difference in depth on a diel scale, with fish occupying shallow water during the day (Fig. 5a; RMANOVA, $F_1 = 492$, $P < 0.001$). Ranges also showed significant differences between day and night (Fig. 5b; RMANOVA, $F_1 = 31.6$, $P < 0.0001$) being greater during the day (Fig. 5b). The consistency of deeper readings at night relative to day, coupled with larger ranges in the early portion of December, is suggestive of small (< 2 m), regular changes in depth under ice.

Spring Warming Phase 1

During spring, heat gain within Lake Opeongo occurs quickly with temperature differences across depths initiated over a few days (Fig. 6a). During this time period,

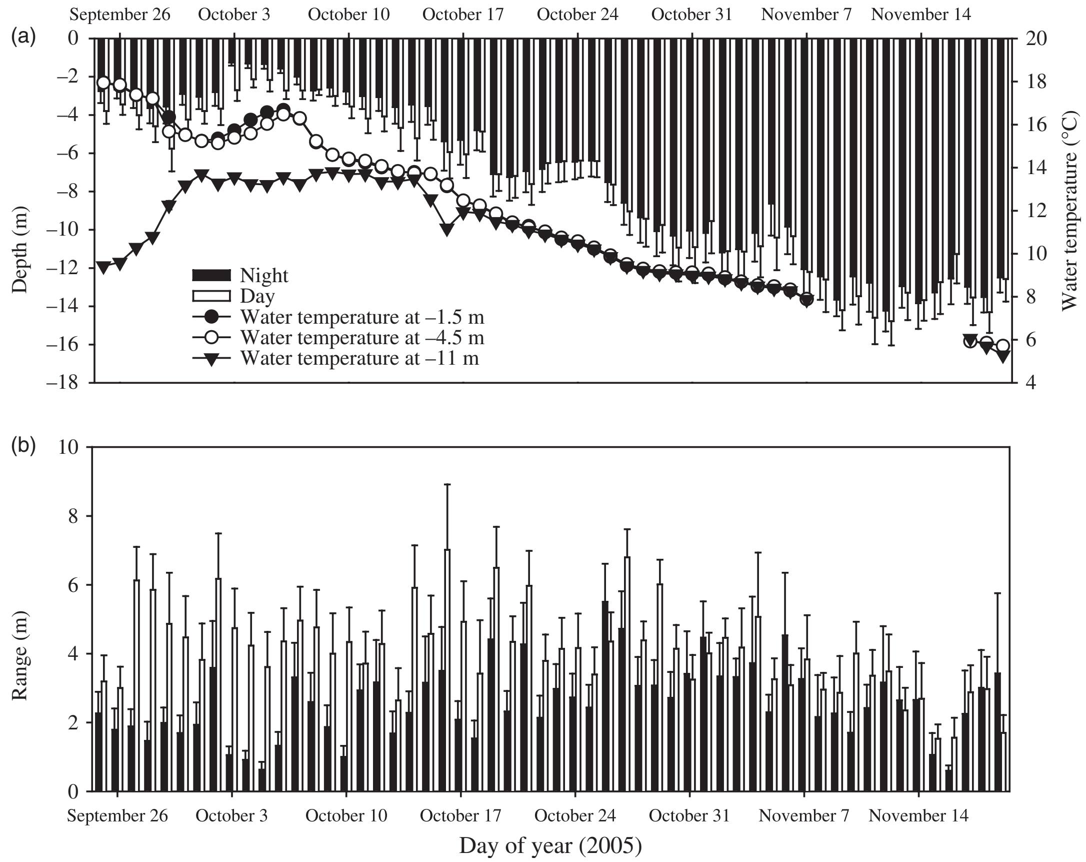

Figure 4 Daily depth (a) and range (maximum depth–minimum depth) (b) of acoustically tagged smallmouth bass *Micropterus dolomieu* monitored over a 56-day period in fall in an oligotrophic lake in Ontario, Canada. Data are divided such that depth/range during daylight hours are shown with open bars, and depth/range during night are shown by black bars. Bars are grouped by day. Daily water temperatures at three different depths are shown by line graphs in (a).

smallmouth bass began ascending from deep winter depths to shallow summer depths (Fig. 6a; RMANOVA, $F_{20} = 2.9$, $P = 0.0003$). During the period of spring stratification, there was no significant difference in the ranges covered by smallmouth bass, either across the days examined (Fig. 6b; RMANOVA, $F_{17} = 1.2$, $P = 0.3$) or between day and night (Fig. 6b; RMANOVA, $F_1 = 3.2$, $P = 0.08$).

Spring Warming Phase 2

This phase in the annual cycle of depth selection is the briefest and stands out from Spring Warming Phase 1 by both shallow depths and a near absence of any depth range movement (Fig. 1a). In 2005, Spring Warming Phase 2 lasted about 2 weeks and in 2006, it lasted about 2–3 weeks (Fig. 1a). This time period is also characterized by relatively sparse data for two potential reasons. First, the acoustic array receivers were set at depths roughly equivalent to the depths selected by smallmouth bass at this time; because detection range is maximized when receivers are oriented above or below the depths of tagged fish (Clements *et al.*, 2005), a reduced number of detections when fish and receivers are oriented at similar depths is possible. Second, based on previous experience with acoustic detection, the spring diatom flush reduces detection distances when monitoring fish with ultrasonic tags.

Discussion

Smallmouth bass in Lake Opeongo demonstrate regular, annual habitat shifts between shallow, summer areas and deeper, overwintering areas. Before the use of an acoustic telemetry array over many months, the seasonal pattern of depth selection for smallmouth was defined by few episodes such as initiation of movement in the spring after a winter of relatively little feeding (Keast, 1968), followed by periods of shallow nesting during spring and summer (Ridgway, 1988). The seasonal movement of lake-dwelling centrarchid fishes to deeper water during the winter was noted by Webster (1954), who documented a predictable movement of smallmouth bass to particular areas of Cayuga Lake, New York. The current study revealed that, for smallmouth bass, the descent during fall and ascent during spring are closely coupled to the erosion and onset of thermal stratification within the lake.

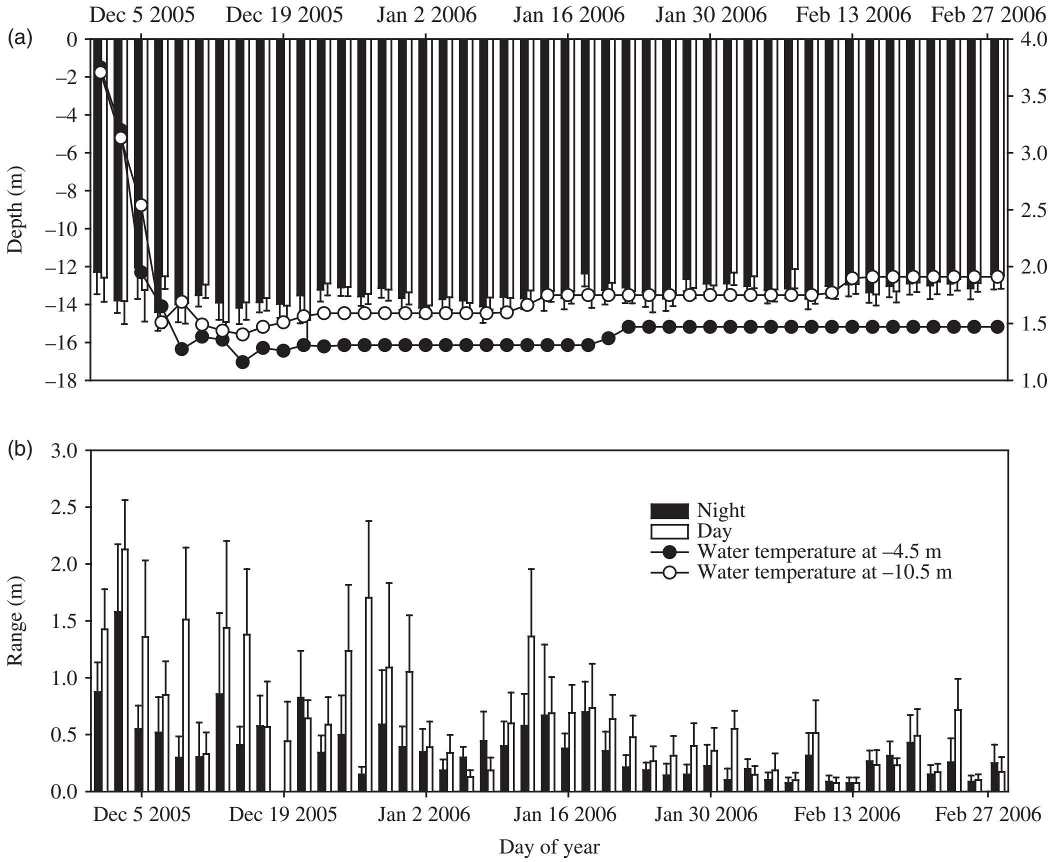

Figure 5 Daily depth (a) and range (maximum depth–minimum depth) (b) of acoustically tagged smallmouth bass *Micropterus dolomieu* monitored over a 90-day period under ice in winter in an oligotrophic lake in Ontario, Canada. Data are divided such that depth/range during daylight hours are shown with open bars, and depth/range during night are shown by black bars. Bars are grouped by day, and, to aid with presentation of data, every second day has been omitted from the figure. Daily water temperatures at two different depths are shown by line graphs in (a).

For several fish species, water temperature has been shown to be a cue that triggers seasonal movements, often across large scales. For example, Gillette *et al.* (2006) showed that decreasing water temperature was one factor that prompted several species of stream-dwelling fishes in the midwestern USA to move between summer and winter habitats. Additionally, our results did not indicate any size-specific differences in this movement pattern, demonstrating this to be a population-level phenomenon across adult smallmouth bass. Together, results from this study demonstrate not only regular, seasonal depth selection patterns for lake-dwelling smallmouth bass, but also that these patterns are largely driven by limnologial features that define habitat.

During the warm summer months, smallmouth bass exhibit pronounced diel behavior patterns, with size-specific variation in occupied habitat. Specifically, smallmouth bass inhabited deeper water during the daylight hours (*c.* 5 m) than at night, although the range of inhabited depths across 1-h intervals was relatively large. After sunset, smallmouth bass ascended to shallow water and remained at these shallow depths until sunrise. This pattern was repeatable across days, although there were differences in depths inhabited across days, and larger fish remained deeper in the water column than smaller conspecifics.

The results of this study show that smallmouth bass rarely crossed significant temperature gradients during summer months in Lake Opeongo indicating that thermoregulatory behavior is not likely occurring. With a mean depth of 2–4 m occupied in summer and a depth range of 6–8 m in 2004 and 4–6 m in 2005, smallmouth bass largely function within the epilimnion and metalimnion especially at dawn when they reach their deepest depths during the day. As well, all smallmouth bass in our study were above 316 mm fork length (adults), making them invulnerable to predation. This suggests that diel vertical movements of the smallmouth bass at night are related to foraging opportunities, possibly for nocturnal crayfish (Gherardi, Barbaresi & Salvi, 2000), while movements down and into the metalimnion may be in pursuit of cisco young of year that occupy this ecotone during the summer months (M. Ridgway, unpubl. data). Cole & Moring (1997) noted that large smallmouth bass (406–520 mm) used deep water (>8 m) more than smaller conspecifics, corroborating observations in the current study that larger individuals either out-compete smaller

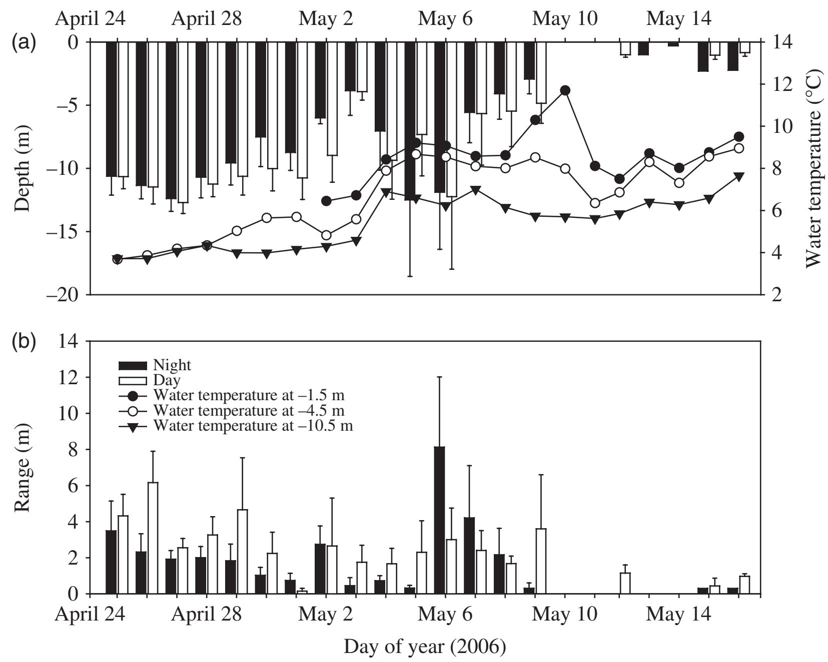

Figure 6 Daily depth (a) and range (maximum depth–minimum depth) (b) of acoustically tagged smallmouth bass *Micropterus dolomieu* monitored over a 3-week period in spring in an oligotrophic lake in Ontario, Canada. Data are divided such that depth/range during daylight hours are shown with open bars, and depth/range during night are shown by black bars. Bars are grouped by day. Daily water temperatures at three different depths are shown by line graphs in (a).

individuals for access to critical habitat parameters (possibly food resources) or that there are size-based differences in habitat preferences. Together, the results of fine-scaled observations of smallmouth bass depth preferences in the summer reveal a strong diel pattern shallow nocturnal depths and deeper depths during daylight.

Winter periods under ice represent a time of both reduced activity and movement of smallmouth bass to deep water. While this trend is true for smallmouth bass in Lake Opeongo, small-scale movement patterns and size-specific differences in habitat selection appear to be occurring. Reduced water temperatures associated with winter have been shown to diminish the swimming ability (Beamish, 1978), metabolic rate and scope for activity in centrarchid fishes (Beamish, 1970). Consequently, earlier studies have characterized overwintering smallmouth bass as 'dormant' with individuals congregating in few, traditional overwintering areas to minimize energy expenditure until spring (Webster, 1954). Acoustically tagged smallmouth bass from the current study remained at *c.* 14 m depth with no significant changes in depth over the 90-day winter observation period, confirming this to be a period of reduced activity relative to summer. Interestingly, smallmouth bass showed significant variation in the range of depths occupied during the winter, with the variation in daily range often exceeding 1.5 m despite the fact that water temperatures were below 2 °C. This increase in range diminished in magnitude as the winter progressed, and suggests that overwintering smallmouth bass are not truly dormant under ice but are quiescent with small movements occurring (Kolok, 1991). In addition, smaller individuals in the current study were shown to remain in deeper water during winter than larger conspecifics. Depth differences across sizes were quite small (*c.* 0.5 m), but may be more pronounced if a greater size range of fish were to be examined. Together, the current study clearly demonstrates that winter represents a significant change in behavior and reduction in activity patterns for smallmouth bass relative to other times of the year, with size-specific differences in depth selection occurring.

During fall, thermal stratification in Lake Opeongo erodes, heat is transferred to the hypolimnion, and water temperature temporally increases at depth. These changes to thermal characteristics appear to be a stimulus for smallmouth bass to occupy increasingly deeper depths while still remaining active. More specifically, the fall cooling period before isothermal conditions within this lake is characterized by smallmouth bass progressing from depths of 6 m in early October to mean depth of 12 m in November, with daily ranges at this time averaging 5–7 m indicating that smallmouth bass are occupying large portions of the isothermal water column. During the fall period, the rate of energy gain is highest on annual basis for smallmouth bass as individuals accumulate lipid reserves before the quiescent overwinter period (Mackereth, Noakes & Ridgway, 1999), and increased depth utilization may allow fish to efficiently forage at depths with temperatures between 10 and 15 °C, a temperature range known to be the operating boundaries for smallmouth bass during the spring warming period (Ridgway, Shuter & Post, 1991*b*). Our temperature data show a clear difference in the duration of the cooling period in 2004 (longer) versus 2005 (shorter). Annual differences in heat accumulation and loss in the lake appear to dictate the duration of accessibility of smallmouth bass to deeper depths in the fall.

The current study demonstrated that smallmouth bass exhibit pronounced, cyclical seasonal depth selection patterns, with fish moving deep in winter and shallow in summer, with patterns closely linked to seasonally changing thermal properties of the lake. Long-term trends in thermocline depth are known to have an effect on nesting success in this population, and climate-induced changes to thermocline depths will likely alter the duration and timing of the fall cooling period when smallmouth bass are most dynamic in depth selection (Suski & Ridgway, 2007). We can therefore expect a change in the timing of significant autumnal energy gains with climate warming for smallmouth bass, with potentially important implications for bioenergetics modeling and energy requirements. Active fish must consume more energy than resting fish, suggesting that smallmouth bass under ice may need to feed if energy requirements are high. Future studies should continue to build upon this work, and examine patterns in the lateral movements of smallmouth bass, coupled with examination of habitat type, substrate type, environmental factors and prey availability to further improve our understanding of factors motivating habitat choices in fish species, especially smallmouth bass.

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