

Behavioural thermoregulation and bioenergetics of riverine smallmouth bass associated with ambient cold-period thermal refuge

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Abstract – Smallmouth bass in thermally heterogeneous streams may behaviourally thermoregulate during the cold period (i.e., groundwater temperature greater than river water temperature) by inhabiting warm areas in the stream that result from high groundwater influence or springs. Our objectives were to determine movement of smallmouth bass (*Micropterus dolomieu*) that use thermal refuge and project differences in growth and consumption among smallmouth bass exhibiting different thermal-use patterns. We implanted radio transmitters in 29 smallmouth bass captured in Alley Spring on the Jacks Fork River, Missouri, USA, during the winter of 2012. Additionally, temperature archival tags were implanted in a subset of nine fish. Fish were tracked using radio telemetry monthly from January 2012 through January of 2013. The greatest upstream movement was 42.5 km, and the greatest downstream movement was 22.2 km. Most radio tagged fish (69%) departed Alley Spring when daily maximum river water temperature first exceeded that of the spring (14 °C) and during increased river discharge. Bioenergetic modelling predicted that a 350 g migrating smallmouth bass that used cold-period thermal refuge would grow 16% slower at the same consumption level as a fish that did not seek thermal refuge. Contrary to the bioenergetics models, extrapolation of growth scope results suggested migrating fish grow 29% more than fish using areas of stream with little groundwater influence. Our results contradict previous findings that smallmouth bass are relatively sedentary, provide information about potential cues for migratory behaviour, and give insight to managers regarding use and growth of smallmouth bass in thermally heterogeneous river systems.

Key words: smallmouth bass; thermal refuge; bioenergetics; movement; growth; archival tag

Introduction

Water temperature is an important driver of fish behaviour, growth, reproduction and movement (Lucas & Batley 1996; Goniea et al. 2006; Whitley et al. 2006; Petty et al. 2012). As ectotherms, freshwater fish are unable to internally regulate their body temperature making behavioural thermoregulation an ideal mechanism for fish to control their body temperature. However, behavioural thermoregulation requires spatial variation in water temperature be

accessible within the system. Fish may experience reduced growth or mortality in some systems if adequate thermal variation is not available because they are only able to tolerate certain temperatures and experience maximum growth in a narrow thermal range (Fry 1947; Reynolds & Casterlin 1979).

Behavioural thermoregulation is achieved when a fish is able to move to an area of water with preferential thermal conditions, termed a thermal refuge (Torgersen et al. 2012). Depending on the system, thermal refuge may be available in the form of a

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tributary, varying water depth, outflow of a hydroelectric dam, discharge from a power plant cooling operation, hyporheic flow or groundwater discharge from a spring (Nielsen et al. 1994; Peterson & Rabeni 1996; Torgersen et al. 1999; Cooke et al. 2004; Young & Isely 2007). Much of our current knowledge about thermal refuge use by fishes is based on salmonids (Torgersen et al. 1999; Ebersole et al. 2001; Howell et al. 2010), but many other species of fish use thermal refuge (Peterson & Rabeni 1996; Labbe & Fausch 2000). Juvenile Coho salmon (*Oncorhynchus kisutch*) that thermoregulate in streams grew faster by moving between cold habitats with abundant food and warmer habitats that provided metabolic and assimilative benefits (Armstrong et al. 2013). Black redhorse (*Moxostoma duquesnei*) may use groundwater sources to avoid lethal temperatures and as refuge from poor water quality in degraded systems (Bunt et al. 2013). Seasonal growth and consumption advantages likely exist for smallmouth bass that use thermal refuge (Peterson & Rabeni 1996; Whitledge et al. 2006), but little else is known about fish behaviour and energetic advantages associated with these refuges.

Thermal refuge use by fishes may be of varying importance based on temporal or spatial scale. Availability of thermal refuge may change temporally whereby areas used as refuge in one season are less desirable in other seasons (Power et al. 1999). This is especially true for many lotic systems influenced by input from springs where water temperatures are driven primarily by groundwater in some stream sections and by ambient air temperatures in other sections (Mugel et al. 2009). At a coarse-spatial scale, groundwater inputs can buffer water temperatures for many km downstream creating large stretches of thermal refuge for fishes (Whitledge et al. 2006). Lotic systems influenced by high groundwater input support robust populations of smallmouth bass (*Micropterus dolomieu*) in the southern part of their U.S. range, whereas streams with little groundwater influence have reduced abundances of smallmouth bass (Brewer 2013). Thermal refuge can also be considered at a fine-spatial scale. Some smallmouth bass use groundwater springs as thermal refuge by leaving the stream itself and inhabiting spring branches or the confluence where a spring enters the river (Peterson & Rabeni 1996; Dauwalter & Fisher 2008).

Bioenergetics models use information on growth, consumption, diet composition, energy density, physiology, water temperature and activity to estimate either fish growth or prey consumption (Rice & Cochran 1984; Whitledge et al. 2003). Wildhaber & Lamberson (2004) point out that bioenergetics models often do not account for fish habitat selection,

resulting in models that do not apply well to natural scenarios. This should be especially true when fish have the choice to use thermal refuge. Berman & Quinn (1991) examined thermoregulation in spring Chinook salmon (*Oncorhynchus tshawytscha*) and reported a 12–20% decrease in basal metabolic demand. Whitledge et al. (2006) predicted that groundwater input and riparian shading at a coarse-spatial scale would result in greater smallmouth bass growth during summer months, but they did not consider potential advantages of winter occupation of thermal refuges. Smallmouth bass have maximum consumption rates and experience optimal growth rates at 22 °C (Zweifel et al. 1999; Whitledge et al. 2002). Below 10 °C, smallmouth bass may cease feeding and growing, and above 27 °C, they are subject to loss of mass from the high cost of metabolic activity at those temperatures (Whitledge et al. 2002, 2006; Brown et al. 2009). Thus, alteration of water temperature inputs while keeping other bioenergetic model inputs constant can provide insight into the energetic differences between smallmouth bass that use thermal refuges, and those that do not.

The threat of global climate change has heightened the awareness of scientists and managers tasked with protecting freshwater organisms and unique aquatic habitats. Coarse-scale shifts (10–100 km) in fish distributions resulting from climate change have been predicted (Comte et al. 2013), and groundwater inflows are predicted to mitigate the effects of climate change in some stream systems (Chu et al. 2008; Brewer 2013). Despite this, mechanistic links between climate change predictions in groundwater-influenced streams and fishes at a fine-spatial scale remain relatively unstudied. Understanding the implications of these issues will better equip managers responsible for protecting aquatic diversity and managing fisheries.

Our study had two major objectives and focused on smallmouth bass, a recreationally important sport-fish known to use thermal refuge (Peterson & Rabeni 1996). The first was to document movement patterns of individual smallmouth bass known to use cold-period thermal refuge created by groundwater inputs (i.e., springs) using both radio and temperature archival tags. We hypothesised that all smallmouth bass occupying groundwater-influenced reaches would leave when river temperature equalled groundwater temperature (14 °C), and return when autumn temperature in the adjacent river again equalled groundwater temperature. We also hypothesised that most fish would move upstream, but remain close (<7.5 km from the release location) based on movement patterns of smallmouth bass within this same river system (Todd & Rabeni 1989). The second objective was to estimate smallmouth bass growth

potential based on three different behavioural thermo-regulation scenarios using two approaches. In the first approach, we used bioenergetics modelling to estimate possible growth or consumption differences for smallmouth bass based on thermal refuge-use behaviours. The second approach was to extrapolate known growth scope values (Whitledge et al. 2002) using the same thermal refuge-behaviour patterns used in the bioenergetics models. We hypothesised that required consumption rates would be lowest, and growth would be greatest, for fish that seasonally migrate to and from groundwater sources. We further hypothesised that fish exclusively using river reaches without groundwater input would have the highest consumption rates and lowest growth. Finally, we predicted fish using river reaches highly influenced by groundwater year-round would have consumption and growth requirements intermediate of the two other strategies.

Methods

Study site

The Jacks Fork and Current Rivers comprise the lotic component of the Ozark National Scenic Riverways (ONSR) in south-central Missouri within the Ozark Highlands (Nigh & Schroeder 2002). The ONSR is characterised by deep valleys overlaying a karst topography which creates many caves and over 270 springs (Mugel et al. 2009). Our study focused on the Jacks Fork River (Fig. 1), an eastern flowing 5th order stream with substrate dominated by coarse chert gravel and large boulders associated with bluff pools

or high gradient reaches (Peterson & Rabeni 2001). The riparian zone was mostly intact along the entirety of the river contained within the ONSR, and the overall catchment was primarily forested with some pasture land.

Alley Spring is the third largest spring on the Current River system (it is the largest on the Jacks Fork), has an estimated annual mean discharge of $2.7 \text{ m}^3 \cdot \text{s}^{-1}$ (Mugel et al. 2009), and an average annual temperature of 14°C (H. Dodd, unpublished data). It rises at the base of a dolomite bluff and is impounded by a small mill dam before flowing approximately 1 km to its confluence with the Jacks Fork River. Smaller springs exist along the length of the Jacks Fork River, but mean annual discharge has been estimated at only Blue Spring (the second largest on the Jacks Fork) and is $0.3 \text{ m}^3 \cdot \text{s}^{-1}$ (Mugel et al. 2009).

Fish tagging

Smallmouth bass were collected using a boat mounted electrofishing system (pulsed DC) on 3 January 2012 from a 200 m stretch of the Jacks Fork River directly below the confluence of Alley Spring. Fish were anaesthetized in a small tub using a mixture of 1:45 seltzer water and river water. Sedation and oxygen supply were maintained during surgery by running this mixture over the gills. Radio transmitters (ATS F1580; Advanced Telemetry Systems, Isanti, MN, USA; 3.6 g in air, battery life of 441 days) were surgically implanted in 28 smallmouth bass. We implanted radio tags in five additional smallmouth bass captured in Alley Spring

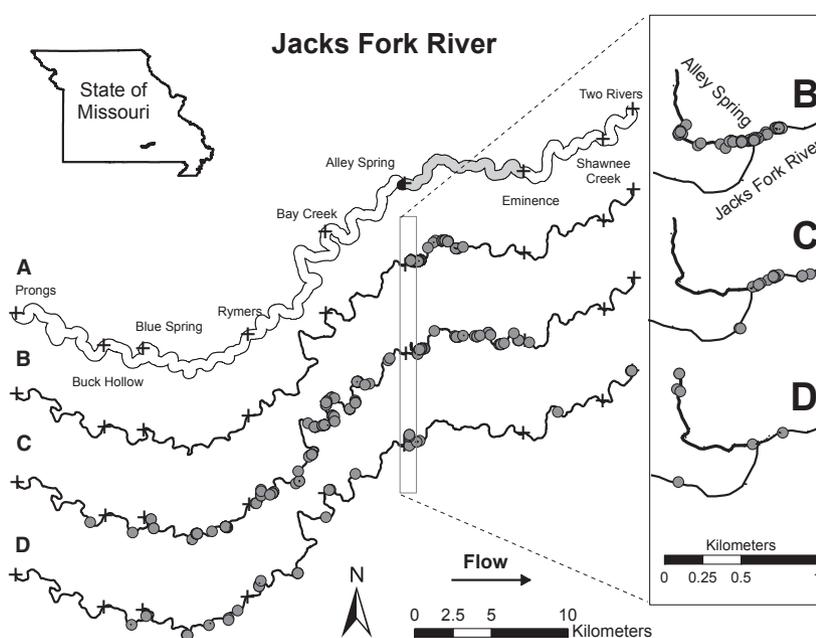


Fig. 1. Location of the Jacks Fork River and all valid locations of radio tagged smallmouth bass *Micropterus dolomieu* depicted according to river temperature. Section A depicts groundwater influence zones; upstream low groundwater influence zone (uLGI; white), spring-confluence zone (SC; black), high groundwater influence zone (HGI; grey) and downstream low groundwater influence zone (dLGI; white). Section B depicts fish locations from 17 January 2012 to 7 March 2012 (when water temperature was $<14^\circ \text{C}$). Section C depicts fish locations from 20 March 2012 to 16 October 2012 (when water temperature was $>14^\circ \text{C}$). Section D depicts fish locations from 6 November 2012 to 17 January 2013 (when water temperature was $<14^\circ \text{C}$). Inset along left provides greater detail of fish locations in and around Alley Spring.

during February and early March 2012 to supplement our sample size and replace fish harvested by anglers early in the study. This resulted in 29 radio tagged smallmouth bass with a range of total length (TL) between 260 and 416 mm (average = 336 mm TL). Temperature archival tags (DST Micro-T; Star-Oddi, Gardabaer, Iceland; 3.3 g in air, battery life >2 years with temperature recorded at 30-min intervals) were inserted into a subset of nine of the 29 smallmouth bass (332–416 mm TL) given radio transmitters. Archival tags were tied to the radio tags using sterilised braided fishing line so the two tags would remain attached if lost from the fish. Surgery was initiated after a sedated fish failed to respond to external stimuli and surgical procedures generally followed the methods of Hart & Summerfelt (1975). Tags were inserted into the body cavity through an incision made posterior to the pelvic fin. Monofilament sutures (PDS 3-0 FS-1) were used to close the incision with the trailing antennae left outside of the body cavity. Fish were allowed to recover in net pens in the river for at least 1 h. Before the fish recovered, a Carlin dangler tag was attached to the dorsal surface of the fish posterior to the dorsal fin and included contact information for anglers and a \$25 reward promise. Fish were then released at the confluence of Alley Spring and the Jacks Fork River.

Fish tracking

Smallmouth bass were tracked from a canoe or on foot every 2 weeks from January 17th, 2012 to 18 April and then monthly ending on 16 January 2013 using a Lotek SRX 600 telemetry receiver (LOTEK Inc., Newmarket, ON, Canada) and a three-element yagi antenna. Search efforts were conducted primarily in an upstream to downstream pattern because fish tracking was performed by traversing approximately 50 km of stream with a canoe. When a fish was encountered, the signal gain was adjusted to pinpoint its location and Global Positioning System (GPS) coordinates were obtained. Test tag relocations yielded location error estimates of less than three metres (J.T. Westhoff, unpublished data).

Several attempts were made during December 2012 and January 2013 to recapture archival tagged fish using boat electrofishing. Both radio tags and archival tags were also recovered over the course of the study from dead fish and from angler returns. Three stationary temperature loggers (HOBO Pendant, Onset Computer Corp., Cape Cod, MA, USA; accuracy ± 0.53 °C) were installed near Alley Spring and collected temperature data every 30 min. One logger was located in Alley Spring Branch, one was in the Jacks Fork River at the Bay Creek Access (10.8 km upstream of Alley Spring) and the other

logger was located in the Jacks Fork River 1.75 km downstream of Alley Spring (Keaton’s Access).

Analysis

Movement of radio tagged fish

We adapted the definition of cold- and warm-period thermal refuge used by Peterson & Rabeni (1996). When daily average water temperature in nongroundwater-influenced sections first equals groundwater temperature (14 °C) in the spring, we term this the vernal equilibrium date (Fig. 2). The autumnal equilibrium date occurs when the same phenomenon first occurs in the autumn. These equilibrium dates divide the year into two periods as related to thermal refuge for aquatic organisms, the cold-water period and the warm-water period (Fig. 2). For our study, the vernal equilibrium date occurred on March 14th, 2012 and the autumnal equilibrium date was October 24th, 2012 resulting in a 228 day warm-period and a 137 day cold-period.

We determined the maximum movement distance (starting location to most distant documented location) of each radio tagged smallmouth bass and calculated the average maximum movement distance for all fish that moved upstream and all fish that moved downstream. To simplify the possible locations of fish within the Jacks Fork River, we defined four zones (Fig. 1) based on thermal characteristics (J.T. Westhoff & C. Paukert, unpublished data). The upstream most zone (upstream low groundwater influence; uLGI) encompassed 45 km of river above Alley Spring characterised by low groundwater influence (only a few, small springs). The spring-confluence (SC) zone included Alley Spring branch and the 200 m of stream directly below the confluence. The third zone, high groundwater influence (HGI) zone was characterised by the substantial groundwater con-

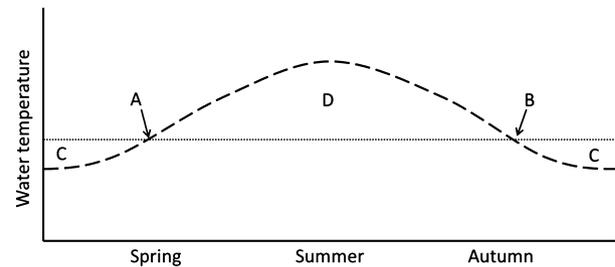


Fig. 2. Theoretical seasonal pattern of surface water temperature (dashed line) compared to groundwater temperature (dotted line) in the northern hemisphere. The intersection of the two lines during the spring season (A) represents the vernal equilibrium date, and the intersection in Autumn (B) represents the autumnal equilibrium date. The area between the lines and below the groundwater temperature (C) is the cold-water period and the area between the lines, and above groundwater temperature (D) is the warm-water period.

tribution from Alley Spring and extended 9 km from the downstream end of the SC zone. The final zone [downstream low groundwater influence (dLGI)] was characterised by low groundwater influence (few small springs and well downstream from Alley Spring) and extended 13 km downstream from the bottom of the HGI zone to the Current River. Range in yearly water temperature for each zone was 2.2–32 °C (uLGI), 13.4–15.7 °C (SC), 7.4–22.2 °C (HGI) and 4.9–27.5 °C (dLGI). The timing and duration of fish movement within and between zones were used to define patterns in fish movement and thermal refuge use.

We collected 340 valid fish locations and averaged (\pm SD) 10.3 ± 5.5 locations per fish. All movement results are based on the 26 tagged smallmouth bass alive at the end of March. We tested whether mean total fish length differed between fish that moved upstream versus those that moved downstream using a two-sample *t*-test. Additionally, we conducted a regression analysis to determine if total fish length was a significant predictor of distance moved.

Movement of archival tagged fish

Temperature archival tags were implanted in the subset of smallmouth bass to provide increased temporal resolution needed for determination of conditions associated with fish movement and thermoregulation behaviours. We recorded the dates, times and durations of thermal conditions encountered by fish throughout the study. This included information on short forays made by tagged fish near Alley Spring, migration movements and differences in temperature that occurred when fish occupied relatively low groundwater-influenced stream reaches during the summer. The time of fish departure from thermal refuge was identified by determining when fish temperature matched upstream river temperatures based on the Bay Creek Access temperature logger. Of the 11 fish implanted with temperature archival tags at Alley Spring (nine original and two replacements), we recovered tags from eight (supporting material). Two fish were harvested by an angler after 22 days, and a third tag malfunctioned after 40 days. Therefore, we used data from the five remaining archival tagged fish which had temperature data that spanned at least 100 days to investigate fish movement related to refuge use at a fine temporal resolution (30 min increments).

Bioenergetics modelling

We used bioenergetics modelling and growth scope extrapolation approaches to investigate smallmouth bass growth potential under three thermal-use patterns. In the first pattern, smallmouth bass remained in areas of the river with relatively low groundwater

influence (LGI; upstream of Alley Spring) and thus experienced a dynamic temperature pattern over the 12-month study. The second pattern focused on fish that remain year-round in areas that are heavily influenced by groundwater (HGI; downstream of Alley Spring) and thus experience a relative stable temperature regime. The third pattern (MIG) focused on migrating fish that occupied groundwater sources (i.e., SC zone at Alley Spring) when ambient river temperatures were below 14 °C (cold-water period) and occupied upstream areas in the LGI zone during the warm-water period. Water temperature inputs for the model were based on conditions during calendar year 2012 measured with the stationary temperature loggers at the Bay Creek Access (LGI conditions) and Keaton's Access (HGI conditions). The MIG group temperature inputs used temperatures from Bay Creek to represent thermal habitat during the warm-water period (water temperature >14 °C) and a value of 14 °C during the cold-water period. This assumes that the fish occupied a groundwater source for the duration of the cold-water period and during no part of the warm-water period. Water temperature values used in the bioenergetic models were input as daily mean values; however, yearly average water temperature (SD) for LGI, HGI and MIG thermal-use patterns was 17.0 °C (7.8), 15.2 °C (3.5) and 19.1 °C (5.3), respectively.

For our bioenergetics modelling approach, we assessed potential growth and consumption differences among the three hypothetical patterns of thermal resource use by smallmouth bass using Fish Bioenergetics 3.0 software (Hanson et al. 1997). Physiological parameters related to consumption, respiration, egestion/excretion and predator energy density for smallmouth bass were obtained from Whitlege et al. (2003). Diet composition and caloric energy density (Joules per gram wet weight) for smallmouth bass in the Jack's Fork River were obtained from Pease & Paukert (2014). Diet composition was modelled at 45% fish, 50% crayfish and 5% insect for the first 150 days and 25% fish, 70% crayfish and 5% insect for the last 215 days. Caloric energy density values were set for fish ($3853 \text{ J}\cdot\text{g}^{-1}$), crayfish ($3063 \text{ J}\cdot\text{g}^{-1}$) and other aquatic invertebrates ($3421 \text{ J}\cdot\text{g}^{-1}$).

We ran 365-day bioenergetics simulations to determine differences in consumption and growth among the three thermal patterns displayed by smallmouth bass. First, we ran static growth simulations for smallmouth bass weighing 350 or 1200 g (about 300 and 450 mm total length), where fish weight was increased by 0, 5, 10, 15 and 20% of the initial weight and used as the final weight in the simulation, which allowed us to determine how much consumption was necessary to achieve these growth

increases under each of the three thermal patterns. Then, we ran static consumption simulations by holding consumption constant at 1500 g for 350 g smallmouth bass and 2000 g for 1200 g smallmouth bass to predict the fish growth under the three thermal patterns. Consumption rates were set at these levels based on results from the static growth simulations.

Growth scope extrapolation was done using the same three thermal-use patterns and temperature data as the bioenergetics modelling approach. Temperature data for each thermal-use pattern were summarised by creating a histogram of mean daily water temperature based on one-degree increments from 11 to 30 °C. All days with mean daily water temperatures ≤10 °C were excluded because smallmouth bass cease feeding and growing at this temperature (Bennett & Childers 1957; Peterson & Rabeni 1996). Growth scope (% body weight gained/day) was known for 114 mm TL smallmouth bass from 18 to 30 °C (Whitledge et al. 2002). Because growth scope values are unknown at colder temperatures, we extrapolated values between 10 and 17 °C by assuming a linear relationship and setting the growth scope value at 10 °C to zero and using the known value at 18 °C. We then multiplied the number of days observed in each thermal-use pattern by the growth scope value for that temperature and summed across all values to obtain an annual growth scope.

Results

Angler harvest and unknown mortality reduced the number of tagged fish available for data collection (Table S1). On 26 January 2012 (23 days after implantation and while the tagged fish were still located at the spring confluence), eight of our 29 fish were caught (three were harvested) by the same angler. Two additional tagged fish were caught (one harvested) from the SC zone in the winter of 2012. Three additional fish disappeared

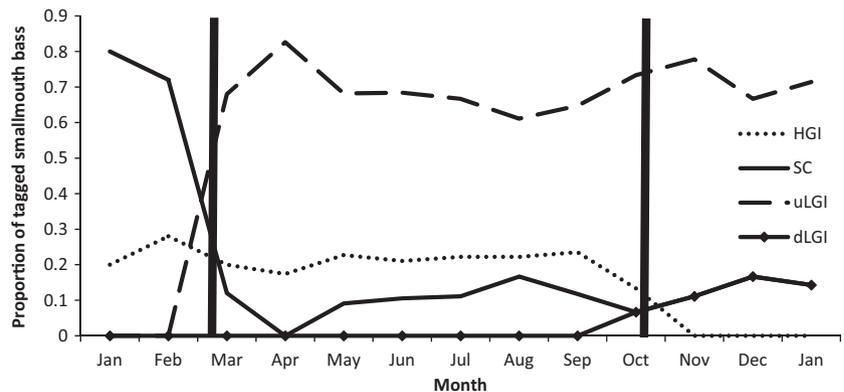
from the spring-confluence area before March and were suspected to have been harvested. Ten fish were caught and released by anglers during the summer and autumn periods based on reward tag returns, and five additional fish were caught and released based on conversations with anglers who did not record tag numbers. In total, a minimum of 19 (58%) of our fish were caught by anglers during the study and a minimum of four (12%) were harvested.

Fourteen fish were confirmed mortalities not directly linked to angling, and the majority of those fish appeared to have died in the fall of 2012. Two additional fish disappeared and may have left the search radius. Combined with harvest numbers, 18 fish were confirmed dead and 24 (73%) were suspected to be dead by the end of the study period. Only 12 fish (36%) were alive in November when water temperatures were consistently below 14 °C (temperature at which we expected return migration to thermal refuge).

Movement of radio tagged fish

The distance, direction and number of movement events varied greatly among tagged fish (Fig. 1). A total of 69% of the fish moved upstream to the uLGI zone between March 7th and March 28th, corresponding to a rise in river water temperature above 14 °C and rain events that caused increased river discharge (USGS Gage 07065495). Three fish (12%) moved upstream between March 28th and April 19th, and five fish (19%) moved from the SC zone to the HGI zone within 2 weeks after tagging, but moved to the uLGI zone by April 19th. Four fish (15%) moved out of the SC zone in March or April and downstream into the HGI zone, where three remained throughout the study. The fourth fish moved further downstream in October through the dLGI zone to the confluence of the Jacks Fork and Current River. One fish (#25) likely left Alley Spring in April and went downstream, but we were unable to locate it again until August. Four fish (15%) left the cold-period

Fig. 3. The proportions of radio tagged smallmouth bass located in each groundwater influence zone during each month from January 2012 to January 2013. Vertical black lines indicate the vernal (14 March) and autumnal (24 October) equilibrium dates. Groundwater influence zones referenced include the upstream low groundwater influence zone (uLGI), spring-confluence zone (SC), high groundwater influence zone (HGI) and downstream low groundwater influence zone (dLGI).



thermal refuge (SC or HGI zones), went upstream and then returned by May or June (Figs 1 and 3).

On average (\pm SE), fish moving upstream travelled 19.0 ± 2.9 km and fish moving downstream travelled 7.2 ± 3.7 km over the entire study period. Fish that moved upstream either selected a location and remained there for the duration of the study or continued to move. Of the 21 fish that moved upstream after leaving Alley Spring, eight moved less than 200 m between their most upstream known location and their June location, when we assumed spawning behaviour was complete because smallmouth bass in the system were no longer observed to occupy nests. Three fish disappeared before June, and the other 10 fish moved >200 m after reaching their upstream most known location, with eight moving more than 1 km. Another fish occupied Alley Spring during most of the warm-period, moved upstream in September and October and returned to Alley Spring in November. At no point did all tagged fish occur in the same zone and the highest percentage of fish occurring in a single zone (83%) occurred in the uLGI zone in April. Four tagged fish returned to the SC zone before July, including one fish that travelled 42.5 km upstream of Alley Spring. A maximum of 17% of tagged fish known to be alive were located in the SC and HGI zones combined after the autumnal equilibrium date (November locations), providing little support to our hypothesis that all the tagged fish would return to the thermal refuge (Fig. 3).

Smallmouth bass range of movement was highly variable (Fig. 1). The greatest observed upstream movement was 42.5 km, and the greatest observed downstream movement was 22.2 km. However, mean total fish length between upstream or downstream moving smallmouth bass did not differ ($t_{24} = -0.55$, $P = 0.59$), and there was no relation between total fish length and total distance moved ($F_{1,25} = 1.12$, $P = 0.30$, $R^2 = 0.04$).

Movement of archival tagged fish

During the cold-water period, two fish used the spring branch and three used the confluence based on a comparison of fish temperature to both river and spring water temperatures. For example, Fish 1 was located in the confluence area as indicated by the temperatures encountered by the fish that were intermediate between the Alley Spring temperatures and upstream river temperatures (Fig. 4). Alternatively, Fish 14.1 occurred only in Alley Spring branch prior to migrating upstream (Fig. 4). However, Fish 14.1 did move <1 km from the spring to the confluence approximately 18 h before it went upstream (Fig. 5) in what might be considered a 'staging' behaviour. None of the fish appeared to make forays between the spring, the confluence or the river while using

cold-water period refuge associated with Alley Spring.

River temperatures and changing discharge levels were associated with movement of archival tagged fish out of Alley Spring and its confluence with the Jacks Fork River (Table 1). Four of the five archival tagged fish left thermal refuge and moved upstream on 12 or 13 March 2012, when river temperatures exceeded that of the spring and discharge was rising or falling. However, one fish left on 7 March 2012 when discharge was steady and before river temperatures exceeded that of the spring. Archival tagged fish left thermal refuge at various times from 0900 to 2030 h, when upstream river temperature was between 11.8 and 14.8 °C. All archival tag fish left the spring/confluence area before the upstream river temperature reached 15 °C. Three fish left during a rise in river discharge and one fish left when discharge was declining, but still at 83% of its peak 19 h earlier (Table 1). Fish 8 left thermal refuge when discharge was steady, but 8 h later discharge began to increase in response to a rain event. Archival tagged fish did not use thermal refuge during the warm-period as evidenced by the <1 °C difference between fish temperature and river temperature upstream of Alley Spring. None of the archival tagged fish returned to the spring, confluence or spent time below the confluence after 12 March 2012.

Bioenergetics modelling

The two approaches we used to estimate growth of smallmouth bass produced different outcomes regarding our predictions of each thermal-use pattern. For the bioenergetics models, our predictions that fish who migrate (MIG pattern) require lower prey consumption levels to experience growth than fish exhibiting HGI patterns or LGI patterns were not supported. A 350 g migrating fish would have to consume 27% more g of prey to maintain its weight (0% growth) compared to a fish using HGI thermal patterns (Fig. 6). A fish in LGI habitat would have to consume 16% more g of prey to maintain its weight than would a fish in HGI habitat. The pattern was similar for 1200 g fish, where MIG or LGI inhabiting fish would have to consume 26 or 15% more g of prey, respectively, than would a fish inhabiting HGI habitat (Fig. 6). These patterns were repeated when modelling consumption needs to achieve 5, 10, 15 or 20% growth; however, consumption needs increased at a greater rate for the 1200 g fish than for the 350 g fish as growth percentage increased (Fig. 6). The timing of growth varied somewhat between strategies whereby growth during the warmest portion of the year was negative for both MIG and LGI strategies, but growth was maximised for the HGI strategy during the same time of year. Additionally, because

Fig. 4. Thermal conditions associated with two tagged smallmouth bass (Fish 1 and 14.1) on the Jacks Fork River near Alley Spring in 2012. All temperatures represent daily average water temperatures. Fish temperature was recorded using a temperature archival tag implanted in the body cavity of the fish; spring water temperature was recorded in Alley Spring Branch; and river temperature was recorded 1 km upstream of Alley Spring in the Jacks Fork River. Discharge values are displayed as average daily discharge and were obtained 800 m upstream of Alley Spring in the Jacks Fork River.

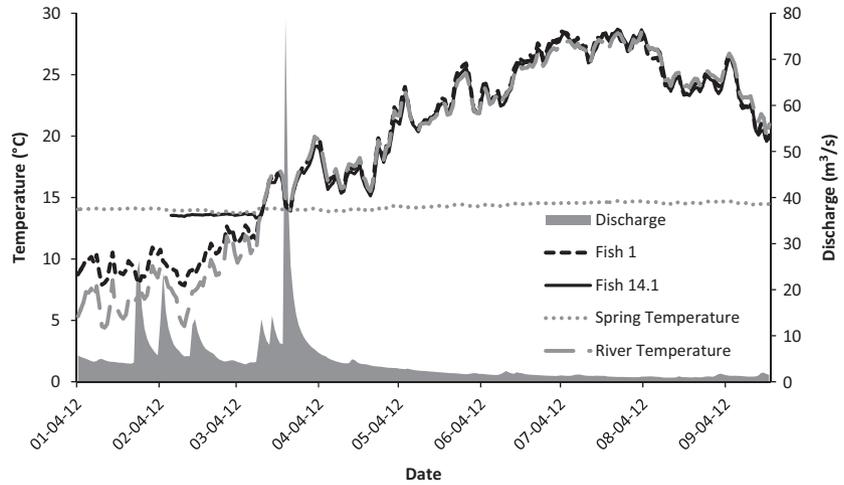
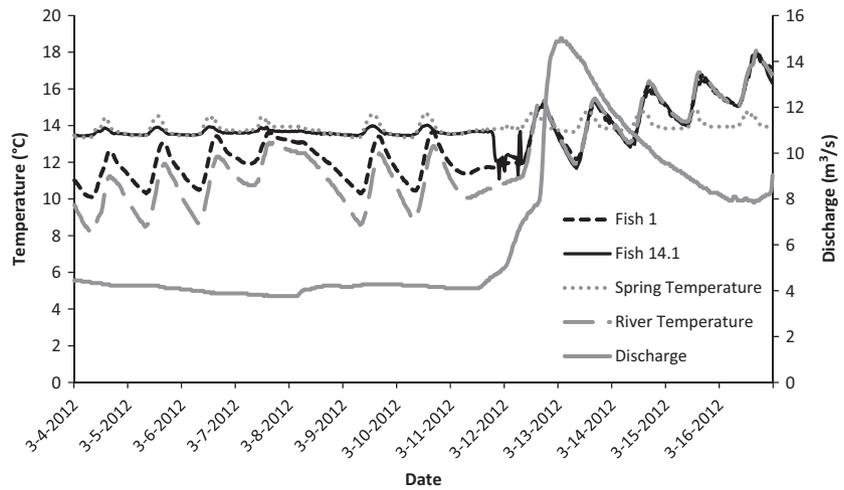


Fig. 5. Fine-scale view of thermal conditions in 2012 associated with two tagged smallmouth bass (Fish 1 and 14.1) corresponding to the time when the fish left thermal refuge associated with Alley Spring and entered the Jacks Fork River. All values represent hourly average water temperature or discharge.



MIG fish experienced some growth during the winter due to use of groundwater-influenced areas as opposed to the LGI inhabiting fish who did not, they required less growth during the summer to reach the same final size as the LGI fish.

Estimates from static consumption rate models showed similar results to the static growth rate models, in that HGI inhabiting fish were expected to grow the fastest and migrating fish the slowest. Both 350 g and 1200 g fish showed a similar pattern of greatest growth for HGI pattern fish and lowest for MIG pattern fish, but the magnitude of growth was less for the larger fish. Potential growth over 365 days for a 350 g fish at 1500 g of consumption was 46.9% for HGI fish, 20.9% for LGI fish and 4.6% for MIG fish. Potential growth over 365 days for a 1200 g fish at 2000 g of consumption was 18.4% for HGI fish, 8.2% for LGI fish and 1.2% for MIG fish.

Results of our growth scope extrapolation approach did support our growth predictions for each thermal-use pattern. Migrating fish (MIG pattern) had an

annual growth scope of 7.34%, which was 5% greater than the HGI pattern (7.0%) and 29% greater than the LGI pattern (5.68%). Mean daily water temperature was <10°C for 101 days in the LGI stream section compared to 33 days in the HGI stream section, and migratory smallmouth bass were assumed to have used groundwater sources (14 °C) during 139 days. Smallmouth bass displaying the HGI pattern were expected to experience 66% of their growth at temperatures from 18 to 20 °C, as water >21 °C was never available (Fig. 7). Fish displaying the MIG pattern were expected to experience 26% of their growth while inhabiting the spring (14 °C). Fish exhibiting the LGI pattern experienced only 4% of their growth when temperatures were below 14 °C (Fig. 7).

Discussion

Our results demonstrate that some individual smallmouth bass exhibit different behavioural thermoregulation strategies based on movement patterns, and there may be energetic advantages to the use of

Table 1. Jack's Fork River conditions when archival tagged smallmouth bass departed the Alley Spring branch or confluence area. River temperature represents the temperature upstream of Alley Spring (Bay Creek Access) at the exact time the fish left thermal refuge. Discharge (Q) trend is based on preceding 12 h.

Fish ID	Departure date	Departure time	River temperature (°C)	Mean daily river discharge (m ³ ·s ⁻¹)	Discharge trend	Spring or confluence	Notes
1	3/12/2012	0900	11.8*	7.1	Up	Confluence	
7.1	3/13/2012	2000	14.8*	12.4	Down	Spring	Q peaked earlier that day
8	3/7/2012	2030	12.9	3.8	Steady	Confluence	Q peaked earlier that day
11	3/12/2012	1400	14.8*	7.7	Up	Confluence	
14.1	3/12/2012	1100	12.7*	7.4	Up	Spring	Fish moved to confluence at 1730 on 3/11 when Q began to rise

*Temperature exceeded 14 °C during that day.

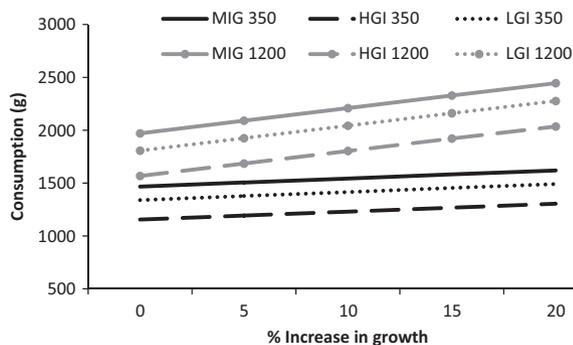


Fig. 6. Results of bioenergetics simulations to predict changes in consumption of prey based on per cent increase in growth for smallmouth bass. Fish weighed either 350 or 1200 g at the start of the simulations and were modelled under three thermal-use patterns (MIG, migrate; HGI, high groundwater influence; LGI, low groundwater influence).

thermal refuge in some scenarios. Our results supported predictions that tagged smallmouth bass using thermal refuge would migrate from the refuge when river temperature equalled spring water temperature and that the majority of smallmouth would move upstream. Contrary to our predictions, all tagged smallmouth did not return to the thermal refuge in autumn and fish moved on average >7.5 km upstream, which contradicts previous studies in the same system (Todd & Rabeni 1989). Our bioenergetics predictions were not universally supported given that the most energetically advantageous thermal-use strategy according to the bioenergetic analysis was to inhabit HGI reaches and the MIG strategy resulted in lower growth and higher required consumption rates than the LGI strategy. The growth scope analysis did support our prediction that migrating fish have a greater growth potential than the other thermal-use strategies.

Our observations on initiation of migratory behaviour in smallmouth bass in response to the combined cues of temperature and discharge mirror the importance of these factors for many other riverine fishes

(Northcote 1984; Modde & Irving 1998; Thorstad et al. 2008). Smallmouth bass in our study left thermal refuge when daily average river temperatures ranged from 11 to 20 °C; however, 69% of our fish left the spring before daily average river temperature exceeded 17 °C during March. The exact time of movement may be modified by physical cues related to rainfall and discharge events as demonstrated by the movement of fish out of thermal refuge both before and after the observed vernal equilibrium date of March 14th. Movement of smallmouth bass to overwintering habitats is known to occur when water temperature fell to 15–16 °C (Webster 1954; Paragamian 1981) or below 18.5 °C (Carter et al. 2012). Todd & Rabeni (1989) documented spawning-related movement of smallmouth bass in the Jacks Fork River during spring, but their fish were not directly associated with thermal refuge. We did not quantify available spawning habitat, but a lack of spawning habitat or ideal thermal conditions for spawning may explain upstream movements.

A total of 17% of tagged fish returned to thermal refuge by November, based on the 12 fish known to be alive at the time. However, the fact that some fish remained in the river and did not return to thermal refuge is an indication that some smallmouth bass do not use thermal refuge annually. The four tagged fish that did return to the thermal refuge did so by the end of June, well before we predicted them to return. Average daily river temperature reached 27 °C on June 25th, which is the temperature at which smallmouth bass are subject to mass loss from thermal stress (Whitledge et al. 2006). Thus, initiation of smallmouth bass migration behaviour related to cold-period refuge occupation coincided with the vernal equilibrium date, but the autumnal equilibrium date was not a reliable predictor of fish movement.

Our results contradict the predictions of the restricted movement paradigm (Gerking 1959; Gowan et al. 1994) which state that adult fish are primarily sedentary. We observed substantial variation

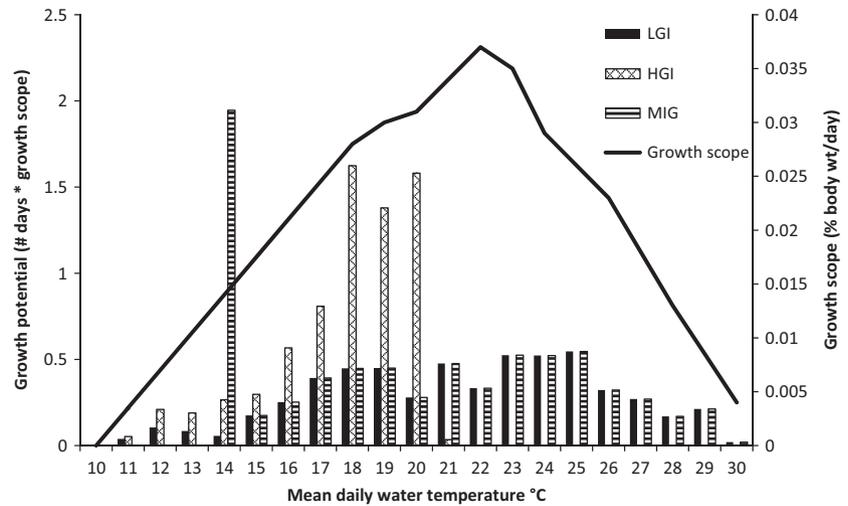


Fig. 7. Results of growth scope extrapolation for smallmouth bass using three different thermal-use patterns (MIG, migrate; HGI, high groundwater influence; LGI, low groundwater influence).

in movement patterns by tagged smallmouth bass, which is known to occur in other streams (Munther 1970; Lyons & Kanehl 2002; Gunderson VanArnum et al. 2004). The longest movement we observed was 42.5 km, which was greater than the maximum 7.5 km movement of smallmouth bass previously documented in this stream (Todd & Rabeni 1989), and our maximum and average movement distances were greater than observed for most smallmouth bass populations, but within the range documented for smallmouth bass (Lyons & Kanehl 2002; Hafs et al. 2010). The longest documented migration by smallmouth bass was 109 km in a Wisconsin stream during autumn when water temperatures fell below 16 °C and in conjunction with a rain event (Langhurst & Schoenike 1990). In our study, the majority of tagged fish moved upstream (81%) into the uLGI zone during spring. Of those, 38% moved less than 200 m after June and appeared to establish a small and static home range. An additional 48% of the fish that moved upstream did not establish a static home range and continued to move throughout the remainder of the study. These findings contrast those of Todd & Rabeni (1989) who documented restricted linear home-ranges (144–176 m) of smallmouth bass in the same river.

The combined results of our study and Todd & Rabeni (1989) demonstrate that some smallmouth bass use winter thermal refuges, but others do not, despite being in close proximity to refuge (2 km of Alley Spring). Other studies have shown that smallmouth bass populations segregate into migrant and resident individuals (Kaemingk et al. 2011). Data from Elkhorn Creek, Kentucky indicated that 69% of tagged smallmouth bass migrated, and 31% remained sedentary (Gunderson VanArnum et al. 2004). Funk (1955) estimated that for riverine smallmouth bass in Missouri 63% were sedentary (<1.6 km movement)

and 37% were mobile (>1.6 km movement), with 8% moving over 40 km. The high amount of variation observed in smallmouth bass movement and migration patterns suggests complex behavioural responses by individual fish are likely, may be age and sex dependent, and likely vary annually (Funk 1955; Lyons & Kanehl 2002). The mixture of migrating and resident individuals demonstrates a pattern of partial migration, which is condition dependent and often closely linked to genetic or phenotypic attributes of individuals (Chapman et al. 2011).

Our study specifically targeted a portion of the smallmouth bass population known to use thermal refuge during 2012. Many other species of fish use thermal refuge (Langhurst & Schoenike 1990; Peterson & Rabeni 1996; Torgersen et al. 1999; Ebersole et al. 2001; Bunt et al. 2013), but the advantages that this behaviour provide are not well understood. Peterson & Rabeni (1996) found that Centrarchids using cold-period thermal refuge had greater stomach contents, were larger, and were heavier per unit length than their congeners. Juvenile coho salmon are known to feed in cold habitats and then move up to 1300 m to warmer habitats to maximise metabolism and assimilation (Armstrong et al. 2013). We observed similar, short forays (a few hours) from a spring into the river by a smallmouth bass tagged with a temperature archival tag in Big Spring in the Current River during the cold-period (J. Westhoff, unpublished data). Thus, the mechanism for use of thermal refuge may be related to foraging or energetics.

The mixed results produced by our two approaches to estimating growth of smallmouth bass displaying different thermal-use patterns were unexpected. Growth scope results followed our predictions and suggest smallmouth bass use cold-period thermal refuge to maximise growth. Although growth scope at

14 °C is only 38% of maximum levels estimated at 22 °C, migratory fish experience those temperatures over long durations of time which allows them to grow when fish using other strategies inhabit water too cold for growth. Contrary to our growth scope results, our bioenergetics models did not indicate that a migratory behaviour incorporating cold-period thermal refuge was the most energetically advantageous. In fact, the migratory strategy required greater overall prey consumption by fish to achieve similar growth, compared to fish exclusively occupying the high and low groundwater influence zones. The HGI strategy was the most energetically advantageous, which likely results from the thermal stability of those stream reaches. Adult smallmouth bass are known to feed and grow at maximum rates near 22 °C (Whitledge et al. 2002), which despite having the lowest yearly average water temperature (15.2 °C), the HGI reach did have the least variation. This may indicate that high variation in water temperature can overshadow the energetic effects of a more desirable mean temperature. Growth, reproductive or survival-related benefits from refuge use must outweigh the risks and cost of refuge use for the strategy to make biological sense and in some cases fish may not use available thermal refuges (e.g., brown trout, *Salmo trutta*, in southern Appalachian streams; Burrell et al. 2000). One explanation for fish adopting the MIG strategy, despite its overall energetic shortcomings, may relate to the timing of growth and energy acquisition. The MIG strategy fish are theoretically able to grow over the winter making them more energetically suited for reproductive activities (e.g., gonad growth) prior to spawn, thus increasing their fitness. Hasler et al. (2012) used bioenergetics models to examine energy density levels for salmonids exhibiting different thermal refuge-use strategies and concluded that fish using refuge had more available energy for spawning. Alternatively, use of refuges can result in increased biotic interactions whereby certain species or individuals receive benefits from their physical environment but suffer increased negative effects of biotic interactions (Magoulick & Kobza 2003; Orrock et al. 2013). Also, the energetic costs of long migrations are unknown for smallmouth bass, but can be great in other fish species (Glebe & Leggett 1981). Given smallmouth bass in our study moved over 40 km, energetic cost of these migrations may be more than previously realised. Differences between the outcomes of our two approaches to estimating growth may relate to differences in sizes of fish considered, or the way the bioenergetics models incorporate more user-defined variables than does the growth scope approach. However, our models did not account for differences in prey availability that likely occur for each strategy or for differences in the

energetic cost of movement. Additional empirical data on these parameters may improve future bioenergetic modelling efforts and growth estimations.

Thermal refuge use by fishes in the southern portion of their range (which is where this study occurred) may be important if the climate warms. Populations of smallmouth bass in the southern portion of their range may require higher prey consumption rates and experience greater growth due to climate change. The Jack's Fork River may have stream temperature increase of up to 4 °C under projected climate scenarios which would lead to 48% increase in consumption by smallmouth bass but only a 9% increase in growth (Pease & Paukert 2014), likely because summer water temperatures may reach above optimal levels and result in decreased growth potential for adult smallmouth bass (Whitledge et al. 2003). Groundwater inputs from spring water discharge may act as a buffer in some of these systems and provide temperature sensitive species thermal refuge despite changing climatic conditions (Torgersen et al. 1999). Although less common, groundwater refuges in the northern part of the smallmouth bass range may have positive bioenergetic and population-level effects as well. The warmer water available during what would be a longer cold-water refuge period may provide more beneficial thermal conditions for foraging, metabolic activity and shelter (Power et al. 1999).

Increases in water temperature will likely cause a shift in timing of the vernal and autumnal equilibrium dates, which may alter the timing of smallmouth bass migration and spawning. If the number of days above 27 °C increases in low groundwater-influenced areas of stream (as predicted by Westhoff & Paukert, unpublished data), the outcome of using the HGI movement strategy may become more advantageous. Other effects of climate change on smallmouth bass movement are unknown, but may include changes in the proportion of fish using thermal refuge. Similarly, earlier warming of river water has been linked to earlier spawning migration of some fishes (Quinn & Adams 1996) and altered migration behaviour and thermal refuge use in response to elevated water temperatures by Chinook salmon (Goniaea et al. 2006).

Our study may provide useful insight into smallmouth bass ecology and movement that can be used to better conserve or manage this species. We demonstrated high harvest rates of fish near the spring, which supports the hypothesis by Peterson & Rabeni (1996) that fish congregating at spring-influenced sections of streams may be more susceptible to harvest by anglers than fish occupying other sections of the river. Although there is a closed season on smallmouth bass harvest from March 1st through May 24th, and no harvest is allowed in Alley Spring

Branch itself at any time, 34% of our fish were legally caught (14% harvested) from the confluence area where they were concentrated during the cold-period of our study (a span of 10 weeks). Behavioural thermoregulation and seasonal migration patterns may also be important to consider when designating special regulation areas for smallmouth bass. A 40 km-long smallmouth bass special management zone exists just upstream (<1 km) of the confluence of Alley Spring in the Jacks Fork River where anglers are allowed to harvest one smallmouth bass per day and it must be >457-mm TL. The rest of the Jacks Fork below and including Alley Spring confluence has a 305-mm minimum length for smallmouth bass with a daily harvest of six fish. Gunderson VanArnum et al. (2004) suggest that the entire migratory range of smallmouth bass may need to be included within a special regulation area to achieve the greatest benefit. However, this approach may not always be feasible given the known migratory capacity of smallmouth bass (>100 km), but protecting various distances upstream and downstream of thermal refugia might protect differing percentages of migrating fish. Given our results, a 15 km protected area both upstream and downstream of Alley Spring may have protected 60% of the migrating fish that survived until at least July ($n = 20$). Protection of 95% of migrating smallmouth bass may require 18 km of special regulation zone based on estimates by Gunderson VanArnum et al. (2004), but we estimate protection of 95% of migrating fish may require 40 km of protection in each direction in our study system. This may allow thermal refuge-seeking fish a way to maximise fitness without incurring high angler mortality.

We were able to document behavioural thermoregulation by smallmouth bass in one stream at one spring, but many unknowns remain regarding thermal refuge and smallmouth bass. Additional information from fish populations using other springs in other systems may expand the application of our findings. Our bioenergetics models predict possible growth and consumption differences for different migratory patterns, but empirical growth and consumption data from fish displaying those patterns may further elucidate the importance of thermal refuge. Finally, a greater understanding of predator-prey dynamics, movement and behaviour of fish while occupying thermal refuges is important in understanding the potential benefits of these systems and for applying appropriate management actions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Information about smallmouth bass used in the telemetry study on the Jacks Fork River including total length (TL), weight, if the fish received an archival tag, the number of days of valid archival tag data, number of valid locations, mortality status at the end of the study, and angling history.