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Journal of Thermal Biology 28 (2003) 445–456

Journal of
THERMAL BIOLOGY

www.elsevier.com/locate/jtherbio

Nesting activity, parental care behavior, and reproductive success of smallmouth bass, *Micropterus dolomieu*, in an unstable thermal environment

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Received 31 January 2003; accepted 1 April 2003

Abstract

Temperature plays a critical role in the reproductive ecology of smallmouth bass, affecting factors such as the timing of spawning, offspring development and survival of the brood. Because temperature also influences the activity rates of fish, it has the potential to alter the chronology of parental care activities and possibly the immediate or future reproductive success of individual fish. We conducted a study in a thermal effluent canal on Lake Erie to examine the influence of fluctuating thermal regimes on parental care and reproductive success of smallmouth bass. In general, parental care activity of these smallmouth bass was higher than previously reported for non-thermally altered environments and did not follow conventional stage-specific patterns. In fact, individual fish exhibited very different patterns, with no consistency among individuals. Despite these behavioral alterations and the thermal instability in the canal, the reproductive success of smallmouth bass (i.e., the percentage of nesting males that successfully produced free-swimming fry) was high relative to other published values. Behavioral alterations observed were variable and did not conform with theory. However, the high level of reproductive success implies that fish are capable of adjusting energetic expenditures in response to a suite of conditions and risks.

Keywords: Behavior; Parental care; Reproduction; Smallmouth bass; Thermal effluent; Predators; Thermal pollution; Thermal variation; Physiological telemetry

1. Introduction

Unstable environments provide unique challenges to animals that provide parental care (Carlisle, 1982; Brommer et al., 2000). This is particularly true for ectothermic animals such as fish, where natural thermal variation is inherent in their environments. Many species of fish provide parental care (Baylis, 1981; Sargent and Gross, 1985), and activity and metabolic rates of fish are affected by both absolute water temperature (Fry, 1971) and by thermal variation (Crawshaw, 1977,1979). Although fish possess suites of physiological adaptations and reproductive behaviors appropriate for the thermal variation they encounter naturally (Wright, 1978), fish are increasingly experiencing anthropogenically induced thermal variability that is more extreme than the thermal conditions under which these fish evolved. A classic example of anthropogenic alterations is the

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doi:10.1016/S0306-4565(03)00038-X

heated effluent from industrial and utility cooling systems. Absolute water temperatures, as well as the magnitude and frequency of thermal fluctuations in these systems, are both influenced by demand for cooling water (Coutant, 1970). These industrial effluents impose unnatural thermal variation on fish over both temporal and spatial scales. Thus, by documenting how fish respond behaviorally to thermal effluents, we can predict the impact of these effluents on fish. In addition, thermal effluents can be viewed as large-scale field experiments that provide an opportunity to examine how fish respond to altered thermal regimes. This study examines how thermal effluents affect the reproductive ecology of a parental care providing fish.

Smallmouth bass *Micropterus dolomieu* is a species of temperate, freshwater fish in which males provide sole parental care to the developing brood for an extended period of time. The reproductive ecology of this species has been well studied, including spawning behavior (Ridgway et al., 1989), timing of reproduction (Goff, 1985; Ridgway et al., 1991), parental care (Ridgway, 1988; Hinch and Collins, 1991; Cooke et al., 2002), and reproductive success (Raffetto et al., 1990). Many aspects of the biology of smallmouth bass are influenced by natural variation in water temperature, including the timing of reproduction and reproductive success (Armour, 1993). Variation in water temperature has the potential to affect parents and young differently, and in so doing, alter the cost-benefit relationships on which patterns of parental care are based. Several studies have reported that thermal variations as small as 2°C may result in nest abandonment (Rawson, 1945; Henderson and Foster, 1957), particularly when water temperatures fall below 15°C (Latta, 1963). Contrary to these results, however, studies of smallmouth bass nesting in thermal effluent canals reported reasonable levels of reproductive success despite widely fluctuating water temperatures (McKinley et al., 2000).

Parental care strategies involve tradeoffs between current and future reproduction, with selection expected to favor strategies that maximize lifetime reproductive success (Trivers, 1972). Parents should, therefore, invest in the current reproductive attempt only to the extent that the tradeoff with potential future reproductive success warrants; i.e., a male bass should abandon a nest because the offspring have died (e.g., due to thermal variation), or abandon viable offspring if by doing so the value of his future reproductive prospects would outweigh that loss. Few studies have examined fish reproductive ecology with a focus on parental care in unstable environments (see Jones and Reynolds, 1997). Because extreme thermal variation, such as that often produced by thermal effluents, imparts an additional mortality risk to the parent that is reasonably independent of parental care effort, it is likely that parental care behavior is impacted. Smallmouth bass represent a unique model system for examining the effects of thermally variable environments on parental care because the extensive research on their reproductive ecology in natural and altered systems provides reference data for comparative purposes.

In 1999 we investigated the reproductive ecology of smallmouth bass in a thermal effluent from a power generation facility on Lake Erie using detailed visual observations and locomotory activity transmitters. We quantified nesting activity, parental care behavior and reproductive success of smallmouth bass in the presence of extreme and highly variable temperatures. We compare our observations with those reported elsewhere, and with our own extensive observations of smallmouth bass reproduction and interpret our results in a life-history framework.

2. Materials and methods

2.1. Study site

This study was conducted at the coal-fired Nanticoke Generating Station (8-unit, 4000 MWe; 500 MWe each), located at 42°48′ N, 80°04′ on the north shore of Lake Erie (Fig. 1). The station uses a once-through condenser cooling water system, taking water from Lake Erie via two submerged intakes that extend approximately 550 m offshore. The maximum design cooling water flow is 154 m^3/s, of which 88 m^3/s is for condenser cooling and 66 m^3/s is for cooling the heated discharge water. The station discharges the heated effluent via a canal 550 m long, 15.25 m wide, and 9.15 m deep. The Nanticoke Thermal Generating Station operates as a peak load station, contributing power to the grid during periods of peak demand. This typically requires that 6–8 units are in operation during the early morning, mid-day, and late afternoon periods. This ‘‘two-shifting’’ mode creates diel fluctuations in effluent temperatures. Additional details on station operation can be found in Wiancko (1981).

2.2. Environmental factors

The inlet temperature was measured in the station forebay, whereas the discharge temperature was measured by two fixed recorders ($T1$) near the head of the outflow canal, just downstream from the tempering pump discharges (Fig. 1). Discharge temperature was taken as the average reading of the two recorders, even though differences >0.1°C were rare. Both inlet and discharge water temperatures were recorded hourly. We used these water temperatures for monitoring trends in activity at gross temporal scales. We also placed a non-fixed temperature recorder (Hobo Tidbit, Onset Inc.) ($T2$) on the bedrock shelf in the area where male smallmouth bass were nesting. This device monitored

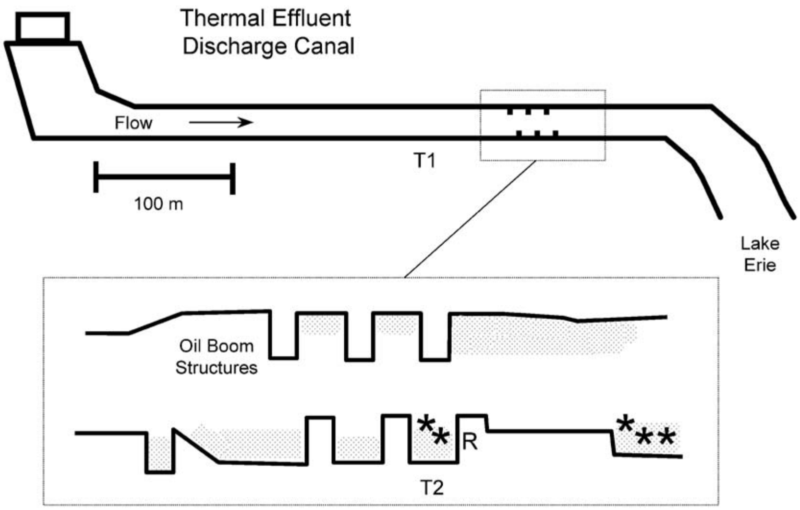

Fig. 1. Overhead schematic of the generating station discharge canal complex with an inset of the region near the oil boom structures where smallmouth bass were observed to spawn. Locations of the nests occupied by fish implanted with activity transmitters are denoted by asterisks. The fixed ($T1$) and the non-fixed ($T2$) temperature probes and the activity receiving system (R) are also noted on the figure. Shaded regions indicate areas where smallmouth bass were observed to nest.

water temperature at 5-min intervals and was used for determining correlations with locomotory activity telemetry at finer resolutions. We determined minimum, maximum, and mean water temperatures and developed an index of temperature variability by using the difference between the previous water temperature and the current water temperature.

2.3. Nesting surveys

We observed smallmouth bass nesting activity daily from above the water using polarized glasses. Individual nests that received eggs were marked with a numbered tile, and the size of the nesting male was estimated to the nearest 5 cm. Nests were also mapped and daily observations of male presence, predator activity, and stage of the developing brood were recorded. We used a modification of Ridgway's (1988) terminology to denote four stages of development (see Cooke et al., 2002); egg (EGG), egg-sac fry (ESF), swim-up fry (SUF), and free-swimming fry (FSF). We considered a nesting male successful if he received eggs that developed to the free-swimming fry stage (Philipp et al., 1997; Suski, 2000). Because a variety of parameters including reproductive success vary seasonally, we divided the spawning season into three spawning periods (April 29–May 14, May 15–31, June 1–15).

2.4. Locomotory activity telemetry

We used locomotory activity telemetry to monitor continuously the parental care activity of free-swimming smallmouth bass in situ. Detailed descriptions of transmitters (Beddow and McKinley, 1999) and surgical techniques for smallmouth bass (Cooke et al., 2001, 2002) are presented elsewhere. Briefly, the transmitters (EMGi radiotelemetry, 51 mm × 13 mm, 18.0 g in air, Lotek Engineering Inc., Newmarket, Ontario) consisted of an epoxy capsule with a single antenna and a pair of gold-tipped electrode wires. When placed in the axial red musculature, the electrodes detect bioelectric potentials. This bioelectric activity is integrated and amplified prior to being transmitted. The signal recorded by the receiver is an EMG pulse interval (ms) that is inversely related to muscular activity.

Once a nesting fish suitable for implantation was located (i.e., a male guarding new eggs), we angled it off his nest. We minimized the stress incurred from angling by landing them in less than 20 s, a duration that in other studies has been used for unstressed controls (e.g., Kieffer et al., 1995). Following capture, fish were placed immediately into a cooler containing an induction bath of anaesthetic (clove oil/ethanol 1:9, 45 PPM). Once each fish was angled from its nest, a researcher wearing polarized glasses kept potential egg predators out of the nest with a blunt pole. All implanted fish had egg scores greater than category 3 (Philipp et al., 1997; Suski, 2000).

After fish lost equilibrium in the anesthetic (3–4 min), they were measured (TL, mm) and weighed (g) before being placed ventral side up in a V-shaped acrylic trough lined with neoprene. During surgery, the gills were continuously irrigated with a maintenance dose of anaesthetic (30 PPM) in oxygenated water. Surgical procedures were similar to those of Cooke et al. (2001). Electrodes were positioned 10 mm apart in the red axial musculature below the lateral line using 16 1/2 g rods (Bunt, 1999). Electrode placement was standardized at the anterior portion of the dorsal fin (Beddow and McKinley, 1999). The incision was closed with four independent braided silk sutures (2/0 Ethicon). A small amount of cyanoacrylate glue (Vet-Bond, 3M Inc.) was applied to the sutures to increase resistance to abrasion that could occur during fanning. The entire procedure lasted less than 5 min, and fish recovered quickly when returned to fresh oxygenated water.

Fish were allowed to recover for 5 min prior to being released directly above the nest site (Cooke et al., 2002). To ensure that any effects of surgery were eliminated, we excluded the first 24 h of data following release (Cooke et al., 2002). In total we implanted five male smallmouth bass (Table 1). Two data-logging receivers (SRX_400, Lotek Engineering Inc.) were used to monitor continuously the activity of radio-tagged fish. The receivers were placed in an environmental chamber and were connected to 2 two-element antennas placed near the implanted fish (Fig. 1). The receiver was set to scan continuously. It cycled through the first antenna, collecting 10 EMGi signals from every fish present, until switching to the second antenna. The receiver system was operational throughout the study, except when downloading data, which took less than 3 h, every 3–4 days.

Data were summarized in SAS (SAS Institute Inc.) creating 30 min averages (Briggs and Post, 1997) for each fish. All EMGi values were adjusted for individual fish, and values were transformed so they could be reported as percent increase over resting (Cooke et al., 2001). Resting values were collected when the fish were stationary while being held in the cooler prior to being released after surgery. Once fish were back in the canal, resting values were corroborated with videography. For each fish, we collected 15 min of videographic observations using a color underwater videocamera (Deep Sea Power and Light Inc, California) and used periods of inactivity to verify resting activity levels. Individual forced swimming calibrations in respirometers were not possible because the fish would have been absent from the nest for an unacceptably extended period. Instead, we used previously developed relationships for smallmouth bass (Cooke et al., 2001) between swimming speed and percent increase in activity to calculate swimming speeds from our field-collected EMG data.

We assessed fish activity at several time scales. First, the mean daily swimming activity (m/d) was calculated for individual fish at each of the different stages of brood development. This examination provided insight into stage-specific patterns and details the stage and species-specific swimming distance equivalents (i.e., a combination of the actual distance traveled and the costs of swimming in place; Hinch and Collins, 1991). We also calculated and compared instantaneous swimming speeds (m/s) for use in the activity multiplier of the bioenergetics model (UW Sea Grant, 1997; see Cooke et al., 2001, 2002). Estimates of daily swimming activity (km/day) were calculated for individual fish using data from the entire 24-h periods (including diurnal, nocturnal and crepuscular).

2.5. Analysis

For locomotory activity transmitter data, we also used ANOVA to test for significant differences in guarding male activity that were related to the different stages of offspring development, mean daily water temperature, and daily variation in water temperature. For all ANOVA procedures, the conservative Tukey post-hoc test was used to identify where significant differences occurred (Day and Quinn, 1989). We used multiple regression to examine the contribution to observed parental care activity arising from age of offspring, mean daily water temperature, and daily variation in water temperature for each fish. For spawning data, we divided the spawning period into three 16-day periods and used ANOVA to test the hypotheses that fish size, mean daily water temperature, and mean daily variation in water temperature did not vary with time of spawning. Reproductive success for each time period was calculated for all individuals that spawned during that period. One sample *t*-tests were used to compare reproductive success values from our study with published values of reproductive success for smallmouth bass from other environments. We also used multiple regression to examine the contribution to observed reproductive success arising from the size of

Table 1
Meristics of smallmouth bass implanted with activity transmitters in the Nanticoke Generating Station thermal effluent on Lake Erie

Transmitter frequency	Total length (mm)	Weight (g)	Date spawned	Date implanted	Fate
149.236	451	1960	May 6	May 10	Successful brood
149.376	437	1620	May 4	May 10	Successful brood
149.415	356	680	May 15	May 19	Successful brood
149.557	437	1420	May 16	May 19	Successful brood
149.579	402	1180	May 16	May 19	Abandoned

the fish, water temperature, and variation in water temperature. We confirmed that our analyses met assumptions of parametric tests by examining graphs of standardized residuals. All analyses were conducted with SYSTAT (Version 8.0, SPSS Inc.). The maximal type 1 error rate was set at $\propto = 0.05$.

3. Results

3.1. Environmental factors

Lake water temperatures generally increased from May through June (Fig. 2). Effluent temperatures mirrored this increase. Smallmouth bass are widely regarded to initiate reproductive activity at a minimum water temperature of 15°C. Lake Erie did not achieve a maximum water temperature of 15°C until May 13, and it was not until June 10 that the minimum water temperature was above 15°C. The discharge canal frequently had daily maximum water temperatures that exceeded 15°C throughout the year, but it was not until June 5 that daily minimum water temperatures in the canal remained above 15°C. Throughout the reproductive period the mean daily water temperature fluctuation in the effluent was 5.4°C, compared to 1.7°C in the lake. Although no obvious temporal trends were evident for thermal stability, upwellings occasionally resulted in greater variability and overall reductions in water temperatures in both the lake and the discharge. Significant upwelling events (decreases of ~5°C or more in one day) occurred on May 2, 13 and 26, and June 13.

3.2. Nesting chronology

We monitored 71 nests in the effluent canal from April 30 to June 15. The first evidence of smallmouth bass spawning occurred on April 29 when fish were observed cruising on the shallow limestone benches near the oil boom structure (Fig. 3). Although nest excavation had begun by some males, no eggs were present in any of the nests. Spawning was first observed on April 30, when mean daily water temperatures were ~15°C. On May 1, additional nests had been excavated, and courting and spawning behaviors among smallmouth bass were observed. Peak spawning (25% of all nests) occurred on May 5 at a mean daily water temperature of

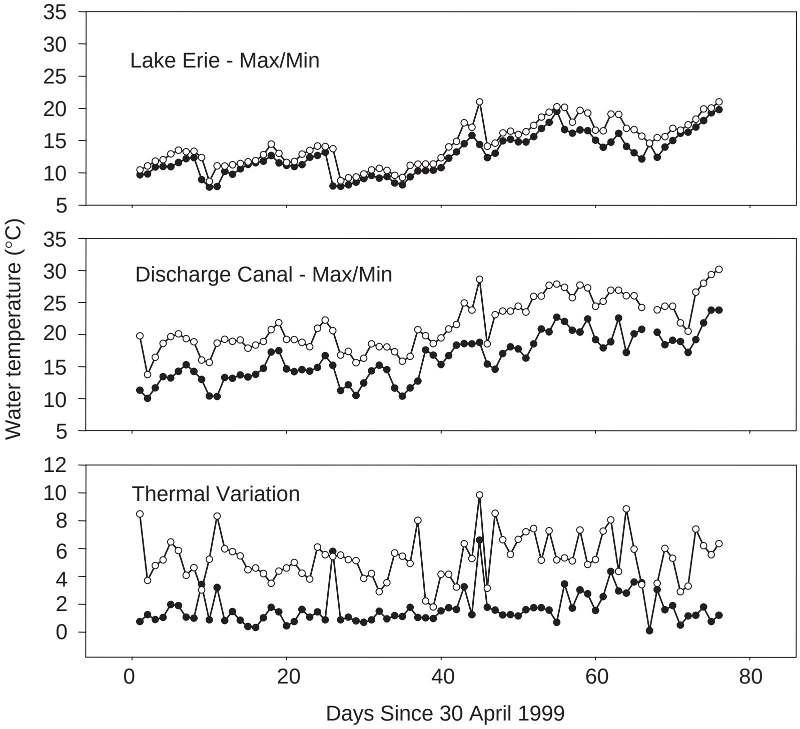

Fig. 2. Daily temperature patterns in Lake Erie and the generating station discharge canal. The upper panel is daily max–min values for Lake Erie. The middle panel is daily max–min values for the discharge canal. The lower panel is the daily thermal variation (i.e., max–min) value for Lake Erie (solid dots) and the effluent canal (open dots).

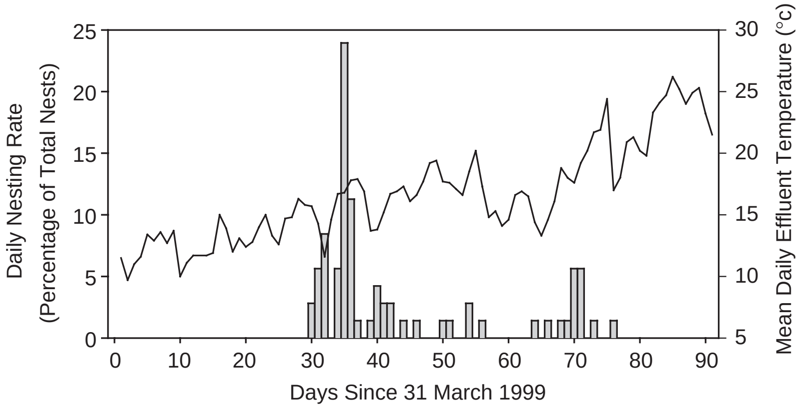

Fig. 3. Chronology of nesting activity of smallmouth bass in the Nanticoke effluent canal. Daily resting rates expressed as a percentage of total nests are plotted (bars). The line is a trace of mean daily water temperature.

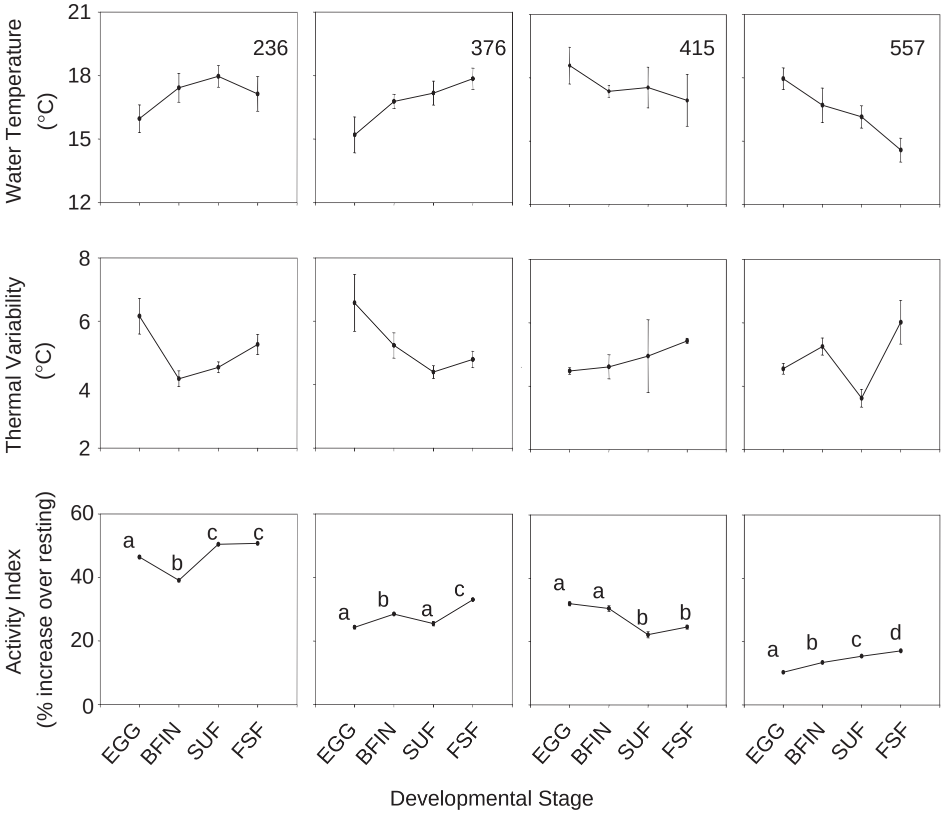

Fig. 4. Stage specific parental care activity of four smallmouth bass implanted with activity transmitters and corresponding stage specific water temperatures and thermal variability values. Offspring developmental stages are described in the text. For water temperature parameters, data are daily means (SE). Plotted activity index values are means of 30 min intervals. Analysis of variance indicated that activity index values varied significantly with stage of offspring development (Fish 236, $F = 159.65$, $P<0.001$; Fish 376, $F = 122.95$, $P<0.001$; Fish 415, $F = 26.12$, $P<0.001$; Fish 557, $F = 76.24$, $P<0.001$). Dissimilar letters indicated statistically different values ($P<0.05$) assessed using the Tukey–Kramer HSD.

~16°C. No or limited spawning was associated with days that were affected by substantial upwelling events. In the non-thermally influenced region near the discharge canal, reproductive activities were first observed on June 14, 47 days later than in the thermal effluent.

Table 2
Multiple regressions for the effects of water temperature, thermal variability, and offspring stage on the parental care activity of nesting males smallmouth bass monitored with activity transmitters

Fish	Sources of variation	Percent model explanation (%)	*F*-Value	*P*-Value
236	Water temperature	2		<0.001
	Thermal variability	17		<0.001
	Offspring stage	<1		0.703
	Entire model	19	159.6518	0.001
376	Water temperature	14		<0.001
	Thermal variability	21		<0.001
	Offspring stage	<1		0.004
	Entire model	35	122.9524	<0.001
415	Water temperature	4		<0.01
	Thermal variability	5		<0.001
	Offspring stage	8		<0.001
	Entire model	17	26.1231	<0.01
557	Water temperature	21		0.015
	Thermal variability	<1		0.315
	Offspring stage	<1		0.968
	Entire model	21	76.3266	<0.001

3.3. *Locomotory activity telemetry*

We collected complete nesting data for four of the five fish implanted with activity transmitters (Table 1). Fish 579 returned briefly to his nest following surgery, but abandoned within 2 h and left the effluent canal by the following day. The remainder of the fish successfully raised broods. Locomotory activity levels varied extensively among individuals, and within individuals across the four offspring development phases (Fig. 4). There were no consistent patterns in locomotory activity of fish. Because fish were implanted on different days and the duration of the different stages differed among individuals, we also present the mean daily water temperature and daily temperature fluctuation for each individual (Fig. 4). Interestingly, there were no consistent relationships between either of these water temperature parameters, or developmental stage of offspring and parental care activity. Multiple regression analysis suggested that only 17–35% of total variation in parental care activity could be explained by these three sources (Table 2). Relative to smallmouth bass studied using activity transmitters and videography where thermal environments were more stable, fish in our study exhibited higher levels of swimming activity (Fig. 5).

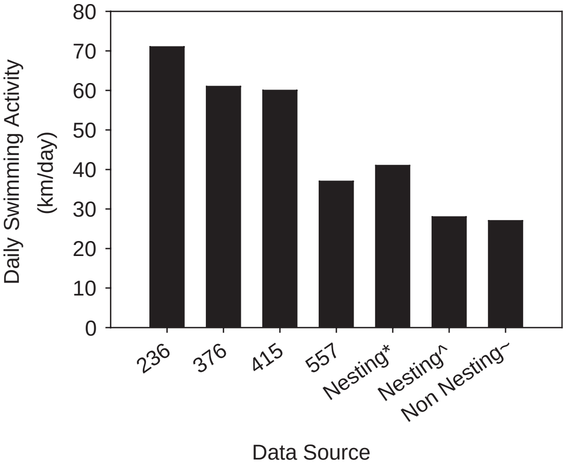

Fig. 5. Daily swimming activity estimates for smallmouth bass in the Nanticoke thermal effluent canal compared to activity rates determined in other environments. The first four bars (236, 376, 415, 557) correspond to mean daily activity rates for smallmouth bass in the Nanticoke thermal effluent. The nesting smallmouth bass represent activity transmitter estimates in Lake Opinicon (*) ($N = 6$, Cooke et al., 2002) and from videography estimates in Lake Opeongo (^) ($N = 2$, Hinch and Collins, 1991). Non-nesting smallmouth bass are from a noneffluent influenced enclosure on Lake Erie ($N = 5$, Cooke et al., 2001).

3.4. *Reproductive success*

Reproductive success for smallmouth bass in our study was generally high, but did decrease for males that spawned later in the reproductive period (early, 95.3%; intermediate, 71.5%; latest, 64.7%) (Fig. 6). A summary of 30 published values indicates that the mean rate of reproductive success for smallmouth bass is 50.6±4.7% (Table 3). Reproductive success rates in our study were

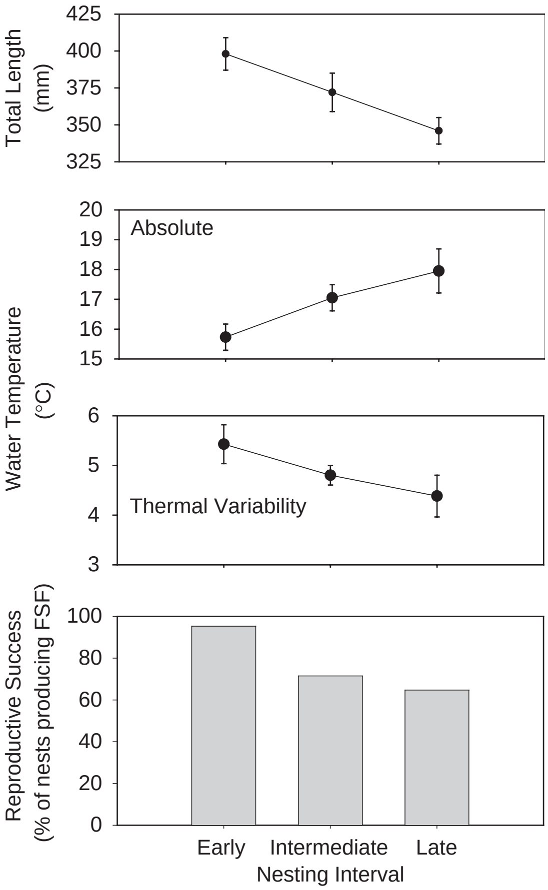

Fig. 6. Characteristics associated with reproductive success levels for smallmouth bass in the effluent canal over three nesting intervals (early, April 29–May 14; intermediate, May 15–31; late, June 1–15). Total lengths of fish (mm), absolute water temperature and thermal variability are also visualized for each nesting interval and are presented as means (SE). Analysis of variance indicated that the size of the fish ($F = 5.15$, $P = 0.010$) and water temperature ($F = 3.95$, $P<0.001$) varied significantly with reproductive timing, whereas thermal variability did not ($F = 5.33$, $P = 0.174$). Dissimilar letters indicated statistically different values ($P<0.05$) assessed using the Tukey–Kramer PSD.

significantly higher (one-sample t; 1st interval, $t = -9.61$, $P<0.001$; 2nd interval, $t = -4.50$, $P<0.001$; 3rd interval, $t = -3.04$, $P = 0.005$) including transmitter implanted fish (80%, $t = -6.32$, $P<0.001$).

Coincident with these seasonal differences in reproductive success was variation in other parameters including fish size, water temperature, and extent of water temperature fluctuations (Fig. 6). The size of fish spawning and water temperature both increased over the spawning period, whereas thermal variability decreased somewhat (Fig. 6). Multiple regression analyses indicate that 97% of the model variation in reproductive success can be explained by absolute mean water temperature (96%) ($P<0.001$) and fish size (1%) ($P<0.001$) (ANOVA $F = 547.19$, $P<0.001$). Thermal stability did not improve the model significantly ($P = 0.082$).

4. Discussion

We found that smallmouth bass reproduced successfully in the Nanticoke effluent canal despite the atypical thermal conditions. Temperatures in the discharge canal were 5–10°C higher than in the adjacent lake, which advanced spawning by a month. In addition, the daily temperature regime was highly variable compared to the lake (a daily fluctuation range of ~5–10°C vs. ~1–2°C). Nest-guarding male smallmouth bass exhibited stage-specific parental care patterns that were not consistent with predicted patterns and that varied substantially among individuals. Nonetheless, many smallmouth bass successfully produced and reared offspring, and their success rates were higher than those reported for undisturbed areas (Table 2). Below, we interpret these results in the context of smallmouth bass thermal ecology and parental care behavior.

Smallmouth bass in the discharge canal in 1999 first spawned on April 29 at a water temperature of 15°C. This temperature is generally considered the minimum thermal threshold for both the initiation and continuation of reproductive activity for this species (Armour, 1993). Spawning in the canal occurred approximately 1 month earlier than in adjacent non-thermally influenced regions, consistent with observations by Shuter et al. (1980) and Balesic (1990). On several occasions, water temperatures fell below 15°C due to upwelling events. Nesting male bass can respond to such events by abandoning their nests while their offspring suffer high mortality directly from lower water temperature (Eipper, 1975), and indirectly through the absence of parental care (Latta, 1963). Interestingly, however, we observed no evidence of such mortality following upwelling in our study, and nesting males continued to provide care for the young and did not abandon their nests. During and following upwelling, few new nests were constructed and spawning was restricted, although spawning resumed quickly once water temperature increased. McKinley et al. (2000) reported that non-nesting smallmouth bass typically left the canal during upwellings, but nesting bass continued to provide care to their young.

In our study, we documented parental care activity that was generally higher than levels of parental care activity observed in smallmouth bass from a non-thermally altered lake in eastern Ontario (Cooke et al., 2002). Variation in activity among studies is exemplified by the estimates of mean daily swimming activity of smallmouth bass plotted for the parental care period in

Table 3
Studies of smallmouth bass in central North America that provide estimates or measures of reproductive success. Reproductive success is generally regarded as raising the brood to the free-swimming stage. Studies conducted in thermal effluents are noted

Nesting success % successful	Location	Thermal effluent	Comments	Citation
100	Lake Opinicon, ON	N	Activity transmitter fish	Cooke et al. (2002)
33	Lake Erie, ON	N	Yr 1	Goff (1985)
88	Lake Erie, ON	N	Yr 2	Goff (1985)
54	Lake Opinicon	N		Gross et al. (1994)
39	Regulated Stream, VA	N	Male abandonment and high flows	Knotek and Orth (1998)
43	Regulated Stream, VA	N	High flow responsible for 85% of failures	Lukas and Orth (1995)
34	Lake Opeongo, ON	N	Yr 1	Mackereth et al. (1999)
51	Lake Opeongo, ON	N	Yr 2	Mackereth et al. (1999)
78	Little Saline Creek, MO	N	Early Bout	Pflieger (1966)
89	Little Saline Creek, MO	N	Later Bout	Pflieger (1966)
73	Lotic Systems, TN	N	Yr 1, low water	Reynolds and O'Bara (1991)
35	Lotic Systems, TN	N	Yr 2, flood condition	Reynolds and O'Bara (1991)
67	Lake Opeongo, ON	N	Yr 1, Unusually warm year	Ridgway and Friesen (1992)
29	Lake Opeongo, ON	N	Yr 2	Ridgway and Friesen (1992)
31	Lake Opeongo, ON	N	Yr 3	Ridgway and Friesen (1992)
38	Lake Opeongo, ON	N	Yr 4	Ridgway and Friesen (1992)
24	Lake Opeongo, ON	N	Yr 1, Only used unfed fish	Ridgway and Shuter (1994)
41	Lake Opeongo, ON	N	Yr 2, Only used unfed fish	Ridgway and Shuter (1994)
60	Not Specific	N	General Comment	Scott and Crossman (1973)
62	Lake Opinicon, ON	N	Inside voluntary angling sanctuary	Suski (2000)
46	Lake Opinicon, ON	N		Suski (2000)
45	Loughborough Lake, ON	N	Inside voluntary angling sanctuary	Suski (2000)
48	Loughborough Lake, ON	N		Suski (2000)
50	Bob's Lake, ON	N	Inside voluntary angling sanctuary	Suski (2000)
50	Bob's Lake, ON	N		Suski (2000)
100	Charleston Lake, ON	N	Control group	Suski (2000)
80	Taughannock Creek, NY	N		Webster (1954)
0	Indian Creek, OH	N	Yr 1, Moderate flooding	Winemiller and Taylor (1982)
29	Indian Creek, OH	N	Yr 2, Light flooding	Winemiller and Taylor (1982)
100	Lake Erie, ON	Y	Radiotransmitter implanted fish	McKinley et al. (2000)
80	Lake Erie, ON	Y	Activity transmitter fish	This Study
95	Lake Erie, ON	Y	Early bout	This Study
72	Lake Erie, ON	Y	Middle bout	This Study
65	Lake Erie, ON	Y	Late bout	This Study

our study (thermal effluent), the parental care period in Lake Opinicon (Cooke et al., 2002) and Lake Opeongo (Hinch and Collins, 1991) and non-nesting smallmouth bass in Lake Erie (Cooke et al., 2001). In general, daily activity levels were highest in our study (Fig. 5). Non-nesting fish in Lake Erie in a stable environment (Cooke et al., 2001) had similar activity rates to the nesting fish from Lake Opeongo (Hinch and Collins, 1991). In smallmouth bass, cardiac output, oxygen requirements, and locomotory activity generally increase with increasing water temperature (Schreer and Cooke, 2002). Although we are aware of only one study (Reebs et al., 1984) that unequivocally determined that parental care activity varies with water temperature, several instances in which temperature did not elicit alterations in parental care behavior have been reported (e.g., Lachance and Fitzgerald, 1992; St. Mary et al., 2001).

Despite the consistency among bass in spawning earlier and displaying higher levels of parental care activity in the thermal effluent, individual smallmouth bass in the discharge canal were inconsistent in how their relative activity levels varied across stages of offspring development. Evidence from relatively stable thermal environments suggests that smallmouth bass parental care activity changes in accordance with the ontogeny of the brood (Ridgway, 1988; Urban, 1991; Ongarato and Snucins, 1993; Cooke et al., 2002) consistent with parental investment theory (Sargent and Gross, 1986). Cooke et al. (2002) used similar activity transmitters to those we employed in this study and report that activity levels increased from the egg stage, peaking at the ESF stage and then gradually decreasing to the low FSF stage. This pattern is consistent with other studies on smallmouth bass (i.e., Ridgway, 1988; Urban, 1991; Ongarato and Snucins, 1993) but differs substantially from patterns we observed in this study. Deviation from the expected pattern, and the inconsistency among the fish we observed was not a consequence of individual fish experiencing different thermal regimes. Both absolute water temperature and thermal variation contributed to the explanation of variance in stage specific activity rates (range 17–36%), but did not account for the patterns exhibited by individuals.

Our results might be attributable to changes in the cost-benefit trade-off of parental care for smallmouth bass in our study. Under natural circumstances, a primary benefit of parental care is protection of eggs and fry from predation (Baylis, 1981). Although we did not quantify potential nest predators, we never observed predators in the vicinity of nesting bass, a much different situation from natural nesting environments (e.g., Cooke et al., 2002). Relaxation of predation pressure, combined with water temperatures that generally allowed higher levels of activity, could have caused individual bass to vary their behavior in response to factors that would normally be unimportant (e.g., proximity of neighbors, feeding opportunities). Thus, apparently stochastic variation in parental behavior could occur while simultaneously allowing all the fish to nest successfully. This hypothesis predicts that bass nesting in thermal effluents with abundant nest predators should behave consistently and follow the stage-specific patterns of bass nesting in natural environments. An alternative explanation is that variation in energetic resources played an important role in parental care behavior (see Mackereth et al., 1999; Gillooly and Baylis, 1999). Lachance and FitzGerald (1992) conclude that energetics may influence parental care decisions in variable environments. Greater allocations to offspring while breeding in harsh (e.g., hypoxic) conditions has been shown to reduce future allocations for nest guarding male fish (Jones and Reynolds, 1999).

This study has shown that despite elevated and highly variable thermal conditions in a thermal effluent, smallmouth bass successfully reproduced at levels higher than most published values from more stable thermal environments. We must caution, however, that in some years the thermal effluent reaches temperatures that are lethal to smallmouth bass (Ryan and Witzel, 1993), so nesting success is far from certain. We also found that nesting bass achieved reproductive success despite altering their usual patterns of parental care and proposed that a lack of nest predators in the canal might explain this result. Because water temperature and threats to the nest should both affect parental investment decisions of nesting bass, thermal effluent canals may provide unique opportunities to the reproductive behavior of smallmouth bass. Studies that systematically vary the level of stability in important environmental variables will be essential for testing and developing hypotheses on the parental care investment decisions of fish in unstable environments (Poysa and Milonoff, 1999).

Acknowledgements

This study benefited from the expert field assistance of Larry DeKoning, Karen Dunmall, Pauline Bloom and Andrea Buckman. Greg Adams and Marko Cicra assisted in the analysis of videographic footage. Logistic support for this project was provided by Gerry McKenna and Rick Ballard. We also thank Scott McKinley for the opportunity to conduct this research. This project was funded by Ontario Power Generation Inc., the Natural Sciences and Engineering Research Council, and the Waterloo Biotelemetry Institute. Support for SJC during analysis and reporting was provided by the University of Waterloo, the Illinois Natural History Survey, the University of Illinois and a Julie Payette Natural Sciences and Engineering Research Council Post-Graduate Scholarship.

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