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Physical activity and behavior of a centrarchid fish, *Micropterus salmoides* (Lacépède), during spawning

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Abstract – The spawning behavior of male and female largemouth bass *Micropterus salmoides* (Lacépède) was studied in central Illinois during the spring of 1998 to examine patterns of muscular activity associated with different spawning related behaviors and to evaluate whether electromyogram (EMG*i*) telemetry could be used to detect spawning activity. Fish were implanted with EMG*i* transmitters (8 females, 16 males) on April 7, prior to the initiation of spawning, and were released in four 0.10-ha earthen research ponds. Continuous EMG*i* records, underwater videography and additional visual observations for one pair of EMG*i* tagged fish were collected throughout the entire spawning event, allowing us to quantify behavioral correlates of physical activity. Male EMG*i* activity patterns were only correlated with female patterns during courting and periods of male aggression toward the female. Overall, EMG*i* activity was highest for the female during shuddering (gamete deposition), whereas male EMG*i* activity was similarly high during periods of nest excavation, shuddering and post-spawn parental care activities. During spawning, female EMG*i* activity was positively correlated to shuddering. Average daily EMG*i* activities for females peaked on the day of spawning. As a result of their engagement in parental care activities, male activity continued to rise even after spawning was completed. EMG*i* telemetry appears to be a useful technique for monitoring the reproductive activity of largemouth bass, especially in areas of high cover or turbid water or during low light conditions. This technology permitted us to quantify and contrast the activity patterns associated with different spawning related activities, information that will be required to construct accurate, gender-specific bioenergetics models for this species.

Key words: largemouth bass; physiological telemetry; electromyograms; reproductive activity; spawning

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Field observations of spawning largemouth bass *Micropterus salmoides* (Lacépède) are limited for several reasons. Firstly, spawning is thought to last for no more than several hours, and it has been suggested that much of this activity may occur during low light conditions (Reighard 1906; Carr 1942; Kelley 1962). Secondly, largemouth bass are known to spawn in areas of shallow water, which could make fish wary, or in heavy cover, which could hinder visual observations (Miller & Kramer 1971). Thirdly, many largemouth bass habitats are too turbid for effective observations. The low probability of observing such acts in the wild has led to alternative approaches for monitoring spawning.

Video equipment has been employed to monitor the behavior of largemouth bass in hatchery conditions (Isaac et al. 1998). Video equipment also has been employed in the field, but usually this activity has been limited to observing nesting behavior, not the actual spawning event (e.g., Shealy 1971; Hinch & Collins 1991). Romero & Allen (1975) provided some information on the spawning behavior of largemouth bass based upon direct observations while snorkeling.

Recent alternative techniques to study the reproductive behavior of fish have included telemetry. Radio and ultrasonic telemetric techniques have been used to locate nest sites of male largemouth bass (Bruno et al. 1990) and smallmouth bass *M. dolomieu* (Lacépède) (Savitz et al. 1993), but observations have been restricted to post-gamete release, during which time the male was guarding the nest. Savitz et al. (1993) acknowledged that their methods precluded them from determining if and when tagged female smallmouth bass spawned. Additional methods were still required to detect and quantify spawning activity and other related behaviors.

More recently, researchers have employed physiological telemetry to monitor spawning activity in fish. In particular, telemetry devices capable of recording and transmitting information on electromyogram (EMG) patterns have been used to identify periods of muscular contraction during the reproductive period (Kaseloo et al. 1996; Weatherley et al. 1996; Økland et al. 2000). These transmitters do not transmit raw EMG, data but instead emit an integrated EMG signal (EMG*i*) that is correlated to axial muscular activity (Økland et al. 1997; Beddow & McKinley 1999; Thorstad et al. 2000). To date, these spawning studies have been limited to lake trout *Salvelinus namaycush* (Walbaum), which spawn at dusk in very deep waters, making verification of spawning difficult (Kaseloo et al. 1996), and Atlantic salmon *Salmo salar* (L) in a semi-natural river environment (Økland et al. 2000). The authors concluded that EMG*i* transmitters could be used as indicators of spawning activity in salmonids (Kaseloo et al. 1996; Økland et al. 2000) and demonstrated their applicability in certain field situations (Weatherley et al. 1996). EMG*i* transmitters have also been used for monitoring the activity of largemouth bass and smallmouth bass, although not during the reproductive period (Demers et al. 1996; Bunt 1999; Cooke et al. 2001).

The objectives of our study were to characterize the activity levels associated with largemouth bass reproduction and to evaluate whether EMG*i* telemetry could be used to detect spawning activity remotely. To accomplish those objectives, a combination of EMG*i* telemetry, underwater videography and visual observations were used to collect qualitative and quantitative information on the intensity of muscular activity during largemouth bass reproductive activities in experimental ponds. Although our focus was on largemouth bass, this can be viewed as a model system to investigate the use of EMG*i* for fish with similar reproductive strategies.

Material and methods

EMG*i* transmitters

The transmitters used (EMG*i*, Lotek Engineering Inc., Newmarket, Ontario, Canada) consisted of an epoxy-coated transmitter package with a pair of electrodes and a single antenna. The tags measured 51 mm in length and 13 mm in diameter and weighed 18.0 g in air. Gold electrodes (9K) measuring 7 mm were affixed to the end of the electrode wires. Kaseloo et al. (1992) and Beddow & McKinley (1998) describe transmitter function in detail.

Study animals

All observations were conducted in four 0.10-ha earthen ponds (mean depth, 0.75 m) at the Illinois Natural History Survey's Aquatic Research Field Laboratory in Champaign, Illinois. In early spring 1998 ponds were filled with water from the municipal water supply, and invertebrates and plants were allowed to colonize. Largemouth bass used for the study were obtained from various local reservoirs by electrofishing and had been held in other ponds for several months. Prior to surgery, fish were maintained in large holding tanks. A total of 8 adult females and 16 adult males were implanted with EMG*i* transmitters on April 7, 1998.

Surgical procedure

Fish were anesthetized in a 60 ppm induction bath of clove oil and ethanol (Anderson et al. 1997; Peake 1998). Fish lost equilibrium after 3–4 minutes and were then measured (TL, mm) and weighed (g) before being placed ventral side up in a V-shaped acrylic trough lined with neoprene on a surgery table. During surgery, the gills were continuously irrigated with a maintenance dose of anaesthetic (30 ppm) in oxygenated water.

Surgical procedures are described in Cooke et al. (2000). Briefly, a small incision was made on the ventral surface. Electrodes were positioned 10 mm apart in the red axial musculature below the lateral line using 16 1/2 gauge rods (Bunt 1999). Electrode placement was standardized at the anterior portion of the dorsal fin (Beddow & McKinley 1999). The transmitter was then inserted into the body cavity and the antenna wire was passed through to the outside of the body through a small puncture wound. The incision was closed using four independent braided silk sutures (2/0 Ethicon Inc.). A small amount of cyanocrylate glue (Vet-Bond, 3M Inc.) was then applied to the sutures to increase resistance to abrasion that might occur during spawning. The entire procedure lasted less than 5 minutes, and fish recovered quickly when returned to fresh oxygenated water. Fish were allowed to recover in a holding raceway for two hours prior to their release into experimental ponds.

Data collection

Fish implanted with radio-transmitters were allocated randomly to one of the four ponds (two females and four males in each pond). Additional untagged fish (2 males and 4 females in each pond) were added to the ponds to assess hindrance to spawning by the tagging process and to provide more spawning opportunities if needed. The fish were allowed to recover for seven days prior to the onset of data collection. Signals were detected and recorded automatically using three SRX–400 radio receivers with W/20 software (Lotek Engineering Inc.). Two of the receivers, each connected to an H-antenna, were placed in environmental chambers positioned between ponds and set to scan continuously. A third receiver was used to collect data when receivers were offline for downloading, or to focus additional monitoring on specific individuals during suspected spawning activity.

Fish behavioral activity was monitored visually several times daily in an effort to detect spawning related activity. This monitoring first involved carefully recording the location of each individual to identify when and where individual males were establishing nesting territories. Once nests were established, activities were observed carefully to detect the potential onset of spawning-related behavior. If it was suspected that a male was constructing a nest, video cameras were positioned near the nest site. A total of four cameras were used for this study, including two black-and-white cameras with night capabilities (Collins et al. 1991), a high resolution color camera, and a micro black-and-white camera for fish that were particularly wary. When fish were wary, we used a rod to place the micro camera near the desired viewing area. Fine camera adjustments were made using poles and flexible focusing-control knobs.

Data analysis

Prior to analysis, data were examined to confirm that they were free from instances of radio interference, which could have contributed erroneous results. In the field we were able to minimize these erroneous signals by adjusting receiver gain and by using a cluster of several antennas very close to the ponds. Data were then summarized in SAS (SAS Institute Inc.) creating averages, standard errors, standard deviations and coefficients of variation for required time intervals for each individual fish. After spawning experimentation was completed, fish were transferred to a shallow raceway. Resting EMG*i* values were recorded while fish were sedentary (Cooke et al. 2000). All EMG*i* values were adjusted for individual fish, and values were transformed to be reported as percent increase over resting (Cooke et al. 2001).

During the study, a total of 11 spawning events were observed or were known to have occurred based on the presence of eggs in a male's nest (Table 1). Not all of the fish observed to have spawned were implanted with transmitters. We attempted to obtain videographic and EMG*i* records (for implanted fish) for all spawns. One pair of fish consisted of individuals that both had EMG*i* transmitters and yielded complete videographic and EMG*i* records. This pair had two dedicated EMG*i* receivers (one to each fish) monitoring continuously from the beginning of nest ex-

Table 1. Eleven EMG*i* tagged fish spawned with a combination of other EMG*i* tagged fish and nontagged individuals. The first two rows denoted in italics are the pair described in results.

Code	Sex	TL (mm)	Wt (g)	Video	Visual	EMG*i*	Spawned with
706	*M*	*314*	*459*	*Yes*	*Yes*	*Yes*	*437*
437	*F*	*401*	*898*	*Yes*	*Yes*	*Yes*	*706*
206	M	352	509	No	Yes	Yes	346
346	F	380	723	No/Yes	Yes	Yes	206 and 741
741	M	372	728	Yes	Yes	Yes	346
537	M	364	795	No	Yes	Yes	Untagged female
128	M	324	480	Yes	Yes	Yes	186 and untagged female
186	F	369	757	Yes	Yes	Yes	128
331	M	373	746	Yes	Yes	Yes	Untagged female
106	M	335	566	No	Yes	Yes	Untagged female
044	F	359	563	No	No	Yes	Untagged male

cavation to the cessation of spawning, when the female departed the area and the male began parental care activities. As a result, we will present detailed observations and analysis for this one complete spawning event between these two individuals, herein referred to as "the pair". An ethogram describes the different behavioral classifications we used for the study (Table 2). For the description of the pair's spawning activities, time is reported in minutes from the beginning of nest construction and is denoted by "*t*".

The data collected for the pair (visual, videographic, and EMG*i* signals) were used to characterize muscular/locomotory activity on the day of spawning. Those characteristics were then used to assess data from other fish to determine whether spawning could be detected remotely using EMG*i* telemetry. Correlations were established by using the Pearson procedure (Zar 1996). Analysis of variance (ANOVA) with the conservative multiple comparison Tukey *post hoc* test (Day & Quinn 1989) was used to assess differences in activity levels during different behavioral phases if the ANOVA results were significant. Where required, data were arcsine transformed. All statistical procedures were carried out using SYSTAT 7.0 (Wilkinson 1997). Values reported are means$\pm$1 SEM, and tests were considered significant at $\propto$=0.05.

Results

Survival and healing

All fish implanted with transmitters survived the entire duration of the study period. Within several

Table 2. Ethogram of spawning behavior for largemouth bass pair analysis. Abbreviations refer to axis descriptions in Fig. 2.

Pre-spawn (PRE) – Male exploring nesting areas, but not yet committed to site or begun nest excavation. Female distant from nest, not interacting with male.

Nest excavation (NEX) – Male produces powerful caudal sweeps of varying intensities and durations to clear silt and debris from substrate of nest site (see Carr 1942). Female still distant from nest.

Courting (CRT) – Courting behavior included all non-contact activities in which the male and female interact, usually limited to approaches and various displays (see Ridgway et al. 1989).

Aggression (AGG) – Male contacts female, usually in the area of the operculum, or genital pore. Male pushes, nudges or leads female to the nest. Male nips tail and shakes the female above the nest (see Miller 1975; Ridgway et al. 1989).

Shuddering (SHUD) – Involves alignment of male and female with low amplitude quivering, vibrations and shuddering (see Romero & Allen 1975; Miller 1975; Ridgway et al. 1989). This could represent actual gamete deposition or false shuddering.

Post-spawn (POST)- Female departs or is chased from nest area. No further participation in spawning with male. Male begins parental care activites, including fanning the eggs and defending the brood against potential predators.

days of implantation fish were observed to behave similarly to untagged fish (i.e., feeding, occupying similar habitats). Wound healing was near complete by the termination of the study. Most sutures were no longer present and the incision sites were closed. Post-mortem dissections indicated that electrodes were generally 10 mm apart. No transmitters were expelled during the study period.

Detailed pair behavior and activity

Beginning on April 23, male #706 was repeatedly observed in the shallows, apparently exploring potential nest sites. On April 25 at 10:25, this male was observed to begin excavating a nest 0.6 m from shore at a depth of 0.5 m. Noon hour surface water temperature on this date was 16°C. The micro camera was then placed between shore and the nest site (at time t_0) and behaviors were recorded visually (Fig. 1). The fish was disturbed by the camera placement for less than 2 minutes. As the fish continued to excavate the nest for the next 104 minutes, the location of the depression shifted somewhat. Camera placement was adjusted slightly using the extension rod at times when the male left the nest to court female #437 in adjacent deeper water. These subsequent camera adjustments did not appear to elicit any response from either fish.

The actual nest construction involved two distinct behaviors. The first and most obvious form of digging was more frequent during the beginning of the nest excavation process. This behavior involved several slow, but powerful caudal beats of high amplitude, as the male propelled itself across the nest area with its head elevated and its mouth partially open. The motion would be completed when the fish burst away, creating a large silt cloud. As the nest area became obvious, these digs became less intense and usually consisted of more gentle and controlled sweeping actions that suspended much less silt. Following these more controlled digs, the male remained close to the nest area.

During the sporadic periods of nest construction, there were several long periods in which the male was away from the nest site. These periods were coincident with major digging events in which the male would disturb the substrate and create regions of high turbidity. Although the camera view was somewhat impaired during this time, visual observations confirmed that the male stayed away from the perimeter of the nest until the water clarity improved. The male would then return and continue nest excavation. During this time the male would depart to deeper water where the female was staging. Occasional gentle nudges to the opercular area would serve to direct the female toward the general area of the nest.

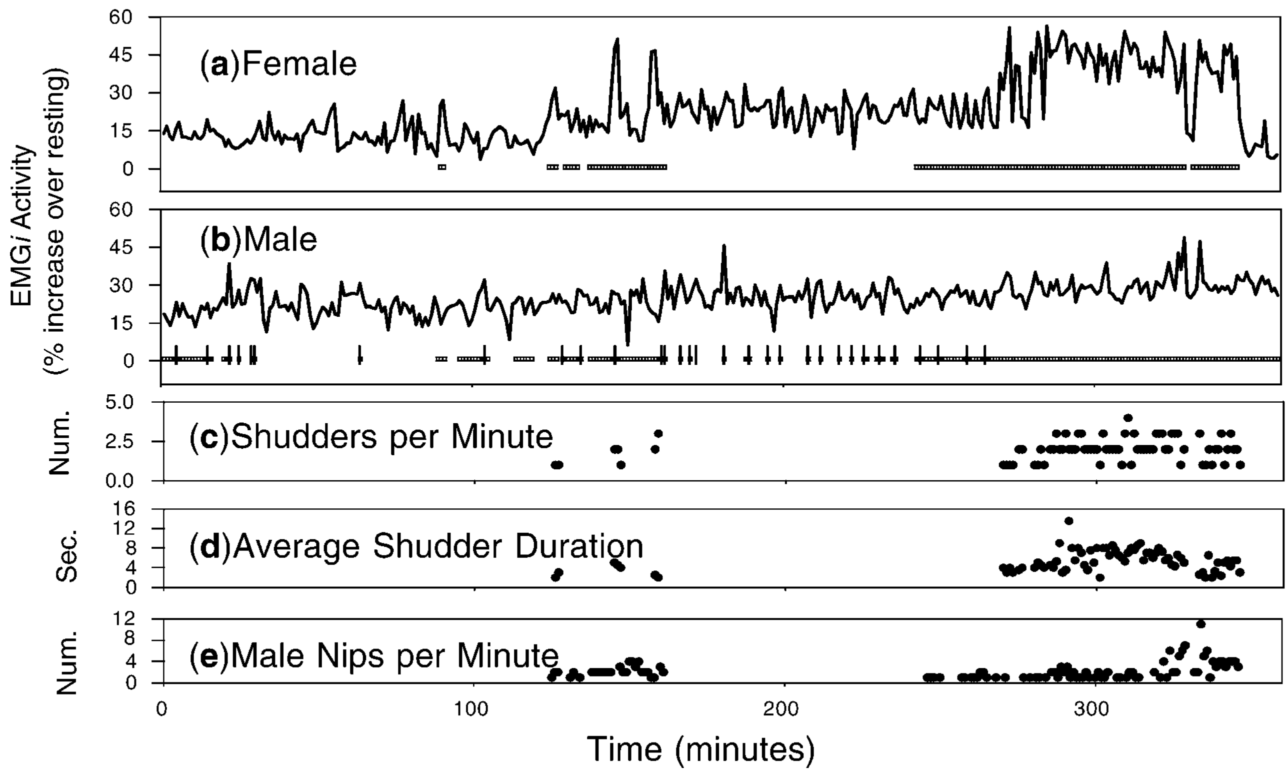

Fig. 1. Detailed patterns of activity during the period in which fish #706 (male) and #437 (female) spawned together over a 360-minute period during which EMG*i* signals, video, and visual observations were conducted. Time 0 represents 10:25. The top trace for the female (**a**) and male (**b**) represents the percentage increase in EMG*i* activity over resting. The hatch marks on the same two panels indicate periods when each of the fish were present within the field of view of the camera. The vertical hatch marks on the male panel (**b**) indicate episodes of nest excavation. **c**. Number of shuddering events initiated during each minute period. **d**. Average duration (s) for each of the shudders initiated during each minute period for which shuddering was observed. **e**. Instances and frequency of male aggressive acts during times when the female was present within the camera's field of view. Note that additional aggressive behavior (although apparently less intense) also occurred when the female and male were away from the nest, but this was difficult to quantify and was generally termed courting.

Prior to spawning, aside from a short appearance (2 min) at t_{91}, the female remained out of the camera's field of view, somewhat near to the nest perimeter, but in deeper water. From t_{125} to t_{162}, the female spent most of her time at the nest. The male became more aggressive with the female at t_{125}, and the first spawning event was observed at t_{126}. After spawning began, the camera was not adjusted. Over the next 33 minutes the female fish shuddered only 12 times, depositing some eggs in the process. At t_{159}, the male resumed major nest digging and egg distribution activities. The female moved into deeper water during this second episode of nest excavation. The male continued to dig aggressively while courting the female for over an hour. The female returned to the nest at t_{243}, the male again began to court the female even more aggressively, and the nest building activities ceased. Spawning recommenced at t_{270} and lasted for 67 minutes. During this time, 137 acts of shuddering were observed. The male aggression peaked at t_{334}, after which the male remained at higher-than-average aggression levels until he finally chased the female away from the nest at t_{347}. The female was observed swimming away and became obscured by cover in deeper water. The male immediately assumed parental care duties, including fanning the newly deposited eggs with gentle movements of the distal portion of his caudal fin and continual beats of his pectoral fins, as he rotated about the nest itself.

Physical activity during various pair behaviors

The EMG*i* activity of each of the pair was recorded continuously from t_0 until spawning was completed at t_{348}, when the female departed and the male assumed parental care activities (Fig. 1). The EMG*i* activity of the female fish was weakly positively correlated to the total amount of shuddering per minute (r=0.233, P=0.047). Male EMG*i* activity, however, was not significantly correlated to the total amount of their shuddering per minute (r=−0.136, P=0.25) or female EMG*i* activity (r=−0.034, P=0.77).

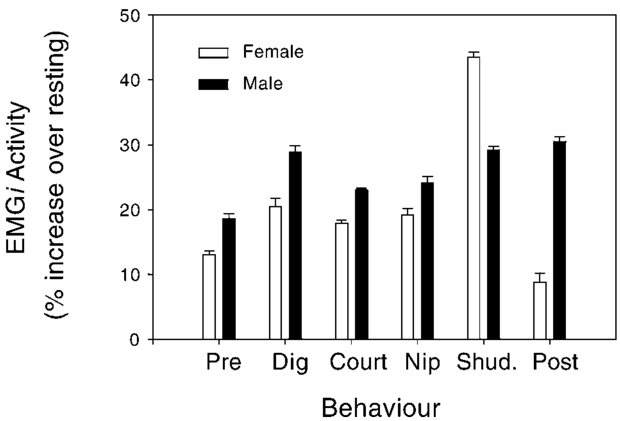

Fig. 2. EMG*i* activity expressed as an increase in activity over resting levels for male and female largemouth bass pair during different spawning related behaviors. Error bars are +1 SE. The different behaviors are described in Table 2.

Overall, male and female EMG*i* activity during the 360 minute spawning period had a moderate coefficient of determination (r=0.399, P<0.001). The only significant correlations of male and female activity when examined on a behavioral basis, however, were for the courting period (r=0.229, P<0.001) and male aggression towards the female, in the form of nips and nudges (r=0.345, P=0.039) (Fig 2).

The EMG*i* activity of the female was higher during shuddering than during all other behaviors (43.4±0.9% increase, P<0.001; Fig. 2). Female post-spawn activity was significantly lower (8.9±1.4% increase, P<0.001) than all other behaviors except pre-spawn activity (13.1±0.6% increase, P=0.50). Pre-spawn activity was lower than during the period of male aggression (19.2±1.1% increase, P=0.025) and male digging events (20.5±1.3% increase, P=0.004). No other significant differences were observed.

Male EMG*i* activity was lowest during pre-spawn periods (18.7±0.7% increase, P<0.001; Fig. 2). The level of activity during shuddering (29.3±0.5% increase) was not significantly different from that during post-spawn parental care activities (30.5±0.8% increase) (P=0.95). EMG*i* activity during digging behavior (28.9±1.0% increase) was significantly higher than all behaviors (P<0.005) except shuddering (29.3±0.5% increase, P=0.99) and post-spawn parental care (30.5±0.8% increase, P=0.91). Activity during courting (24.2±1.0% increase) and male aggressive acts (23.0±0.3% increase) were not significantly different (P=0.728).

Changes in daily activity resulting from spawning activity in the pair

Increases in EMG*i* activity were observed on the date of spawning for both the male and female fish of the pair. Female activity was maximal on the day

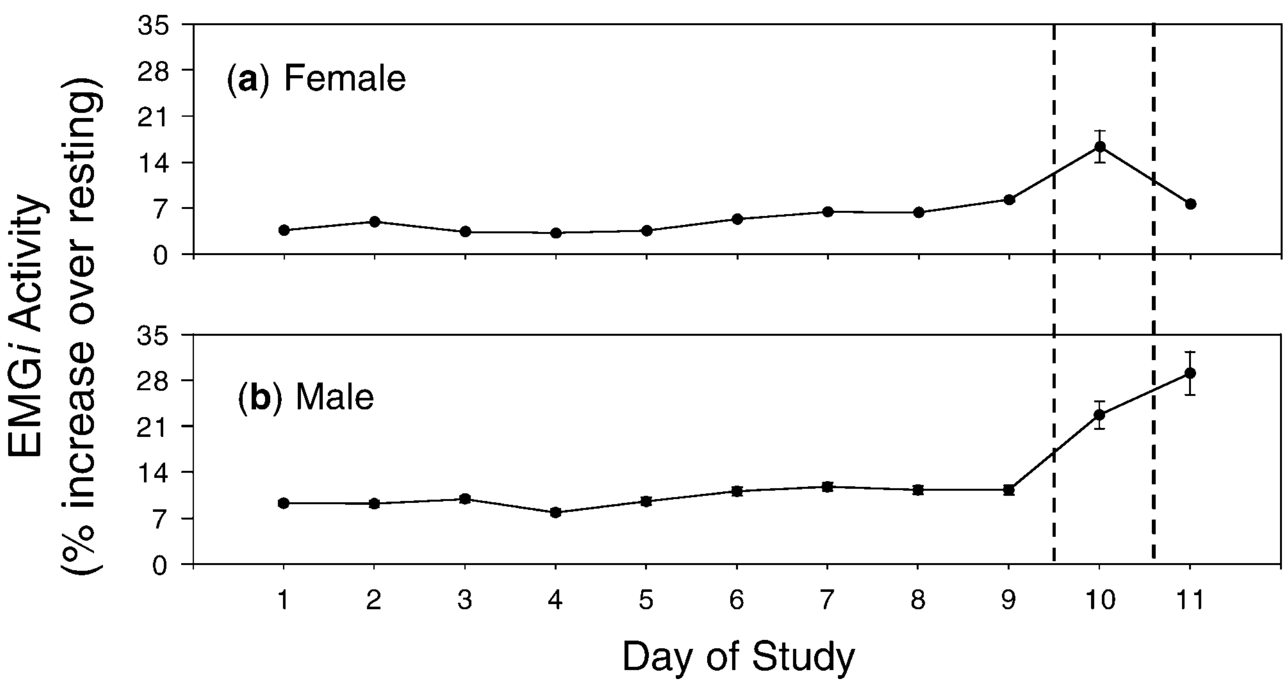

Fig. 3. Mean daily EMG*i* records estimated from mean hourly EMG*i* signals for the female (**a**) and male (**b**) fish implanted with EMG*i* transmitters. Data for each fish are calibrated to reflect increases in activity over resting levels and the standard deviation of the activity. The first day of the study represents the first day for which EMG*i* signals were analyzed, providing a one-week recovery period. The daily period indicated between the two marked lines denotes the date of spawning (day 10, April 25).

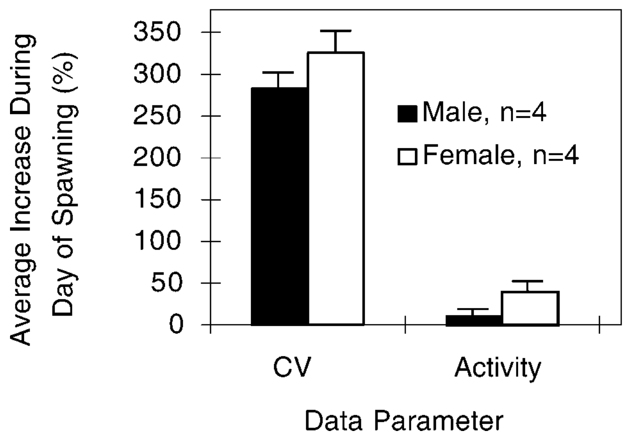

Fig. 4. Summary of spawning detection parameters for 4 EMG*i* tagged males and 4 EMG*i* tagged females for which spawning was visually confirmed. Coefficients of variation (CV) increases are calculated for a 24-hour period and are compared to the average daily CV from the 7 previous days. Daily EMG*i* activity values are calculated the same way. SE (+1) for these detection parameter estimates are also present on each bar.

of spawning, whereas male activity continued to rise coincident with the male's parental care duties including continuous nest defence and fanning (Hinch & Collins 1991). The female fish had more than a 10-fold increase in the SD of EMG*i* activity during the day of spawning (Fig. 3). The day following spawning, the SD of EMG*i* activity returned to pre-spawn levels. For the male fish, however, the SD increased only about three times over pre-spawn activity levels during the date of spawning, but continued to rise to over four times pre-spawn levels on the day following spawning (Fig. 3).

Detection of spawning in other fish

Overall, female fish spawning on a daily basis was easily detected by at least a one fold increase of the CV (up to 10 times) for estimates of activity levels and an increase in actual EMG*i* activity (Fig. 4). Similar, but less extreme trends were observed for males; (Fig. 4). For female fish EMG*i* levels were significantly lower on pre-spawning days and the first post-spawn days, than on days of known spawning ($P<0.001$). That same pattern was seen for males, however, in contrast to females, activity on the first day post-spawn was significantly higher than pre-spawn levels ($P<0.001$).

Spawning of four different radio-tagged females was detected and confirmed by videography or visual observations (Table 1). In addition, one female, according to EMG*i* records, also spawned during the night but there was no verification with videography. Visual observations the following morning, however, indicated that an untagged male was observed on a nest with a new complement of eggs that were deposited overnight. In addition, at the conclusion of the experiment, that tagged female showed obvious signs of spawning (flacid abdomen and red, swollen genital opening). With untagged females also present in the pond, it was impossible to be sure that the EMG*i* records do indeed reflect spawning activity for that female.

EMG*i* records also detected all the known male spawns that occurred. One of these spawns occurred in a very turbid pond, and water levels in that pond were lowered to verify the presence of eggs in the male's nest. The telemetry data suggested that this fish had spawned 2 days prior to pond draining (probably with an untagged female), which was confirmed by visual inspection of the developmental stages of the eggs present in his nest (Philipp et al. 1997). Some slight variability in EMG*i* activity was noted in the days immediately prior to spawning, which may be indicative of heightened activity as males court females, explore potential nest sites, or begin nest excavation. Based on this, we would also likely be able to detect false nesting and nest abandonment during the parental care period and to assess the changes in activity during different developmental stages of the offspring.

Discussion

Experimental approach

An inherent assumption in all telemetric studies is that neither the transmitter nor the mode of attachment alters the behavior or health of the study organism. Such an assumption is particularly important when attempting to study the spawning behavior of fish. Because centrarchids likely incur substantial bioenergetic expenses during spawning and parental care periods (e.g., Hinch & Collins 1991; Mackereth 1995; Gillooly & Baylis 1999), the potential for telemetric studies interfering with behavior and physiology is increased. Numerous researchers have implanted conventional transmitters into largemouth bass prior to spawning (e.g., Bruno et al. 1990). Crumpton (1982) and Richardson et al. (1995) studied the effects of dummy transmitters on spawning behavior of largemouth bass and found no effects. Additional field studies have provided further qualitative observations that bass implanted with transmitters prior to spawning were still capable of reproduction (e.g., Tranquilli et al. 1981; Bruno et al. 1990).

The only other published study employing EMG*i* transmitters similar to those used in this study concluded that largemouth bass can be implanted successfully with this method (Demers et al. 1996). The authors observed one of the two implanted largemouth bass guarding a nest in each of the three years following implantation with an expired transmitter. The transmitter to body mass ratio ranged from 2.0% to 3.9%, more than the generally accepted 2% rule (Winter 1996). However, due to the lack of observed transmitter effects and a growing body of literature liberalizing the 2% rule (e.g., Brown et al. 1998), we are confident that the behaviors we observed were natural. Indeed, the behaviors of the transmitter-implanted largemouth bass in our study were consistent with previously reported spawning behaviors (Breder & Rosen 1966; Heidinger 1975). This body of evidence helps to support the supposition that implanting largemouth bass with EMG*i* transmitters prior to the initiation of spawning allows successful collection of data on physical activity.

Spawning activity and behavior

To date, no other studies have quantified the relative activity costs to largemouth bass of spawning. Videographic observations of nest guarding activities of male largemouth bass (Shealey 1971) and smallmouth bass (Hinch & Collins 1991) proposed that the males expend significant amounts of energy while maintaining high levels of vigilance against potential brood predators. Data presented in this study indicate that during the parental care period, the activity of nesting male largemouth bass is nearly twice that of prespawning levels. In addition, recent information on proximate body composition indicates that smallmouth bass lipid reserves and lean muscle mass of nesting males are extensively depleted during the parental care period (Mackereth 1995; Gillooly & Baylis 1999).

The data from our study suggest that, for males, the excavation of nests is also an energetically costly activity. Similarly, Grantner & Taborsky (1998) report that the digging behavior of a cichlid, *Neolamprologus pulcher* (Trowavas and Poll), was an energetically costly activity, resulting in a six-fold increase of routine metabolic rates. In fact, in our study, all of the activities associated with nest excavation, courting, aggression, spawning and post-spawn parental care was higher than prespawning activities for the male fish. Grantner & Taborsky (1998) also reported that agonistic/aggressive behavior, defined similarly to our study, resulted in a nearly four-fold increase over routine metabolic rate. Earlier studies by Brett & Groves (1979) measured the change in standard metabolic rate during aggressive interactions of juvenile sockeye salmon, *Oncorhynchus nerka* (Walbaum). Their results also indicated that aggressive behaviors can be costly, elevating standard metabolic rates four times.

In largemouth bass, although the female has a larger gametic investment, the EMG*i* activity of the female was generally low for all behaviors except the actual shuddering, when gametes were deposited. In another study, Kaseloo et al. (1996) report that for lake trout shuddering activities were not considered to be demanding of high muscular activity. Species and gender specific differences in the trunk musculature recruited for gamete deposition and patterns of muscular discharge may exist, as has been noted for sockeye salmon (Matsushima et al. 1986) and chum salmon, *Oncorhynchus keta* (Walbaum) (Uematsu et al. 1980; Uematsu & Yamamori 1982). In general, however, these authors suggest that strong contractions of the main trunk musculature are required to increase the inner pressure of the body cavity and exude eggs. It is possible that, depending on the placement of electrodes, EMG*i* transmitters may not be capturing the most intense muscular activity associated with shuddering, which may explain the findings of Kaseloo et al. (1996). Based upon the placement of our electrodes in the *M. lateralis superficialis*, a comparably thin band in largemouth bass relative to lake trout, we may have also detected the muscular contractions of other trunk muscles. It must also be noted that Beddow & McKinley (1999) report that in Atlantic salmon, EMG*i* telemetry electrodes in the red muscle were largely isolated from the effects of white muscle activation; this may not be the case with largemouth bass. To date, no studies have examined the raw electromyograms of largemouth bass during the reproductive phase.

An additional consideration in the importance of muscular activation for oviposition by female largemouth bass is that it is nearly impossible to manually strip eggs from these fish until immediately prior to spawning. This may signify the importance of behavioral cues during the short courtship period that may be required to induce oviposition (Mark Ridgway, personal communication; Cooke & Philipp, personal observations). There are also weak anecdotal observations suggesting that female largemouth bass may strike their bodies against objects prior to spawning (Miller 1975). These two contradictory suppositions have yet to be completely explored. It is clear, however, that the relative cost of the spawning event for the female is far less in terms of energetic expenditure; the male devotes more energy to nest construction and courting, two behaviors in which the female is rather passive. In addition, the female does not participate in parental care activities (Breder & Rosen 1966; Cooke & Philipp, personal observations). This may help to explain the sexual dimorphism in size, in that females reach larger ultimate sizes and better condition than males (Carlander 1977).

Our method of documenting the relative energetic costs of different behaviors is based upon physical activity. Oxygen consumption can also be altered rapidly by changes in cardiac output, which itself may be responding to factors other than physical activity, such as hormonal activity (Priede 1983). As a result, when a fish increases respiration, resulting in an elevated standard metabolic rate, monitoring locomotory activity using electromyogram telemetry may not reveal these changes unless it results in increased physical activity (Anderson et al. 1998). In addition, if shuddering activity required the utilization of white musculature, post-spawn females may remain motionless until an oxygen debt has been repaid (Scarabello et al. 1991). It is possible, therefore, that the EMG*i* activity that we report is not completely representative of the entire costs of activity. Although this is a current limitation of EMG*i* telemetry, this tool still provides the best indicator of *in situ* physical activity.

Detection of spawning activity

This study represents the first attempt to quantitatively describe the pattern of male and female muscular activity relative to specific spawning behaviors using EMG*i* telemetry in free swimming largemouth bass. Our study showed that female largemouth bass EMG*i* activity increased during the spawning event and elevated the average daily EMG*i* values to the point at which they were readily detectable and distinct from other days before or after that event. The resumption of lower activity levels similar to pre-spawning periods indicated that the peak in EMG*i* activity could be used for determining when female largemouth bass spawn.

Male EMG*i* values increased during the spawning period, but this was not completely attributed to the shuddering. Although the male exhibited heightened activity during specific behaviors (i.e., nest digging, spawning), these activities were not any higher than those observed during the first day of parental care. Because the male is expending energy by continually fanning the nest and defending the brood from nest predators, it is more difficult to determine the day of spawning than for females. The elevated mean daily EMG*i* records are likely a combination of the actual spawning event and the commencement of parental care activity. The relative muscular activity required to deposit gametes (measured as the percentage increase in EMG*i* during shuddering) by the male is 30% less than that of the female. The male simply rotates outward and is able to release sperm without major muscular contractions of axial musculature. Females, however, required significant muscular output to deposit eggs in the nest. This was not only evident in EMG*i* signals but also in the intense vibrations observed using underwater videography. Kaseloo et al. (1996) had reasonable success detecting actual spawning activity of male lake trout because there was an apparently larger amount of axial muscular output during the actual deposition of gametes. In addition, because male lake trout do not provide parental care, the EMG*i* signals from the spawning activity were not obscured by any heightened activity from parental care after gamete deposition. The male lake trout daily activity patterns are therefore more similar to the female largemouth bass.

As such, EMG*i* transmitters would be most useful for detecting the timing and duration of spawning (i.e., gamete deposition) for female largemouth bass, and the initiation of reproductive activities (i.e., nest building) for male largemouth bass. The high levels of EMG*i* activity associated with some of the male behaviors, particularly the nest guarding activity would provide the opportunity to speculate on the timing of the actual spawning event. However, this would not provide the same precision as is apparently possible with the female fish, being that male activity does not drop following the termination of spawning. This research further indicates the need for species-specific calibrations of EMG*i* transmitters in controlled situations before they can be applied to field studies of reproduction in other species.

Conclusion

As more studies of spawning activity using this technology are conducted, it may become possible to use calibrations from fish with similar spawning behavior and reproductive tactics. Future studies should still attempt to obtain some form of visual observation (e.g., videography (see Økland et al. 2000), snorkeling) or use of other confirmatory methods (e.g., egg baskets, gonadosomatic index (GSI) changes, semelparous death). This will ensure that the EMG*i* transmitters are serving as surrogates for detecting reproductive activity and not just bouts of rapid locomotory activity. These kinds of observations will also be required in instances where researchers are attempting to quantify the physical activity patterns and intensities associated with different spawning behaviors.

In summary, our results suggest that largemouth bass spawning expenditures may be substantial. The spawning related activity and behaviours differed between male and female fish; female activity clearly peaks at spawning, male activity rises during spawning and remains heightened during the parental care period. These differences likely represent substantially different energetic investments for each gender. Furthermore, our data suggest that EMG*i* transmitters are an appropriate tool for studying and documenting the reproductive activity of largemouth bass and likely other large centrarchid fishes (e.g., smallmouth bass). Additional investigations focusing on the chronology of brood development and activity levels of the nesting male will be particularly useful at quantifying the full energetic implications of reproduction in centrarchid fish. This information is essential for the development of gender specific bioenergetic models that incorporate the costs of reproduction.

Resumen

1. Estudiamos el comportamiento reproductivo de machos y hembras de *Micropterus salmoides* (Lacépède) en Illinois central durante la primavera de 1998 con el fin de examinar patrones de actividad muscular asociados a diferentes comportamientos relacionados con la reproducción tanto como para evaluar si la telemetría de electromiograma (EMG*i*) puede ser utilizada para detectar actividad reproductora.
2. Los peces fueron implantados with transmisores EMG*i* (8 hembras y 16 machos) el dia 7 de abril (antes de iniarse la puesta), y fueron soltados en cuatro lagunas de investigación de 0.10 ha. Observaciones continuas de los EMG*i*, videografía bajo el agua y observaciones visuales adicionales de una pareja de peces marcados con EMG*i* fueron obtenidos a lo largo del todo el evento reproductivo lo que nos permitió cuantificar pautas de comportamientos de la actividad física.
3. Los patrones de actividad EMG*i* en machos estuvieron solamente correlacionados con los patrones de las hembras durante el cortejo y con periodos de agresión de los machos hacia la hembras. En general, la actividad EMG*i* fue mayor para las hembras durante la puesta mientras que para los machos, esta actividad EMG*i* fue similarmente alta durante los periodos de excavación de los nidos, durante la puesta y durante las actividades de cuidado parentel post-puesta.
4. Durante la reproducción, la actividad EMG*i* de las hembras estuvo positivamente correlacionada con la puesta. La actividad EMG*i* diaria media para las hembras tuvo un pico el dia de la puesta. Como resultado de la actividad de cuidado parental, la actividad de los machos continuó ascendiendo depues de completar la puesta.
5. La telemetría EMG*i* parece ser una técnica util para monitorear la actividad reproductiva de *M. salmoides*, especialmente en áreas de mucha cubierta vegetal, aguas turbias y en condiciones de baja luminosidad. Esta tecnología nos permitió cuantificar y contrastar los patrones de actividad asociados a diferentes actividades relacionadas con la puesta, información que será requerida para construir modelos bioenergéticos precisos para esta especie.

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