Parental care patterns and energetics of smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*) monitored with activity transmitters

Steven J. Cooke, David P. Philipp, and Patrick J. Weatherhead

Abstract: Male smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*) care for their offspring from fertilization until the offspring disperse after becoming capable of avoiding predators. We used activity transmitters to monitor round-the-clock parental activity of both species throughout the nesting period, coupled with direct observational data collected while snorkeling, to determine whether nocturnal behaviour varied similarly to diurnal behaviour. In general, nesting males of both species were equally active during day and night, developmental-stage-specific patterns being evident during both periods. Consistent with theory, parental males of both species exhibited elevated levels of burst swimming (indicative of chasing nest predators) early in the nesting period. Unlike male smallmouth bass, however, male largemouth bass showed no decline in overall activity and energy expenditure in the later nesting stages as predicted from the greater mobility and dispersion of their broods, although burst-swimming activity decreased. Activity of nesting fish was approximately double that of non-nesting conspecifics, causing an increase in respiration rates of fish, estimated using a bioenergetics model. The results of our study suggest that physiological telemetry devices which provide both behavioural and energetic information enhance the study of parental care activity in centrarchid fishes, and may be equally useful in a variety of other taxa.

Résumé : Les mâles de l'achigan à grande bouche (*Micropterus dolomieu*) et de l'achigan à petite bouche (*Micropterus salmoides*) s'occupent de leurs petits de leur éclosion jusqu'à leur dispersion, qui se produit lorsqu'ils sont en mesure d'éviter les prédateurs. Nous avons utilisé des données provenant d'appareils capables d'enregistrer et de transmettre l'activité parentale 24 h par jour pendant toute la durée de la nidification et les avons combinées à des données obtenues par observation directe au cours de plongées en apnée, pour vérifier si les variations du comportement nocturne sont semblables à celles du comportement diurne. De façon générale, les mâles nicheurs des deux espèces sont aussi actifs le jour que la nuit avec des patterns d'activité spécifiques au stade de développement durant les deux périodes. Comme on pouvait s'y attendre, les parents mâles des deux espèces utilisent beaucoup la nage précipitée (à la poursuite de prédateurs) au début de la période de nidification. Contrairement aux mâles de l'achigan à petite bouche, les mâles de l'achigan à grande bouche ne subissent pas de baisse de leur activité ou de leur dépense énergétique aux stades avancés de la nidification comme on aurait lieu de croire vu la plus grande mobilité et dispersion de leur progéniture; toutefois, ils utilisent moins la nage précipitée. L'activité chez les poissons qui nichent équivaut à peu près au double de l'activité enregistrée chez les poissons qui ne nichent pas, ce qui donne lieu, d'après un modèle bioénergétique, à des taux respiratoires plus élevés. Nos résultats indiquent que les appareils de télémétrie physiologiques qui donnent à la fois des informations comportementales et énergétiques rehaussent la valeur des études sur les soins parentaux chez les Centrarchidae et pourront s'avérer utiles chez bon nombre d'autres taxons.

[Traduit par la Rédaction]

Introduction

An early review of the comparative ethology of black basses (*Micropterus* spp.) by Miller (1975) included only a brief section on parental care, reflecting the paucity of information at the time. Knowledge of parental care in centrarchids was limited to several anecdotal observations and the early descriptive work of Breder (1936). Since Miller's (1975) review, major advances have been made in understanding parental care in both smallmouth bass, *Micropterus dolomieu* (e.g., Ridgway 1988; Hinch and Collins 1991; Urban 1991; Ongarato and Snucins 1993; Wiegmann and Baylis 1995; Mackereth et al. 1999), and largemouth bass, *Micropterus salmoides* (e.g., Brown 1985; Colgan and Brown 1988), as

---

Received 18 September 2001. Accepted 8 March 2002. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 3 May 2002.

S.J. Cooke,[1] D.P. Philipp, and P.J. Weatherhead. Center for Aquatic Ecology, Illinois Natural History Survey and Program in Natural Resource Ecology and Conservation Biology, Department of Natural Resources and Environmental Sciences, University of Illinois, 607 East Peabody Drive, Champaign, IL 61820, U.S.A.

[1] Corresponding author (e-mail: scooke@uiuc.edu).

DOI: 10.1139/Z02-048

well as most other common centrarchids (e.g., Keenleyside 1971; Colgan and Gross 1977; Bain and Helfrich 1983; Colgan and Brown 1988; Coleman and Fischer 1991). Nonetheless, large gaps in our knowledge remain, reflecting, at least in part, technological constraints associated with observing parental care behaviour in the wild. Here we use data collected with activity transmitters to provide the first documentation of round-the-clock parental care patterns in free-swimming male smallmouth bass and largemouth bass monitored throughout the period of parental care.

Parental-investment theory (Trivers 1972) predicts that parents will vary the care provided to their offspring in response to several factors. Because offspring become more valuable to the parent as they approach independence, parents should invest more and take greater risks protecting older offspring. However, because parental investment in current offspring is expected to reduce opportunities to invest in future offspring, parents should reduce care given to older offspring as the offspring become self-sufficient. Sargent and Gross (1986) proposed a model that incorporates these proposed reproductive trade-offs at different stages of offspring development in teleost fish. This model recognizes that the dynamics of parental care reflect not solely the requirements of the offspring, but also the trade-offs between present and future reproduction. The model of Sargent and Gross (1986) predicts that for fish such as basses, one should expect parental care activity to increase from the egg stage, peak at the egg-sac fry or swim-up fry stage, and then decrease as the fry become free-swimming (i.e., increasingly independent).

Evidence that parents vary parental care as predicted by theory has come from both laboratory and field studies of several taxa, including birds (Montgomerie and Weatherhead 1988) and fishes (Pressley 1981; Colgan and Brown 1988; Ridgway 1988). Studies of black basses have shown that parental care peaks around the time of hatching and then declines gradually as the offspring become increasingly independent (Colgan and Brown 1988; Ridgway 1988; Urban 1991; Ongarato and Snucins 1993; Mackereth et al. 1999). Brown (1985) showed that male largemouth bass guard their broods until the predator-avoidance behaviour of the fry is well developed. To date, most observations of bass parental care have been made during the day because of the difficulties associated with observing fish under water in low-light conditions (but see Hinch and Collins 1991). As a result, it is not known whether the nocturnal behaviour of basses is similar to their diurnal behaviour, and thus whether it follows the same pattern over the different phases of offspring development.

Adult centrarchid fish are typically more active during the diurnal and crepuscular periods than at night (Davis 1964; Emery 1973; Demers et al. 1996). Parental activities, however, likely require that nesting males be active during both day and night because eggs should require fanning as much at night as during the day, and because eggs and fry may also require protection from nocturnally active predators. Alternatively, nest-guarding males may exhibit the same diel patterns as observed in non-nesting fish, particularly if the predation risk to fry is lower at night. Studies by Hinch and Collins (1991) and Cooke et al. (2000) showed that parental male basses are active at night, but neither of these studies examined all of the phases of offspring development and both had small sample sizes. Scott et al. (1997) examined the dispersion of smallmouth bass fry and the associated nest-guarding males at night, but their study only provided information on the location of the male relative to the offspring. Our first objective was to use activity transmitters to determine whether the nocturnal behaviour of parental male basses is similar to their behaviour during the day at each of the four offspring-development stages.

In addition to being conducted only during the day, previous studies of black bass parental care may have had other methodological limitations. Conventional means of experimentally testing whether patterns of brood defence conform to life-history models of parental care have involved assessing the intensity of aggression and threat behaviour at different developmental stages. This usually involves snorkelers eliciting aggressive behaviours from nesting males by presenting a series of staged nest intrusions using brood-predator models. Researchers have employed both conspecific (Ridgway 1988) and heterospecific models (Ongarato and Snucins 1993), which also may have influenced the results. Furthermore, few studies have controlled for repetition of model presentation (Lavery and Colgan 1991). An alternative approach that does not require the use of models and repetitive presentation is the use of natural-predator intrusions, although studies using this approach are rare (see Colgan and Brown 1988; Urban 1991). It has also been difficult to make comparisons among studies, and hence to make intra- and interspecific comparisons, owing to variability in the stage of brood development examined and inconsistency in defining developmental stages. Our second objective was to determine whether activity patterns reported from studies using conventional model presentations are representative of natural activity patterns of nesting bass determined using 24 h activity transmitters.

Like the study of patterns of parental investment in centrachids outlined above, attempts to estimate the energetic costs of parental care in centrarchids have also relied on indirect measurements. These indirect approaches have included estimating the extent to which parental care reduces foraging (Adams et al. 1982; Thorp et al. 1989), estimating increases in swimming activity and fanning frequency from videography (Coleman and Fischer 1991; Hinch and Collins 1991), and measuring decreases in wet mass over the nesting period (Coleman et al. 1985; Coleman and Fischer 1991; Sabat 1994). More recently, direct measurements have been used, including terminal proximate body composition studies (Coleman and Fischer 1991; Mackereth 1995; Mackereth et al. 1999) and nonterminal total body electrical conductivity readings (Gillooly and Baylis 1999). None of these approaches has been successful in quantifying the in situ behaviour and associated energetic costs of parental care activity continuously from egg deposition through completion of the free-swimming fry stage. Our third objective was to estimate the energetic costs of reproduction for male bass over the nesting period using data from activity monitors.

Quantifying the activity of free-ranging organisms has long been a challenge in ecology (Butler 1989) and fisheries science (Lucas et al. 1993). The recent development of devices capable of detecting axial-musculature activity and transmitting data via radio signals has provided an objective and quantifiable means of assessing the locomotory activity of fishes (Kaseloo et al. 1992). These activity transmitters have been successfully implanted and calibrated in both smallmouth bass and largemouth bass (e.g., Demers et al. 1996; Bunt 1999; Cooke et al. 2000; Cooke et al. 2001*a*, 2001*b*). The activity transmitters allowed us to collect two kinds of data relevant to the objectives outlined above. First, data on proximity to the brood and burst-swimming behaviour (the latter being indicative of chasing predators from the nest) provided information on parental care duration and intensity. Second, data on overall activity were used to generate estimates of energy expenditure during brood rearing.

In this study we chose to investigate the in situ locomotory activity of both smallmouth bass and largemouth bass, for two reasons. First, because the parental-care activity of smallmouth bass has been well studied using conventional approaches, we were able to compare our results obtained using activity transmitters with published data for this species. Second, by also including largemouth bass, we could determine whether patterns of parental care activity of these two species were similar across developmental stages. We predicted that parental care activity of the two species should be similar until the free-swimming fry stage. However, differences in the ontogeny of fry behaviour in the two species after swim-up should result in differences in parental care. Smallmouth bass fry generally remain close to the nest during the day and return to the nest site at night (Scott et al. 1997). In contrast, largemouth bass fry typically leave the area of the nest upon becoming free-swimming and become increasingly mobile as they move about in search of patchy food resources (Brown 1984, 1985). We predicted that parental male largemouth bass would become more active during the free-swimming fry stage relative to smallmouth bass at the same stage and to both species at earlier developmental stages.

Materials and methods

Study site and animals

We conducted the study in Lake Opinicon (44°33′30′′N, 76°20′00′′W), Ontario, from 15 May to 9 June 1998. The study site was a littoral region in which both largemouth bass and smallmouth bass were known to spawn (Keast et al. 1978; Suski 2000). The proximity of the site to the Queen's University Biological Station facilitated frequent downloading of data (see below) and allowed us to discourage recreational angling within the study site. Signs affixed to anchored buoys alerted anglers that a research program was underway and that fishing was not permitted within the study site. Previous research in the study area (Keast and Webb 1966; Keast 1978; Keast et al. 1978) confirmed the presence of fish species that have been identified as potential bass nest intruders and predators in Lake Opinicon; these include pumpkinseed, *Lepomis gibossus*, bluegill, *Lepomis macrochirus*, rock bass, *Ambloplites rupestris*, black crappie, *Pomoxis nigromaculatus*, brown bullhead, *Ameiurus nebulosus*, northern pike, *Esox lucius*, blackchin shiner, *Notropis heterodon*, bluntnose minnow, *Pimephales notatus*, eastern banded killifish, *Fundulus diaphanus*, yellow perch, *Perca flavescens*, johnny darter, *Ethesotoma nigrum*, tesselated darter, *Ethesotoma olmstedi*, and log perch, *Percina caprodes*, in addition to juvenile smallmouth bass and largemouth bass. Of these species, bluegill and pumpkinseed are the most frequent intruders at nests (Colgan and Brown 1988) and have the highest densities in Lake Opinicon (Keast 1980).

Activity transmitters and implantation

The transmitters (EMG*i*, Lotek Engineering Inc., Newmarket, Ontario) were coated in epoxy and had a pair of electrodes and a single antenna extending from the package. The transmitters were 51 mm long and 13 mm in diameter and weighed 18.0 g in air. Gold electrodes (9 karat) measuring 7 × 1 mm were affixed to the end of the electrode wires. The electrodes detect electromyographic activity within the axial red muscle, which then charges a capacitor. When the capacitance has been reached, a pulse is emitted from the transmitter. This signal provides information on integrated electromyographical activity (EMG*i*) rather than data on individual muscle contractions. The signal recorded by the receiver is an electromyogram (EMG) pulse interval (ms), which is inversely related to muscular activity. As muscle activity increases, the muscle EMGs increase, charging the capacitor more rapidly, thereby decreasing the interval between pulses. Kaseloo et al. (1992) and Beddow and McKinley (1998) describe the transmitters in detail. The transmitters used in this study have been used successfully for other studies of smallmouth bass (Demers et al. 1996; Cooke et al. 2001*a*) and largemouth bass (Demers et al. 1996; Cooke et al. 2000, 2001*b*).

Once nesting fish were located (by snorkeling or from a boat), a diver examined the nest. Only fish that had recently spawned, as evidenced by translucent eggs, were used for this study. Fish that were observed spawning were allowed to complete spawning before being captured for implantation. All six smallmouth bass nests studied were located close to shore or on a gravel bar in less than 1 m of water. Nests were constructed on sand, gravel, and pebble substrates in areas without aquatic macrophytes. The five largemouth bass nests studied were in deeper water (1–2 m) and were constructed over pebble and silt substrates with scattered aquatic macrophytes. To capture the fish, we angled the guarding male off his nest with a jig. We minimized the stress incurred by angled fish by landing them in less than 20 s, a period that in other studies has been used for unangled controls (e.g., Kieffer et al. 1995). Following capture, fish were placed immediately in an onboard cooler containing an induction bath of anaesthetic (clove oil : ethanol 1:9, 45 ppm). This anesthetic appears to allow fish to recover more rapidly than fish anaesthetized with the more conventional MS 222 (Anderson et al. 1997; Keene et al. 1998; Peake 1998). After a fish was angled from its nest, the diver remained beside the nest to ward off any potential brood predators. Pumpkinseed, bluegill, rock bass, yellow perch, black crappie, and log perch all attempted to make nest intrusions during our snorkeling observations. The diver also placed an individually numbered tile near the nest and quantified the eggs using the categorical scoring method of Philipp et al. (1997) (1 = lowest, 5 = highest). Only fish with egg scores greater than category 3 were implanted. Thus, our results must be interpreted in the context that we selected individuals which were more likely to invest more in parental care than those with small, depauperate broods (e.g., Suski 2000).

Table 1. Meristics of largemouth bass, *Micropterus salmoides* (L1–L5), and smallmouth bass, *Micropterus dolomieu* (S1–S6), implanted with activity transmitters.

Fish ID No.	Total length (mm)	Fork length (mm)	Mass (g)
L1	319	304	436
L2	374	360	766
L3	369	356	712
L4	394	381	844
L5	364	352	640
S1	396	374	926
S2	306	291	354
S3	325	307	430
S4	359	336	496
S5	314	296	396
S6	371	350	642

Surgery was conducted on board a boat anchored near the nest site. Fish lost equilibrium in the anaesthetic after 3–4 min and were then measured (total length, 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. (2000). A 3 cm long incision was made on the ventral surface, just posterior to the pectoral girdle. Electrodes were positioned 10 mm apart in the red axial musculature below the lateral line using 16 1/2 g rods (Bunt 1999). The red oxidative musculature is located in a superficial wedge-shaped layer, subcutaneous to the lateral line in centrarchids (Bone 1966; Jayne and Lauder 1993, 1995). Jayne and Lauder (1993) report that during chase responses elicited in bluegill, both white and red muscle were activated during burst swimming. Performing an EMG of red musculature is therefore an appropriate technique for assessing both aerobic and anaerobic activity. Electrode placement was standardized at the anterior portion of the dorsal fin (Beddow and McKinley 1999). Once they were in place, a plunger was used to secure the electrodes in the muscle, allowing the rods to be removed. The transmitter was inserted through the incision and pushed anteriorly into the body cavity. A 16 1/2 g hypodermic needle was then pushed through the body-cavity wall using the shielded-needle technique and the antenna wire was passed through to the outside of the body. 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. Divers remained at the nest and observed the post-release behaviour of the fish. The diver continued to fend off intruders if necessary following release until the fish was able to exclude predators on its own. All fish resumed parental care in less than 1 min. Other studies also indicate that nest-guarding smallmouth bass actively engage intruders immediately following surgery (Scott et al. 1997; S.J. Cooke, unpublished data). Nonetheless, we excluded the first 24 h of data to ensure that any effects of surgery were eliminated. In total we implanted six male smallmouth bass and five male largemouth bass (Table 1).

Data collection and analysis

Nest observations following surgery were made on a daily basis by snorkeling to monitor fish behaviour, relative brood size, predator activity, and brood developmental stage. We used a modification of Ridgway's (1988) terminology to denote four stages of development: egg, egg-sac fry, swim-up, and free-swimming fry. Ridgway (1988) termed the second stage wrigglers, but we term this stage egg-sac fry. The developmental stages are depicted in Hubbs and Bailey (1938). Two data-logging receivers (SRX_400, Lotek Engineering Inc.) were used to continuously monitor the activity of radio-tagged fish. We were able to minimize erroneous signals due to interference by using low receiver gain and a cluster of several antennas within 100 m of the nesting fish.

Data were summarized in SAS (SAS Institute Inc.), creating 30-min averages (Briggs and Post 1997*a*, 1997*b*) for each fish. All EMG*i* values were adjusted for each fish, and values were transformed so that they could be reported as percent increase over resting values (Cooke et al. 2001*a*). 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 lake, resting values were corroborated by snorkelers using timers that corresponded to the exact time on the receivers. Individual forced-swimming calibrations in respirometers were not possible because the fish would have been absent from the nest for an extended period and exhausted upon return. Therefore, we used a previously developed relationship (Cooke et al. 2001*a*) between swimming speed and percent increase in activity to predict swimming speeds from our field-collected EMG data.

We examined the activity of fish on several time scales. First, mean daily swimming activity (m) was calculated for individual fish and for each of the different stages of brood development. This examination provided insight into stage-specific patterns and detailed 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)). Next we examined diel patterns of relative activity. Like Hinch and Collins (1991) we excluded crepuscular-period data (05:00–07:59 and 19:00–20:59) and divided the remaining time into diurnal (08:00–18:59) and nocturnal (21:00–04:59) periods. We used the crepuscular periods for downloading receivers and performing maintenance on the automated monitoring system. Nocturnal and diurnal data for each species and all four of the developmental stages were treated individually for analysis.

We quantified the burst-swimming bouts assuming that any EMG signals corresponding to swimming speeds over 0.8 m/s represented burst-swimming activity for adult basses (Bunt et al. 1999; Cooke and Bunt 2001; Cooke et al. 2001*a*; S.J. Cooke, unpublished data). We summed all the signals from a single fish during a given period in milliseconds and determined the proportion of time that each fish spent burst swimming. It is not possible to determine from EMG signals exactly when burst-swimming activity begins. By using the relationship developed in a respirometer (Cooke et al. 2001*a*), however, we can infer the EMG activity levels consistent with burst swimming, which would be characterized by the fish swimming at speeds greater than 80% of critical swimming speed (U_{crit}) (Lauder 1989). Many fish species are capable of generating speeds up to 80% of U_{crit} while using aerobic musculature (e.g., Webb 1971; Jones 1982; Burgetz et al. 1998). Speeds above ca. 80% of U_{crit} usually require activation of both white muscle and red muscle. For the burst-swimming activity that basses exhibit during nest defence (i.e., chases, aggression), this combination of red and white musculature would also be used. In a study employing videography, EMG transmitters, and intruder models in Illinois ponds, spikes in EMG activity were found when nest-guarding male largemouth bass swam rapidly towards the staged intruder threat and during angling (Cooke et al. 2000; S.J. Cooke, unpublished data). Collected data were divided into diurnal and nocturnal components as described above.

The proximity of guarding male centrarchids to the developing brood has typically been assessed using conventional telemetry. Here we used the relative power strength of the logged EMG*i* signals to examine the proximity of fish to the nest site. Power strength is a dimensionless number expressed in relative power strength units ranging from 0 to 232 (see Cooke and Bunt 2001). Receiver sensitivity (gain) and antenna location were fixed for the study to minimize baseline signal strength shifts. Fish that made more frequent forays from the nest site exhibited greater variation in signal strength than fish that remained closer to the nest. It should be noted that if the fish changed location slowly over time, particularly during the free-swimming fry period (see Scott et al. 1997), the short-term variation in signal strength would not change. Thus, gradual movements of a brood and parent away from the nest would not be misinterpreted as short-term movements of the parent away from the nest or brood. We quantified variation in signal strength of each fish in each period with the coefficient of variation (CV) using SAS (SAS Institute Inc.). These data were divided into diurnal and nocturnal components as described above.

Lastly, we calculated and compared instantaneous swimming speeds (m/s) for use in the activity multiplier of the bioenergetics model. The mean instantaneous swimming speed was calculated for individual fish, the two different species, and the different stages of brood development. Data for entire 24-h periods (including diurnal, nocturnal, and crepuscular where possible) were used to derive these values.

We used analysis of variance (ANOVA) to test for significant differences among stages of offspring development for all of the metrics we examined. Tukey's HSD test was then applied a posteriori to identify differences between stages (Day and Quinn 1989). Assumptions of parametric tests were examined using graphical analysis of standardized residuals. Where appropriate, variance was stabilized and normality was corrected with log transformations (Sokal and Rohlf 1995). All analyses were conducted with SYSTAT (Version 8.0, SPSS Inc.). The maximal type 1 error rate was set at $\alpha = 0.05$. To control type 1 errors for multiple comparisons we used Bonferroni-adjusted probabilities for paired *t* tests (Zar 1996).

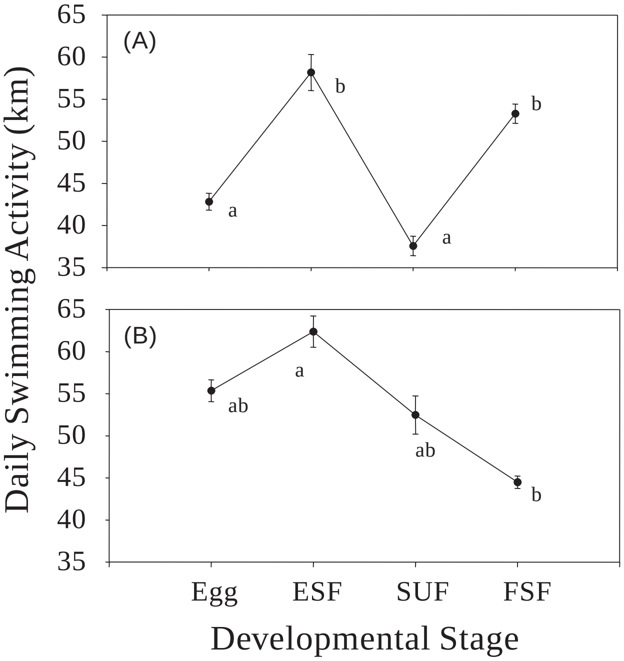
Bioenergetics modeling

We conducted a series of energetics simulations with the software Fish Bioenergetics 3.0 for Windows (University of Wisconsin System Sea Grant Institute 1997). For all simulations we used the model parameters developed by Rice (1981). Water temperature was set at a constant 18°C because temperatures approximating this were maintained for most of the monitoring period. Data for the activity multiplier, RTO (swimming speed as a constant (m/s)), of the respiration component of the model (model 1) were derived from developmental-stage-specific values for each individual monitored. Unlike our assessment of day and night activity levels, we did not exclude crepuscular periods for which such data were available. Swimming-activity data were collected for individual fish continuously throughout the 22-day study. Consecutive models were run for each developmental stage for the period during which the brood was at a given stage for each fish. Because water temperatures were reasonably similar for all test males over the course of the study, developmental stages were of similar duration among the broods (3 days for egg, 2 days for egg-sac fry, 2 days for swim-up fry, and 15 days for free-swimming fry). We used the mass measured when each fish was caught for implantation as the initial mass of the fish for the simulations.

For the first set of simulations we were interested in the effects of nest guarding on growth and respiration of parental males over the 22-day study. We assumed that some of the effects of nest guarding would be attributable to males not feeding while caring for eggs or fry. The general consensus in the literature is that centrarchid fishes do not feed during the parental care period (Coble 1975; Heidinger 1975; Miller 1975), although there is some evidence that they may feed opportunistically in some situations (Hinch and Collins 1991). We assumed that the fish did not eat at all, based upon our unpublished videography data (S.J. Cooke, unpublished data).

We also compared the costs incurred by nest-guarding fish with those of free-swimming non-nesting fish at similar water temperatures. Data for free-swimming, non-nesting smallmouth bass from Lake Erie were provided in Cooke et al. (2001*a*). The instantaneous free-swimming speed for smallmouth bass (0.317 m/s at 18°C) was determined using the same activity transmitters as used in this study. Data for free-swimming, non-nesting largemouth bass were collected in ponds in central Illinois (for details see Cooke et al. 2000). The instantaneous swimming speed of largemouth bass at 18°C was 0.139 m/s. The mean stage-specific swimming-activity values for the five largemouth bass and six smallmouth bass that we monitored were used to represent nesting fish. For this set of simulations we set the initial (day 0) mass of all fish to 1000 g. We then modeled the change in mass and growth over a 22-day period for nesting smallmouth bass, nesting largemouth bass, non-nesting smallmouth bass, and non-nesting largemouth bass. We again assumed that nesting bass do not feed, but assumed that non-nesting fish would be actively feeding and therefore assigned them a ration of 10 g/day of fish with an energy content of 4000 J/g wet mass. Model 1 regression analysis was used to examine the relationship of the initial mass of smallmouth bass and largemouth bass with both the estimated absolute body mass loss over the nesting period and the proportion of total body mass lost. Two-tailed *t* tests were used to test the hypothesis that the slope was equal to zero. All analyses were conducted with SYSTAT (Version

Fig. 1. Daily swimming activity of male largemouth bass (*Micropterus salmoides*; *N* = 5) (A) and smallmouth bass (*Micropterus dolomieu*; *N* = 6) (B) during four brood-development stages (egg, egg-sac fry (ESF), swim-up fry (SUF), and free-swimming fry (FSF)). Values are expressed as the mean ± 1 SE. Identical letters denote statistical similarity between estimates of daily swimming activity at different developmental stages.



8.0, SPSS Inc.). The maximal type 1 error rate was set at $\alpha = 0.05$.

Results

Daily swimming activity

Patterns of daily swimming activity of parental male smallmouth bass were expected to follow the model described by Sargent and Gross (1986). Consistent with that prediction, daily swimming activity of male smallmouth bass varied significantly among developmental stages of the offspring ($F = 4.567$, df = 3,20, $P = 0.003$; Fig. 1), increasing from the egg to the egg-sac fry stage, then decreasing through the swim-up and free-swimming fry stages. For parental male largemouth bass, we hypothesized that swimming activity would be high during the free-swimming fry stage, owing to the mobility of the fry and the accompanying increase in activity required for the parental male to patrol that region. Male largemouth bass swimming activity did differ by stage ($F = 23.526$, df = 3,16, $P < 0.001$) and conformed to the predicted pattern. After declining from the egg-sac fry to the swim-up fry stage, swimming activity of the male largemouth bass increased at the free-swimming fry stage (Fig. 1).

Diel relative-activity patterns

General patterns of relative activity of both species for day and night at each stage were similar to those described for the 24-h periods above and were consistent with our predictions (Fig. 2). Day and night activity for males of both species differed among the various stages of offspring development. For both largemouth bass and smallmouth bass, activity levels during the egg, egg-sac fry, and swim-up fry stages were similar for nocturnal and diurnal periods ($P = 0.111$–0.804) (Fig. 2). However, during the free-swimming fry stage, nocturnal activity levels were slightly lower than during the day for both largemouth bass and smallmouth bass.

Diel burst-swimming activity index

Consistent with our prediction, the burst-swimming-activity index (indicative of predator defence, or potential prey pursuit) generally followed the pattern proposed by Sargent and Gross (1986) for both species (Fig. 3). Largemouth bass burst-swimming activity varied across developmental stages ($F = 4.664$, df = 3,16, $P < 0.001$). During both day and at night, burst-swimming activity peaked during the egg-sac fry stage, with significantly higher levels than at earlier or later stages (Fig. 3). Smallmouth bass burst-swimming activity did not vary significantly over the developmental stages ($F = 0.770$, df = 3,20, $P = 0.613$). For both species, burst-swimming activity tended to be lower at night, although none of these differences was significant ($P = 0.199$–0.917).

Diel signal-strength variation

Signal-strength variations (indicative of the variation in proximity of the male to the developing brood, presumably generated by chasing off potential predators) also conformed to predicted patterns. Signal strength varied across stages and followed similar trends in both species, peaking at the egg-sac fry stage and then declining ($F_L = 31.175$, df = 3,16, $P < 0.001$; $F_S = 72.073$, df = 3,20, $P < 0.001$; Fig. 4). The signal-strength coefficient of variation (CV) was similar between day and night periods for largemouth bass across all stages ($P = 0.080$–0.677). Signal-strength variation for smallmouth bass was higher during diurnal periods for both the egg and free-swimming fry stages (Fig. 4), but similar to nocturnal levels for the other stages ($P = 0.319$ and 0.773, nonsignificant).

Energetics simulations

Simulations revealed that all nest-guarding smallmouth bass and largemouth bass that we monitored would have had negative growth rates and a mean daily energy loss exceeding 10 000 J (Table 2). The absolute mass loss during the nest-guarding period for both smallmouth bass and largemouth bass was positively correlated with the initial mass of the fish (Fig. 5). Despite the fact that larger fish lost more mass absolutely, large fish lost proportionately less mass than smaller fish. The proportion of initial mass lost was negatively correlated with initial mass ($P < 0.05$) for both largemouth bass and smallmouth bass (Fig. 5). The respiration component of the energetics model required inputs of both swimming speed as a constant and the slope of the allometric mass function for standard metabolism. The strong relationship presented above is largely a result of the allometric mass function, although the generally high respiration rates were due to the heightened activity levels of the nest-guarding fish.

The models using the standard 1000-g fish also indicated that growth would be negative (Fig. 6) for nest-guarding fish. Smallmouth bass would lose 115 g and largemouth bass would lose 125 g (Fig. 7) over the 22-day period. The models indicated that non-nest-guarding fish that did not eat

Fig. 2. Relative EMG activity (mean ± SE) of nesting male largemouth bass ($N = 5$) (A) and smallmouth bass ($N = 6$) (B) during four brood-development stages, expressed as percent increase in activity over resting values (0). Solid bars represent nocturnal activity and open bars represent diurnal activity. Identical letters denote statistical similarity between estimates of daily relative EMG activity at different developmental stages (egg, egg-sac fry (ESF), swim-up fry (SUF), and free-swimming fry (FSF)). The letters to the left of the paired bars are for nocturnal activity and those to the right are for diurnal activity. An asterisk indicates a significant difference in activity between nocturnal and diurnal periods for a developmental stage.

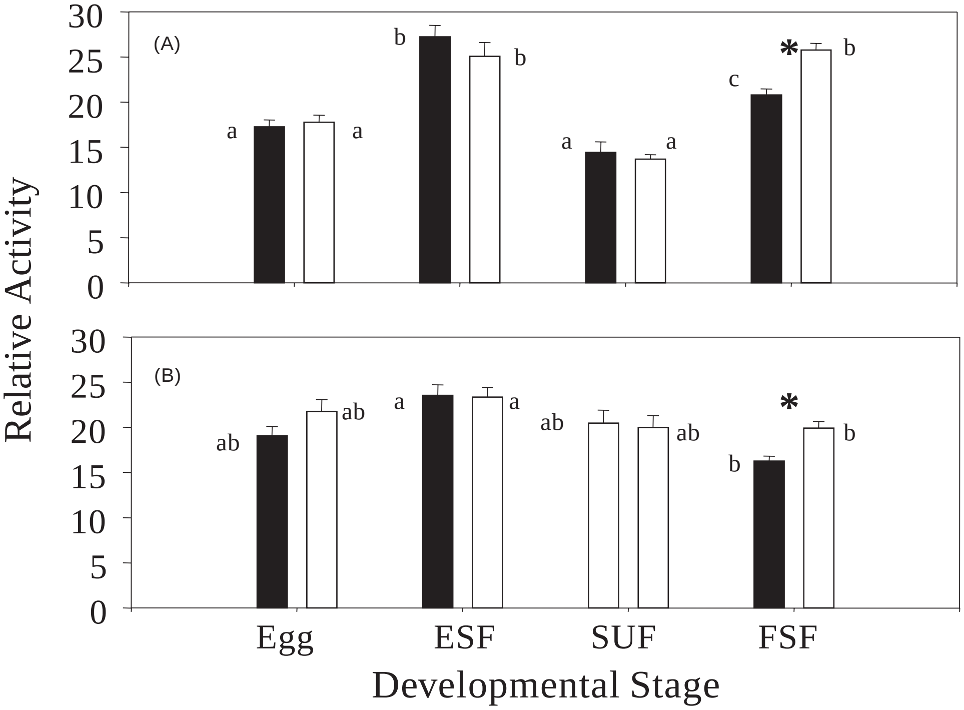


Fig. 3. Burst-swimming frequency (mean ± SE) for male largemouth bass ($N = 5$) (A) and smallmouth bass ($N = 6$) (B) during four brood-development stages, expressed as the proportion of time engaged in swim speeds in excess of 80% of U_{crit}. Solid bars represent nocturnal activity and open bars represent diurnal activity. Identical letters denote statistical similarity between burst-swimming frequencies at different developmental stages (egg, egg-sac fry (ESF), swim-up fry (SUF), and free-swimming fry (FSF)). The letters to the left of the paired bars are for nocturnal activity and those to the right are for diurnal activity.

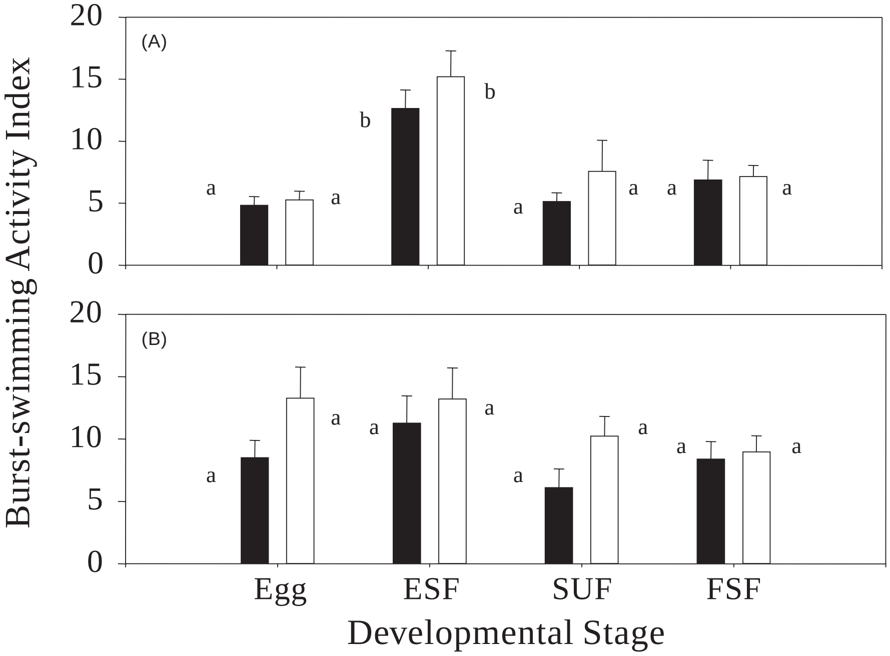
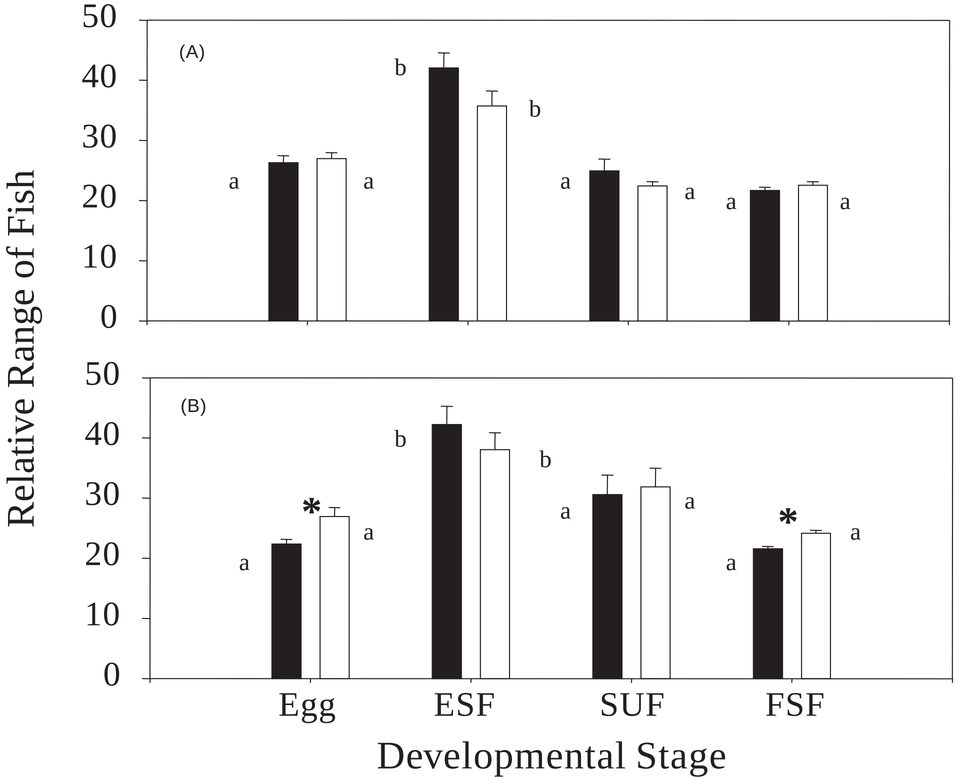


Fig. 4. Power strength (mean ± SE) of logged signals during four brood-development stages in largemouth bass ($N = 5$) (A) and smallmouth bass ($N = 6$), expressed as the coefficient of variation. Solid bars represent nocturnal activity and open bars represent diurnal activity. Identical letters denote statistical similarity between variation in signal strength at different developmental stages (egg, egg-sac fry (ESF), swim-up fry (SUF), and free-swimming fry (FSF)). The letters to the left of the paired bars are for nocturnal activity and those to the right are for diurnal activity. An asterisk indicates a significant difference in signal strength variation between nocturnal and diurnal periods for a developmental stage.



would also lose mass, but much less than nest-guarding fish. Specifically, we estimated that smallmouth bass from Lake Erie would lose 98 g and largemouth bass from Illinois ponds would lose 83 g if they were operating at non-nesting activity levels, but without food. If an estimated ration of 10 g/day was provided to the same non-nesting fish, smallmouth bass would gain 42 g and largemouth bass would gain 58 g. Thus, the extreme energetic costs of nest guarding are due to the heightened parental care activity levels relative to non-nesting fish, but are magnified by the lack of food consumption during the nest-guarding phase. Based on this direct comparison, nest guarding for the 22-day period that we modeled appears to be more costly to largemouth bass than to smallmouth bass, though this is subject to the assumptions and limitations of the model inputs. Evidence to support the differential costs of parental care includes the observation that the specific respiration rate for a nesting 1000-g largemouth bass would be 52.6% higher than that for non-nesting individuals in Illinois ponds. The specific respiration rate for a nesting 1000-g smallmouth bass was only 17.6% higher than that for non-nesting fish in Lake Erie (Fig. 8).

Discussion

Diel activity patterns

Our first objective was to use activity transmitters to determine whether parental male bass behave the same at night as they do during the day at each of four offspring developmental stages. The fish in our study were equally active nocturnally and diurnally during the first three offspring developmental stages. This is consistent with Hinch and Collins (1991), who examined diel parental-care activity of smallmouth bass during the first two developmental stages and found that the number of turns per hour and the caudal- and pectoral-fin beat frequencies were similar during the day and at night. However, during the free-swimming fry stage, both largemouth bass and smallmouth bass were less active at night than during the day. In addition to monitoring relative activity we also monitored diel burst-swimming activity, which is indicative of chasing predators. Burst-swimming activity followed a general pattern of reduced nocturnal activity, particularly during the second and third stages of nest development. However, none of the differences was significant. Hinch and Collins (1991) reported that the number of hourly departures was higher during the day than at night and that males departed the nest to threaten or attack nearby fish. It is likely that predation attempts by other fish are reduced at night, reflecting their inactivity (Emery 1973). However, brown bullhead, which have been identified as centrarchid nest predators (Ongarato and Snucins 1993), are abundant in Lake Opinicon, and are active only at night.

Prior to Hinch and Collins' (1991) study, it was generally believed that because smallmouth bass are visual predators, they were quiescent at night, which was supported by SCUBA

Table 2. Output from energetics modeling of individual fish in our study.

Fish ID No.	Initial wet mass (g)	Projected final wet mass (g)	Projected total mass loss (g)	Predicted proportion of total mass loss (g)	Gross daily mass loss (g)[a]	Gross daily energy loss (J)[a]	Daily specific growth rate (g)[a]	Daily specific respiration rate ($J \cdot g^{-1} \cdot d^{-1}$)[a]
L1	436	367.3	68.8	15.8	–3.234 (0.037)	–13 536 (156)	–0.00802 (0.000114)	33.579 (0.476)
L2	766	660.3	105.7	13.8	–4.802 (0.054)	–20 101 (227)	–0.00672 (–0.00009)	28.142 (0.379)
L3	712	614.0	98.0	13.8	–4.456 (0.052)	–18 651 (219)	–0.00671 (0.000096)	28.088 (0.400)
L4	844	743.1	100.9	12.0	–4.586 (0.087)	–19 196 (364)	–0.00577 (0.00008)	24.153 (0.335)
L5	640	546.6	93.4	14.6	–4.247 (0.048)	–17 779 (199)	–0.00715 (0.000089)	29.921 (0.372)
S1	926	816.4	109.6	11.8	–4.984 (0.072)	–20 857 (300)	–0.00571 (0.000046)	23.903 (0.190)
S2	354	296.8	57.2	16.2	–2.601 (0.039)	–10 886 (162)	–0.00798 (0.000052)	33.403 (0.217)
S3	430	363.4	66.6	15.5	–3.031 (0.053)	–12 685 (222)	–0.00763 (0.000068)	31.931 (0.285)
S4	496	423.7	72.3	14.6	–3.288 (0.050)	–13 765 (207)	–0.00714 (0.000057)	29.890 (0.238)
S5	396	33.0	63.0	15.9	–2.865 (0.049)	–11 991 (203)	–0.00785 (0.000063)	32.848 (0.264)
S6	642	555.8	86.2	13.4	–3.918 (0.055)	–16 398 (230)	–0.00653 (0.000056)	27.338 (0.236)

Note: We modeled various parameters over a 22-day parental care period and provided the fish in the model with no food.
[a] Values are given as the mean with 1 SE in parentheses.

Fig. 5. Size-specific trends in absolute and proportional loss of body mass for nesting largemouth bass (N = 5) (●) and smallmouth bass (N = 6) (○). The activity rates from nesting fish are based on empirical data from this study with the activity multiplier changed to reflect the instantaneous swimming speed of each fish at each stage of development.

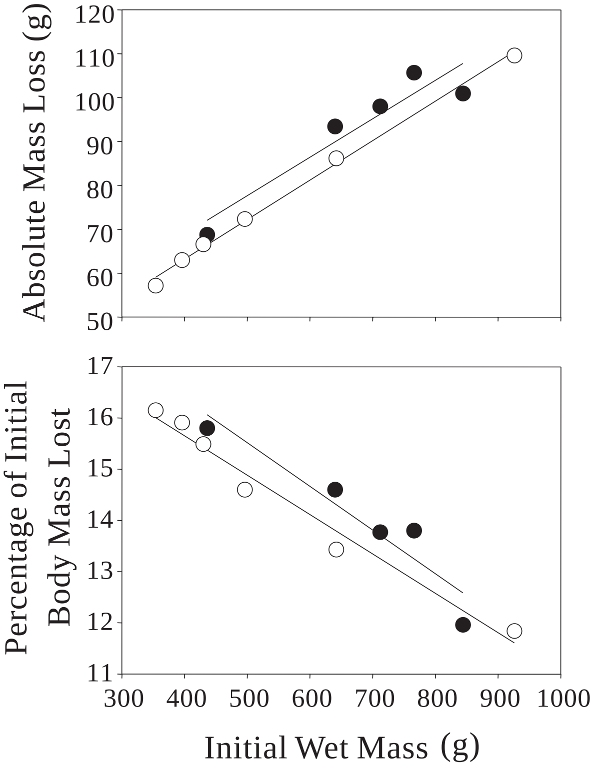
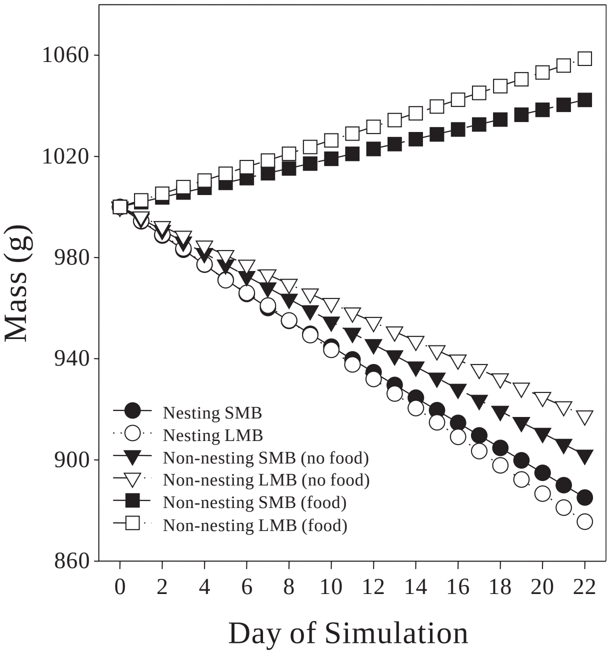


Fig. 6. Daily output from a 22-day simulation of growth at 18°C of largemouth bass (LMB) and smallmouth bass (SMB) with an initial mass of 1000 g. The activity rates from nesting fish are based on empirical data from this study with the activity multiplier changed to reflect the mean instantaneous swimming speed from Fig. 1. The activity rates for the non-nesting fish are derived from the literature and unpublished data. Consumption was set to 0 for all groups except the non-nesting "food" groups, which were provided with a ration of 10 g/day of fish with a prey value of 4000 J/g.



observations made using a flashlight (Emery 1973). Since these studies, Demers et al. (1996) have used EMG telemetry to determine that non-nesting smallmouth bass and largemouth bass both exhibited pronounced diel activity patterns (more active diurnally) under field conditions. Somewhat disparate results have been generated in laboratory experiments (e.g., Davis 1964; Reynolds and Casterlin 1976) suggesting that bass exhibit crepuscular activity. Reebs (1992) reviewed the phenomenon of changes in activity patterns in response to parental care requirements. There is evidence that most circadian organization is repressed during the parental phase. It must be noted, however, that rhythms of activity still differ between light and dark periods. For example, Reebs and Colgan (1991) concluded that variation in egg fanning by parental males in light versus dark periods is the result of an endogenous rhythm whose amplitude is modified by light intensity. None of the previous staged intrusion studies of *Micropterus* species were conducted at night, and most were conducted near midday (e.g., Ridgway 1988; Ongarato and Snucins 1993). Fish in our study were more active during the day than at night during the free-swimming fry stage, the difference in activity being greater than at any other stage. This discrepancy likely reflects the behaviour of the offspring, which are also likely more active during the day than at night (e.g., Scott et al. 1997; see discussion below). Resumption of non-reproductive diurnal activity patterns probably begins upon abandonment of the fry.

Parental care relative to brood ontogeny

Our second objective was to determine whether activity patterns that have been reported from studies using conventional model presentations are representative of natural activity patterns of nesting basses determined using 24 h activity transmitters. The patterns in daily swimming activity over the parental care period that we observed for smallmouth bass were roughly similar to patterns of nest defence reported in the literature. Ridgway (1988) noted that parental defence increased from the egg to the wriggler (egg-sac fry) stage and then declined drastically after swim-up. The frequency of aggressive behaviours was also lowest during the free-swimming fry stage. Ongarato and Snucins (1993) and Suski (2000) report similar findings, with the frequency of aggressive behaviour increasing from the egg to the egg-sac fry stage. Models were not presented during other stages. Urban (1991) studied the effect of offspring age and frequency of nest intrusions on the defence behaviour of parental smallmouth bass and reported that the proportion of time males spent close to the brood declined once the fry were free-swimming. Rock bass, the primary nest intruders in that study, were chased away most frequently when offspring were midstage. The decline observed at later offspring stages corresponded to reductions in intrusion attempts by predators. Wiegmann and Baylis (1995) reported that smallmouth bass guarding eggs were more tenacious than those guarding larvae and attributed this inconsistency with the results of

Fig. 7. Summary of results of the model output illustrating the change in mass of largemouth bass (LMB) and smallmouth bass (SMB) over the 22-day simulation, based on an initial mass of 1000 g and 18°C. The activity rates from nesting fish are based on empirical data from this study with the activity multiplier changed to reflect the mean instantaneous swimming speed from Fig. 6. The activity rates for the non-nesting fish are derived from the literature and unpublished data. Consumption was set to 0 for all groups except the non-nesting "food" groups, which were provided with a ration of 10 g/day of fish with a prey value of 4000 J/g.

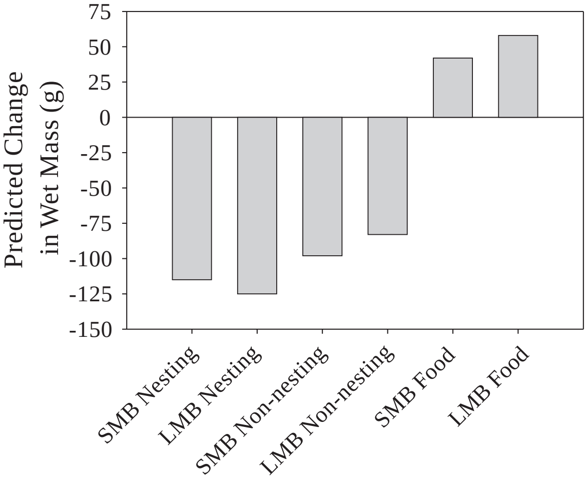
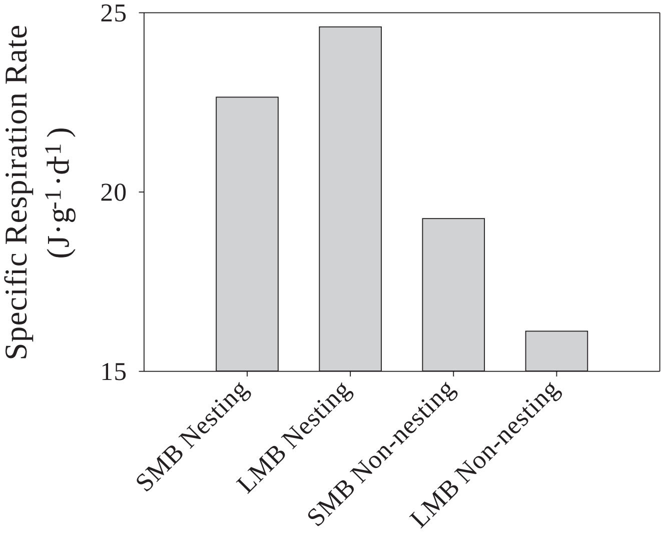


Fig. 8. Specific respiration rates of nesting and non-nesting 1000-g smallmouth bass (SMB) and largemouth bass (LMB) at 18°C. The activity rates from nesting fish are based on empirical data from this study with the activity multiplier changed to reflect the mean instantaneous swimming speed from Fig. 6. The activity rates for the non-nesting fish are derived from the literature and unpublished data.



previous studies to differences in type of intruder, physiological demands of the progeny, and the manner in which risk is perceived.

These changes in parental care over the nesting period (e.g., Ridgway 1988; Ongarato and Snucins 1993; this study) likely reflect the increasing reproductive value of the developing brood combined with the decreasing ability of the parent to enhance their fry's survival (Sargent and Gross 1986). Our observations did deviate slightly from the model in that smallmouth bass appeared to reduce parental care after the egg-sac fry stage rather than immediately after the eggs hatched. Generally, increasing levels of defence were observed from oviposition through to the swim-up of the larvae. After this, the level of defence is generally expected to decline, owing to the increasing independence of the larvae and a reduction in the parents' ability to improve survival further. Because the offspring are still in or close to the nest until they become free-swimming, at which time they are still distributed in a reasonably compact manner (relative to largemouth bass free-swimming fry), the reduction in activity could be a consequence of the male being able to defend the fry effectively with little locomotory activity.

The pattern of locomotory activity exhibited by guarding male largemouth bass deviated from conventional patterns of parental care. Initially, largemouth bass showed a typical response, with nest defence peaking early in the parental care period and then declining during the swim-up fry stage. However, during the final phase (free-swimming fry), the activity of the male showed a dramatic increase. The only previous information on largemouth bass parental care activity was collected by Colgan and Brown (1988). Although they used different terminology and stages, they found that that largemouth bass would attack model predators at increasing distances through the late wriggler stage (similar to our swim-up fry stage); this was followed by a decrease in distance as the fry became free-swimming. Some of our data for largemouth bass are more contradictory to the predictions of Sargent and Gross (1986) than the discrepancies noted by Colgan and Brown (1988). Specifically, the secondary spike in locomotory activity that we noted during the free-swimming fry stage is not predicted by the model. The reduction in largemouth bass activity during the swim-up fry stage may reflect a cessation of fanning behaviour and other activities that are not essential to offspring survival at this stage. The simplest explanation for the increase in activity at the free-swimming fry stage may be that the mobility, size, and loss of cohesion in the "fry ball" as the fry become older requires parental bass to swim more just to maintain contact with the fry (see Brown 1985). The behaviour of free-swimming smallmouth bass fry differs from that of free-swimming largemouth bass fry in that the former stay relatively close to the nest during the later stages of parental care / fry development, often returning to the nest itself at night (Scott et al. 1997; Friesen and Ridgway 2000). We found no spike in burst swimming of parental male smallmouth bass during the free-swimming fry stage, which is consistent with Sargent and Gross' (1986) model. Thus, the spatial distribution of the fry may affect some aspects of parental care independently of offspring value. Indeed, to compensate for the increased parental-care needs during the free-swimming fry stage relative to smallmouth bass, largemouth bass may begin to forage. This may not only be necessary to provide sufficient energy resources (immediately and for the future (see below)), but may also reflect increased opportunities associated with the mobility of the fry ball.

Energetics

Our third objective was to estimate the energetic costs of reproduction for male bass over the nesting period using data from activity monitors. Our results clearly indicate that parental fish are more active than non-nesting fish. Heightened activity during parental care resulted in higher respiration rates. Using videography, Hinch and Collins (1991) quantified the energetic costs associated with nest defence in one smallmouth bass. They estimated that the fish used the equivalent energy of swimming a distance of approximately 28 km per day. Although this value seems high, Cooke et al. (2001*a*) recently reported that even non-nesting smallmouth in Lake Erie swam the equivalent of about 27 km per day. Similar activity estimates are rare for largemouth bass, although in small Illinois ponds, non-nesting fish swim about 12 km per day (S.J. Cooke, unpublished data). In our study, mean daily swimming activity over the entire parental care period was 41 km for smallmouth bass and 49 km for largemouth bass. During the early stages of development, the parental male must fan the nest in addition to defending the nest against predators (Blumer 1979). Fanning enhances the survival of the developing embryos by keeping them oxygenated and free from silt and debris (Gross 1980; Sargent and Gebler 1980; Zoran and Ward 1983). Fanning can also be costly and although it may not result in a net displacement of the fish, it is the energetic equivalent to swimming in place (Coleman and Fischer 1991; Hinch and Collins 1991).

Two recent studies have examined the depletion of somatic energy reserves of smallmouth bass during parental care. Mackereth et al. (1999) found that energy stores were lowest at the end of the parental care period and exhibited size-specific variation. Small fish showed the greatest decline in parental care activity, and thus the rate of energy depletion was lower in small fish than in larger fish. The authors attribute this variation to a possible increase in reliance on exogenous energy sources (i.e., feeding) by small fish relative to larger fish. Gillooly and Baylis (1999) determined that larger fish have higher lipid reserves, although this was not reflected in size-specific percent changes in body mass or lean mass. Our modeled changes in absolute mass were similar to the values reported by Gillooly and Baylis (1999) if their data are extended from the 8-day period that elapsed between their measurements to the 22-day period that we simulated. Contrary to the empirical data of Mackereth et al. (1999) and Gillooly and Baylis (1999), we found size-specific patterns in both the absolute and the proportionate loss of wet mass using theoretical model simulations. It must be noted that although this model provides estimates of changes in wet body mass, when lipids and lean muscle mass are metabolized/catabolized, leading to loss of lipid and lean muscle mass, cells may hydrate. The resulting slight reductions in mass (Mackereth et al. 1999) would mask the significant loss of energy reserves.

There are several limitations to the model inputs that we used to estimate the energetic costs of parental care. For the modeling exercise that we present, we restricted the comparison to a 22-day period to reflect the period during which we monitored fish in the wild. We terminated the experiment prior to the dispersal of fry. We also assumed that nesting fish did not ingest any food during this period. Support for this assumption comes from evidence that males provided with supplemental food exhibit increased survival or reproductive success (Ridgway and Shuter 1994), suggesting that nesting males are food-stressed. More directly, video-monitored nesting smallmouth bass rarely feed (Hinch and Collins 1991). However, nesting smallmouth bass that were terminally sampled from Lake Opeongo, Ontario, frequently had food in their stomachs (~0.47–1.33 g mean dry mass) (Mackereth et al. 1999). Thus, it is currently not known when the males of both species resume active feeding or the degree to which they may acquire resources opportunistically during the parental care period.

The activity estimates that we present for non-nesting largemouth bass and smallmouth bass come from only two other studies. Although it was not possible for this study, it would be desirable to monitor simultaneously the activity of nesting and non-nesting fish in the same water body to eliminate some of the potential sources of error involved in our estimates. While we are confident that our modeling output is indicative of the relative energetic costs of parental care between nesting and non-nesting bass, the model can be refined as necessary to provide more accurate outputs as further insights into the parental care biology of these fishes are gained. Indeed, energetics models are only as good as the inputs (Ney 1993).

Methodological implications

When assessing patterns of behaviour and energetics over the parental care period, a variety of different indicators can be used. For example, quantifiable aspects of nest defence can be used to assess the response of the parent to perceived or actual threats using natural or staged intrusions. This may include the number of aggressive acts, attack distance (Colgan and Brown 1988), or time spent away from nest. Similarly, one can also employ energetics approaches such as quantification of indicators of locomotory activity (distance moved, tail- or wing-beat frequency), remote measurement of a physiological parameter (i.e., heart rate, EMG), or direct estimation of energetic costs using techniques like the doubly labeled water technique or parameters such as proximate body composition, body mass, or condition factor). Frequently, studies are based upon only one of these, thus providing information on either behaviour or energetics. Our use of activity monitors in this study allowed us to use a variety of indicators of both the defence activities and the general activity and energetics of fish during the parental care period.

Despite its advantages, the approach that we employed is not without limitations. For example, activity monitors can only quantify defence behaviours that involve a locomotory response. Non-locomotory behaviours such as yawns may be used to discourage other fish from approaching, thereby minimizing possible future energetic costs or physical injury. The energetic costs of such acts are minimal compared with a burst-swimming action where the fish chases predators from the nest area. However, in some instances these inexpensive defence behaviours may be important, especially in reducing the frequency of more costly behaviours.

An important component of using activity transmitters is their calibration for generating estimates of swimming speed.

Because we captured fish that were already providing parental care, we had to return the fish to the water without calibrating individual fish in a respirometer. Our results are thus based upon the use of calibrations developed in another laboratory study (Cooke et al. 2001*a*). The baseline resting values of locomotory activity collected while the fish were in the cooler prior to release are similar to the lowest activity levels that we record in the field as determined by timers carried by snorkelers. Furthermore, videographic observations on nesting largemouth bass implanted with activity transmitters in ponds in Illinois suggest that occasional periods of inactivity (stationary with no caudal flexion) yield data similar to those that we collect during our cooler calibration method (S.J. Cooke, unpublished data). An additional concern is the shifting of signals over the period of observation (22 days in this case). However, Beddow and McKinley (1999) report that EMG activity in Atlantic salmon, *Salmo salar*, monitored by activity transmitters did not differ until periods of more than 3 months post implantation had elapsed. Thus, although we had to rely on calibrations not developed for the individual fish used in this experiment, we believe that the data we present are indicative of what occurs in the field. We encourage researchers who use this approach in the future to couple their telemetry data with detailed observations (i.e., snorkeling, videography) and, where possible, use techniques that do not require instruments that need calibrating (e.g., tail-beat transmitter, heart-rate transmitter).

It is not surprising that our results for largemouth bass deviate somewhat from those from previous studies of parental care activity. The majority of other studies were based upon defence behaviours quantified from staged intrusions using models, and the frequency and type of response and the distance from which it was elicited (e.g., Colgan and Brown 1988). Our study attempted to quantify several surrogates of defensive behaviour, but it also includes non-defence behaviours, including fanning, distant patrolling, and the general locomotory activity of the fish. The heightened activity of largemouth bass during the free-swimming fry stage was based upon data collected after the fry had left the region of the nest. Using other methods it would be difficult to locate nest-guarding males and their fry balls in order to present models.

In our study, nesting males were faced with a variety of potential predators in addition to conspecific predation. The abundance of potential brood predators in the littoral zone of Lake Opinicon could be considered extreme relative to other commonly studied systems (i.e., Canadian Shield lakes). Other studies on Lake Opinicon showed that the removal of male smallmouth bass by angling for even short periods of time resulted in heavy nest predation (Kieffer et al. 1995; Philipp et al. 1997). Other studies have used both conspecific and heterospecific models. For example, Ridgway (1988) used conspecific models (smallmouth bass) matched to within 1 cm of the nesting males’ fork length to elicit responses. Ongarato and Snucins (1993) investigated smallmouth bass aggression towards conspecific, yellow perch, and brown bullhead models. They found no difference in response to the three models. However, brown bullhead are not regarded as nest predators, and yellow perch were not found in the lake they studied. Rock bass was the only natural brood predator found in the lake, but the response to this fish was not studied. Both of these studies involved repeated presentation of models, something that is rarely controlled for (Lavery and Colgan 1991). Only Colgan and Brown (1988) and Urban (1991) used natural intrusion frequencies to examine parental defence by centrarchid fish. By using activity monitors, we relied upon natural predators and associated natural intrusion frequencies, permitting us to quantify the real expenses associated with parental care.

Obviously all current methods of assessing parental care by fishes, when used on their own, have limitations. Studies incorporating several methods that incorporate real-time energetic measurements of the activity of free-ranging organisms and the collection of quantitative and qualitative behavioural observations will be the most robust for assessing the relationships between behaviour and physiological energetics. To date, studies of this nature are limited, but several examples do exist (i.e., Chappell et al. 1993). As recently discussed by Siegel et al. (1999), the biology of the taxa in question must drive the decisions on how best to quantify parental effort. Furthermore, there is a need to compare methods of assessing parental activity to reveal the level of disparity that can be attributable to study method (Knight and Temple 1986; Siegel et al. 1999). Our results indicate that physiological telemetry is an appropriate method for gaining insight into the parental care activity of largemouth bass and smallmouth bass. By quantifying an energetic equivalent, we are able to provide insights into the behaviour and physiological energetics of the parental care period that will facilitate the development of seasonal, gender-specific energetics models (Hansen et al. 1993). With appropriate validation this approach may be applicable to other species of fish and other groups of organisms, including birds and mammals (Butler 1989).

Acknowledgements

Field assistance was provided by Anders Koed, Matt Deters, Cory Suski, Jana Svec, Jimmy Ludden, Julie Claussen, Amy McAninch, and Andrea Weckworth. This work was conducted at the Queen’s University Biological Station with the support of station manager, Frank Phelan, and director, Raleigh Robertson. We thank Scott McKinley for providing access to equipment in the spirit of scientific collaboration. Kate Deters assisted with manuscript preparation. Assistance with statistical analysis was provided by Jason F. Schreer. We also thank Derek Aday, Nick Collins, and Stephan Reebs for providing constructive comments on the manuscript. This project was partially funded by Scott McKinley of the University of Waterloo. Additional funding was provided by the Illinois Natural History Survey, the University of Illinois, and Natural Sciences and Engineering Research Council of Canada postgraduate scholarships to S.J.C.

References

Adams, S.M., McLean, R.B., and Parotta, J.A. 1982. Energy partitioning in largemouth bass under conditions of seasonally fluctuating prey availability. Trans. Am. Fish. Soc. **111**: 549–558.

Anderson, W.G., McKinley, R.S., and Colavecchia, M. 1997. The use of clove oil as an anesthetic for rainbow trout and its effects on swimming performance. N. Am. J. Fish. Manag. **17**: 301–307.

Bain, M.B., and Helfrich, L.A. 1983. Role of male parental care in survival of larval bluegills. Trans. Am. Fish. Soc. **112**: 47–52.

Beddow, T.A., and McKinley, R.S. 1998. Effects of thermal environment on electromyographical signals obtained from Atlantic salmon (*Salmo salar* L.) during forced swimming. Hydrobiologia, **371/372**: 225–232.

Beddow, T.A., and McKinley, R.S. 1999. Importance of electrode position in biotelemetry studies estimating muscle activity in fish. J. Fish Biol. **54**: 819–831.

Blumer, L.S. 1979. Male parental care in the bony fishes. Q. Rev. Biol. **54**: 149–161.

Bone, Q. 1966. On the function of the two types of myotomal muscle fibres in elasmobranch fish. J. Mar. Biol. Assoc. U.K. **46**: 321–349.

Bone, Q. 1978. Locomotor muscle. *In* Fish physiology. Vol. VII. Locomotion. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 361–424.

Breder, C.M., Jr. 1936. The reproductive habits of the North American sunfish (family Centrarchidae). Zoologica, **21**: 1–47.

Briggs, C.T., and Post, J.R. 1997*a*. Field metabolic rates of rainbow trout estimated using electromyogram telemetry. J. Fish Biol. **51**: 807–823.

Briggs, C.T., and Post, J.R. 1997*b*. *In situ* activity metabolism of rainbow trout (*Oncorhynchus mykiss*): estimates obtained from telemetry of axial muscle electromyograms. Can. J. Fish. Aquat. Sci. **54**: 859–866.

Brown, J.A. 1984. Parental care and the ontogeny of predator-avoidance in two species of centrarchid fish. Anim. Behav. **32**: 113–119.

Brown, J.A. 1985. The adaptive significance of behavioral ontogeny in some centrarchid fishes. Environ. Biol. Fishes, **13**: 25–34.

Bunt, C.M. 1999. A tool to facilitate implantation of electrodes for electromyographic telemetry experiments. J. Fish Biol. **55**: 1123–1128.

Bunt, C.M., Katopodis, C., and McKinley, R.S. 1999. Attraction and passage efficiency of white suckers and smallmouth bass by two Denil fishways. N. Am. J. Fish. Manag. **19**: 793–803.

Burgetz, I.J., Rojas-Vargas, A., Hinch, S.G., and Randall, D.J. 1998. Initial recruitment of anaerobic metabolism during submaximal swimming in rainbow trout (*Oncorhynchus mykiss*). J. Exp. Biol. **201**: 2711–2721.

Butler, P.J. 1989. Telemetric recording of physiological data from free-living animals. *In* Towards a more exact ecology. *Edited by* P.J. Grubb and J.B. Whittaker. Blackwell Scientific Publications, Oxford. pp. 63–84.

Chappell, M.A., Shoemaker, V.H., Janes, D.N., Maloney, S.K., and Bucher, T.L. 1993. Energetics of foraging in breeding Adélie penguins. Ecology, **74**: 2450–2461.

Coble, D.W. 1975. Smallmouth bass. *In* Black bass biology and management. *Edited by* H. Clepper. Sport Fishing Institute, Washington, D.C. pp. 21–33.

Coleman, R.M., and Fischer, R.U. 1991. Brood size, male fanning effort and the energetics of a nonshareable parental investment in bluegill sunfish, *Lepomis macrochirus* (Teleostei: Centrarchidae). Ethology, **87**: 177–188.

Coleman, R.M., Gross, M.R., and Sargeant, R.C. 1985. Parental investment decision rules: a test in bluegill sunfish. Behav. Ecol. Sociobiol. **18**: 59–66.

Colgan, P.W., and Brown, J.A. 1988. Dynamics of nest defense by male centrarchid fish. Behav. Proc. **17**: 17–26.

Colgan, P.W., and Gross, M.R. 1977. Dynamics of aggression in male pumpkinseed sunfish (*Lepomis gibossus*) over the reproductive phase. Z. Tierpsychol. **43**: 139–151.

Cooke, S.J., and Bunt, C.M. 2001. Assessment of internal and external antenna configurations of radio transmitters implanted in smallmouth bass. N. Am. J. Fish. Manag. **21**: 236–241.

Cooke, S.J., Philipp, D.P., Schreer, J.F., and McKinley, R.S. 2000. Locomotory impairment of nesting male largemouth bass following catch-and-release angling. N. Am. J. Fish. Manag. **20**: 968–977.

Cooke, S.J., Bunt, C.M., Schreer, J.F., and Wahl, D.H. 2001*a*. Comparison of several techniques for mobility and activity estimates of smallmouth bass in lentic environments. J. Fish Biol. **58**: 573–587.

Cooke, S.J., McKinley, R.S., and Philipp, D.P. 2001*b*. Physical activity and behaviour of a centrarchid fish, *Micropterus salmoides* (Lacépède), during spawning. Ecol. Freshw. Fish, **10**: 227–237.

Davis, R.E. 1964. Daily “predawn” peak of locomotion in fish. Anim. Behav. **12**: 272–283.

Day, R.W., and Quinn, G.P. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. **59**: 433–463.

Demers, E., McKinley, R.S., Weatherley, A.H., and McQueen, D.J. 1996. Activity patterns of largemouth and smallmouth bass determined with electromyogram biotelemetry. Trans. Am. Fish. Soc. **125**: 434–439.

Emery, A.R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. J. Fish. Res. Board Can. **30**: 761–774.

Friesen, T.G., and Ridgway, M.S. 2000. Brood size does not influence the behaviour or density of larval and juvenile smallmouth bass under parental care. Behaviour, **137**: 61–74.

Gillooly, J.F., and Baylis, J.R. 1999. Reproductive success and the energetic cost of parental care in male smallmouth bass. J. Fish Biol. **54**: 573–584.

Gross, M.R. 1980. Sexual selection and the evolution of reproductive strategies in sunfishes (Lepomis: Centrarchidae). Ph.D. dissertation, University of Utah, Salt Lake City.

Hansen, M.J., Boisclair, D., Brandt, S.B., Hewett, S.W., Kitchell, J.F., Lucas, M.C., and Ney, J.J. 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here? Trans. Am. Fish. Soc. **122**: 1019–1030.

Heidinger, R.C. 1975. Life history and biology of the largemouth bass. *In* Black bass biology and management. *Edited by* H. Clepper. Sport Fishing Institute, Washington, D.C. pp. 11–20.

Hinch, S.G., and Collins, N.C. 1991. Importance of diurnal and nocturnal nest defense in the energy budget of male smallmouth bass: insights from direct video observations. Trans. Am. Fish. Soc. **120**: 657–663.

Hubbs, C.L., and Bailey, R.M. 1938. The small-mouthed bass. Bull. No. 10, Cranbrook Institute of Science, Bloomfield Hills, Mich.

Jayne, B.C., and Lauder, G.V. 1993. Red and white muscle activity and kinematics of the escape response of the bluegill sunfish during swimming. J. Comp. Physiol. A, **173**: 495–508.

Jayne, B.C., and Lauder, G.V. 1995. Speed effects on midline kinematics during steady undulatory swimming of largemouth bass, *Micropterus salmoides*. J. Exp. Biol. **198**: 585–602.

Jones, D.R. 1982. Anaerobic exercise in teleost fish. Can. J. Zool. **60**: 1131–1134.

Kaseloo, P.A., Weatherley, A.H., Lotimer, J., and Farina, M.D. 1992. A biotelemetry system recording fish activity. J. Fish Biol. **40**: 165–179.

Keast, A. 1978. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Environ. Biol. Fishes, **3**: 7–31.

Keast, A. 1980. Food and feeding relationships of young fish in the first weeks after the beginning of exogenous feeding in Lake Opinicon, Ontario. Environ. Biol. Fishes, **5**: 305–314.

Keast, A., and Webb, D. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board. Can. **23**: 1845–1874.

Keast, A., Harker, J., and Turnbull, D. 1978. Nearshore fish habitat utilization and species associations in Lake Opinicon (Ontario, Canada). Environ. Biol. Fishes, **3**: 173–184.

Keene, J.L., Noakes, D.L.G., Moccia, R.D., and Soto, C.G. 1998. The efficacy of clove oil as an anaesthetic for rainbow trout, *Oncorhynchus mykiss* (Walbaum). Aquacult. Res. **29**: 89–101.

Keenleyside, M.H.A. 1971. Aggressive behavior of male longear sunfish (*Lepomis megalotis*). Z. Tierpsychol. **28**: 227–240.

Kieffer, J.D., Kubacki, M.R., Phelan, F.J.S., Philipp, D.P., and Tufts, B.L. 1995. Effects of catch-and-release angling on nesting male smallmouth bass. Trans. Am. Fish. Soc. **124**: 70–76.

Knight, R.L., and Temple, S.A. 1986. Methodological problems in studies of avian nest defence. Anim. Behav. **34**: 561–566.

Lauder, G.V. 1989. Caudal fin locomotion in ray-finned fishes: historical and functional analyses. Am. Zool. **29**: 85–102.

Lavery, R.J., and Colgan, P.W. 1991. Brood age and parental defence in the convict cichlid, *Cichlasoma nigrofasciatum* (Pisces: Cichlidae). Anim. Behav. **41**: 945–951.

Lucas, M.C., Johnstone, A.D.F., and Priede, I.G. 1993. Use of physiological telemetry as a method of estimating metabolism of fish in the natural environment. Trans. Am. Fish. Soc. **122**: 822–833.

Mackereth, R.W. 1995. Size-based variation in the allocation of energy to parental care by male smallmouth bass (*Micropterus dolomieu*). Ph.D. dissertation, University of Guelph, Guelph, Ont.

Mackereth, R.W., Noakes, D.L.G., and Ridgway, M.S. 1999. Size-based variation in somatic energy reserves and parental expenditure by male smallmouth bass, *Micrpoterus dolomieu*. Environ. Biol. Fishes, **56**: 263–275.

Miller, R.J. 1975. Comparative behavior of centrarchid basses. *In* Black bass biology and management. *Edited by* H. Clepper. Sport Fishing Institute, Washington, D.C. pp. 85–94.

Montgomerie, R.D., and Weatherhead, P.J. 1988. Risks and rewards of nest defence by parent birds. Q. Rev. Biol. **63**: 167–187.

Ney, J.J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Trans. Am. Fish. Soc. **122**: 736–748.

Ongarato, R.J., and Snucins, E.J. 1993. Aggression of guarding male smallmouth bass (*Micropterus dolomieui*) towards potential brood predators near the nest. Can. J. Zool. **71**: 437–440.

Peake, S. 1998. Sodium bicarbonate and clove oil as potential anaesthetics for nonsalmonid fishes. N. Am. J. Fish. Manag. **18**: 919–924.

Philipp, D.P., Toline, C.A., Kubacki, M.F., Philipp, D.B.F., and Phelan, F.J.S. 1997. The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. N. Am. J. Fish. Manag. **17**: 557–567.

Pressley, P.H. 1981. Parental effort and the evolution of nest-guarding tactics in the threespine stickleback, *Gasterosteus aculeatus* L. Evolution, **35**: 282–295.

Reebs, S. 1992. Sleep, inactivity and circadian rhythms in fish. *In* Rhythms in fishes. *Edited by* M.A. Ali. Plenum Press, New York. pp. 127–135.

Reebs, S.G., and Colgan, P.W. 1991. Nocturnal care of eggs and circadian rhythms of fanning activity in two normally diurnal cichlid fishes, *Cichlasoma nigrofasciatum* and *Herotilapia multispinosa*. Anim. Behav. **41**: 303–311.

Reynolds, W.W., and Casterlin, M.E. 1976. Activity rhythms and light intensity preferences of *Micropterus salmoides* and *M. dolomieu*. Trans. Am. Fish. Soc. **105**: 400–403.

Rice, J.A. 1981. Derivation and application of a bioenergetics model for largemouth bass (*Micropterus salmoides*). Ph.D. dissertation, University of Wisconsin, Madison.

Ridgway, M.S. 1988. Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus dolomieui*). Can. J. Zool. **66**: 1722–1728.

Ridgway, M.S., and Shuter, B.J. 1994. The effects of supplemental food on reproduction in parental male smallmouth bass. Environ. Biol. Fishes, **39**: 201–207.

Sabat, A.M. 1994. Costs and benefits of parental effort in a brood-guarding fish (*Ambloplites rupestris*, Centrarchidae). Behav. Ecol. **5**: 195–201.

Sargent, R.C., and Gebler, J.B. 1980. Effects of nest concealment on hatching success, reproductive success, and parental behavior of the threespined stickleback, *Gasterosteus aculeatus*. Behav. Ecol. Sociobiol. **7**: 137–142.

Sargent, R.C., and Gross, M.R. 1986. Williams' principle: an explanation of parental care in teleost fishes. *In* The behaviour of teleost fishes. *Edited by* T.J. Pitcher. Croom-Helm, London. pp. 275–293.

Scott, R.J., Ridgway, M.S., and Noakes, D.L.G. 1997. The nest range of smallmouth bass (*Micropterus dolomieu*): parental care after swim-up. Can. J. Zool. **75**: 2058–2062.

Siegel, R.B., Weathers, W.W., and Beissinger, S.R. 1999. Assessing parental effort in a Neotropical parrot: a comparison of methods. Anim. Behav. **57**: 73–79.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. 3rd ed. W.H. Freeman and Co., New York.

Suski, C.D. 2000. Linking reproduction with conservation for the largemouth bass (*Micropterus salmoides*) and smallmouth bass (*M. dololmieu*). M.S. thesis, University of Illinois at Urbana–Champaign, Urbana.

Thorp, J.H., Goldsmith, L.D., Polgreen, J.A., and Mayer, L.M. 1989. Foraging patterns of nesting and nonnesting sunfish (Centrarchidae: *Lepomis auritis* and *L. gibbosus*). Can. J. Fish. Aquat. Sci. **46**: 1342–1346.

Trivers, R.L. 1972. Parental investment and sexual selection. *In* Sexual selection and the descent of man. *Edited by* B. Campbell. Heinemann Press, London. pp. 139–179.

Urban, D.K. 1991. The effect of offspring age on the changes in the parental defense response of smallmouth bass (*Micropterus dolomieui*) to predators. M.Sc. thesis, Trent University, Peterborough, Ont.

University of Wisconsin System Sea Grant Institute. 1997. Fish bioenergetics 3.0 for Windows. Board of Regents, Sea Grant Institute, Center for Limnology, University of Wisconsin System, Madison.

Wiegmann, D.D., and Baylis, J.R. 1995. Male body size and parental behaviour in smallmouth bass, *Micropterus dolomieui* (Pisces: Centrarchidae). Anim. Behav. **50**: 1543–1555.

Zar, J.H. 1996. Biostatistical analysis. 3rd ed. Prentice Hall Inc., Englewood Cliffs, N.J.

Zoran, M.J., and Ward, J.A. 1983. Parental egg care behavior and fanning activity for the orange chromidae, *Etroplus maculatus*. *In* Predators and prey in fishes. *Edited by* D.L.G. Noakes. Dr. W. Junk Publishers, The Hague. pp. 139–148.