

## Size-based variation in somatic energy reserves and parental expenditure by male smallmouth bass, *Micropterus dolomieu*

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### Synopsis

Male smallmouth bass show size-based variation in both probability and timing of reproduction. The objective of this research was to determine seasonal and size-based patterns of depletion of energy reserves and determine if parental defense is related to males' energy reserves. We sampled male smallmouth bass in the spring, during the parental care period and in the fall to measure energy reserves (lipid stores in muscle and viscera tissue) over a two year period. Energy stores, which were not built up before nesting, declined to a minimum level by the end of the parental care period. Small males had consistently lower energy reserves than larger males and did not utilize these reserves at the same rate during the parental care period. All parental males complimented endogenous energy reserves by feeding during parental care, however, small males appear to rely proportionately more on exogenous energy intake than do larger males. Parental defense by all sizes of males declined over the parental care period, the decline being the most obvious by small males. Small males' lower energy budget may make them less effective parents and decrease their probability of survival over the following winter relative to larger males.

### Introduction

Several studies have demonstrated that fishes with parental care lose weight or deplete stored energy during the parental care period. Male threespine sticklebacks, *Gasterosteus aculeatus*, showed large declines in tissue dry weights as well as in lipid and glycogen levels in their livers, gonads and carcasses (Chellappa et al. 1989, FitzGerald et al. 1989). This weight loss and reduction in stored energy was correlated with a higher rate of mortality for breeding males compared to non-reproductive males (Chellappa et al. 1989, Dufrense et al. 1990). For European river bullheads, *Cottus gobio*, there was significant weight loss and increased

mortality for males during the parental care period (Marconato et al. 1993). Somatic growth was reduced for parental male longear sunfish, *Lepomis megalotis*, in response to reproductive investment (Jennings & Philipp 1992). The body weight of parental male bluegill sunfish, *L. macrochirus*, declined significantly during the parental care period due in part to declines in stored lipids (Coleman & Fisher 1991). Body weight declined during the parental care period for male rock bass, *Ambloplites rupestris*, with increased weight loss corresponding to a reduced probability of recapture in subsequent years (Sabat 1994).

The observed decline in the physiological state of parental male fish is constrained by allometric

relationships between body size and metabolic rate (negatively allometric), body size and cost of locomotion (negatively allometric), and body size and energy reserves (positively allometric) (Schmidt-Nielsen 1972, Brett & Groves 1979, Robinson et al. 1983, Shuter & Post 1990). These allometric relationships suggest that small males may require relatively more stored energy and utilize these reserves at a faster rate than larger males. As a consequence of these constraints large males may be able to acquire the energy reserves required to provide parental care prior to small males within a season, as hypothesized for smallmouth bass (Ridgway et al. 1991a), and large males would lose relatively less weight than small parental males (*A. rupestris*: Sabat 1994).

Male smallmouth bass, *M. dolomieu*, provide solitary parental care of their offspring for a number of weeks (Ridgway & Friesen 1992), and sustain a high level of fanning and guarding 24 hours per day through most of this period (Hinch & Collins 1991). Foraging opportunities for nesting males are limited because their nest range is substantially smaller than the summer home ranges they use for foraging (Scott et al. 1997, Ridgway & Shuter 1996). In a number of smallmouth bass populations, large males precede small males in initiating parental care (Ridgway et al. 1991a, Wiegmann et al. 1992), an observation consistent with the reproductive constraints hypothesis based on allometric relationships between body size and various energetic parameters (Ridgway et al. 1991a, Schultz et al. 1991).

The first objective of this study is to determine the seasonal and size-based patterns of energy depletion for male smallmouth bass. Smallmouth bass should be subject to two periods of energy depletion in each year, although these have not been previously measured. One period should occur during the quiescent period of late fall and winter months, when smallmouth bass gather in large groups and remain inactive until the following spring (Webster 1954, Kolok 1991). The other period should occur in the reproductive season when parental males are restricted to a habitat patch defined by their nest site (Scott et al. 1997). We will examine the hypothesis that large males should have larger energy reserves relative to smaller males before, during and after each depletion period.

The second objective of this study is to determine if parental defense of offspring reflects the size-based patterns of energy depletion among males of different size. Because aggressive defense of offspring has

an energetic cost that may be higher than other activity costs (Chellappa & Huntingford 1989), changes in parental investment that occur as a result of offspring development and number (Ridgway 1988, 1989) may be modified by these size-based patterns of energy depletion.

## Materials and methods

Data were collected from the population of smallmouth bass in Lake Opeongo, in the south eastern region of Algonquin Park, Ontario. Lake Opeongo (45°42'N, 78°22'W) is a large oligotrophic lake with a total surface area of 58.6 km<sup>2</sup>, mean and maximum depths of 14.8 m and 52 m respectively and secchi disc readings of 6 m (Martin & Fry 1972). Additional physical and biological descriptions are provided in Martin & Fry (1972) and Ridgway et al. (1991).

Male bass were sampled in the spring, during the nesting season and in the fall of 1991 and 1992. In order to minimize the sample size required to address our question we treated size as a discrete, rather than continuous, variable by dividing the size range of male bass into three categories: 21–25 cm, 28–32 cm and 35–39 cm fork length which we refer to as small, medium and large, respectively. The categories were chosen to be representative of the full range of sizes of mature male bass in the population (Ridgway et al. 1991a, Ridgway & Friesen 1992) and to insure that fish in each category were as different in size as was reasonably possible to test our size-based hypotheses.

Spring and fall samples were taken using trap nets set at several locations throughout the lake in the littoral zone and checked daily. Spring sampling began after the ice cover completely melted and smallmouth bass began moving into the littoral zone (between 7–19 May 1991 and between 19–25 May 1992). Fall sampling occurred between 21–23 September 1991 and between 25 September and 1 October 1992. Nesting males were collected at three times during the nesting period. Timing of the sample was determined by the developmental period of young in the nest. Parental males were sampled early in the embryo period (embryo), generally when the egg envelope was still intact, at the time of transformation from embryo to larva period (larva) and at the time of transformation from larva to juvenile (juvenile). Nesting males were mainly angled from the nest by a diver who could insure that the appropriate fish was caught.

### *Energetic analyses*

When males of appropriate size were sampled they were killed by a blow to the head and returned to the laboratory for dissection. Dissection involved measuring and weighing the fish (to the nearest 0.01 g), separating the testes, liver and the remaining visceral tissue and emptying all gut contents. Gut contents were dried and weighed (to the nearest 0.01 g). Testes were weighed (to the nearest 0.01 g) and this weight was then divided by the total body weight to calculate a gonadosomatic index (GSI). Muscle tissue was removed from the fish and skin was removed from the muscle. The muscle tissue was then homogenized in a Waring blender. All tissue samples were weighed and then frozen at  $-25^{\circ}\text{C}$  until drying.

Liver, testes, viscera and a subsample of homogenized muscle tissue were freeze-dried (VirTis RePP sublimator) to a constant weight. Lipid content of the dried muscle and viscera samples were determined using a chloroform-methanol extraction technique adapted from the Herbes & Allen (1983) modification of the method of Bligh & Dyer (1959). Two replicates of each sample were analyzed. The total lipid content of each tissue type was calculated by multiplying the dry tissue weight by the proportion of lipid in the sample. Energy stored as lipid in the tissue was determined by multiplying total lipid content by the constant of  $9.3 \text{ Kcal g}^{-1}$  (Voet & Voet 1990). An index of stored energy (energy index) was calculated to compare the relative amount of energy, stored as lipid, in the tissue of different sized fish. An energy index was calculated by dividing total energy stores (Kcal) by fork length (cm) cubed ( $\text{FL}^3$ ).

### *Parental defense behaviour*

During the 1992 season the nest defense behaviour of males was recorded prior to sampling. Conspecific models were used to elicit male nest defense behaviour. Models were prepared following Ridgway's (1988) modification of Helfman's (1983) procedure of preparing resin-coated fishes. Briefly, smallmouth bass were captured, fixed in strong formalin solution ( $>20\%$ ), coated in fiber glass resin, painted with acrylic paint to restore natural colours and mounted on a metal fork. Model sizes were 23 cm, 30 cm, and 37 cm fork length. These model sizes ensured that nesting males were presented models within 2 cm of their own fork length in an attempt to standardize the threat posed by the model.

During behaviour recording, the model was presented to a nesting male by inserting the end of the metal fork into the end of a 1.2 m aluminum pole. A swimmer could then use the pole to position the model. Models were positioned at the edge of the nest for the embryo and larva period recordings and in the centre of the school during the juvenile recording. These positions have been shown to be effective in eliciting parental defense behaviour (Ridgway 1988).

Behaviour recording followed a standard procedure and occurred between 10:00 h and 16:00 h. Two swimmers (with mask and snorkel) would approach the nest and position themselves side by side approximately 2 m from the nest and the presenter would extend the pole to the appropriate position. After a 2 min period for the nesting male to become accustomed to the observers the model was placed in position and behaviour was recorded for 5 min. The observer used a stopwatch and a plastic slate to record behaviour. The behaviours recorded (jaw display, lateral display, opercular display, approach model, bite and tail beat) are described by Ridgway (1988). The amount of time the parental male spent within approximately 2 body lengths of its brood (time with brood) was recorded.

### *Data analysis*

All energetic data were analyzed using factorial analysis of variance (ANOVA). All interaction terms were included in the ANOVA models, however, interaction terms are referred to only if they were significant. All percentage and proportion data were arcsine square root transformed to normalize variance (Zar 1984). Independent variables used in the analyses were size (small, medium and large) and sample period (spring, embryo period, larva period, juvenile period and fall). In preliminary analyses, year (1991 and 1992) was also included as an independent variable, however, in no case did it explain a significant proportion of the variation in the dependent variable or contribute to a significant interaction term. Data from both years were subsequently combined to reduce the imbalance of sample sizes within cells, particularly for the juvenile period. In addition, lipid analysis was done on a subsample of 7 fish of each size taken from the spring sample in 1991 to balance the sample sizes.

Behaviour data were analyzed as total parental defense behaviour per minute (all parental defense behaviours performed by the nesting male divided by the time with brood (min), hereafter called 'total

defense') to control for variation in time with brood. Total defense behaviours per min were also divided into 2 categories: contact and non-contact defense. Contact parental defense behaviours (bite and tailbeat) were assumed to be the most aggressive behaviours because the male made physical contact with the model. Non-contact defense (jaw display, lateral display, opercular spread and approach model) were assumed to be less aggressive than contact defense. Data were analyzed using factorial ANOVA with sample period and male size as independent variables and an interaction term. Behaviour data were square root transformed  $((x + 0.5)^{1/2})$  to normalize the variation in the data (Zar 1984). Brood number and time with brood were log transformed  $(\ln(x + 1))$  for analyses.

In all analyses a significance level of 5% ( $\alpha = 0.05$ ) was chosen as the critical level of difference among groups. Interpretation of analyses was limited to describing the patterns of variation that contributed significant effects in 2-way ANOVA models.

## Results

### Seasonal energetics

In total 174 male bass were sampled over the 2 years. The sample size is broken down by year, size and sampling period in Table 1. In 1991 it was not possible to reach the target sample size of 7 fish in each size category at each sampling period. Many nests failed before the young reached the juvenile period, possibly due to high winds and rough water late in the parental care period, and as a result the 1991 juvenile period

sample was incomplete. Preliminary analyses of 1991 data showed that sample size could be reduced to 5 fish in each category without a large increase in variance. After subsampling fish captured in spring 1991 the remaining sample size used for analyses of tissue lipid content was 153 fish.

The muscle lipid content of male bass tissue varied significantly among the sample periods over the year (sample period:  $F_{4,152} = 58.774$ ,  $p < 0.001$ ). Muscle lipid level remained relatively constant between spring and embryo samples in medium and large males and declined slightly in small males (Figure 1). During the parental care period muscle lipid levels declined from the embryo to the larva sample and again from the larva to the juvenile sample. Fish sampled in the fall had the highest muscle lipid levels, approximately 1.5 times higher than in the spring. Although the pattern of variation was consistent for males in the three size classes there were significant differences among the size classes in muscle lipid levels (size:  $F_{2,152} = 26.55$ ,  $p < 0.001$ ). Large males had higher levels of muscle lipid than medium sized males which had higher levels than small males.

The seasonal variation in visceral lipid content showed the same general pattern as muscle lipid variation (Figure 2). Visceral lipid levels varied significantly among the samples (sample period:  $F_{4,152} = 66.719$ ,  $p < 0.001$ ), however, the magnitude of the variation was higher than in muscle lipids. This was particularly obvious in the fall sample when visceral lipid levels were more than double levels in the spring. Size differences in visceral lipid levels were significant (size:  $F_{2,152} = 19.166$ ,  $p < 0.001$ ) with lipid levels positively related to male size. One difference

Table 1. Numbers of male smallmouth bass sampled during 5 sampling periods in 1991 and 1992 (sample date denotes beginning and end of sample period). Total sample size = 174.

Year	Fork length (cm)	Sampling period				
		Spring	Embryo	Larva	Juvenile	Fall
1991	21–25	14	7	4	0	5
	28–32	14	7	5	3	5
	35–39	14	7	5	5	5
	Sample date	7–19 May	27 May to 5 Jun	4–19 Jun	18–24 Jun	21–23 Sep
1992	21–25	5	5	5	5	5
	28–32	5	5	5	5	5
	35–39	5	5	5	5	4
	Sample date	19–25 May	5–15 Jun	18 Jun to 2 Jul	6–16 Jul	24 Sep to 1 Oct

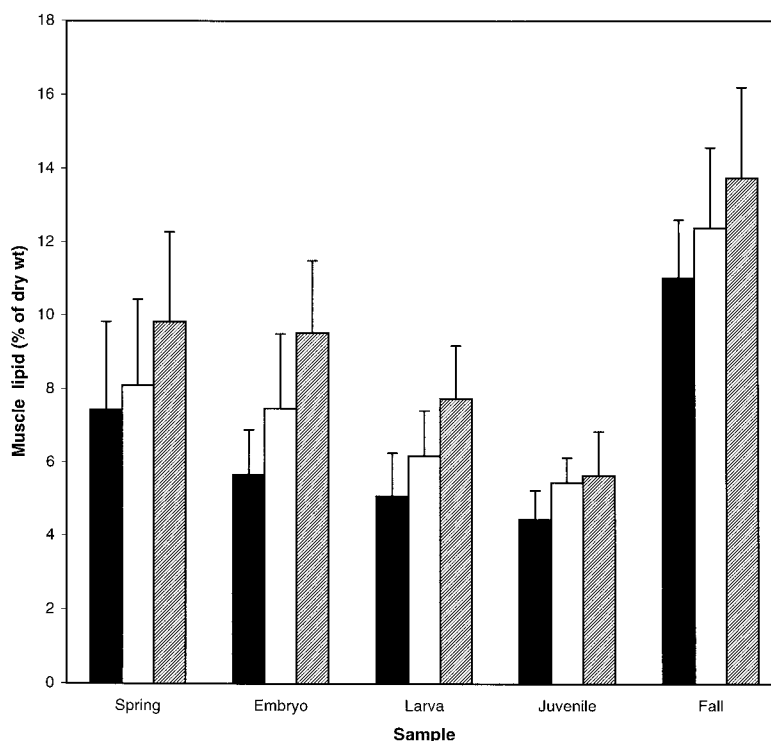


Figure 1. The mean (+ S.D.) amount of lipid in muscle tissue, as a percentage of total muscle dry weight, of small (fork length 21–25 cm: solid bars), medium (28–32 cm: open bars) and large (35–39 cm: hatched bars) male smallmouth bass sampled in the spring, when the males' young were at the embryo, larva and juvenile period, and in the fall. Sample sizes are presented in Table 1 (total  $n = 153$ ).

between muscle and visceral lipid levels was seen in small males whose visceral lipid levels remained at a constant, low level throughout the parental care period, although this difference did not result in a significant interaction between size and sample period.

There were significant differences in the energy indices of males among sample periods (sample period:  $F_{4,152} = 115.72$ ,  $p < 0.001$ , Figure 3). The energy index did not change between spring and embryo samples for medium and large males and declined in small males. Energy index declined over the parental care period for all males and increased to a maximum in the fall. There was also a significant positive relationship between energy index and size (size:  $F_{2,152} = 33.09$ ,  $p < 0.001$ ). The decline in energy index from the embryo to juvenile period was 45.5% in large males, 30.4% in medium males and 17.0% in small males, however, this trend did not result in a significant size by sample period interaction.

Although the proportion of lipid in muscle tissue was not high compared to viscera (Figures 1, 2) the majority of total energy stored as lipid was in the muscle.

From the spring to the end of the parental care period between 70% and 75% of lipid energy was stored in the muscle. In the fall, muscle lipid increased but the proportion of total lipid energy stored in the muscle declined significantly to approximately 50% (sample period:  $F_{4,152} = 43.361$ ,  $p < 0.001$ ). This is because bass sampled in the fall had very large quantities of lipid in the visceral tissue. There were no significant differences among the different sized males in the proportions of total lipid energy stored in muscle.

GSI increased to a maximum from spring to the embryo period and then declined during the parental care period, particularly in large males (Figure 4). In the fall, GSI increased in larger males to levels similar to the embryo period. This seasonal variation, along with the greater variation in GSI for larger males, contributed to a significant interaction between sample period and size ( $F_{8,152} = 4.431$ ,  $p < 0.001$ ).

During the parental care period the majority of males had some gut contents, however, the proportion of males with gut contents was independent of size and sample period ( $X^2_{0.05,4} = 0.108$ ,  $p = 0.99$ ). For the

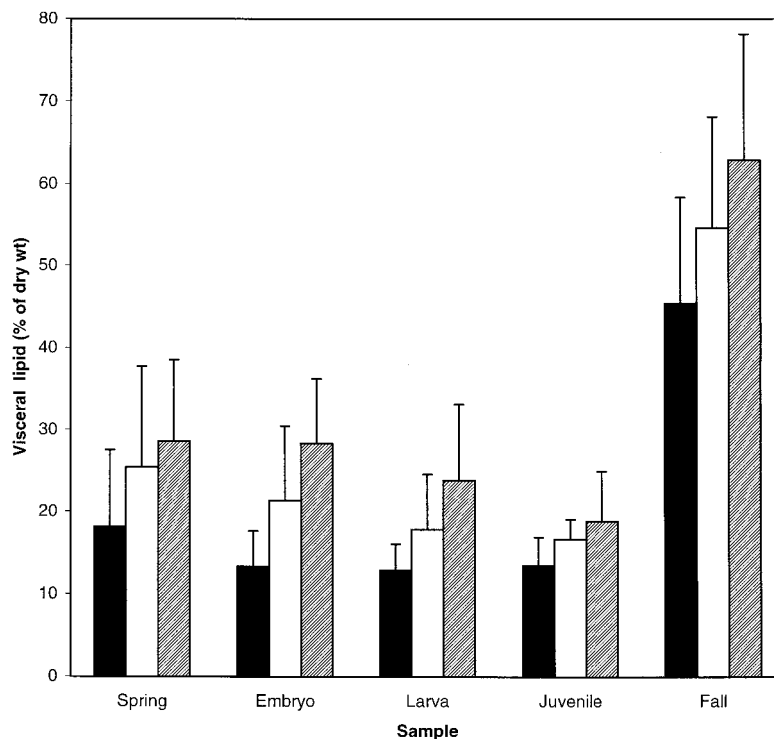


Figure 2. The mean (+ S.D.) amount of lipid in visceral tissue, as a percentage of total visceral dry weight, of small (solid bars), medium (open bars) and large (hatched bars) male smallmouth bass sampled in the spring, during parental care (embryo, larva and juvenile period) and in the fall (total  $n = 153$ ).

males with gut contents there were no significant differences in the dry weight of gut contents among different sized males ( $F_{2,58} = 0.67$ ,  $p = 0.548$ ) or among the three sample periods ( $F_{2,58} = 1.201$ ,  $p = 0.308$ ; Table 2). Gut contents were not identified but generally consisted of crayfish, aquatic insects and fish. Because males caught in trap nets were in the nets for a variable length of time and often regurgitated when they were removed from the net, gut contents data from these males were not included in Table 2.

#### Parental defense behaviour

In total 45 males were sampled during the 1992 nesting season (sample dates in Table 1). Behaviours were recorded for 43 males prior to sampling; 5 males of each size during the embryo and larva periods, and for 5 small, 4 medium and 4 large males at the juvenile period.

Brood number varied significantly among sampling periods (sample period:  $F_{2,42} = 62.693$ ,  $p < 0.001$ ; Figure 5) and was largest at the embryo period. During

the larva period, brood number of small and large males tended to be slightly less than during the embryo period, whereas brood number was about equal between the 2 periods for medium males. Brood number at the juvenile period was an order of magnitude lower than at the embryo or larva periods. Brood number did not differ significantly among the three size classes of males at each period although large males had slightly larger broods than small males at all periods.

Time with brood differed significantly among the three sample periods (sample period:  $F_{2,42} = 15.365$ ,  $p < 0.001$ ; Figure 6). Males' time with brood was highest at the embryo period, slightly lower at the larva period and by the juvenile period males spent only about 10% of the 5 min observation period with their brood. Time with brood did not differ among different sized males.

Total defense behaviour (per min) did not differ significantly among the three sample periods (Figure 7a). There were significant differences among the three size classes (size:  $F_{2,42} = 3.346$ ,  $p = 0.046$ ). Large males showed a consistent level of defense over the three

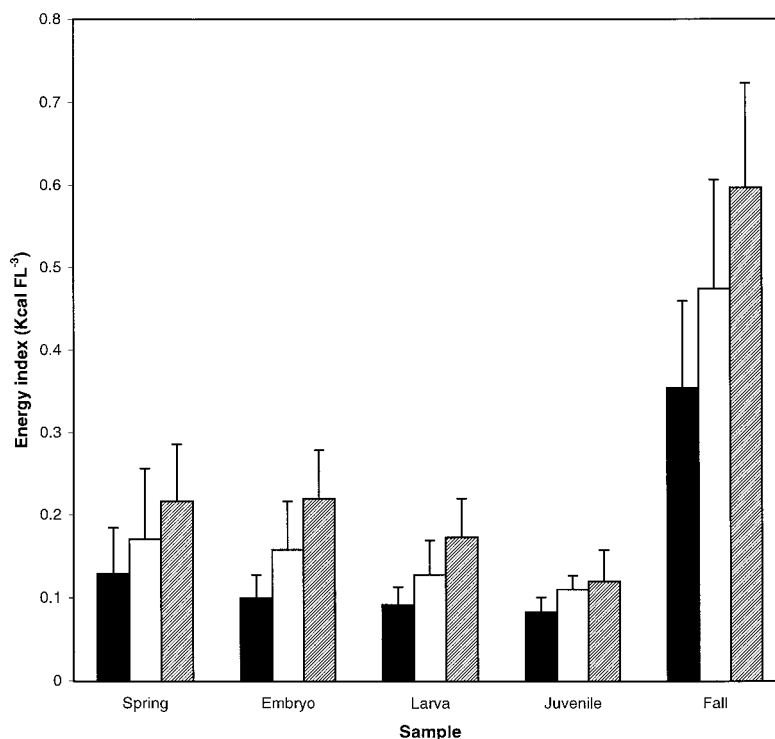


Figure 3. Mean (+ S.D.) energy index (calculated as total lipid energy (Kcal) divided by  $FL^3$ ) of small (solid bars), medium (open bars) and large (hatched bars) male smallmouth bass sampled in the spring, during parental care (embryo, larva and juvenile period) and in the fall (total  $n = 153$ ).

sample periods which was higher than the level of defense shown by medium males. Small males showed parental defense during the embryo and larva period, but none of the small males sampled at the juvenile period showed any defense.

Total defense (per min) was divided into contact and non-contact defense. Contact defense was infrequent and occurred mainly at the embryo period (Figure 7b). In the larva period contact defense was performed mainly by large males and by the juvenile period no males performed any contact defense. The reduction in contact defense over the sampling period was significant (sample period:  $F_{2,42} = 4.415$ ,  $p = 0.019$ ), but there were no significant differences due to male size.

Non-contact defense made up the majority of total defense (Figure 7c) and, therefore, showed the same pattern as total defense. The level of non-contact defense differed slightly among sample periods (sample period:  $F_{2,42} = 2.597$ ,  $p = 0.088$ ). There were no significant differences in non-contact defense due to male size.

## Discussion

The results of this study show that male smallmouth bass are subject to two periods of energy depletion through the year. Energy depletion occurred during the winter, as shown by the large drop in lipid levels from the fall to the spring samples. Energy depletion also occurred during the parental care period, as shown by a decline in lipid levels from embryo to larva period and again from larva to juvenile period. The reduction in lipid levels during both periods was consistent between muscle and viscera. While the majority of total lipid energy was stored in the muscle, as has been reported for other fishes (Brett & Groves 1979), visceral lipid levels were more dynamic, particularly in the fall when they comprise almost half of the fish's total lipid energy stores.

One potentially confounding factor in this study was that different males were sampled at each time during the parental care period. Use of stored energy during nesting would be ideally measured by repeatedly

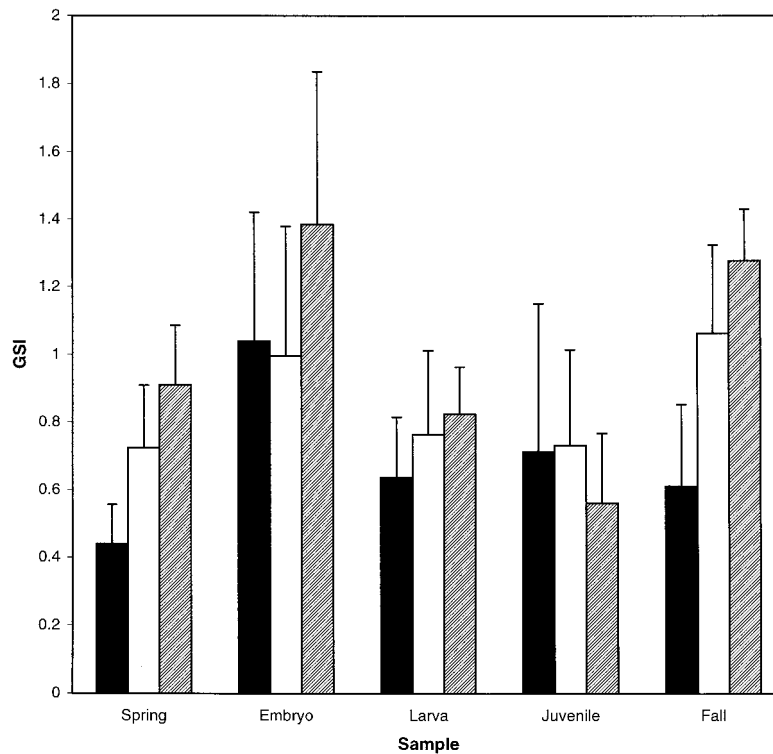


Figure 4. The mean ( $\pm$ S.D.) gonadosomatic index (GSI) of small (solid bars), medium (open bars) and large (hatched bars) male smallmouth bass sampled in the spring, during parental care (embryo, larva and juvenile period) and in the fall (total  $n = 153$ ).

Table 2. The percentage of male smallmouth bass in each size category with gut contents and the mean dry weight in grams ( $\pm$ S.D.) of gut contents (see Table 1 for sample sizes, total  $n = 88$ ).

Fork length (cm)	Sampling period		
	Embryo	Larva	Juvenile
21–25	67% 0.47 $\pm$ 0.54 g	78% 0.48 $\pm$ 0.39 g	100% 1.21 $\pm$ 1.54 g
28–32	83% 0.73 $\pm$ 0.86 g	80% 0.91 $\pm$ 0.76 g	75% 1.12 $\pm$ 1.07 g
35–39	83% 0.83 $\pm$ 0.94 g	70% 1.33 $\pm$ 1.20 g	60% 0.83 $\pm$ 0.92 g

measuring the energy stores in the same individual during nesting. This type of repeated sampling was not technically possible. The potential problem of destructive sampling is that by the juvenile period only a fraction of the original nesting stock remains (34% in 1991 and 52% in 1992) and these may be the males with the largest energy reserves. Those males that have abandoned their nests may have done so because

their energy reserves were too low to continue parental care. Therefore, the decline in energy reserves we have demonstrated for successful males may be an underestimate of the overall rate of decline of stored energy for all nesting males.

Although males build large lipid stores in the fall, which are depleted during the winter, we did not find a similar increase in lipid levels between the spring



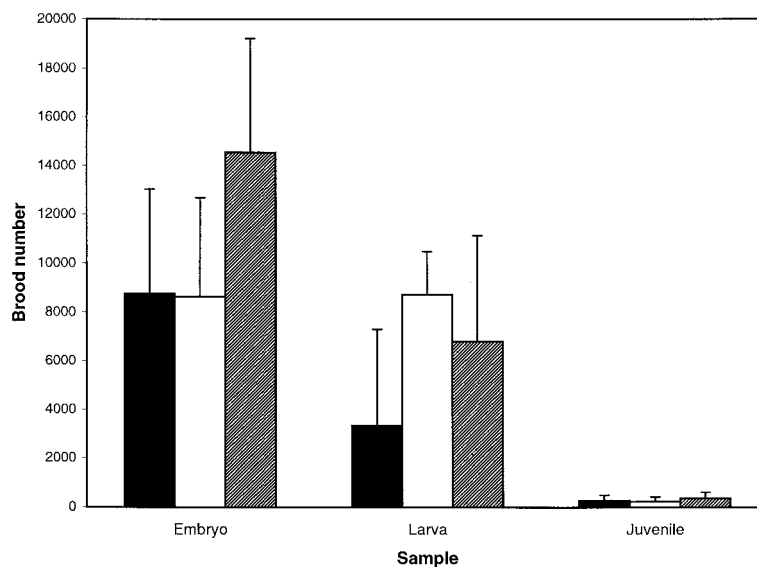


Figure 5. The mean (+ S.D.) brood number of small (solid bars), medium (open bars) and large (hatched bars) male smallmouth bass with young at the embryo, larva and juvenile period of development (total n = 43).

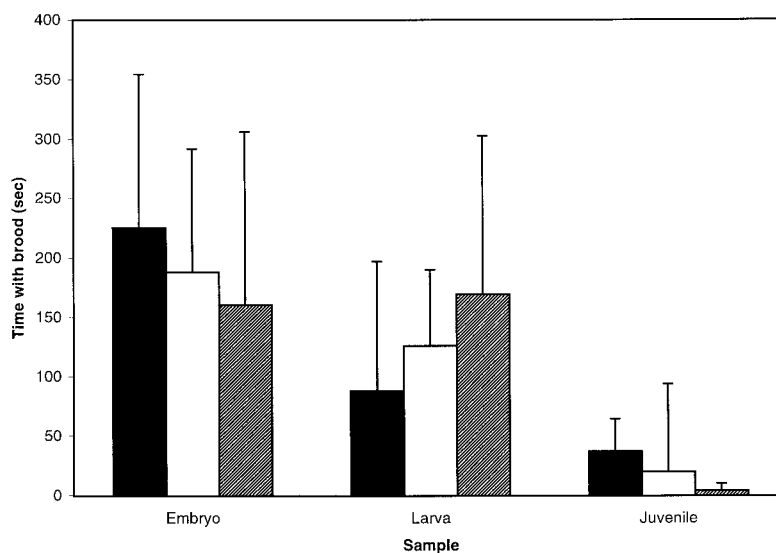


Figure 6. The mean (+ S.D.) time (seconds), per 300 sec model presentation, within 2 body lengths of their brood by small (solid bars), medium (open bars) and large (hatched bars) male smallmouth bass with young at the embryo, larva and juvenile period of development (total n = 43).

and embryo samples. One contributing factor could be that energy is directed towards gonad development during the spring rather than to somatic lipid stores. The large increase in GSI between the spring and embryo samples requires an energetic investment (Wootton

1985). While the GSI of smallmouth bass is smaller than in species such as longear sunfish (Jennings & Philipp 1992), three-spined sticklebacks (Chellappa et al. 1989), and northern pike (*Esox lucius*: Medford & Mackay 1978), there are two lines of evidence that

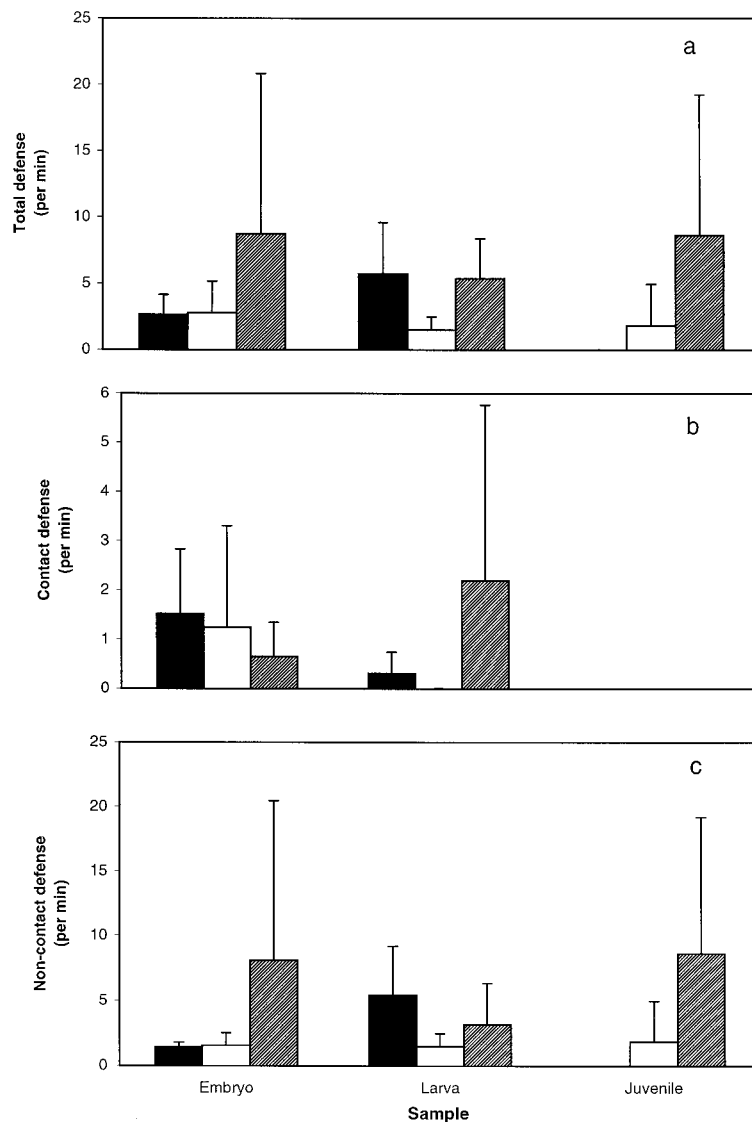


Figure 7. Mean frequency (+ S.D.) of defense behaviour, per minute with brood, of small (solid bars), medium (open bars) and large (hatched bars) male smallmouth bass with young at the embryo, larva and juvenile period of development (total  $n = 43$  for each). a – total defense behaviour, b – contact defense behaviour and c – non-contact defense behaviour.

gonad development is energetically costly for male bass. First, males do not maintain GSI over the parental care period possibly because energy stored in the gonads is utilized. Second, males invest energy in gonad development in the fall which could reduce the time and energy required for gonad development in the spring.

It is important to consider that our expectation that males would build energy stores prior to the nesting period was based on the assumption that successful

nesting is constrained by the availability of stored energy. A previous explanation for larger males nesting earlier in the season is that they are in relatively better condition in the spring and require less time to build reserves (Ridgway et al. 1991). An alternative, though not necessarily mutually exclusive hypothesis, is that nesting males rely on a combination of endogenous (somatic lipids) and exogenous (available food) reserves during the nesting period. This explanation is consistent with the reserve complementation model

of Shultz et al. 1991. Further evidence for reliance on exogenous reserves comes from the fact that the majority of nesting males sampled had food in their stomachs. While foraging is likely opportunistic, because males remain in their territory (Hinch & Collins 1991, Scott et al. 1997), this energy may be an important supplement to endogenous reserves.

We also predicted that small males would deplete relatively more stored energy than large males. The results show that there was size-based variation in how parental males used somatic energy reserves during the parental care period. However, although small males had consistently lower energy indices than larger males, they did not deplete energy reserves at a greater rate than larger males as predicted. Indeed, during the parental care period, when energy stores declined significantly for all males, the percentage decline in energy stores tended to be less for small males (energy index decline of 17%) than for medium (30.4% decline) and large (45.5% decline) males.

Size-based variation in the level of stored energy may occur because differences exist in the relative reliance on endogenous and exogenous energy reserves among different sized males. Large males, with larger somatic reserves, may be able to nest earlier in the season and utilize somatic energy reserves during parental care. The greater energetic cost of reproduction, which large males incur by nesting earlier and relying more heavily on endogenous reserves, may give their young the advantage of a longer growing season. The young can grow to a larger size before the winter starvation period and thus have a greater chance of survival (Shuter et al. 1980). Small parental males may nest later in the season, when food availability may be greater, and rely mainly on exogenous energy reserves to supplement lower endogenous reserves (Schultz 1991). Although nesting later in the season may put the young of small males at a growth disadvantage, small males use relatively less endogenous energy which may increase their probability of survival during the winter starvation period. These results support the use of the reserve complementation model to explain size based variation in nesting patterns, which appear more complex than can be explained by the allometrically based reproductive constraints hypothesis (Ridgway et al. 1991).

Prior to sampling parental males, we recorded parental defense behaviour to determine if parental defense levels were related to endogenous energy stores. Parental defense behaviour directed towards a

model predator has been used by other investigators as a measure of parental expenditure and the level of risk the parent takes during parental care (Pressley 1981, Sargent & Gross 1986). The results are consistent with the prediction that parental expenditure by smaller males would be less than that of larger males. Parental defense declined over the sampling periods for all males but the decline was greatest for small males who ceased parental defense behaviour by the juvenile period. Total defense was highly variable for all sizes of males at all sample periods but, on average, did not differ among sample periods within size classes (Figure 7a). Larger males performed more parental defense than medium sized males at all sample periods while small males only performed parental defense behaviour during the embryo and larva periods.

Although total defense did not differ among sample periods, the amount of contact defense performed by all males was significantly lower during the juvenile period. Because contact defense is more likely to result in injury to the nesting male (Pressley 1981, Ridgway 1988), and may require more energy than less active behaviour (Chellappa & Huntingford 1989), it may represent a greater risk of mortality to the parent and higher parental expenditure than non-contact defense. Therefore, although males continue to defend their brood, they may reduce their parental expenditure and potential risk of injury by switching to less risky defense behaviour.

Another indicator of parental expenditure is the amount of time that the parent spends with the young (Clutton-Brock & Godfray 1991). Time with the brood was highest during the embryo period, lower at the larva period and very low at the juvenile period (Figure 6). The low time with brood at the juvenile period is complicated by the fact that the young are free swimming and both the area occupied by the young and the male's territory are larger than at earlier periods (Ridgway 1988, Scott 1993). The larger territory of the male may partially explain the decline of time with the brood, but the model, in the centre of the group of young, still represents a risk to the male's brood. Both the decline in time with the brood and total parental defense behaviour directed towards the model suggests that parental males reduce parental expenditure during the juvenile period.

The decline in parental defense can be explained by the decline in the value of the current brood as it develops which is predicted to reduce the optimal level of parental effort (Sargent & Gross 1986). This

pattern of decline in parental defense has been previously observed in male smallmouth bass (Ridgway 1988). While variation in the value of the current brood may partly explain the decline in male parental defense over sample periods, it does not explain the size-based variation in parental defense. Brood number, which does decline as the young develop, did not differ among different sized males. The probability of the young surviving without parental care is likely also independent of male size. Therefore, the value of the current brood is probably similar for all sizes of males.

Our results suggest that size-based differences in available energy may influence parental defense. While nesting males utilize both endogenous and exogenous energy, their ability to utilize endogenous reserves may be constrained by their energetic requirements over the winter. Because males rely on endogenous reserves to survive the winter, depletion of reserves during parental care may increase the probability of overwinter mortality for parental males. Increased probability of mortality may represent a greater cost to small males, in terms of reduced future reproduction, because they have more potential breeding seasons in the future than large males. Small males may rely on exogenous energy to a much greater extent than larger males and this relatively lower energy budget, along with relatively higher metabolic demands, means they are not able to expend energy on parental defense as long as larger males can. Further study, including manipulation of energy budgets, is required to clarify size-based energy budget differences.

The present study demonstrates that male smallmouth bass utilize stored energy during both the winter and the parental care period. Energy stores, which were not built up before nesting, declined to a minimum level by the end of the parental care period. Small males had consistently lower energy reserves than larger males and did not utilize these reserves at the same rate during the parental care period. All parental males complemented endogenous energy reserves by feeding during parental care, however, small males appear to rely proportionately more on exogenous energy intake than do larger males. Parental defense by all sizes of males declined over the parental care period, the decline being the most obvious in parental defense by small males. Small males' lower energy budget may make them less effective parents and decrease their probability of survival over the following winter relative to larger males.

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