

BROOD SIZE DOES NOT INFLUENCE THE BEHAVIOUR OR DENSITY OF LARVAL AND JUVENILE SMALLMOUTH BASS UNDER PARENTAL CARE

by

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Summary

We used fine scale observations of individual broods of smallmouth bass (*Micropterus dolomieu*) to ask whether brood size had an effect on feeding behaviour, agonistic behaviour, nearest-neighbour distance or brood density of larvae and juveniles. Developmental phase, and not brood size, provided the only significant effect on individual behaviour. The dispersion of broods in the nearshore zone of the lake increased throughout the parental care period in response to both developmental phase and brood size. The density of fish in broods (number of fish/m² of lake surface/brood) declined sharply before metamorphosis and remained relatively constant throughout the remaining parental care period. However, at any particular developmental phase, the density of fish in broods was unrelated to the total numbers of fish in a brood. The observation of increasing dispersion of broods during parental care while, at any developmental phase, the density of fish remains independent of brood size has important implications for the ecology of young-of-year smallmouth bass. The possible mechanisms governing this phenomenon may be similar to those proposed for schooling fish and the movements of large migratory mammals.

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Introduction

Under natural conditions, examining the dynamics of larval and juvenile fish requires a level of resolution where the behaviour of fish is in response to gradients in predator, food and competitor density (Rothschild, 1986; Sale, 1998). Unfortunately, traditional sampling schemes for larval and juvenile fish have operated at scales too large to discern behavioural interactions. Despite this lack of resolution, there is a broad emphasis on the importance of behaviour for understanding recruitment processes in fish (Miller *et al.*, 1988, 1992; Mackenzie *et al.*, 1990; Mackenzie & Leggett, 1991; Walters & Juanes, 1993; Williams *et al.*, 1996; Dower *et al.*, 1997). However, addressing behavioural questions by direct observation under field conditions can be difficult because of the dispersion of larval and juvenile cohorts over wide areas.

The behaviour and ecology of larval and juvenile smallmouth bass (*Micropterus dolomieu*) during the parental care period can overcome the problem between method and mechanism in research on larval and juvenile fish. Adult males establish nest sites in the shallow littoral zone of lakes and rivers in spring (Ridgway *et al.*, 1991a), court females (Ridgway *et al.*, 1989) and provide sole parental care that can range from 19 to 45 days (Ridgway, 1988; Ridgway & Friesen, 1992). Young-of-year (YOY) smallmouth bass under parental care remain near the nest site with the brood occupying an increasing area of the littoral zone as the offspring develop from larvae into juveniles (Scott *et al.*, 1997). Nesting habitat is not a limiting resource and nest density ranges from 0 to 6 nests/100 m of shoreline which effectively isolates nesting males and their broods from their neighbours (Ridgway *et al.*, 1991b; Rejwan *et al.*, 1997).

The objective of this study is to determine whether foraging rate, agonistic behaviour and brood density of larval and juvenile smallmouth bass are governed by the number of offspring in a brood or simply by changes in body size as offspring grow throughout their free-swimming period while under parental care. Smallmouth bass broods can be observed at close range in the field and at scales sufficient to record larval and juvenile behaviour. We use this perspective and the relatively sparse nest density to treat each brood as a unique and well-defined 'cohort'. Most studies examining the behaviour of larval fish are based on changes in body size (*e.g.* Miller *et al.*, 1988). This study is a departure from this approach since we incorporate brood size

(i.e. 'cohort' size) as a factor that could influence the behaviour and density of larval and juvenile fish. We recorded individual (foraging rate, agonistic interactions and nearest-neighbour distance) and brood-level (dispersion and density) behaviours which are thought to be important in larval and juvenile fish ecology.

Methods

Data were collected in 1991, 1992 (brood dispersion) and 1993 (behaviour) in the near-shore zone of Jones Bay, Lake Opeongo (45° 42' N, 78° 22' W), Ontario, Canada. Lake Opeongo is a large (58.6 km²) oligotrophic lake and the site of a long-term study on the ecology of smallmouth bass (Ridgway *et al.*, 1991b). Smallmouth bass nest throughout the lake with the highest concentration of nesting males occurring in Jones Bay. Observers using mask and snorkel swam daily surveys of the shoreline to detect and monitor nest sites in Jones Bay. Nests were individually marked with numbered bricks placed adjacent to nests and the location of each nest was recorded on topographic maps.

Daily estimates of brood size began at swim-up, the first day of exogenous feeding in the larval period, and ended when no offspring were observed at the nest site. The lack of offspring occurred because either the brood was lost to predators or they dispersed from the nest site as juveniles. One of us (TGF) estimated brood size using underwater visual counts of individuals, or groups of individuals within broods. Three estimates of brood size were made on each date and brood size recorded as the mean of the three estimates. In conducting behavioural observations, brood sizes were grouped into three brood size categories: small (≤ 500), medium (501-1500) and large (> 1500 individuals).

We verified brood size estimates on a subset of nests ($N = 21$) from outside the study area. Following a visual estimate, a large dip net was used to capture the entire brood. Individuals in a netted brood were subsequently counted (actual brood size) and returned to their nest of origin. A comparison of our estimates of brood size using underwater observations with the actual count of offspring in a brood revealed a close agreement between the two methods (Fig. 1):

$$\text{Actual brood size} = 33.65 + 1.12 (\text{Estimated brood size}); r^2 = 0.87.$$

We recorded the behaviour of larval and juvenile fish in the field at four developmental phases within the larval and juvenile periods of development: (1) larvae at swim-up (9.5 mm total length (TL)); (2) larvae at pre-metamorphosis (14.0 mm TL); (3) juveniles at post-metamorphosis (18.5 mm TL), and (4) juveniles at pre-dispersal (28.0 mm TL). Larvae averaging 9.5 and 14.0 mm in length represented early and late larval phases of development (Balon, 1975). Juveniles averaging 18.5 and 28 mm in length represented the early and late juvenile phases while under parental care. Age-specific length of larvae and juveniles under parental care differed slightly among years due to temperature-mediated variation in developmental rates (Ridgway & Friesen, 1992).

Little information is available on the diurnal patterns of dispersion in YOY smallmouth bass while under parental care. However, preliminary field observations indicate a consistent pattern in the dispersion of YOY across the early larval, late larval and early juvenile phases of

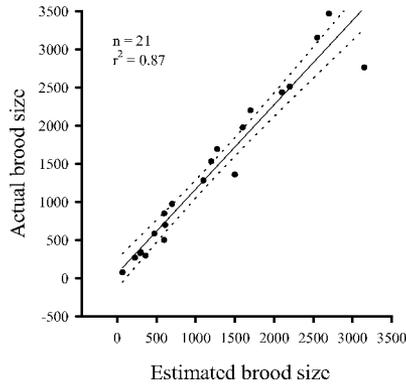


Fig. 1. The relationship between estimated brood size (number of individuals in a brood) and actual brood size for smallmouth bass in Lake Opeongo. Dashed lines indicate 95% confidence limits. Sample size and coefficient of determination are shown.

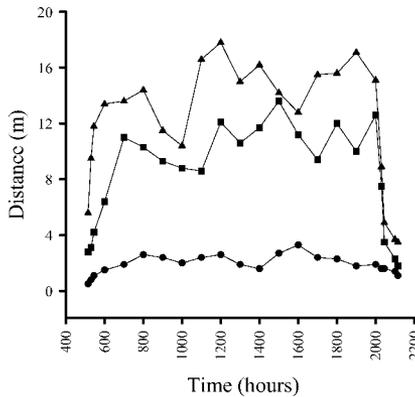


Fig. 2. Maximum dispersion distance (m) plotted against time of day (h) for a single large smallmouth bass brood ($N = 3000$) at the early larval (closed circle), late larval (closed square) and early juvenile (closed triangle) phases of development.

development (Fig. 2). YOY disperse away from the nest at dawn and return to the vicinity of the nest at dusk. Soon after initiating feeding at dawn, brood dispersion reaches a maximum and remains relatively stable until dusk, when broods return to their overnight resting sites. Because of YOY dispersion patterns, we conducted behavioural observations between 1000 and 1700 h on all days.

We recorded the foraging and agonistic behaviour of fish in each of the four developmental phases in both the small (≤ 500 individuals) and large ($> 1,500$ individuals) brood size categories. Individual fish were observed using the focal animal technique (Altman, 1974). Each focal period was 2 min during which time the behaviour of one randomly selected fish was recorded. We recorded time with a stopwatch and the focal period commenced 10 s after

initial identification of the trial fish. Observations were recorded using an underwater slate and pencil by a swimmer who remained motionless while observing fish.

For foraging behaviour, ten randomly chosen fish from each of three randomly chosen broods were observed in the four developmental phases in both the small and large brood size categories ($N = 240$ fish). We did not estimate foraging success of YOY, because of the small size of prey they consumed. However, we could observe foraging attempts (bites and S-shape strikes) and estimated foraging rate as the sum of all foraging attempts divided by foraging time.

For agonistic behaviour, ten fish from each of five randomly chosen broods in both the small and large brood size categories were observed in all but pre-metamorphic larval phase ($N = 300$ fish). The frequency of agonistic behaviour was low during the larval period relative to foraging rate. We recorded the following agonistic behaviours: (1) *Chase*; a rapid darting approach toward another fish without making direct contact, (2) *Escape*; a rapid acceleration away from an approaching fish, (3) *Avoid*; an obvious change in direction of movement of the focal animal away from another fish that was approaching (or being approached by the focal animal).

We recorded nearest-neighbour distance (NND) at central and peripheral positions in a brood in each of the four developmental phases between large and small brood size categories. Fifteen fish were randomly selected for observation in both the central and peripheral positions in each of three randomly chosen broods. A fish was defined as central if the distance between it and the estimated central point of the brood was less than the shortest distance between the fish and the nearest edge of the brood. For a fish to be defined as peripheral, the distance between it and the nearest outer edge of the brood could be no greater than approximately one quarter the distance between it and the centre of the brood. Defined in this way, a region existed between centrally and peripherally positioned fish in which no observations were recorded.

We estimated NND as the distance between the nose of the focal fish and the nearest part of the closest neighbouring fish. This distance is expressed in terms of 'YOY body lengths' and assigned to one of four nearest neighbour intervals. Intervals correspond to 4-body lengths and the mid-point for the four intervals equals 2, 6, 10 and 14 body lengths. NND's > 16 body lengths are arbitrarily adjusted to 16 to maintain consistency among intervals. NND was expressed in millimetres for each sample time-nearest neighbour interval by multiplying YOY TL by the midpoint for each nearest neighbour interval.

Brood dispersion was measured in all developmental phases except the late juvenile phase in each of the three brood size categories (small, medium, and large). Ten nests in each brood size category were randomly selected from the entire set of active nests in the study area for measurement at each of the three sampling times.

Brood dispersion was measured between 1000 and 1600 h by two swimmers. Swimmers swam slowly around the periphery of a brood placing 10 to 15 coloured stones on the substrate to outline the brood's perimeter position. After stones were positioned, the bearing (degrees) and distance (cm) of each marker from the centre of the guarding male's nest was measured using a compass and tape measure. Bearing and distance measurements were converted to Cartesian co-ordinates and the minimum convex polygon method (White & Garrott, 1990) was used as an estimator of lake surface area occupied by the brood. The density of any particular brood was based on the brood size estimate divided by the lake surface area occupied by the brood. An insufficient number of nests in the large brood size category at the final sample time resulted in an unbalanced ANOVA design.

Two-way ANOVA models that included the interaction term (brood size and developmental phase) were used to analyse both individual- and brood-level behaviour, with the following exceptions. A two-sample *t*-test was used to test for the one-tailed hypothesis that mean frequency of agonistic acts of juvenile SMB (TL = 18.5 mm) in the small brood size category was less than that of juveniles in the large brood size category. To analyze NND we used a repeated measures ANOVA, with two grouping factors (body size and brood size category) and one trial factor (centre/edge). In all foraging, agonistic and NND analyses, individual fish selected for observation were treated as sub-samples and mean brood values for each behaviour were used in further analyses. Data were log transformed [$\ln(x + 1)$] to normalize for analyses (Zar, 1984). In all analyses the level of significance was set at 5% ($\alpha = 0.05$). Tukey's *a posteriori* multiple comparison test was used to distinguish between treatment means.

Results

Brood size

A total of 72, 92 and 76 nests were found in South Jones Bay in 1991, 1992 and 1993, respectively, of which 34 (47%), 71 (77%) and 62 (86%) reached the larval period (first-feeding) of development. Brood size estimates of first-feeding larvae averaged 495, 1910 and 1570 in 1991, 1992 and 1993 and brood size distributions were highly skewed to lower numbers in all years (Fig. 3).

Behaviour of individuals

Foraging behaviour

There was considerable variation in first-feeding date among broods, which reflects the consistent inverse relationship between male size and the seasonal timing of spawning. The median spawning date for males ranged from 22nd of May 1991 to 7th of June 1993. The duration of the spawning period ranged from 11 d in 1991 to 27 days in 1993 and the mean spawning date varied significantly among years ($F_{2,230} = 152.56$, $p < 0.01$). Offspring from nests spawned early in the season began active feeding on the 2nd, 16th, and 18th of June in 1991, 1992 and 1993, respectively.

Foraging rate did not differ between brood size categories ($F_{1,12} = 0.02$, $p = 0.85$). However, ANOVA showed that foraging rate increased with developmental phase of fish ($F_{2,12} = 31.55$, $p < 0.01$; Fig. 4). Tukey's test showed that it increased during both the first (larval) and second (juvenile) sampling periods. Less than 10% of first-feeding larvae made no feeding attempts during the two-minute focal period and the percentage of non-feeders declined to nearly zero in late larvae and early juveniles.

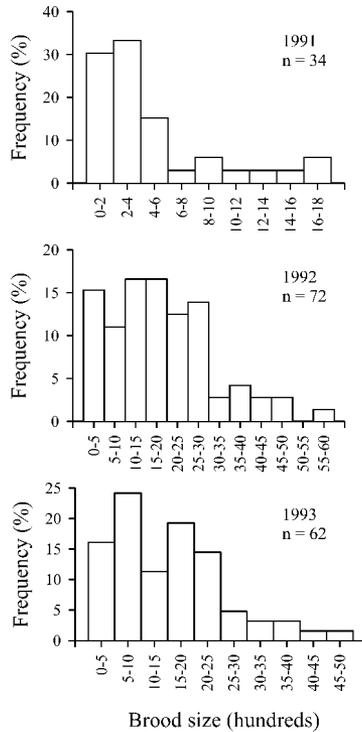


Fig. 3. Frequency distribution of brood size at swim-up for smallmouth bass broods in Lake Opeongo during three spawning seasons.

Agonistic interactions

Larvae showed little interaction with siblings at first feeding. There was a significant positive increase in agonistic behaviours with developmental phase (Fig. 5; Chase, $F_{2,24} = 154.04$, $p < 0.01$; Escape, $F_{2,24} = 190.90$, $p < 0.01$; Avoid, $F_{2,24} = 294.76$, $p < 0.01$). The frequency of Chase, Escape and Avoid increased by an average 125, 157 and 126%, respectively, between metamorphosis and dispersal of young from nesting territories. In contrast, the frequency of agonistic behaviours in recently metamorphosed juveniles was not related to brood size category (Chase, $F_{1,24} = 0.74$, NS; Escape, $F_{1,24} = 0.24$, NS; Avoid, $F_{1,24} = 1.65$, NS). The interaction terms between brood size and developmental phase for any of the agonistic behaviours were also not significant.

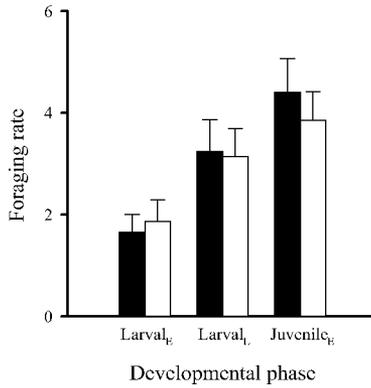


Fig. 4. The relationship between foraging rate (bites/minute) and developmental phase (Larval_E = early larvae, TL = 9.5 mm; Larval_L = late larvae, TL = 14.0 mm; Juvenile_E = early juvenile, TL = 18.5 mm) for small (≤ 500 individuals; black bar) and large (> 1500 individuals; white bar) brood size categories.

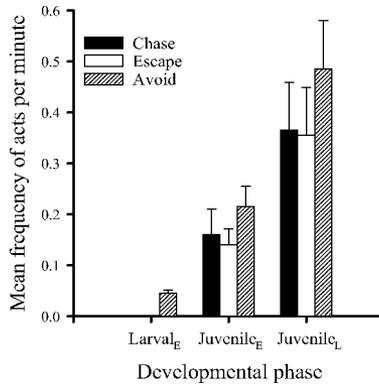


Fig. 5. The mean frequency (+ SD) of chase (black bar), escape (open bar) and avoid (hatched bar) for young-of-year smallmouth bass in Lake Opeongo plotted against developmental phase (Larval_E = early larvae, TL = 9.5 mm; Juvenile_E = early juvenile, TL = 18.5 mm and Juvenile_L = late juvenile, TL = 28.0 mm).

Nearest-neighbour distance

There was a positive increase in NND with increasing body size ($F_{2,12} = 559.78$, $p < 0.01$; Fig. 6), but brood size category had no effect on NND ($F_{1,12} = 4.02$, $p = 0.08$). NND was also greater among young located peripherally than for centrally located young ($F_{1,12} = 103.40$, $p < 0.01$). The NND for early larvae (TL = 9.5 mm), late larvae (TL = 14.0 mm) and early juveniles (TL = 18.5 mm) located in the periphery of the brood

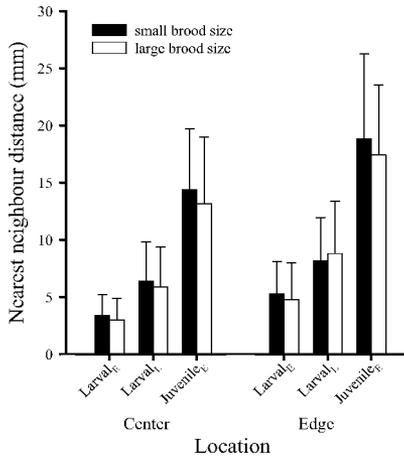


Fig. 6. Mean nearest-neighbour distance (+ SD) plotted against brood size category (small ≤ 500 , large > 1500), developmental phase (early larval, late larval and early juvenile) and location (centre, edge) in smallmouth bass broods in Lake Opeongo. Refer to figure four caption for young-of-year body sizes.

was 57, 35 and 33% greater, respectively, than that for YOY located in the centre of the brood. The location-body size interaction term was significant ($F_{2,12} = 9.30$, $p = 0.01$) and suggests that the effect on NND of body size differed between centrally and peripherally-located fish.

Brood dispersion

The area of water occupied by broods increased with increasing developmental phase ($F_{2,81} = 149.55$, $p < 0.01$) and brood size category ($F_{2,81} = 67.21$, $p < 0.01$). At first-feeding (TL = 9.5 mm), brood dispersion averaged 0.8, 2.6 and 5.8 m^{-2} for the small, medium and large brood size categories, respectively (Fig. 7). Upon reaching metamorphosis, dispersion averaged 14.8, 36.7 and 64.1 m^{-2} for the small, medium and large brood size categories, an order of magnitude higher than that at first-feeding, regardless of brood size category. Tukey's test showed that the area of water occupied by broods differed among all three body sizes and across all three brood size categories. Brood density showed a seasonal decline with body size ($F_{2,81} = 196.52$, $p < 0.01$), however, it did not differ across brood size category at any of the developmental phases ($F_{2,81} = 2.31$, $p = 0.29$).

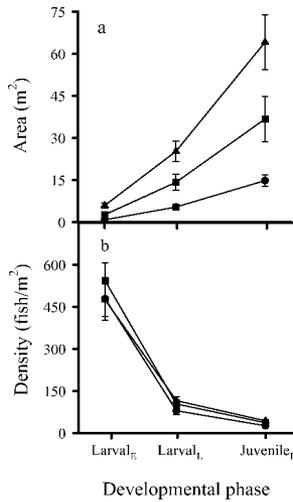


Fig. 7. The mean (a) area of water occupied by broods and (b) density (number fish/m² of surface area/brood) of young-of-year within broods plotted against developmental phase (Larval_E = early larvae, Larval_L = late larvae, and Juvenile_E = early juvenile) for small (≤ 500 ; circle), medium (501-1500; square) and large (> 1500 ; triangle) brood size categories.

Discussion

Brood size had no measurable effect on the frequency of feeding and agonistic behaviours in smallmouth bass broods. Since broods remain in limited areas in the nearshore environment for many weeks (Ridgway & Friesen, 1992; Scott *et al.*, 1997), we assumed that food limitation and competition for prey would be high given the order of magnitude difference among brood size categories and the high density of fish in broods.

Changes in body size and developmental phase had significant effects on feeding and agonistic behaviour. Agonistic behaviour was absent or at very low frequency during the early larval phase, but increased significantly after metamorphosis prior to dispersal. Based on studies of behavioural development in other centrarchid fishes, Brown (1985) proposed that the presence of agonistic behaviour late in the parental care period may be responsible for the dispersal of the brood. Certainly, the appearance of frequent agonistic acts after metamorphosis may account in part for the increase in nearest-neighbour distance and the corresponding sharp decline in brood density that we observed at this developmental phase. However, in contrast to previous work which focused on social behaviour of centrarchids

under laboratory conditions (Brown & Colgan, 1985a,b) or on agonistic interactions of juveniles later in the first year (Sabo *et al.*, 1996), we were able to demonstrate that significant social interactions between individuals are apparent immediately after metamorphosis and days before dispersal from the nest site.

Our inability to detect brood size effects on feeding and agonistic behaviour appears to be related to the intriguing observation of similar spacing among nearest-neighbours in broods of different size (Fig. 7). The net effect of this consistency is similar densities of young bass independent of brood size at any given developmental phase. The sharp decline in the density of fish in broods prior to metamorphosis appears to result simply from increased dispersion of the brood as offspring grow from larvae to juveniles possibly as a consequence of increased agonistic behaviour that was observed at this time.

Two additional mechanisms may also account for the sharp decline in density. First, predation risk of larval smallmouth bass may change prior to metamorphosis. Fish swimming speeds and escape tactics increase significantly at metamorphosis (Miller *et al.*, 1988; Williams *et al.*, 1996; Sogard, 1997), suggesting that predation risk may decline at this phase of development. If predation does decline prior to metamorphosis, then increased nearest-neighbour distances that correspond to increased dispersion of broods at this time may represent a social change in anti-predator behaviour as a response to declines in vulnerability. Second, male movements around the brood during and after metamorphosis may in some way act as a possible mechanism for causing increased dispersion of broods. However, the nest range of parental males changes in response to the movements of the brood (Scott *et al.*, 1997), indicating that brood dispersion itself is not governed by male movements.

One clear implication of our results is that individual fish are following a simple rule of maintaining visual contact with their nearest-neighbour based on our observation that brood dispersion increases with brood size while density remains unchanged at any developmental phase. Bass broods reach their daily maximum in dispersion soon after initiating feeding in early morning hours. Dispersion then remains relatively stable throughout the day until sunset when the brood concentrates in a dense aggregation near the nest site. Maintaining consistent levels of dispersion throughout the feeding period likely involves, to some extent, visual contact with neighbours. This

possibility has an interesting parallel with an individual-based model of wildebeest herds where a simple rule of awareness of your neighbour is sufficient for organizing travelling waves during migration (Gueron & Levin, 1993) as well as with the organization of schooling fish (Hueth & Wissel, 1992, 1994). Simulations of fish schools point to different outcomes in terms of school polarity and cohesion depending on nearest neighbour rules (Hueth & Wissel, 1992). If fish 'average' the influence of neighbours then the schools can in theory appear to be more polarized and cohesive. If fish respond to only a single neighbour, then schooling is less polarized and cohesive with individuals pointing and swimming in different directions within the school. The behaviour of larval and juvenile fish in smallmouth bass broods appears to follow the single neighbour model. Based on our field observations, individuals orient in different directions and rarely swim in a cohesive manner while within the area occupied by the brood.

In this study, we treated individual broods as small, independent cohorts of larval and juvenile smallmouth bass. This was a reasonable assumption since nesting densities in this population are low and independent of the availability of nesting habitat (Ridgway *et al.*, 1991b; Rejwan *et al.*, 1997). Other approaches to conceptualizing cohorts in research on larval fish ecology have relied on enclosure methods (*e.g.* Cowan & Houde, 1990), or in the case of field studies, separate egg batches produced at different times within a spawning season (Rutherford & Houde, 1995; Dorsey *et al.*, 1996; Betsill & Van den Avyle, 1997). Research reported in this study is one of the few cases where field-based underwater observations of well-defined, identifiable groups of larval and juvenile fish have addressed traditional hypotheses of larval fish ecology. Theoretically, density-dependent mechanisms may affect larval growth rates (Ware, 1975; Rothschild, 1986) and the ability of larvae to reduce prey levels below that required for maximum growth remains a critical assumption in some theoretical treatments of density-dependence in larval fish ecology. In this study, the lack of any influence of brood size on foraging rate, agonistic behaviour, or brood density suggests that food is not a limiting resource governing the dynamics of smallmouth bass larvae and juveniles while under parental care. One mechanism that might maintain sufficient food resources to meet consumption demands of foraging fish in broods is plankton renewal of the littoral zone from the pelagic or near-pelagic zone of the lake adjacent to the nesting area. Enclosure experiments that examine the effects of food supplementation and predator exclusion are

needed to resolve the relative importance of these mechanisms governing the dynamics of young smallmouth bass.

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