Environmental Biology of Fishes **39**: 119–127, 1994.

Age and size-dependent variation in the seasonal timing and probability of reproduction among mature female pumpkinseed, *Lepomis gibbosus*

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Received 25.3.1993 Accepted 29.7.1993

Key words: Body size, Centrarchidae, Life history, Energy allocation, Energetic deficits, Sunfish

Synopsis

In this study, we used pumpkinseed, *Lepomis gibbosus*, populations in two east-central Ontario lakes to test for age and size-dependent effects on the probability and timing of reproduction of mature females. Pumpkinseed body size characteristics differed in the two lakes; Little Round Lake harbours a stunted population and Beloporine Lake does not. Age-class distribution of mature females was determined by a maturity assessment on fish collected just prior to spawning and at the mid-spawning period, combined with an early-season capture-mark-recapture survey. Spawning females were collected throughout the breeding season to assess age and size-related temporal trends, and to compare their age and size distribution with that of mature females at large. The proportion of age 2 females in Little Round Lake that actually spawned was considerably lower than the proportion of mature age 2 females at large. Furthermore, age 2 females that spawned in this lake did not do so until late in the breeding season. In contrast, the proportion of young/small females spawning in Beloporine Lake was comparable to the proportion of young/small mature females at large, and both small and large females spawned throughout the breeding season. Small mature females in Little Round Lake may have had no other option but to spawn late in the season because of their poor body condition. In Beloporine Lake, condition factor early in the breeding season in age 2–4 females was higher than that of Little Round Lake females, suggesting that limited energy reserves in the spring may have prevented young Little Round Lake females from early spawning. Our results show that the likelihood and timing of reproduction are both age and size-dependent in some populations. Small individuals that delay seasonal maturation and spawn late in the summer probably contribute little to the population due to the restricted growth and reduced overwinter survival of their progeny.

Introduction

The energetic trade-off between growth and reproduction has been the focus of a number of studies with fish. Many studies have shown that life-history components such as somatic maintenance (Wootton 1979), present and future somatic growth (Jennings 1991), present and future survivorship (Roff 1981, Wootton 1985, Hutchings 1993), and future fecundity (Wootton 1979, Vøllestad & L'Abée-Lund 1990) are reduced when present reproductive effort is high.

The reproductive characteristics of centrarchids have been extensively described; however, the majority of research has concentrated on males (e.g. Keenleyside 1971, 1972, Colgan & Ealey 1973, Colgan & Gross 1977, Gross 1979, Bietz 1981, Noltie & Keenleyside 1987, Jennings 1991, Ridgway et al. 1991). The life histories of male centrarchids have been a focal point of behavioural ecology because of the varied patterns of male parental care in this family and the presence of alternative male reproductive styles in some species (Gross 1982, 1991). The ease of studying male centrarchids is that unlike females, parental males remain at their nests immediately after spawning, making direct quantitative measures of seasonal and individual reproductive success more reliable (Raffetto et al. 1990). However, since the majority of seasonal reproductive energy in males is not allocated solely to gonads, a measure of female gonadal development is a more reliable indicator of reproductive effort (Miller 1963, Gross 1979, Vøllestad & L'Abée-Lund 1990).

Ridgway et al. (1991) showed that a significant proportion of adult male smallmouth bass, *Micropterus dolomieui*, do not nest in a given year. Nesting habitat was shown not to be a limiting factor, and no alternative male reproductive styles have been shown for smallmouth bass. In a closed population of smallmouth bass, Raffetto et al. (1990) also found that a large proportion of non-breeding adults from both sexes are present in each year. Raffetto et al. (1990) suggested that by assuming all individuals spawn, the use of factors such as female fecundity estimates from the population at large may grossly overestimate reproductive potential.

Ridgway et al. (1991) also showed that nesting in smallmouth bass was asynchronous, with small males nesting later in the season than large males. Based on allometric differences in metabolism and energy reserves (Shuter & Post 1990), Ridgway et al. (1991) hypothesized that small males emerge from winter with a higher energetic deficit than large males, and are therefore incapable of allocating energy to reproduction until later in the season. They also suggested that this energetic hypothesis could apply to the timing of female reproduction; however their support for this hypothesis was based on size-dependent patterns of gonad development, not observations of females that actually spawned.

In this study, we test for the presence of size and age-dependent variation in the likelihood of reproduction in mature female pumpkinseed, *Lepomis gibbosus*, a common centrarchid in eastern North America that nests in the littoral zone of many lakes. We also test a prediction that follows from the overwinter energetic deficit hypothesis; that smaller/younger females will spawn later in the season than larger/older females.

Methods

Study sites

The study was conducted during the 1991 and 1992 breeding seasons in two east-central Ontario lakes, one of which was known to contain a stunted pumpkinseed population. Little Round (LR) is a 7.5 ha lake located in eastern Ontario (44° 48′ north, 76° 42′ west), approximately 60 km north of the city of Kingston. Little Round is a deep meromictic lake (mean depth 11 m) with a narrow littoral zone, the result of its 'teacup' morphology (McNeely 1975). Pumpkinseeds in this lake exhibit very slow growth; few individuals attain a body length of 100 mm (M. Fox unpublished data).

Beloporine (BP) is a 7.2 ha lake located in central Ontario (44° 29′ north, 77° 57′ west), approximately 35 km east of the city of Peterborough. It is a shallow lake (mean depth 2.2 m) that is almost entirely littoral zone. An elevated weir at the outlet of the lake maintains its present basin characteristics.

In addition to pumpkinseed, both of the study lakes are inhabited by yellow perch, *Perca flavescens*, and several cyprinid species. Beloporine Lake also contains white sucker, *Catostomus commersoni*, and brown bullhead, *Ictalurus nebulosus*, whereas Little Round Lake contains banded killifish, *Fundulus diaphanus*, and stocked rainbow trout, *Oncorhynchus mykiss*. Neither lake is likely to contain piscine predators of adult pumpkinseed, as no northern pike, *Esox lucius*, or largemouth bass, *Micropterus salmoides*, were observed while snorkeling, captured in traps or seines, or angled.

Determination of the age-class distribution of mature females

A two step process was used to determine the age breakdown of mature females in each study population. The first step was to estimate percent maturity of each age-class. To accomplish this, we collected a random sample of females from littoral zone areas with wire funnel traps 1 m (length) x 40 cm (diameter). Samples were collected over a two year time frame during 'prespawn' periods immediately prior to the onset of nesting activity, and mid-spawn periods when spawning activity was at or near peak (A. Danylchuk & M. Fox unpublished data) (Table 1). Collected fish were sacrificed by ice water shock and stored frozen prior to laboratory analysis.

Maturity was assessed by inspection of eggs within the ovaries. A pumpkinseed was defined as mature if the ovaries contained yolked eggs. Individuals were measured total length, nearest 1 mm) and weighed (wet weight, nearest 0.1 g). Age was determined by reading acetate impressions of scales, and annuli were identified using the criteria outlined by Regier (1962). We validated our scale aging technique by comparing scale and otolith ages (Casselman 1987) for a subsample of 10 fish from each population. Ages determined from both methods were identical in all fish examined. Length at age was backcalculated on each fish, using the Fraser-Lee method (Bagenal & Tesch 1978) and a standard body-scale length intercept (Carlander 1982) calculated as the mean of 27 pumpkinseed populations surveyed in eastern and central Ontario (M. Fox unpublished data).

The second step was a capture-mark-recapture survey to assess the age/size structure of each population. During mid-August, 1991 (Little Round) and early June, 1992 (Beloporine), eight to ten funnel traps were randomly set throughout the shallow littoral zone area in each lake. Funnel traps were set for 12-24 h periods, emptied, and then moved to another location. Captured pumpkinseeds were measured, marked by clipping the upper lobe of the caudal fin, and then released. This capture-mark-recapture process was repeated over a 6 d (Little Round) and 9 d (Beloporine) period, by which time nearly 2000 pumpkinseeds were captured in each lake.

Determination of the age-class distribution of spawning females

Nests occupied by parental males were monitored throughout the 1991 spawning season in Little Round Lake and 1992 in Beloporine Lake. Nests were observed while snorkeling in randomly selected areas of spawning habitat within each lake. Nests in Little Round Lake could also be monitored from the shore due to the narrow littoral zone within its perimeter. When a spawning bout was observed, the female was captured using a dip net or by chasing her into a wire funnel trap. Captured spawning females were measured, weighed, and scales were removed for aging. Age was determined using criteria outlined earlier in this paper.

Data analysis

Capture-mark-recapture data were used to determine the length and age-class distribution of each population. Population estimates were derived separately for size ranges that displayed a different recapture frequency, using the Darroch method (Bagenal & Tesch 1978, Youngs & Robson 1978). By

Table 1. Sampling periods in the two study lakes.

	Little Round Lake	Beloporine Lake
Maturity assessment		
Prespawn	27 May 1992	28 May 1992
Mid-spawn	1 July 1990, 23 June 1992	11 June 1992
Mark-recapture	August 1991	May 1992
Capture of spawning females	31 May–27 July 1991	8 June–17 July 1992

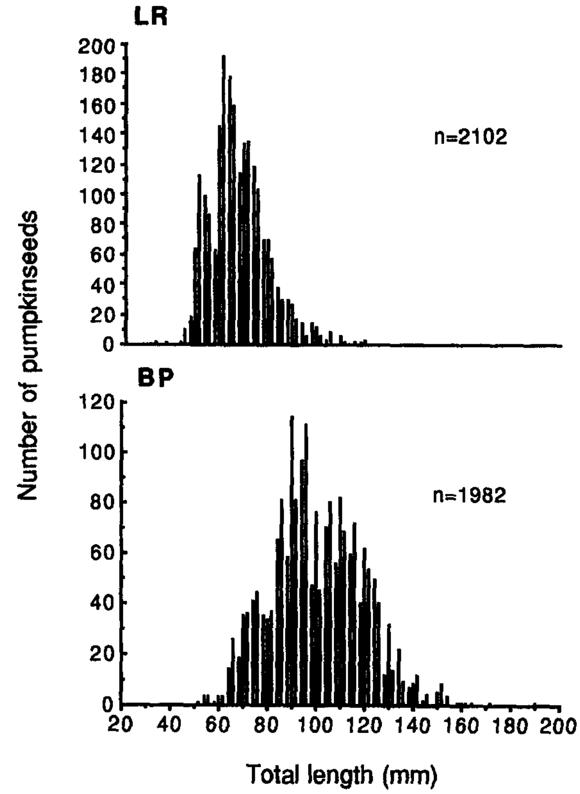

Fig. 1. Length-frequency distribution of pumpkinseeds from capture-mark-recapture surveys; Little Round Lake (LR) August 1991, Beloporine Lake (BP) May 1992.

combining estimates of the proportion of mature individuals at each age-class (estimated from prespawn and mid-spawn sampling) with relative estimates of age-class-frequency (from capture-mark-recapture), we determined the age-class distribution of mature females during these periods.

In the case of Little Round Lake, we assumed that the proportion of mature females by age, as assessed in 1990 and 1992, were representative of this proportion in 1991 when the capture-mark-recapture and spawning assessments were conducted. This is a reasonable assumption because our data suggest that percent maturity does not have a high degree of annual variation in this lake. For the mid-spawn period, assessments conducted in 1990 and 1992 showed 100% maturity in age 3 and older females, and 90 vs. 87% maturity in age 2 females in the two respective years. The proportion of age 2 females mature in the prespawn assessment in 1992 was 57%, whereas this proportion in a sample of females captured in early June, 1993 was 62%. Neither of these differences in age 2 females was statistically significant (prespawn: $\chi^2 = 0.04$, $p = 0.85$; mid-spawn: $\chi^2 = 0.07$, $p = 0.79$).

To assess whether the proportion of mature females that actually spawn increases with body size/age, a chi-square test was used to compare the age-class distribution of mature females during prespawn and mid-spawn periods with the age-class distribution of spawning females. To test whether younger/smaller females spawn later in the season than older/larger females, the period over which spawning females were captured was divided into three equal intervals. We then compared the age of females captured during each trimester of the spawning season in each lake, using one-way analysis of variance. A probability level of $p < 0.05$ was accepted as significant in both statistical tests.

As an indicator of gross nutritional state, we calculated Fulton's condition factor [K= 100 x weight (g) x (length (cm))$^{-3}$] on females collected during the prespawn and mid-spawn periods for each population and determined mean condition factor of each age-class (Weatherley 1972). To determine if body condition could account for size-related variation in the timing of reproduction, we compared mean condition at age in the prespawn and mid-spawn periods in the two populations.

Table 2. Age-class distribution of pumpkinseeds in the two study lakes, based on multiple capture-mark-recapture analysis. Little Round Lake, August 1991; Beloporine Lake, May 1992.

Lake	Population estimate (age 2 and above)	Age-class distribution (%)				
		2	3	4	5	6
Little Round	10 207	84	10	3	1	–
Beloporine	41 143	52	29	15	4	0.3

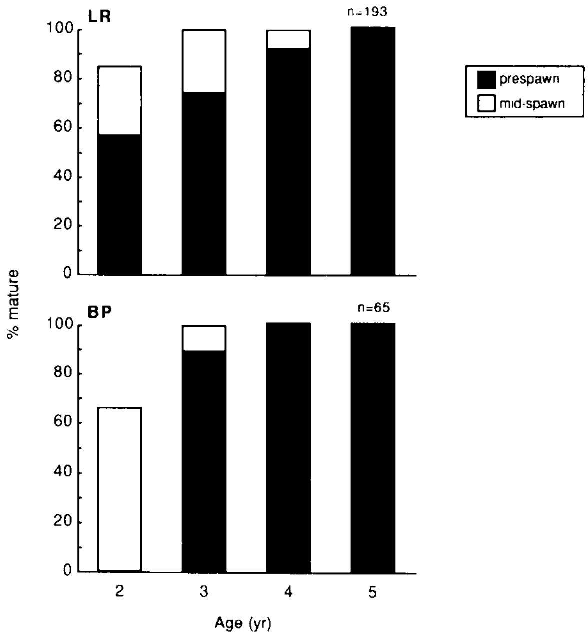

Fig. 2. Percent mature at age of females collected during the prespawn and mid-spawn periods; Little Round Lake (LR) and Beloporine Lake (BP). Dates of data collection for these periods are given in Table 1.

Results

The pumpkinseed population of Little Round Lake was comprised of a large proportion of small fish when compared to the population of Beloporine Lake (Fig. 1). Although the age-class distribution was particularly skewed towards the youngest fish in Little Round Lake, both populations consisted mainly of fish ≤ age 5 (Table 2).

Pumpkinseeds in Little Round Lake were observed spawning mainly between 28 May and 27 July 1991, although a few spawning bouts were observed until August 13. The spawning period observed in Beloporine Lake was more compressed, as bouts were observed between 2 June and 19 July. The proportion of mature female pumpkinseeds of all age-classes increased between pre-spawn and mid-spawn periods in both populations, with the largest increase occurring in the youngest fish (Fig. 2). More than 70% of females ≥ age 3 were mature during the prespawn period in both populations, and more than half of age 2 females in Little Round Lake were also mature at this time.

The age distribution of mature females in the Little Round population during prespawn and mid-spawn periods was significantly different than the age distribution of females that were captured spawning (prespawn matures vs. spawning fish, χ^2= 22.9, p ≤ 0.0001; mid-spawn matures vs. spawning fish, χ^2 = 27.1, p≤ 0.0001). The proportion of spawning females that were age 2 was low when compared with the proportion of mature females that were age 2 in either the prespawn and mid-spawn periods (Fig. 3). In Beloporine Lake, the proportion of spawning females that were age 2 was higher than the proportion of mature females that were age 2 in the prespawning period, but lower than this proportion during the mid-spawning period. However, only one 2 year-old fish was actually captured spawning in Beloporine Lake, so it is more meaningful to make this comparison with age 3 females. The proportion of mature females that were age 3 during the prespawn and mid-spawn period was virtually the same as the proportion of spawning females that were age 3. Furthermore, there was no significant difference in the age distribution of

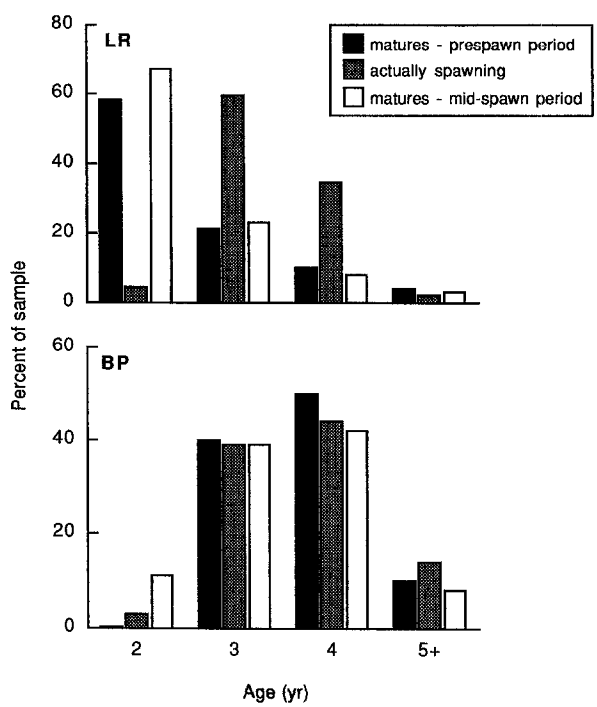

Fig. 3. Comparison of the age-class distribution of mature females during the prespawn and midspawn periods with the distribution of females collected while spawning. LR = Little Round Lake, BP = Beloporine Lake.

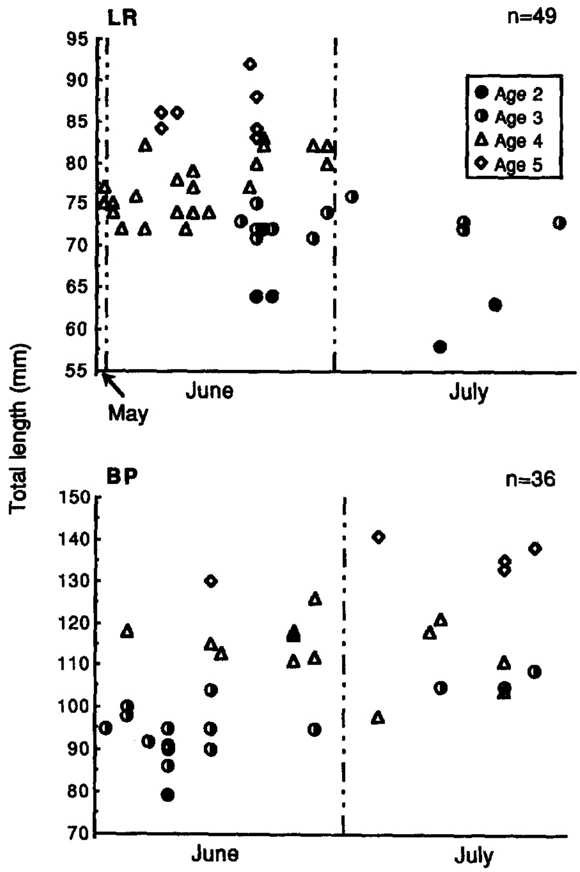

Fig. 4. Length and age of spawning females collected during the spawning season (Little Round Lake (LR) 1991; Beloporine Lake (BP) 1992).

spawning females and either the pre-spawn or mid-spawn age distribution of mature females in Beloporine Lake (prespawn matures vs. spawning fish, $\chi^2 = 4.1$, $p > 0.1$; midspawn matures vs. spawning fish, $\chi^2 = 6.25$, $p > 0.1$).

Although the mean age of spawning females was significantly different among early, middle, and late periods in both populations (Little Round Lake $F_{2,46} = 8.1$, $p = 0.001$; Beloporine $F_{2,33} = 5.9$, $p = 0.006$), the temporal pattern of age and size distribution of spawning females differed between lakes (Fig. 4). In Little Round Lake, age 4 and 5 females tended to spawn early in the season, whereas the younger/smaller females apparently did not begin to spawn until mid-June. No females ≥ age 3 were captured spawning after June. In Beloporine Lake, the distribution of spawners by age-class was more even throughout the season compared with Little Round Lake, although there was some tendency for the oldest females to spawn late in the season. The length of spawning females increased significantly over the season in Beloporine Lake ($r = 0.56$, $p = 0.003$, d.f. = 35), but part of this increase can be explained by seasonal growth of the fish.

Within populations, early season condition factors were similar among age-classes, but the females in Beloporine Lake tended to be in better condition (Fig. 5). Average body condition either changed little or decreased from the prespawn to mid-spawn period in both populations, except for age 2 Little Round Lake females. The condition of these small mature females improved substantially from the prespawn to mid-spawn period, by which time several were captured spawning.

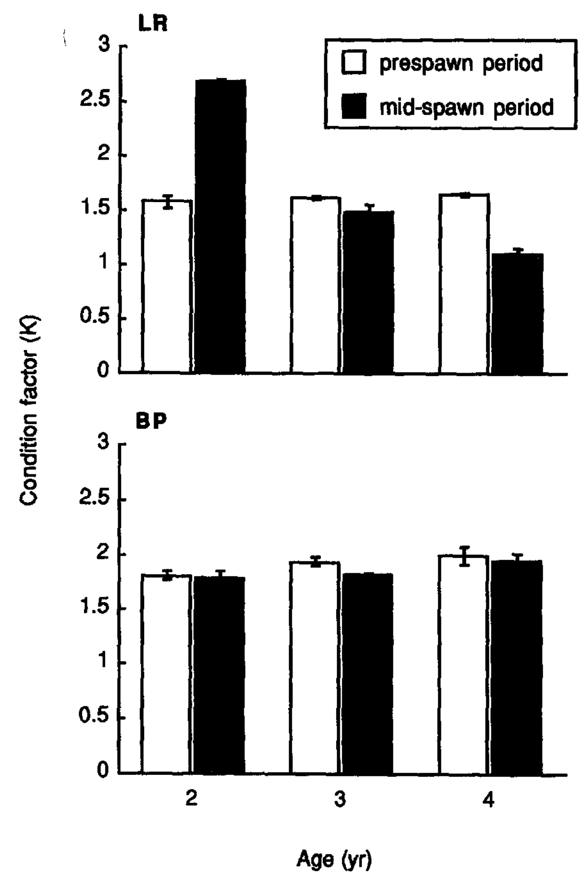

Fig. 5. Condition factor of mature females sampled during the prespawn and mid-spawn periods of 1992. LR = Little Round Lake, BP = Beloporine Lake. Vertical bars represent ± 1 SE.

Discussion

Our predictions were only partly supported by the results of our study, since trends in size/age distribution of spawning females were not consistent between the two populations studied. In the stunted population of Little Round Lake, age 2 pumpkinseeds were significantly underrepresented among the fish captured while spawning, despite high representation of these small females in the mature segment of the population. These small females also spawned later in the season than their larger conspecifics, as predicted. In contrast, the age/size distribution of females spawning in Beloporine Lake was representative of the age/size distribution of mature fish in the population, and there was no evidence that smaller/younger Beloporine females spawn later in the season than larger/older females.

Our study suggests that a high proportion of small, mature females in certain populations may not reproduce in a given season. This result is consistent with the finding of Raffetto et al. (1990) that a large contingent of adult females (as well as males) in a smallmouth bass population fail to breed in a given year. Raffetto et al. (1990) did not examine the relative size or age-class distribution of these non-breeding adults. Our study suggests that, at least in Little Round Lake, many of these non-breeding pumpkinseeds are the youngest/smallest fish, but since we did not attempt to census breeding fish, we cannot rule out the possibility that there are many non-breeding adult females of all size and age-classes in both of our study lakes.

Ridgway et al. (1991) suggest that spacing behaviour and exploitative competition for food resources may play an important role in determining why a low proportion of young, mature male smallmouth bass nest in a given year. Small females in Little Round Lake may also be under resource constraints early in the season, but may nevertheless mature in order to spawn if the opportunity arises. Even if the probability of spawning is low, it may nevertheless pay in fitness terms for a small female to mature. This is because maturation without subsequent spawning may not be costly energetically, since female pumpkinseeds can resorb their eggs late in the season (Crivelli & Mestre 1988).

A high energetic deficit accumulated overwinter by small fish could account for the delay in the seasonal timing of reproduction of small females in Little Round Lake. Shuter et al. (1980) showed that smaller fish accumulated a higher overwinter energy deficit than larger fish. Danylchuk & Fox (1994) also found that peak gonadal development in pumpkinseed occurred later in the season in populations with small adult body size, and that small individuals within populations delayed seasonal maturation. These results are consistent with the Ridgway et al. (1991) hypothesis that small fish may have to rebuild depleted energy reserves before allocating resources to reproduction.

Small adult females in Beloporine Lake may have been able to quickly rebuild energy deficits and therefore spawn earlier in the season than small adult females in Little Round Lake. The better condition of these fish suggests that higher food availability relative to population density may account for the ability of small Beloporine females to rebuild energy stores lost overwinter. The low proportion of mature age 2 females in this population relative to that of Little Round Lake might also be a result of genetic differences between these populations.

Ridgway et al. (1991) found a consistent relationship between the size of individual male smallmouth bass, the timing of nesting activity, and their thermal history prior to nesting. This suggests that temperature may have a size-dependent influence on seasonal reproductive activity. However, Danylchuk & Fox (1994) found that differences in the initiation of nesting activity among six pumpkinseed populations with varying adult body size characteristics could not be attributed to early season water temperatures. Early spring littoral zone temperatures in Little Round Lake were actually 3 to 5° C warmer than those in Beloporine Lake during the years of their respective spawning assessments. Since the warming of water in the spring has been shown to induces gonadal recrudescence in centrarchids such as green sunfish, *Lepomis cyanellus*, (Kaya & Hasler 1972), it is unlikely that the presence of a size-related spawning effect in Little Round and its absence in Beloporine can be attributed to differences in temperature regime.

It may be beneficial to spawn early in the season to allow for maximum accumulation of energy reserves in the young-of-year produced. Several studies have shown that first year overwinter survival for species such as smallmouth bass, *Micropterus dolemieui* (Oliver et al. 1979, Shuter et al. 1980), yellow perch (Newsome & Leduc 1975, Post & Evans 1989) and brook charr, *Salvelinus fontinalis* (Hunt 1969), is size-dependent and likely the result of allometric differences in body fat reserves (Post & Evans 1989, Shuter & Post 1990). Shuter & Post (1990) suggested that population viability hinges on the ability of young-of-year to complete a minimum amount of growth during their first year of life. Individuals born late in the season are less likely to accumulate sufficient energy to maintain themselves during the winter. Therefore, recruitment from spawning events late in the season may have a low contribution to the future of the population, thus contributing minimally to an individual's reproductive fitness.

Although the reproductive fitness of individuals spawning late in the season may be low, it may represent the only opportunity to reproduce if adult mortality is high. Hutchings (1993) found that reduced adult survival favoured increased reproductive effort at an early age of maturity in brook charr. Fox & Keast (1991) showed that short-lived pumpkinseeds in winterkill ponds matured at an early age and allocated more energy to gonadal development than pumpkinseeds in a stable lake environment. Therefore, small fish may mature precociously in order to maximize fitness, even when energetic considerations force them to delay spawning until relatively late in the season.

In summary, our study provides evidence that small/young female pumpkinseeds that mature in a given year may have a relatively low probability of actually spawning. For those that do spawn, energetic constraints on these small females may result in a seasonal delay in this activity. In populations where these size-dependent effects do occur, it is necessary to question the contribution of small, mature individuals to the strength of the year class for the season in which they first spawn. To further assess the generality of size-related effects in the probability and the timing of reproduction, the reproductive fitness of individuals spawning throughout the season in a larger sample of lakes should be examined.

Acknowledgements

We gratefully acknowledge the field and laboratory assistance of Joseph Justus, Ian McDonald and Kim Westcott. We extend our appreciation to the Newton family for allowing us access to Beloporine Lake. Finally, we acknowledge Erica Nol and Michael Berrill and two anonymous reviewers for constructive comments on an earlier version of this article. This study was supported by a Natural Sciences and Engineering Research Council of Canada grant to M. Fox.

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