Seasonal Reproductive Patterns of Pumpkinseed (*Lepomis gibbosus*) Populations with Varying Body Size Characteristics

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To assess the implications of reproduction on body size and the potential physiological constraint imposed by small body size on reproductive patterns, we examined seasonal nesting patterns and gonad allocation in six pumpkinseed (*Lepomis gibbosus*) populations exhibiting a range of adult body size characteristics. We found that the two populations exhibiting stunted adult body size initiated nesting activity 1-wk later and had nesting periods 3–7 wk longer than the other four populations. Mean adult body size showed a significant negative correlation with both length of spawning season and gonadosomatic index in the six populations. Within populations, smaller females matured later in the season than larger females. Our results suggest that small adult body size is associated with high reproductive effort and that variation in the timing of reproduction is a consequence of differences in energy reserves between small and large individuals. The extended spawning season of some populations may result in a higher cost of reproduction than that which would be predicted from gonad size alone. Small individuals forced by energy limitations to spawn late in the season are likely to produce offspring with lower survival rates, and their reproductive fitness should be discounted accordingly.

Pour évaluer les liens entre la reproduction et la taille corporelle, et les contraintes physiologiques potentielles imposées par la faible taille du corps aux schèmes de reproduction, nous avons examiné les modes saisonniers de nidification et la distribution de la taille des gonades chez six populations de crapet soleil (*Lepomis gibbosus*) présentant des caractéristiques diverses de taille à l'âge adulte. Nous avons trouvé que les deux populations dont les adultes avaient une taille chétive commençaient leur nidification 1 sem plus tard et la poursuivaient pendant 3 à 7 sem de plus que les quatre autres populations. La taille moyenne des adultes montrait une corrélation négative significative avec la durée de la saison de ponte et l'index gonadosomatique dans les six populations. Au sein des populations, les femelles de plus petite taille atteignaient la maturité plus tard dans la saison que celles de grande taille. Nos résultats semblent indiquer que la faible taille des adultes est associée à un effort reproductif élevé, et que la variation dans la période de reproduction est une conséquence des différences dans les réserves énergétiques entre les individus de petite et de grande taille. L'allongement de la saison de ponte dans certaines populations peut avoir pour effet un coût de reproduction supérieur à celui qu'on aurait pu prédire à partir de la taille des gonades seulement. Les petits individus forcés par les limitations énergétiques à frayer tard dans la saison vont vraisemblablement produire des rejetons dont le taux de survie sera plus faible, et ont donc une faible valeur adaptative.

Growth and reproduction are processes that compete for the same limited energetic resources (Roff 1984; Calow 1985). A central concept of life-history theory is that a trade-off exists between present and future reproduction, growth, and survival (Stearns 1977; Wootton 1990; Kozlowski 1992). Two critical factors concerning this trade-off are the amount of energy directed from somatic growth to reproductive processes and the size at which investment into reproduction should occur (reviewed in Calow 1985).

Fish have frequently been used to examine the trade-offs predicted by life-history theory because of the large variation in body size among breeding adults (Roff 1981; 1984; Ridgway et al. 1991). Since body size and fecundity are positively correlated in fish, decreased growth associated with increased reproductive investment can reduce future fecundity (Wootton 1979; Reznick 1983).

Studies with fish have shown that present reproduction is costly, as it occurs at the expense of postspawning growth, reproduction, and survivorship (Roff 1982; 1984; Reznick 1983; Wootton 1985; Stearns and Koella 1986; Hutchings 1993). Spawning fish have been shown to be in poorer somatic condition, making them more susceptible to predation, disease, or physiological stress than nonreproductive fish (Wootton 1977; Pressley 1981; Roff 1982). Reproduction can also place a heavy burden on energy reserves. For example, in American plaice (*Hippoglossoides platessoides*) the flesh becomes jellied as fish break down their body tissues to provide energy for gonadal development (Roff 1981).

The evidence relating reproductive effort to body size and survival suggests that stunting (small adult body size) may be a consequence of early maturation and high reproductive effort (Jennings 1991). However, the link between

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TABLE 1. Body size and maturity characteristics of pumpkinseed in the six study lakes. Body size and maturity data were collected during 1988–1991.

| Lake | Physical characteristics | | Body size characteristics | | |
	Surface area (ha)	Mean depth (m)	Maximum length (mm)	Mean total length at age 5 (mm)	Mean length at maturity (males/females) (mm)
Little Round	8	11	97	96	55/64
Warrens	34	2.6	133	123	77/82
Black	40	7.8	152	132	82/91
Beloporine	7	2.6	154	141	102/92
Opinicon	787	2.5	170	128	116/108
Duncan	45	n/a	169	146	127/125

characteristics of stunted fish such as early maturation (reviewed in Murnyak et al. 1984) and slow growth (Alm 1946; Roff 1986) has not been demonstrated at the population level.

The energy available for reproduction can be restricted by body size. Several studies have shown that smaller fish have lower fat stores and higher rates of energy use than larger fish (reviewed by Shuter and Post 1990). Ridgway et al. (1991) showed that body size affected the timing of reproduction in smallmouth bass (*Micropterus dolomieu*, previously *M. dolomieui*). They found that large male bass nested earlier in the season than small males, and they hypothesized that these differences are linked to size-dependent energy deficits. Their results suggest that smaller fish require more time to rebuild overwinter energy deficits, resulting in a delay in the allocation of energy to reproduction. However, their study was within one population and the timing of female reproduction was not directly assessed.

The purpose of this study was to examine the nature of size-related energetic trade-offs in pumpkinseed (*Lepomis gibbosus*), a common centrarchid species in many north temperate lakes. Given that reproductive patterns are a product of available energy stores, and that smaller fish accumulate a higher overwinter energy deficit than larger fish (Shuter et al. 1980), we predicted that (1) pumpkinseed populations exhibiting small adult body size would initiate reproductive activity later in the spring than populations with comparatively larger adults, (2) smaller fish within populations should initiate reproductive activity later in the season than larger fish, and (3) smaller fish within populations should allocate energy to gonads later in the season than larger fish.

Given that there is a high cost to reproduction, we further predicted that body size at the population level would be negatively associated with reproductive effort and predicted that (4) pumpkinseed populations exhibiting small adult body size would have a protracted spawning season and (5) would allocate more energy to gonads than populations with normal adult body size characteristics.

Materials and Methods

Study Sites

Pumpkinseed populations used for this study were selected from a data base of 23 eastern and central Ontario populations used in an ongoing study (Fox 1994). Pumpkinseed from these waterbodies had been collected during the pre-

reproductive periods from 1988 to 1991 to define the life-history characteristics of each population. To test the predictions of this study, six populations were selected encompassing a broad range of body size characteristics (Table 1). Little Round Lake (LR) and Warrens Lake (WA) populations exhibit stunted growth and small adult body size whereas populations in Lake Opinicon (OP) and Duncan Lake (DU) exhibit growth and adult body size characteristics typical of populations in eastern and central Ontario. Black Lake (BL) and Beloporine Lake (BP) populations exhibit intermediate adult body size characteristics.

The study lakes were geographically proximate (within 125 km and 20′ of latitude of each other) (Fig. 1). Lake area ranged from 7 to 787 ha, with mean depths ranging from 2.5 to 11 m (Table 1).

Assessment of Seasonal Nesting Patterns

Male pumpkinseed nest in diffuse colonies and aggregate in favoured habitat within the littoral zone (Breder 1936; Clark and Keenleyside 1967; Gross 1979). The location of nests constructed early in the season tends to define areas where the majority of nesting is to occur (Colgan and Ealey 1973; Gross 1979; Ridgway et al. 1991). Therefore, transects were established in suitable nesting habitat where parental males had initiated nest construction early in the spring. Two transects were used in each of Little Round, Warrens, Opinicon, and Beloporine lakes (Table 2). Three transects were established in Duncan and Black in order to increase the number of nests surveyed, since nest density early in the season was comparatively low in these two lakes. Transect dimensions varied within and between lakes and were dependent upon the location of nests early in the season and the morphological characteristics of the littoral zone.

Transects were examined for nesting activity on a biweekly basis from May to August 1992 and weekly at the initiation of the study to more precisely define when nesting was initiated in each lake. Nests within transects were marked and surveyed during each assessment period for parental occupation and the presence of eggs or larvae. Previously unmarked or "new" nests occupied by parental male pumpkinseed were marked and included in the assessment. Whole-lake inspections of other nesting areas conducted on each day of transect assessments confirmed that seasonal trends in parental occupation and nest content observed in transects were representative of the lake as a whole. All inspections were carried out by divers using mask and snorkel.

To compare reproductive activity to trends in water temperature, a minimum/maximum thermometer was placed in
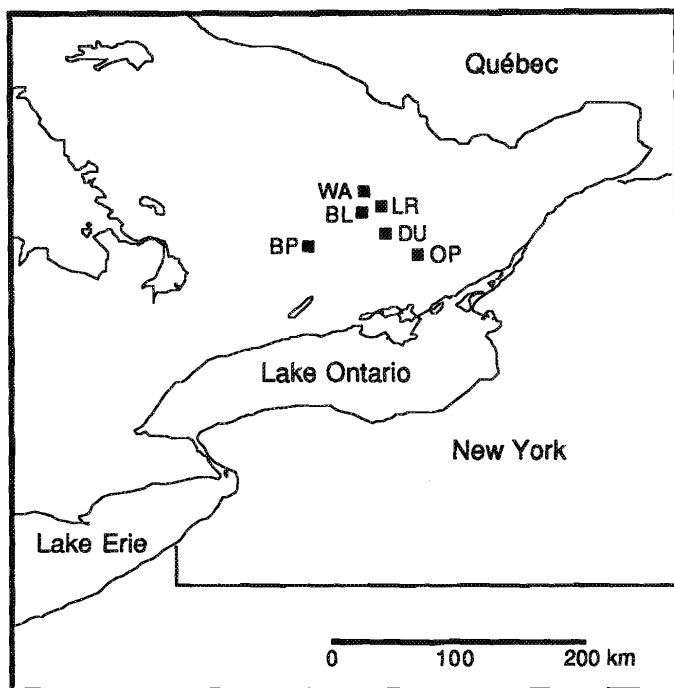
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FIG. 1. Location of study lakes in eastern-central Ontario. LR = Little Round, WA = Warrens, BL = Black, BP = Beloporine, OP = Opinicon, and DU = Duncan.

TABLE 2. Number of transects and total transect area for the study lakes.

Lake	Number	Total area (m^2)
Little Round	2	392
Warrens	2	450
Black	3	1898
Beloporine	2	492
Opinicon	2	1185
Duncan	3	2624

approximately 1 m of water at or near one of the transects in each lake. Temperature data were read on the date that transects were surveyed, although some readings could not be made due to equipment damage and theft.

Assessment of Seasonal Allocation Patterns

Female pumpkinseed were collected from each waterbody on the day of transect assessments. Females were selected for this analysis, since the majority of seasonal reproductive energy in females is allocated to gonad development and not to secondary reproductive behaviour such as brood care (Miller 1963; Gross 1979; Vøllestad and L'Abée-Lund 1990). Collections were made in littoral zone areas with a bag seine and 1 m (length) × 40 cm (diameter) wire funnel traps set at a depth of approximately 1 m (Keast and Fox 1990). Collections were made away from transects to avoid disturbing survey nests.

Total length and wet weight were measured for each individual. Age was determined by reading acetate impressions of scales. Annuli were identified using the criteria outlined by Regier (1962). We validated our scale aging technique by comparing scale and otolith ages (Casselman 1987) in 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 and Tesch 1978) and a standard body-scale length intercept (Carlander 1982) calculated as the mean of 23 populations surveyed (Fox 1994).

The proportion of gonad weight to total body weight (gonadosomatic index, GSI) was calculated for each mature fish. A fish was defined as mature if the ovaries contained yolked eggs. Spent females were also counted as mature. These females were identified by the presence of flaccid gonads containing a few yolked eggs and the protrusion of the gonadal papilla (Miller 1963). GSI was calculated for each population, collection period, and age-class.

Analysis of Seasonal Nesting Patterns

The number and density of occupied nests were calculated for each assessment period as an indicator of seasonal reproductive activity in each lake. Nest density was plotted according to assessment date to observe interpopulation trends in nesting activity, including initiation date, peak activity, and season duration. The number of occupied nests and those containing eggs and larvae were also plotted according to assessment date to observe interpopulation patterns in spawning and hatching.

Duration of the spawning season was defined as the number of weeks between the initiation of nesting activity and the complete abandonment of nests. The number of occupied nests with larvae and the accumulation of silt within those nests were also used to indicate the completion of the spawning season. Transects were surveyed 2 wk after total nest abandonment to ensure that a resurgence of reproductive activity did not occur.

Pearson correlations were used to test the prediction that seasonal duration is inversely related to female body size across populations. The 90th percentile length of all females was determined for each population and used as an indicator of maximum body size. The 90th percentile length was used instead of the length of the largest fish collected because the former is less subject to sampling error. Mean length of mature females was used as an indicator of average body size of reproductive fish. Both indicators were determined by backcalculating fish length to the beginning of the season (formation of the 1992 annulus) to standardize the length of mature fish collected at different times throughout the season.

Patterns of reproduction in centrarchids, including the time of initiation, duration, and proportion of energy allocated to gonads, can potentially be affected by water temperature (Kaya and Hasler 1972; Burns 1976; Ridgway et al. 1991). We therefore examined the water temperature regime within our study lakes to determine if interpopulation differences in reproductive activity were related to early season trends in water temperature. A Pearson correlation was used to examine the relationship between the time until peak nest density (in weeks) and thermal history, expressed as the number of degree-days greater than 16°C (Burns 1976) accumulated by that time. If temperature is the critical factor in determining interpopulation differences in the timing of reproductive activity, then peak nest density should occur in all of the waterbodies when a given number of degree-days is reached. We also examined the relationship between maximum body size and thermal history to determine if populations with comparatively smaller adults accumulated a

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TABLE 3. Female body size and reproductive characteristics determined from samples taken during the 1992 spawning season.

Lake	Body size characteristics[a]		Reproductive characteristics[b]	
	90th percentile length (mm)	Mean length of matures (mm)	90th percentile GSI	Peak GSI[c]
Little Round	80	70	11.2	8.6
	(333)	(287)		
Warrens	95	78	10.4	7.9
	(204)	(194)		
Black	124	94	9.5	6.2
	(172)	(110)		
Beloporine	117	100	10.2	8.5
	(223)	(160)		
Opinicon	145	125	7.7	5.8
	(145)	(102)		
Duncan	155	128	6.4	4.3
	(139)	(81)		

[a]Standardized to the beginning of the season by backcalculation from scales (sample size in parentheses).
[b]Sample size of GSI characteristics is the same as that of mean length of mature fish.
[c]Highest mean GSI in any assessment period.

greater number of degree-days before the peak in nesting activity (Ridgway et al. 1991).

To examine growth trajectories of females in each population, mean length at age was calculated by averaging the backcalculated length of each age and the two successive older age-classes (for example, mean length at age 2 was calculated by averaging the backcalculated length for age-classes 2, 3, and 4). Older age-classes were not used in this calculation because several populations showed Lee's phenomenon, in which older fish appear to be slower growing as a result of selective mortality on faster growing individuals (Bagenal and Tesch 1978). Mean age at maturity was calculated according to the method of DeMaster (1978).

Analysis of Seasonal Allocation Patterns

Mean GSI and 90th percentile GSI for all mature females were determined and plotted according to assessment date to observe interpopulation trends in seasonal allocation of energy to gonads. Mean GSI was used as a value of average allocation whereas the 90th percentile GSI was an indicator of maximum allocation.

Pearson correlations were used to test the prediction that populations of small adult body size should allocate more energy to gonads. The 90th percentile GSI (maximum allocation) and the highest mean GSI during the assessment period (peak allocation) were used as two indicators of energy allocated to gonads. The latter indicator removed the confounding influence of date sampled and eliminated spent fish and those without fully developed gonads from the analysis. As an indicator of total seasonal reproductive allocation, we examined the combined effects of seasonal allocation and seasonal duration of reproductive activity by calculating the area under the mean GSI × date curve.

To test whether smaller fish within populations delay the allocation of energy to gonads and therefore initiate reproduction later in the season than larger fish, we determined the proportion of mature females for the first three age-classes that contained mature females for each population. To compare age-class trends in maturation, percent mature was
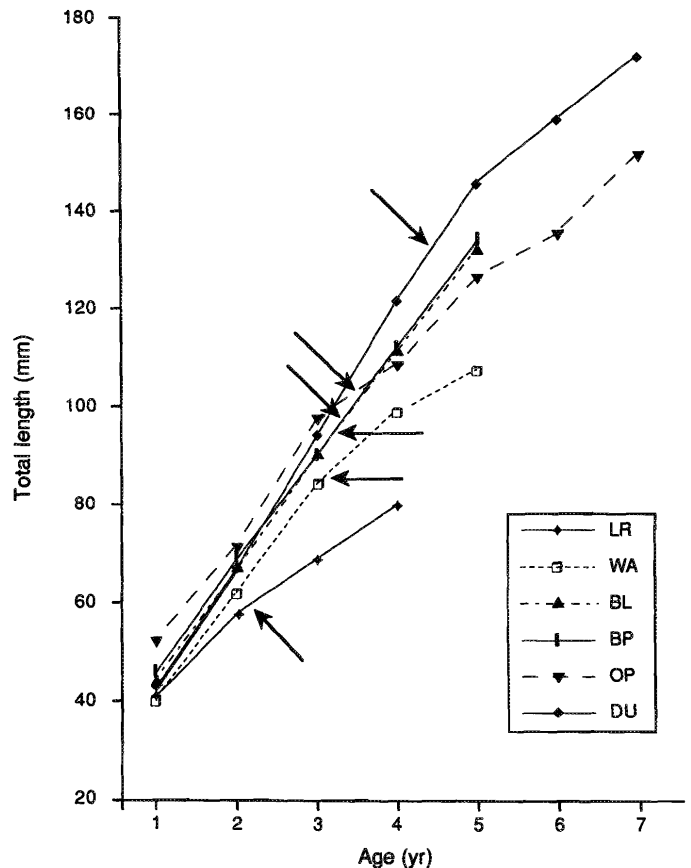

FIG. 2. Mean length at age for females from the six study populations. Mean age at maturity for each population is indicated by an arrow.

plotted against assessment date until the youngest age-class reached peak maturity .

Bonferroni adjustments were used with multiple factor correlations to give guaranteed family-wise probability levels. We defined probability levels of <0.05 as signifi-
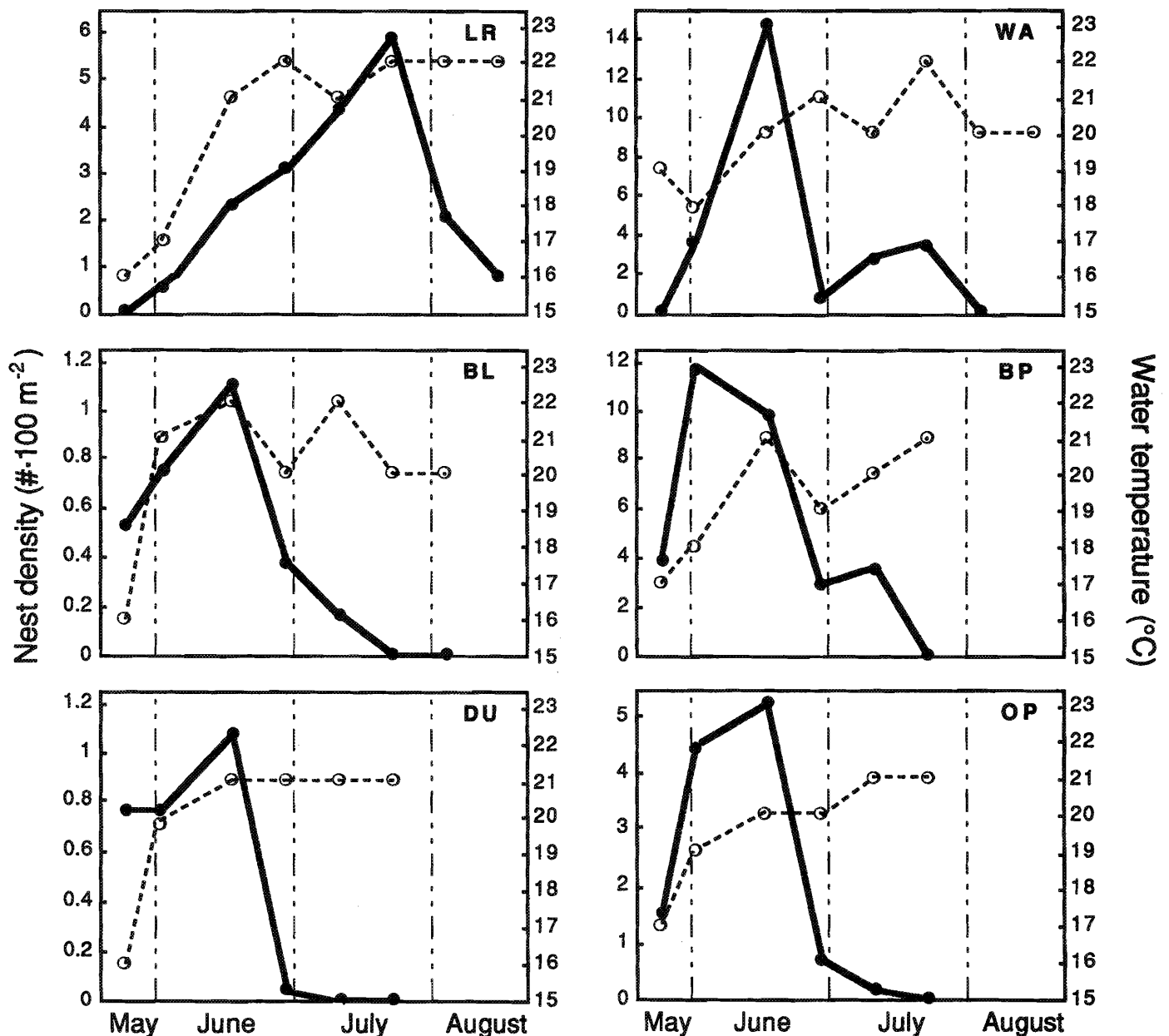
FIG. 3. Nest density and mean water temperature for the study lakes during the 1992 spawning season. Nest density is represented by solid circles/solid lines and mean water temperature by open circles/broken lines.

cant and denoted probability levels between 0.05 and 0.1 as marginally significant.

Results

Body Size, Growth, and Reproductive Allocation

Females from Little Round and Warrens exhibited the smallest body size and the greatest allocation to gonads (Table 3). The body size characteristics of Black and Beloporine females were intermediate to those of the other populations. GSI of Beloporine females was as high as those of the stunted populations.

A downward shift in the growth trajectory coincident with the mean age of maturation was evident in four of the six populations (Fig. 2). Females from Little Round and Warrens exhibited the earliest age at maturity and a major decline

in the annual growth increment following the mean age at maturity (Fig. 2). Small adult body size in these two populations was coincident with small juvenile body size, but there was no correspondence between juvenile and adult body size in the other four populations.

Seasonal Nesting Patterns

Nesting activity began in late May or early June, with the stunted populations of Little Round and Warrens initiating nesting activity 1 wk later than other populations. Seasonal nest density ranged from 1 to 15 nests·100 m^{-2} (Fig. 3), and maximum seasonal nest density was not significantly correlated with either of the body size indicators (Table 4). Peak nest density occurred from early June to late June in all lakes except Little Round, which peaked in late July. Although nest density peaked latest in the most stunted pop-

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TABLE 4. Correlation between female body size and reproductive characteristics in the six study populations.

| | Body size characteristics | | | |
| | 90th percentile length | | Mean length of matures | |
Reproductive characteristics	r	P^a	r	P^a
Seasonal duration	−0.94	0.005**	−0.89	0.01*
90th percentile GSI	−0.89	0.010*	−0.95	0.003**
Peak GSI	−0.96	0.003**	−0.83	0.04
Total seasonal allocation	−0.99	0.0001**	−0.97	0.001**
Maximum nest density	−0.55	0.27	−0.47	0.34

^{a}Individual probability values are given. Asterisks denote Bonferroni-adjusted family-wise level of significance: $*P < 0.1$ and $**P < 0.05$.

ulation, the timing of this peak was not ordered by body size in the rest of the populations.

Water temperature at the initiation of nesting ranged from 16 to 18°C, and water temperature at peak nest density ranged from 20 to 22°C. The initiation of nesting did not occur in sequence with the warming of the lakes (see Fig. 3). In addition, peak nest density occurred in each lake after a different number of degree-days was accumulated (Fig. 4); thus, thermal regime does not explain the variation among lakes in the timing of nesting activity. There was a tendency for the number of thermal units until peak nesting occurs to decrease with increasing body size of the population (Fig. 4), but the relationship between these variables was not significant ($r = -0.58$, $P = 0.20$).

The nesting period of the stunted populations in Little Round and Warrens occurred for 12 and 10 wk, respectively, whereas Black, Beloporine, and Opinicon populations nested for 7 wk, and the Duncan Lake population nested for 5 wk. There was a significant negative correlation between seasonal duration of nesting and body size (Table 4). The underlying cause of this relationship was apparently not competition for mates or nesting sites because neither mean nor maximum nest density was significantly correlated with seasonal duration ($r = 0.39$, $P = 0.44$ and $r = 0.45$, $P = 0.37$ respectively).

Seasonal peaks in the number of occupied nests and the number of those nests that contained eggs were either synchronous or sequential for each lake (Fig. 5). The number of nests observed with larvae ranged in these lakes from 7 to 51% of the number of nests observed with eggs, and this proportion was unrelated to body size characteristics of the populations ($r = 0.59$, $P = 0.29$).

Seasonal Allocation and Maturity Patterns

Within-lake trends in mean GSI and 90th percentile GSI (Fig. 6) generally corresponded with seasonal nesting patterns for each lake (Fig. 3). Peak allocation occurred early in the season for each population except that of Little Round. Mean and 90th percentile GSI in Little Round Lake did not peak until mid-June and did not decrease until early July. Mean and 90th percentile GSI also remained near the seasonal peak for a longer period of time in the stunted populations.

Both measures of GSI as well as total seasonal allocation were highly correlated with adult body size (Table 4). Thus, populations exhibiting stunted body size characteristics allocated more energy to gonads on a seasonal basis
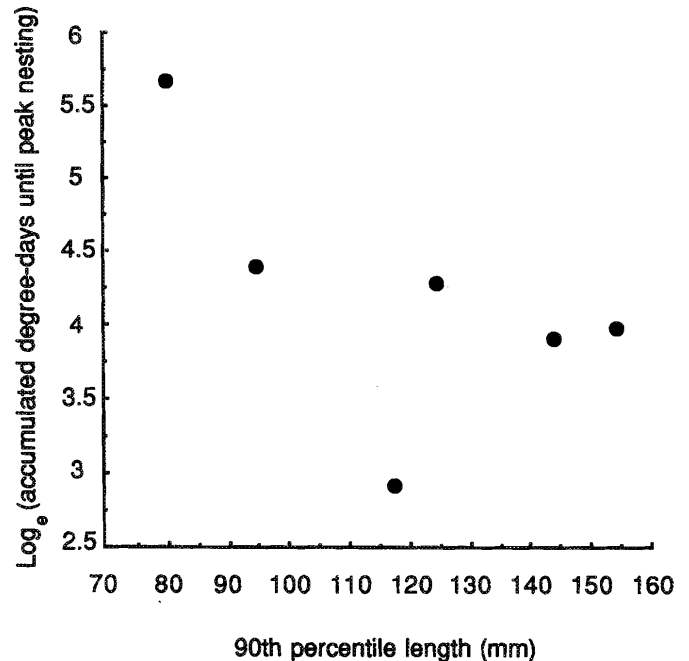

FIG. 4. Relationship between adult body size in the six study populations and accumulated degree-days prior to peak nest density.

and had higher seasonal peaks than populations with larger adult body size.

Within populations, a lower proportion of smaller/younger females were mature at the onset of nesting activity than larger/older females (Fig. 7). The proportion of the youngest age-class of females maturing increased over the reproductive season in each lake except Opinicon. In addition, age 2 females peaked in percent maturity 2–5 wk later than older fish in the four populations with age 2 mature fish.

Discussion

Our study showed that high reproductive effort is associated with small adult body size in pumpkinseed. We found that the populations exhibiting a longer spawning season, delayed seasonal reproductive activity, and greater gonad development were those with the smallest adult body size.

Size-specific differences in energy stores prior to reproduction could account for the delay in seasonal reproductive activity by stunted populations and by small maturing
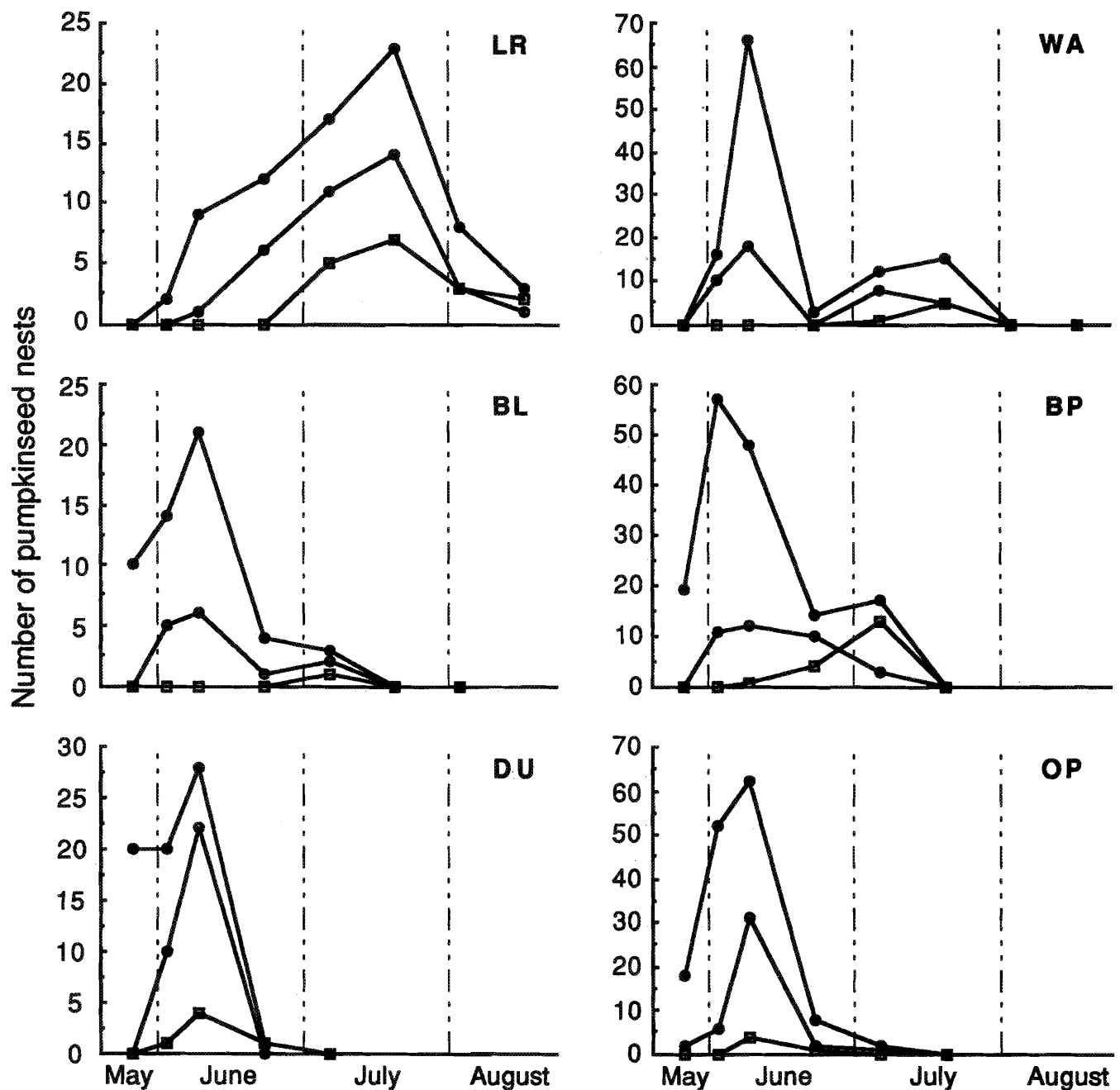
FIG. 5. Number of occupied nests (solid circles) and the number of those nests that contained eggs (open circles) or larvae (open squares) for the study lakes during the 1992 spawning season.

fish within populations. Trippel and Harvey (1989) showed that the onset of maturation in white sucker, (*Catostomus commersoni*) was energy dependent. Ridgway et al. (1991) postulated that more time should be required by smaller fish to replenish energy stores early in the spring, resulting in the delay of energy allocation to gonads. Our results are consistent with the hypothesis of Ridgway et al. (1991) and emphasize the importance of the overwinter period to the reproductive potential of small fish.

Burns (1976) showed that the seasonal timing of maturation in pumpkinseed is primarily a function of water temperature. Gonadal recrudescence in green sunfish (*Lepomis cyanellus*) was shown to be stimulated by a combination of elevated water temperature and extended photoperiod (Kaya

and Hasler 1972). However, the initiation of nesting in our six lakes was not ordered by early season temperature; nor did nest density in these lakes peak at a set number of accumulated degree-days. While this does not mean that thermal regime is unimportant in regulating the timing of reproductive activity within a lake, it does show that thermal regime cannot account for the among-population differences in reproductive patterns demonstrated in our study.

Given that energy availability and energy stores are limited in the pumpkinseed populations we studied, it is reasonable to assume a cause–effect explanation for the negative relationship between reproductive effort and adult body size. Jennings (1991) had previously demonstrated such a relationship in two longear sunfish (*Lepomis megalotis*) sub-
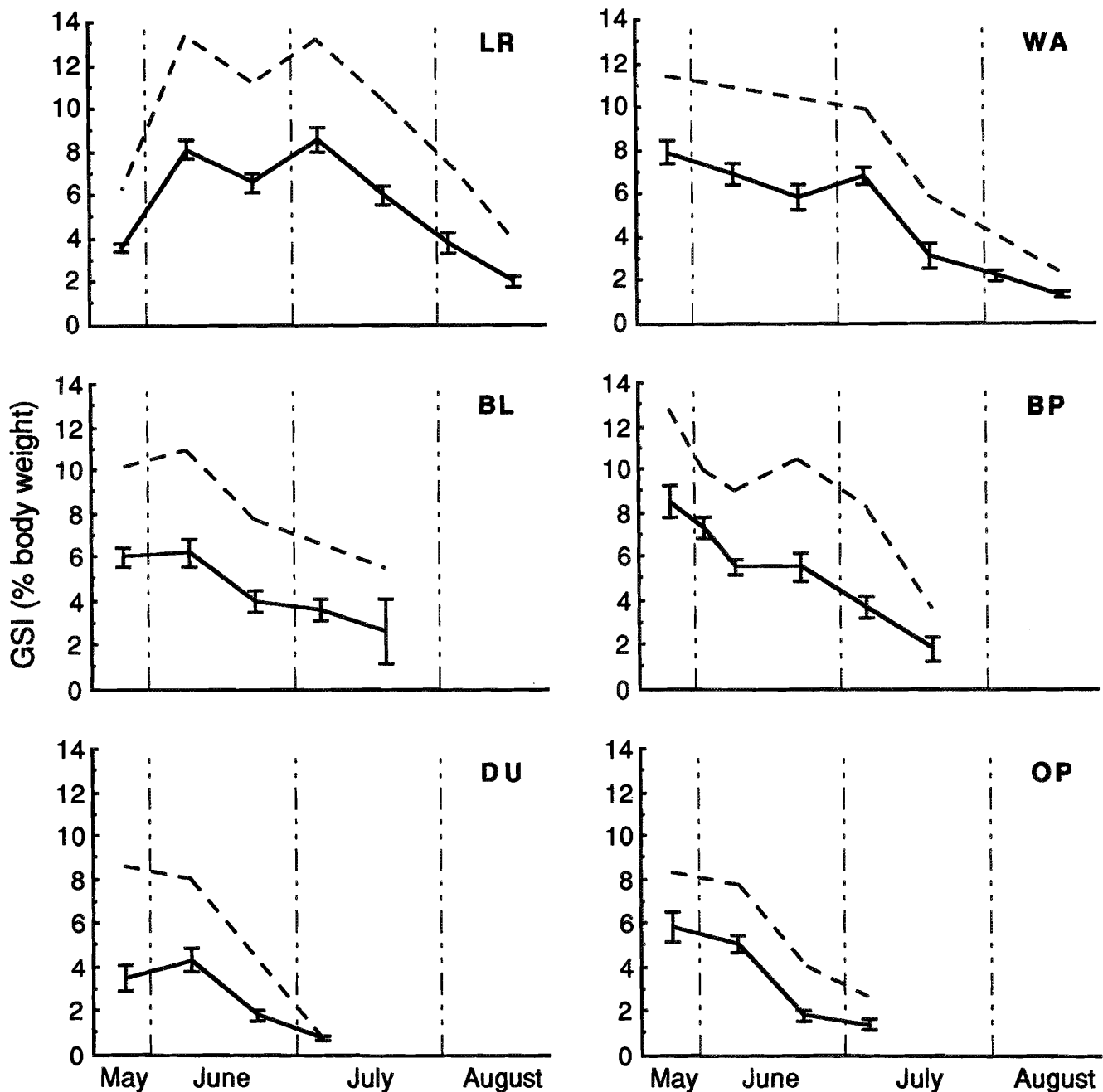
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FIG. 6. Mean GSI (±1 SE) and 90th percentile GSI of females sampled from each study lake during the 1992 spawning season. Mean GSI is represented by solid lines and 90th percentile GSI by broken lines.

species; our work demonstrates that the relationship also applies at the population level. However, factors such as population density and resource availability can also influence adult body size in fish (Alm 1946; Murnyak et al. 1984; Deacon and Keast 1987; Fox and Keast 1990). Thus, although our data suggest that reproductive effort may account for much of the variation in adult body size among populations, its importance relative to other factors was not determined.

Values of energy allocated to reproduction are typically based on GSI (Vøllestad and L'Abée-Lund 1990), fecundity (Wootton 1979; Vøllestad and L'Abée-Lund 1990; Schultz and Warner 1991), and the energy content of gonads (Constantz 1979; Reznick 1983). Our study suggests that the traditional use of gonad data may actually underesti-

mate the relative cost of reproduction in different populations. While conducting reciprocal transplants experiments with sculpin (*Cottus gobio*) between northern and southern streams, Mann et al. (1984) found that females that allocated more energy to reproduction also had longer spawning periods than females that allocated less energy to reproduction. On the other hand, gonad data may overestimate the absolute reproductive effort of some mature females, since it has been shown that mature individuals do not necessarily spawn in a given year (Raffetto et al. 1990; Ridgway et al. 1991; Danylchuk and Fox 1994).

An extended spawning season incurs a high energy cost, assuming that individuals are repeatedly spawning throughout the season. Repeat spawning throughout the season has been shown to occur in other centrarchids such as bluegill

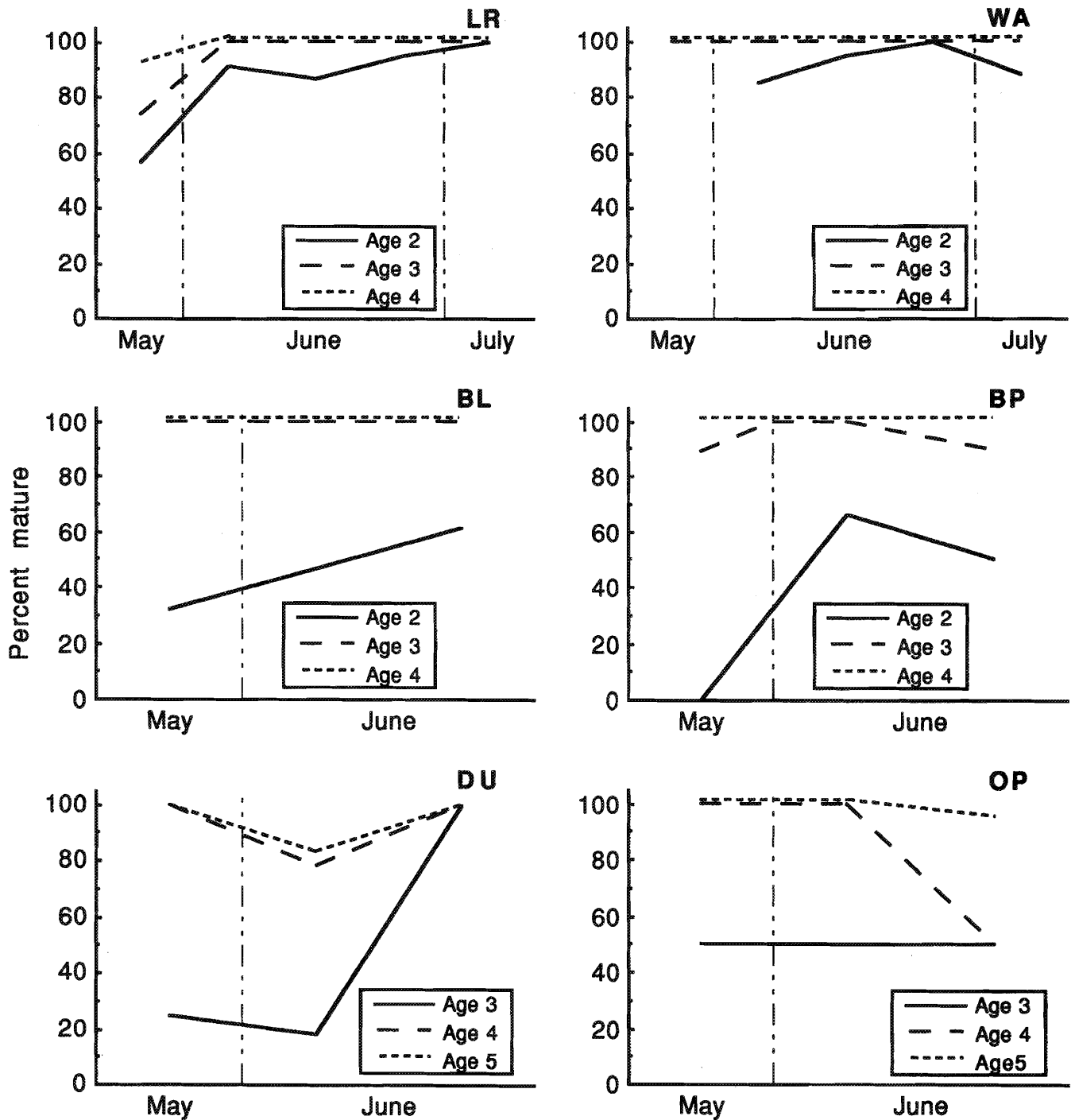*Can. J. Fish. Aquat. Sci., Vol. 51, 1994*

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FIG. 7. Proportion of mature females collected from each study lake for the first three age-classes with mature fish. Proportions plotted until the youngest age class reached peak maturity.

(*Lepomis macrochirus*) (Gross 1982) and rock bass (*Amblo-plites rupestris*) (Gross and Nowell 1980) and has been suggested for pumpkinseed (Miller 1963; Deacon and Keast 1987; Crivelli and Mestre 1988).

An issue raised by our study is whether size-dependent timing of reproduction may result in smaller individuals having lower reproductive fitness than larger individuals capable of spawning earlier in the season. Given that overwinter survival of young-of-the-year fish is highly size-dependent (Oliver et al. 1979; Post and Evans 1989), young born at the end of an extended spawning season may con-

tribute minimally to the reproductive fitness of the parents. Thus, in trying to determine the fitness value of early maturity within a population, it would be necessary to discount the value of offspring production according to the time in the season when it occurs.

In summary, our study shows that the seasonal timing of reproductive activity is related to body size of the individual and that differences in adult body size among populations are linked to differences in reproductive allocation. Given that the energy available for growth and reproduction is limited, our results suggest that small adult body size can be a con-

sequence of high reproductive effort. Our study provides support for the life-history assumptions relating energetic trade-offs between body size and reproduction. To further assess the consequences of reproductive effort on pumpkinseed populations, interpopulation differences in reproductive success and postreproductive survivorship should be addressed.

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