

# The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*)

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**Abstract:** Many fish species are protracted spawners, producing fry over a several-week breeding season. We demonstrate that this time dimension has important implications for recruitment by relating the body size and survival of yearlings to the day that they were born. The production of bluegill sunfish fry was estimated throughout the 1993 spawning season in Lake Opinicon, Ontario. In 1994, yearlings were collected and otolith daily growth rings used to determine their 1993 date of birth. We found that yearling body size decreased with date of birth in 1993. There was a progressive decline in body size across the eight spawning bouts, resulting in a 50% difference in the size at age 1 of early- and late-born fry. This difference is apparently due to the longer growing season available to early-born fry. Fry born earlier in the season also had strikingly higher survivorship to age 1 than fry from the middle- or late-season bouts. Fry produced during the first trimester increased 231% in representation among yearlings. This increased survivorship is probably due to increased over-winter survivorship and possibly also size-selective predation. These results highlight the importance of the temporal dimension in understanding the nature of fish recruitment.

**Résumé :** De nombreuses espèces de poissons ont une saison de fraye relativement longue, de sorte que les alevins naissent sur une période de plusieurs semaines. Nous démontrons que cette dimension temporelle a des implications importantes pour le recrutement en établissant un rapport entre d'une part la taille corporelle et le taux de survie des poissons d'un an, et d'autre part le jour de leur naissance. On a estimé la production d'alevins de crapet arlequin pendant toute la saison de fraye de 1993 dans le lac Opinicon (Ontario). En 1994, on a prélevé des poissons d'un an et on a utilisé les anneaux de croissance quotidienne des otolithes pour déterminer la date de leur naissance (en 1993). On a observé un déclin progressif de la taille corporelle en fonction de la date de naissance en 1993, soit à la suite de huit épisodes de fraye, qui entraînait à 1 an une différence de taille de 50% entre les alevins nés au début et à la fin de la saison de fraye. Cette différence est apparemment due à la saison de croissance plus longue dont pouvaient profiter les alevins nés au début de la période. De plus, on observait chez ces derniers un taux de survie à 1 an notablement plus élevé par rapport à celui des alevins nés au milieu ou à la fin de la saison. La représentation des alevins nés au cours du premier trimestre a augmenté de 231% dans le groupe des poissons d'un an. Cette augmentation du taux de survie est probablement due à un taux de survie accru après hivernage et peut-être aussi à des facteurs de prédation dépendant de la taille. Ces résultats soulignent l'importance de la dimension temporelle des études visant à améliorer la compréhension du processus de recrutement des poissons.

[Traduit par la Rédaction]

## Introduction

Recruitment, the addition of new members to a population through reproduction (Fogarty et al. 1991), is a central issue in fish population biology. Recruitment, and the variability associated with it, affects not only population size, but also population structure, stability, and genetic composition. Recent research has indicated that the early life history stages are critical to determining adult population sizes, and a number of important processes that influence recruitment and year-class strength have been identified, including size-selective predation

(Post and Prankevicius 1987; Post and Evans 1989a; Litvak and Leggett 1992), size-dependent feeding and starvation (Miller et al. 1988), and size-dependent over-winter mortality (Oliver et al. 1979; Toney and Coble 1979; Shuter et al. 1980; Post and Evans 1989b; Smith and Griffith 1994). These studies show that survivorship can be biased towards larger individuals in a population (for an exception see Litvak and Leggett 1992).

An important dimension to survival has not been previously addressed. No study has related body size and survival to actual spawning times. Many temperate fish species have breeding seasons that span a substantial portion of the summer growing season. For example, about 74% of Canadian freshwater fish species have breeding seasons that extend for more than 1 month ( $n = 86$  species from 26 families; data in Scott and Crossman 1973). This temporal dimension within a season may result in a wide range of birth dates and potential growth opportunities, and may be important to understanding recruitment and year-class strength of temperate fish populations.

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In this study, we examine within-season temporal variation in recruitment, yearling body size, and survival of young-of-the-year bluegill sunfish, *Lepomis macrochirus*. We link survival to age 1 with individual birth dates from the previous year. We find that early-born individuals attain the largest body size and have the highest survivorship to age 1. We discuss the implications of these results for recruitment theory, year-class strength, and the size structure of temperate fish populations.

## Methods

### Bluegill reproductive biology

The bluegill sunfish is a synchronously breeding, colonial centrarchid found in eastern and central North America (Scott and Crossman 1973). In Lake Opinicon, the breeding season ranges from as early as 21 May to as late as 24 July (data from 1985–1993). Spawning is initiated by males entering the littoral zone and building nests in the substrate (Gross 1980, 1982). Colonies, varying in size from 1 to 300 nests, are formed by parental males in water 0.5–3.5 m deep. These males range in age from 7 to 11 years. Gravid females, 4–7 years of age, approach male colonies in schools and individually enter nests where they spawn with parental males. When spawning is complete, females leave the colony and retreat to deeper waters while parental males remain on their nests to care for the embryos in their nests. Depending on water temperatures, fry reach swim-up in 5–12 days and then the parental male abandons the nest (L.M. Cargnelli and M.R. Gross, University of Toronto, unpublished data).

Spawning occurs in distinct bouts, in which a number of colonies form and spawn synchronously. There are at least several days of colony inactivity before the next spawning bout. As a result, all colonies formed during a bout are at approximately the same stage of development. The number of spawning bouts during a season ranges from five to eight (data from 1985–1993).

### Study site

The bluegill population is from Lake Opinicon, an 890-ha mesotrophic lake typical of those in southeastern Ontario (Keast 1978). It has a maximum depth of 11 m and an average depth of 4.5 m, and is usually covered with ice from December to April. Ice-out occurs in the spring as early as the first week in April and as late as the first few days in May. In 1994 ice-out occurred on approximately 21 April.

Shallow littoral areas are abundant and make up approximately 10% of the lake surface area (Curran et al. 1947). Lake Opinicon sustains a large natural population of bluegill sunfish and a total community of 18 species including 5 other species of centrarchids (Keast 1978). The reproductive biology of bluegill sunfish has been studied in the lake annually since the mid-1970s (e.g., Colgan et al. 1979; Gross 1980, 1982; Coleman et al. 1985; Claussen 1991; Gross 1991; Cargnelli and Gross<sup>2</sup>).

### Reproductive activity surveys

Bluegill reproductive activity was studied in an area bounding 2 km of littoral zone along the northern shore of the lake. This zone, referred to as the fish reproduction study area (FRSA), includes a variety of habitat types characterizing the wide biological and physical diversity in which bluegill are known to spawn. The FRSA was monitored by snorkellers on a daily basis during the 1993 spawning season beginning several days before the onset of spawning activity and continuing for as long as males remained on nests. Thus, a complete record of all reproductive activity occurring within the study site during 1993 was obtained.

Dates of male colony formation, female spawning, egg hatch, and swim-up as well as the number of nests formed, the number of nests in which fish spawned, and the number of nests to produce free swimming fry were recorded for each colony that formed. Fry swim-up was not directly observed; instead, empty nests that on the previous day had contained parental males and larvae at the golden-eyed stage, the final larval stage in the nest, were taken as an indication that swim-up had occurred. Since surveys were performed in the mornings, the date of swim-up for each colony was assigned to the previous day, even though swim-up may have occurred earlier in the morning before our survey. Thus, the number of days from first to last swim-up in 1993 has an error of 1 day in either direction.

There were eight spawning bouts in 1993, with the first spawning occurring on 6 June (bout 1) and the final spawning on 13 July (bout 8). The first swim-up occurred on 14–15 June and the final swim-up on 17–18 July, a range of 32–34 days.

### Estimates of egg number

The number of eggs within each nest on the day following spawning was estimated using a standard method developed in our laboratory. A diver visually examines the mass of eggs in a nest and assigns an egg score ranging from 0 to 5, with 0 indicating no eggs and each higher score representing increased numbers of eggs. Visual egg scores and the actual number of eggs in the nest are significantly correlated with little overlap between egg score categories (Claussen 1991). The number of eggs per egg score, determined by collecting and counting full clutches of eggs that had been scored, is as follows: score 1, 1–4900 eggs ( $n = 9$  nests); score 2, 4600 – 29 000 ( $n = 8$ ); score 3, 27 000 – 53 000 ( $n = 7$ ); score 4, 49 000 – 87 000 ( $n = 5$ ); score 5, 82 000 – 113 000 ( $n = 3$ ) (data in Claussen 1991). Thus, although there is variability within each egg score, a reasonably accurate representation of differences among nests can be obtained.

Egg scores were estimated for all males that spawned within a colony and for all 106 colonies that formed within the FRSA in 1993. For some very large colonies ( $n > 100$  nests), however, only a sample of nests including at least 50% of the individuals randomly distributed throughout the colony was scored. Egg scoring was tested for repeatability in two ways. First, all 49 nests in one colony were scored by two individuals and concordance was tested (Spearman rank correlation:  $n = 49$ ,  $r = 0.7255$ ,  $p < 0.001$ ). Second, the average scores from all nests within five colonies scored by the two observers were compared ( $2.231 \pm 0.787$  (mean  $\pm$  standard deviation) versus  $2.359 \pm 0.816$ ; Mann–Whitney  $U$  test:  $df = 311$ ,  $Z = -1.67$ ,  $p = 0.095$ ).

### Estimates of fry production

We define production by the number of fry leaving the nest. There is a significant positive correlation between egg scores and the number of fry present in a nest on the final day of parental care (Spearman rank correlation:  $n = 31$  nests,  $r = 0.878$ ,  $p = 0.0001$ , data in Claussen 1991). Production from each colony that formed in 1993 was therefore calculated by multiplying the average egg score of a colony by the number of males in the colony that produced free-swimming fry. We used average egg scores instead of individual egg scores because we could not keep track of which individual nests in a colony were successful. The total production for each of the eight spawning bouts in 1993 was determined by summing the production estimates of each colony within each spawning bout.

### Recruitment to age 1

Age-1 bluegill sunfish were captured using seine and minnow traps from within the FRSA on 24 May 1994. The total length (in millimetres) and wet weight (in grams) of each of the 400 fish were measured and all samples frozen. Otolith daily growth rings were used to age and obtain growth data on each fish. The presence of otolith daily growth rings has been verified in bluegill (Taubert and

<sup>2</sup> L.M. Cargnelli and M.R. Gross. Fish energetics: larger individuals emerge from winter in better condition (bluegill sunfish: *Lepomis macrochirus*). Submitted for publication.

Coble 1977) and in other centrarchids (Miller and Storck 1982; Taubert and Tranquilli 1982).

The saggital otoliths, the largest of the three pairs found in the inner ear, were removed from thawed fish using forceps and a dissecting microscope. Any soft tissue that adhered to the otolith was removed. The otoliths were then placed in 80% ethanol and the cleaning process was completed with fine forceps under a dissecting scope. The otoliths were allowed to air dry before their length was measured using a compound microscope and ocular micrometer (range: 1.6–2.1 mm). Otoliths were then mounted onto microscope slides.

The otoliths were embedded in Araldite GY-502 epoxy, which has been found to be the best medium for mounting otoliths because it is hard and clear and has a low refractive index (Casselman and Barnes<sup>3</sup>). A thin layer of epoxy was placed on a microscope slide and the otoliths were positioned with the convex side up. After hardening for 24 h, the epoxy-embedded otoliths were ground and polished to thin the nucleus and increase optical resolution. Generally, otoliths smaller than 2 mm in length are thin enough that they need only be ground and polished on one side (Casselman and Barnes<sup>3</sup>). The otoliths were ground lightly on a 600 grit disk and then more finely ground and polished with 12- and 0.3- $\mu$ m aluminum oxide lapping film until the nucleus, the portion of the otolith produced during embryonic development (Taubert and Coble 1977), was exposed.

Daily rings were counted using a compound microscope at a magnification of 200–400 $\times$ . The microscope was equipped with a camera lucida, which allowed the image to be projected onto a flat surface. This facilitated reading of the microzonation and allowed the otolith to be traced. Counts were made at the posterior end of the otolith as this is where optical microzonation is best resolved (Pannella 1974; Casselman and Barnes<sup>3</sup>). Microstructure during the over-winter period could not be resolved because of the close proximity of the rings. Thus, counts were made from nucleus to annulus and represented the number of days from swim-up to the termination of growth in the fall.

Problems encountered while reading otoliths were similar to those described by Parrish et al. (1994). Cracks, accessory primordia, and loss of the nucleus or otolith margin made otolith analysis difficult, and uninterrupted viewing of the growth record was not always possible. In such cases, a single counting axis was not used; instead, multiple axes, which allowed rings to be read from nucleus to edge, were utilized. Where ring structure could not be discerned, the otolith was discarded. Counts were successfully made on 161 of 195 otoliths (83%).

Each individual's ring count was converted to the date of swim-up in the following manner. We expected a range of 32–34 days in the ring counts obtained from the 1994 yearlings because this was the number of days between the first and last swim-up observed in 1993. We assumed that the largest ring count corresponded to the first swim-up date, the smallest to the final swim-up date, and each count in between to the intervening dates. In this manner, each individual was assigned to one of the eight spawning bouts in 1993. Each individual was also assigned to an early-, middle-, or late-season trimester in 1993, each 11 days in length.

To estimate actual birth dates from our measures of the number of growth days, we assumed that growth in the fall ceased on the same day for each individual. This assumption seems generally reasonable from several lines of evidence. First, there is a strong relationship between feeding activity and temperature (e.g., Hathaway 1927; Marcus 1932; Gerking 1966; Keast 1977; Shuter and Post

1990) and between growth and temperature (e.g., Gerking 1966; Brett and Groves 1979; Peters 1983; Weatherley and Gill 1987; Shuter and Post 1990) in fish. The bluegill stops feeding with even a 0.5°C temperature drop. It is possible that all of the fish experience similar temperatures and thus respond similarly. Second, studies of seasonal growth cycles in bluegill (Gerking 1966; Keast 1995) suggest that even different age-classes stop growing at the same time in the fall. We expect much less variation within than among year-classes. Finally, and most importantly, the number of days of growth indicated by our otolith study corresponds exactly to the number of days predicted by the data collected from the reproductive activity surveys, a correspondence unlikely to occur by chance.

### Fry size and growth

The average daily growth increments of yearlings were calculated as the total length of the fish divided by its age (millimetres per day). To examine if growth rate differed through the spawning season, regression analysis of yearling total length against yearling age was used. A separate regression was performed for early-, middle-, and late-season periods, and the homogeneity of the regression lines (slopes and intercepts) from each trimester was tested using an analysis of covariance. Significant differences in slopes among lines would indicate that growth rates varied at different times in the season. We used this technique to analyze trends in growth rather than simply analyzing the average daily growth increments over time because of the difficulties in dealing with spurious correlations (Jackson and Somers 1991).

To quantify fry sizes among spawning bouts in 1993, samples of 10 fry were collected with a turkey baster from several nests from each spawning bout and preserved in 90% alcohol. The total length of each fry was measured using a dissecting microscope and ocular micrometer. Only fry that had reached the final golden-eyed stage, where the yolk sac is almost completely depleted and growth in the nest is complete, were used. Fry collected from the first and second bouts of spawning possessed visible yolk sacs and thus were discarded from the analysis.

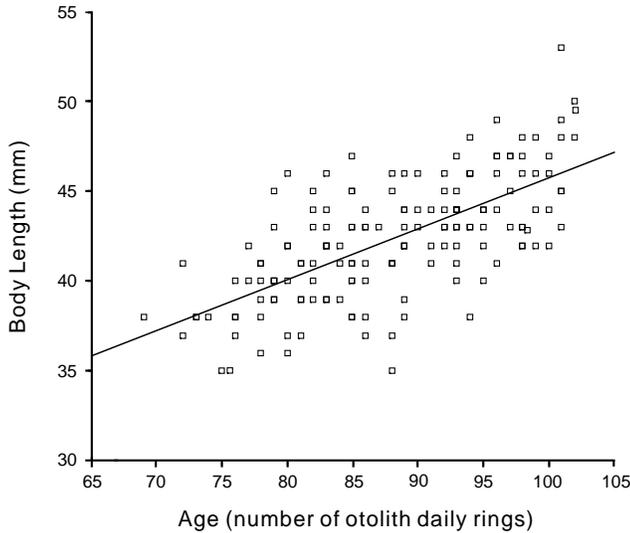
## Results

There was a 34-day range of ring counts made from yearling otoliths, from 69 to 102. This corresponds very closely to the 32–34 days expected on the basis of the first and last observed swim-up dates in 1993. Fish with the largest ring count were therefore assigned the date of 15 June, the first date on which fry were recruited. This implies that 1993 recruits stopped growing by 24 September 1993 (June 15 + 102 days), which is consistent with results of several studies of seasonal growth cycles in bluegill indicating that body growth ceases between mid-September and early October (Gerking 1966; Keast and Eadie 1984).

The 1993 recruits varied considerably in body size by the spring of 1994, ranging in size from 35 to 53 mm total length. These individuals were collected before significant spring growth had occurred, as evidenced by the small number of distinct postannulus growth rings. Thus, spring length is probably a good approximation of fall 1993 body size. Yearling body size was found to be highly correlated with the number of daily growth rings counted (Fig. 1). Older individuals, produced early in 1993, achieved a larger size at age 1 than those born later. Moreover, there was a progressive decrease in yearling body size with each successive spawning bout in 1993 (Fig. 2a;  $df = 7$ ,  $F = 20.06$ ,  $p < 0.001$ ). These data are also summarized for early-, middle-, and late-born 1993 recruits (Fig. 3a;  $df = 2$ ,  $F = 48.98$ ,  $p < 0.0001$ ). Recruits born early in

<sup>3</sup> J.M. Casselman and L.E. Barnes. Removal, storage, and preparation of fish otoliths for studies of microzonation: with special reference to young-of-the-year walleye. Presented at the Age and Growth Workshop – Otolith Method, Maple, Ont., 1987.

**Fig. 1.** Relationship between the number of otolith daily rings from nucleus to annulus in 1993 recruits and the fish's total body length in spring 1994 ( $n = 161$ ,  $r^2 = 0.451$ ,  $p < 0.0001$ ). Larger ring numbers correspond to earlier birth dates in 1993.



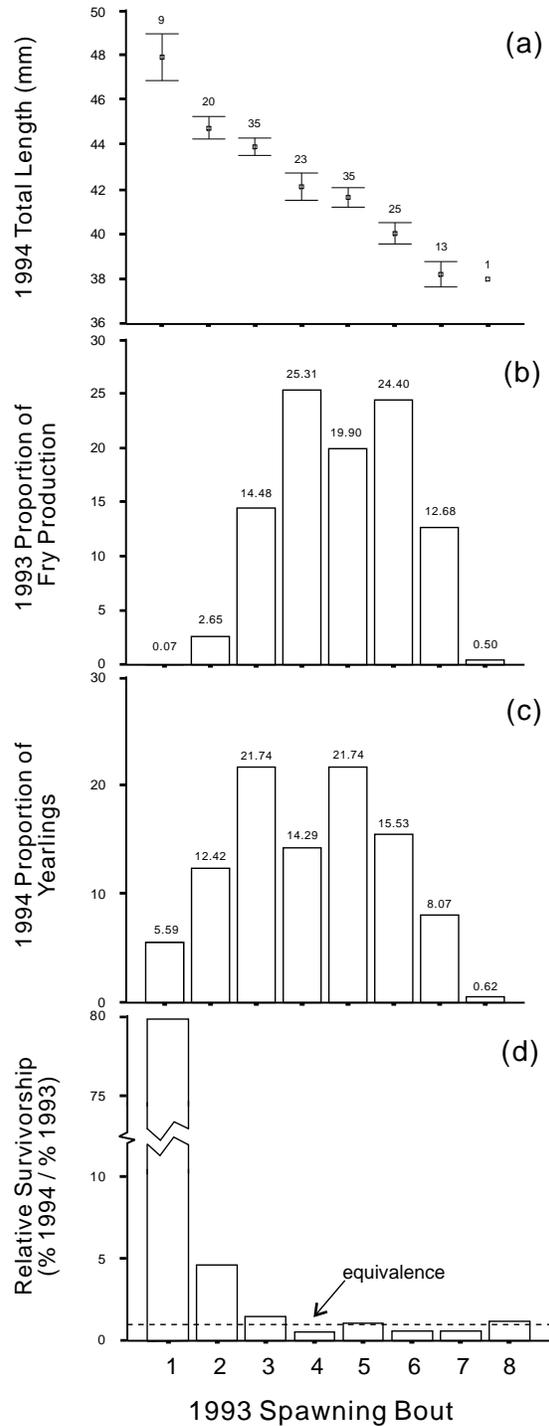
1993 were 7.4% larger than midseason recruits and 13.6% larger than late-season recruits.

The average daily growth increment determined from the regression of total length plotted against ring number (Fig. 1) was 0.55 mm/day. However, growth increments varied among individuals from 0.40 to 0.57 mm/day. This variation was not time dependent as there was no significant difference in growth rates among early-, middle-, and late-season recruits on the basis of results from the analysis of covariance (Table 1). The interaction term in the first part of Table 1 indicates that regression slopes were equal across trimesters ( $p = 0.677$ ), suggesting that all fry increased in size at the same rate through the growth season. The trimester term in the second part of Table 1 indicates that the y intercepts were significantly different ( $p < 0.001$ ). This is expected, since early-season fry are larger at age 1 than middle- and late-season fry.

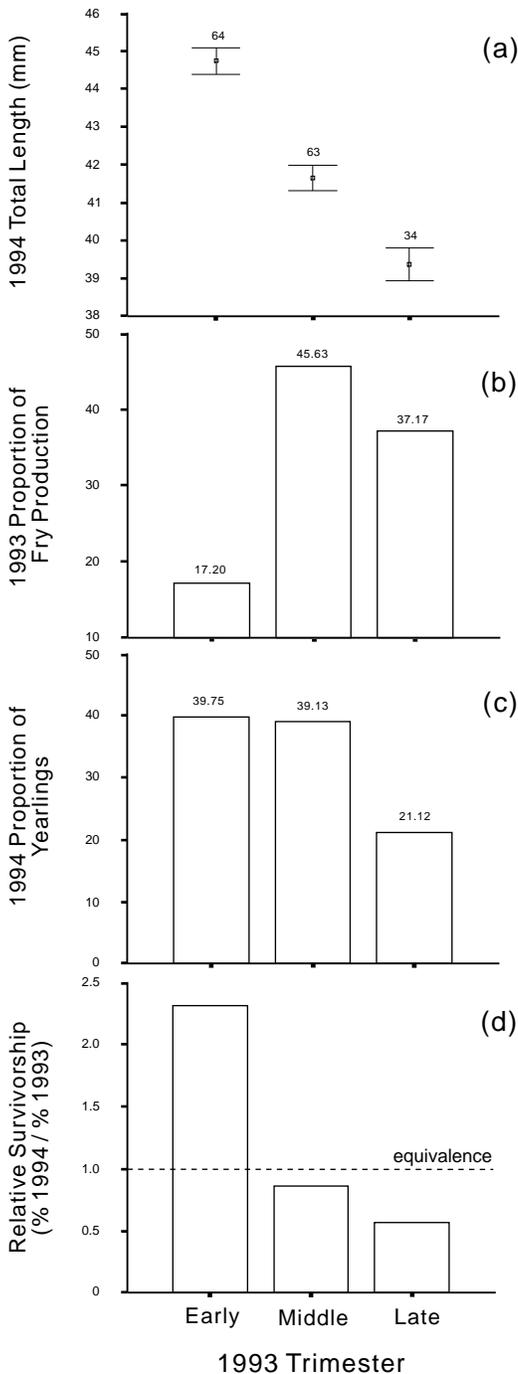
The body size of fry leaving the nest ranged from approximately 4.3 to 6.7 mm and was negatively correlated with spawn date ( $n = 433$ ,  $r^2 = 0.202$ ,  $p < 0.001$ ). Thus, fry from earlier in the season were larger at swim-up than those from later. However, fry size did not make a statistically significant contribution to final recruit size as indicated by a multiple regression analysis with fall size as the dependent variable and spawning bout and fry size the independent variables (Table 2). Thus, the length of the 1993 growing season, as determined by otolith ring counts, appeared to be the most important factor in determining eventual body size in spring 1994.

Numbers of fry produced varied considerably throughout the 1993 breeding season, with the majority of fry being produced during the middle part of the season (Fig. 2b). The early season contributed a much smaller proportion of the total fry production than the middle or late season (Fig. 3b). The early parts of the season were only 37.7% as productive as the middle-season bouts and 46.3% as productive as the late-season bouts. However, the early season produced a relatively larger proportion of recruits into 1994 (Figs. 2c, 3c). If survival of

**Fig. 2.** Data summarized by 1993 spawning bout. (a) Total length (mm) ( $\pm 1$  SE) of yearlings in spring 1994 from each 1993 bout. Numbers represent sample sizes. (b) Proportion of the total fry produced in 1993 from each 1993 bout. Numbers represent actual proportions. (c) Proportion of recruits from each 1993 bout in spring 1994. Numbers represent actual proportions. (d) Relative proportional survivorship to spring 1994 for each 1993 bout, calculated by dividing the proportion of fry produced in 1993 (b) into the proportion of recruits in 1994 (c). The broken line represents a survival value of 1.0. A value above the line indicates an increase in representation; a value below indicates a decrease.



**Fig. 3.** Data summarized by 1993 trimester. (a) Total length (mm) ( $\pm 1$  SE) of yearlings in spring 1994 from each 1993 trimester. Numbers represent sample sizes. (b) Proportion of the total fry produced in 1993 from each 1993 trimester. Numbers represent actual proportions. (c) Proportion of recruits from each 1993 trimester in spring 1994. Numbers represent actual proportions. (d) Relative proportional survivorship to spring 1994 for each 1993 bout, calculated by dividing the proportion of fry produced in 1993 (b) into the proportion of recruits in 1994 (c). The broken line represents a survival value of 1.0. A value greater than 1.0 indicates an increase in representation; a value less than 1.0 indicates a decrease.



fry to age 1 were uniform across time, then we would expect the distribution of age-1 bluegill in 1994 to be the same as the distribution of fry in 1993. Chi-square tests indicated that the distribution of age-1 fish in 1994 was significantly different than that expected from 1993 fry production (by trimester:  $df = 2$ ,  $\chi^2 = 37.42$ ,  $p < 0.0001$ ; by bout:  $df = 7$ ,  $\chi^2 = 484.83$ ,  $p < 0.0001$ ).

The ratio of 1994 to 1993 proportions yields a measure of survival that can be compared across spawning bouts (Fig. 2d). For example, fry produced during the first bout of spawning in 1993 made up 0.07% of all 1993 fry, but made up 5.59% of recruits into 1994. This resulted in a relative proportional survivorship of 79.81 (5.59/0.07), indicating that the first bout produced about 80 times more recruits than expected on the basis of the 1993 numbers. The relative proportional survivorship tended to decrease with successive bouts, a trend that was more clear when the breeding season was divided into trimesters (Fig. 3d). Early-born individuals increased dramatically in representation (231% of 1993); middle-season individuals decreased slightly, and late-season individuals dropped sharply. Note that survivorship in the final bout (Fig. 2d) looks higher than might be expected. However, this may simply be an artifact of sampling bias as this was the only age-1 individual found to be from the eighth spawning bout.

## Discussion

This study directly links the production of free-swimming fry from bluegill sunfish nests to recruitment into the age-1 year-class. Fry from the first trimester contributed substantially (40%) to year-class composition even though they represented a small proportion of the total fry production (17%), a 231% increase. Thus, early-season fry contributed disproportionately to the cohort. Moreover, the study shows that early-season fry obtain larger body sizes as 1 year olds, probably because of the longer growing season, which may account for their increased survivorship.

Past studies of survivorship to age 1 have not made the connection between survivorship and date of birth. We know that size-dependent processes can have considerable effects on the survivorship of young-of-the-year individuals. A number of studies have demonstrated that predation can be size selective, affecting more intensely the smaller individuals in a population (Post and Prankevicus 1987; Post and Evans 1989a; but for an exception see Litvak and Leggett 1992). Other studies indicate that larger individuals have a greater probability of surviving winter starvation periods (Oliver et al. 1979; Toney and Coble 1979; Shuter et al. 1980; Post and Evans 1989b; Smith and Griffith 1994). On the basis of these results, we expect the larger individuals in a population or cohort to be favored and to show the highest survivorship. But who are the larger individuals in a cohort and from where do they come? This issue has not been previously addressed, and no study has demonstrated the link between fry production and actual recruitment to age 1. Thus, the results of this study advance our understanding of the relationship between recruitment and size-dependent processes.

The data clearly show that early-emerging fry attain the largest body size by winter. The most obvious explanation for this is that early-season young of the year have available to them a longer growing season. The earliest born fry in 1993

**Table 1.** Results from an analysis of covariance comparing changes in body size with age of early-, middle-, and late-season recruits.

	SS	df	MS	F	p
Test for differences in slopes					
Error	812.93	129	6.30		
Age	171.67	10	17.17	2.72	0.005
Trimester	628.67	2	314.33	49.88	<0.001
Trimester × age	98.47	19	5.18	0.82	0.677
Test for differences in intercepts					
Error	994.47	157	6.33		
Age	124.36	1	124.36	19.63	<0.001
Trimester	810.03	2	405.02	63.94	<0.001

**Note:** Regression lines from each trimester are tested for significant differences in slopes, and intercepts. SS, sum of squares; df, degrees of freedom; MS, mean square.

had 48% more growing days than the latest born. Moreover, there is a progressive decline in fall body size with each successive bout of spawning. Therefore, the more time they have to grow, the larger they get. Alternative explanations of the trend seem less plausible. First, if early-season fry have greater food resources available to them, then larger daily growth increments should be associated with early-born individuals. However, growth rates were highly variable and showed no relationship with birth date. Second, our data indicate that fry size at swim-up decreases slightly through the spawning season. However, relative to the length of the growing season, fry size does not make a statistically significant contribution to the variation in age-1 body size. Third, early- and late-season fry obtained similar size at age.

Early-emerging fry also have the highest survival to age 1. There are three potential hypotheses that can explain this result. First, the larger fall body size attained by early-season fry may result in greater over-winter survival. Since body size is allometrically related to metabolic rate and energy reserves (Brett and Groves 1979; Shuter and Post 1990), and bluegill do not feed during the winter (Keast 1968; Keast 1977), larger individuals should have the highest probability of surviving to spring (Cargnelli and Gross, see footnote 2). Our data are consistent with this, as body size and survival are highly correlated.

A second explanation to consider is size-selective predation during the growing season. Post and Prankevicius (1987) found that growth rates and the composition of the predator population determine whether predation has a significant size-dependent effect. Early-emerging bluegill fry did not have the advantage of faster growth rates, and so all young of the year spent similar amounts of time within vulnerable size-classes (Werner and Gilliam 1984). Predation on age-0 bluegill in Lake Opinicon comes from a number of sources (Keast 1985): (i) all age-classes of bass, *Micropterus dolomieu* and *Micropterus salmoides*; (ii) older age-classes of yellow perch, *Perca flavescens*; and (iii) all age-classes of northern pike, *Esox lucius*. These predators are present throughout the growing season and are probably not gape limited. Thus, all young of the year were probably exposed to similar predation pressures. This does not, however, fully exclude the possibility of size-selective predation during the growing season, since other fac-

**Table 2.** Results of a multiple regression analysis testing the relative contributions of birth date (spawning bout) and fry size to the body size attained by bluegill sunfish recruits ( $r^2 = 0.983$ ,  $F = 56.373$ ,  $p = 0.0087$ ).

Variable	$\beta$	t	p
Spawning bout	-1.055	-9.214	0.0116
Fry size at swim-up	-0.118	-1.033	0.4103
Constant		10.622	0.0087

tors such as predator-avoidance capability may be size dependent.

Third, middle- and late-season fry may experience greater mortality relative to early-season fry as a result of food limitation. However, this is unlikely because middle- and late-season fry grew at approximately the same rate as early-emerging fry and attained a size at age similar to that of the early-season fry.

The phenomenon of size-dependent over-winter mortality is receiving increasing attention, in both experimental (Oliver et al. 1979; Toney and Coble 1979; Post and Evans 1989b; Smith and Griffith 1994) and descriptive studies (Toney and Coble 1979; Shuter et al. 1980; Post and Evans 1989b). Our results correlate survivorship with actual spawning dates, showing that larger individuals with higher survivorship are coming from the early parts of the season. This suggests that size-dependent over-winter mortality can be an important process operating within a cohort and indicates the value of early season spawning to the year-class and population. If the size and survivorship advantages of early season fry were to accumulate each year to adulthood (Baylis et al. 1993), then the value of early spawning would be even greater than indicated by our results. Yearlings in our study varied in size by 18 mm, or 50%, after less than 1 year. Parental males of age 8, the most common breeding age-class, vary in size by 59 mm, or 38% ( $n = 197$ ), a result, at least in part, of this variation in yearling size. Larger males have significantly higher breeding success (Gross 1980), and thus early-season fry contribute the most to the population in terms of numbers, and probably also as the largest, most valuable fish in the population.

Our study also suggests that variation in the length and quality of the growing season will strongly affect year-class strength. Small changes in the growing season, either by a delayed spring or early fall, may prevent individuals from attaining a minimum body size required to survive the winter. Thus, in a year in which the spring is cold and spawning is delayed, the average fall size attained by young of the year would decrease, resulting in increased total over-winter mortality and a weak year-class. Conversely, in an early season the average fall body size is increased and the total over-winter mortality should decrease. Although very simplistic, these scenarios show the importance of understanding the temporal dimension within a cohort to understand year-class dynamics.

Finally, the results of this study hold interesting implications for the breeding structure of bluegill sunfish. First, the higher value of early-season fry will favor adult males and females that spawn early. However, there are costs associated with early nesting for males and only individuals that can afford to pay these costs will nest early (L.M. Cargnelli and M.R. Gross, University of Toronto, unpublished data). As

well, differences in the value of offspring at various times in the season (from Fig. 3d: 2.3 versus 0.9 versus 0.6) will have important impacts on the investment decisions of parental males (Coleman et al. 1985). For example, early-spawning parental males should invest more effort in a clutch of the same size as one spawned later in the season, all else being equal. Third, the size and survivorship advantages of early fry may accumulate through to maturity at age 7 or 8 years for parental males and age 5 or 6 years for females (Gross 1980). Since only the largest and fastest growing males in the parental life history mature at 7 years (Gross and Charnov 1980), this would save 1 year of mortality and further ensures the breeding contribution of early-season fry. Finally, the relationship between seasonal birth date and the relative production of males to the alternative life histories of cuckolder and parental males (Gross 1982, 1991) remains to be explored. Males maturing as cuckolders do so at age 2 and sneak fertilizations from the nests of parental males. If body size is more important to the cuckolder than parental life history, then cuckolder males may constitute a greater proportion of early-season recruits.

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