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PROTRACTED REPRODUCTION IN SUNFISH: THE TEMPORAL DIMENSION IN FISH RECRUITMENT REVISITED

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Abstract. Understanding how life histories influence reproductive success under uncertain conditions is necessary to predict population dynamics. For many organisms, protracted reproduction may increase expected offspring recruitment in variable environments, requiring that temporal patterns of reproduction be considered when developing management or conservation strategies. We explored the interrelationships among birth date, production of embryos on nests, survival of larvae to the open-water stage, and survival of juveniles through the first fall and winter of life for bluegill and pumpkinseed sunfish (*Lepomis macrochirus* and *L. gibbosus*) in Lake Opinicon, Ontario, during May 1998 through May 1999. Age-0 sunfish were sampled with nesting surveys for embryos, surface tows for free-swimming larvae, and seining/trawling for juveniles. Age of juveniles (days post swim-up) was quantified using otoliths. The abundance of embryos on nests and the density of open-water larvae were unrelated across all dates and sites. Although 40% of larvae had appeared in the open water by 12 June, most juveniles sampled in the fall were produced after that time, suggesting that high mortality of early produced larvae occurred. Larval survival to the juvenile stage was generally unrelated to the abundance of edible zooplankton taxa during swim-up from nests. Larval survival was often highest at temperatures >23.5°C. Fall length of age-0 sunfish increased with increasing age. Both age-specific length and mean lengths shifted positively between October 1998 and May 1999, suggesting that growth of all individuals and perhaps selective mortality of small juveniles occurred.

Although early reproduction may increase sizes reached by fall and thereby improve overwinter survival, early hatched larvae are subject to variable environmental factors that may reduce survival. Late-hatched larvae may reach relatively smaller sizes by fall, but have higher survival probabilities during this life stage. Protracted reproduction appears to be a response to variable environmental factors influencing growth and survival across multiple life stages. As such, all reproducing adults, rather than those perceived to produce offspring during typically favorable times, must be protected from exploitation or other human-induced perturbations.

Key words: environmental variability; Lake Opinicon (Ontario, Canada); Lepomis; *management decisions and population sustainability; population management; recruitment to reproductive age; reproduction, protracted; stage-specific survival; sunfish, larvae and juveniles.*

INTRODUCTION

Many organisms including amphibians (Wilbur 1997), insects (Tauber et al. 1986), and fish (Winemiller and Rose 1992) must contend with environmental variation that threatens to reduce their success. To develop sound strategies for sustaining, enhancing, or controlling (e.g., pest insects) these species, conservationists and managers must appreciate how environmental variation affects their population dynamics. Understanding how life histories are adapted to maximize fitness under uncertain conditions is a critical requisite for accomplishing this goal.

Many species residing in variable environments experience their highest mortality during the first year of life (Werner and Gilliam 1984). These species must possess phenotypic traits that offset the high environmental variability driving first-year mortality (Stearns 1976, Roff 1992). Indeed, variance in life-history traits may largely be explained by the trade-offs among offspring survivorship, adult fecundity, and age at maturity that maximize recruitment to the reproductive age (Leggett and Carscadden 1978, Winemiller and Rose 1992). How these traits interact to affect recruitment must be considered when developing conservation or management strategies (e.g., Alford and Richards [1999] for amphibians; Frank and Leggett [1994] for fish).

Trade-offs between offspring survival and other life-history traits differ broadly both among populations and among taxa as a function of system-specific en-

vironmental variability (Leggett and Carscadden 1978, Drake et al. 1997, Doughty and Shine 1998, Johansson and Rowe 1999). For fish, differences in environmental variation inherent in marine or freshwater systems may determine whether survival varies more during larval or juvenile stages (Houde 1994; also see Houde 1997). If such generalizations hold, research elucidating processes that regulate cohort strength may be focused on the appropriate, system-specific critical life stage (May 1974, Leggett and DeBlois 1994, Sogard 1997).

Although identifying critical life stages may be a crucial first step for predicting fluctuations in population abundances and developing stage-specific management strategies, processes regulating growth and survival in any given life stage are certainly not isolated (Ludsin and DeVries 1997). Events occurring during early life stages regulate events later in life in many organisms (Alford and Wilbur 1985, Sredl and Collins 1991, Tonn et al. 1992, Lawler and Morin 1993, Wilbur 1997, Garvey et al. 1998a, Post et al. 1998). For many piscivorous fish, subtle differences in the timing of hatching of eggs may determine whether gape-limited juveniles grow sufficiently large to consume piscine prey, increase their energy intake, grow rapidly, and reach large fall size (Adams and DeAngelis 1987, Goodgame and Miranda 1993, Phillips et al. 1995). Because large size as a function of early interactions often increases the probability of winter survival in temperate-latitude fish (Post and Evans 1989, Miranda and Hubbard 1994, Garvey et al. 1998c) and amphibians (Dratnal and Davies 1990, Jiang and Claussen 1992), interactions among life stages and their consequences for first-year growth have important implications for recruitment to reproductive age.

Linkages among life stages are likely to be important in organisms that have protracted reproduction because temporally variable conditions may translate into variable success within a cohort. Similar to classic r-strategists (MacArthur and Wilson 1967), fish species that spawn multiple times during a year are typically small bodied and produce small clutches during each reproductive event (Winemiller and Rose 1992). This "opportunistic" strategy (Winemiller and Rose 1992) effectively increases total reproductive output, presumably as a response to highly unpredictable environmental conditions. Sunfishes Lepomis spp. have a prolonged spawning season that often persists for periods greater than one month (Claussen 1991, Danylchuk and Fox 1994b, Fox and Crivelli 1998). In departure from an opportunistic strategy, the total annual reproductive output of sunfish is lower than that expected for a typical multiple-batch-spawning species, perhaps as a consequence of the high energy cost of nest building and parental care characteristic of this group (Fox and Crivelli 1998).

Although protracted reproduction may increase lifetime expected fitness in variable environments, many investigators have suggested that early spawning con-

veys a distinct advantage in fish (Atlantic cod: Tupper and Boutilier 1995; largemouth bass: Trebitz 1991). Because large adults often reproduce earlier than small counterparts (Goodgame and Miranda 1993), adult size structure may then have important implications for offspring success (Danylchuk and Fox 1994a, b). During one year in Lake Opinicon, Ontario, offspring produced early in the season by large adults grew to larger sizes and experienced disproportionately higher survival through their first winter than those produced by small, late-spawning adults (Cargnelli and Gross 1996). The specific life stages at which most mortality occurred were not identified. Large male sunfish reproduce more successfully than small counterparts because they attract more females and produce more offspring (Claussen 1991), further ensuring that large adults contribute markedly to future cohorts.

If the probability of offspring success declines precipitously through the season and reproductive costs are quite high, why do some organisms in temperate environments reproduce late in the season? In particular, protracted spawning appears disadvantageous for small adult sunfish with low expected reproductive success. So if it occurs, late spawning by small adults must provide some benefit. Failing this it would be excluded in favor of delayed reproduction later in life. To understand implications of fisheries management that alters adult size structure or temporal reproductive patterns, we must (1) refine our understanding of how linkages among interdependent life stages affect cohort strength and (2) assess the relative reproductive consequences of protracted reproduction. We returned to the sunfish assemblage in Lake Opinicon originally studied by Cargnelli and Gross (1996) to revisit the process they coined the "temporal dimension in fish recruitment."

MATERIALS AND METHODS

Study site and organisms

Patterns of adult sunfish reproduction and the recruitment of their offspring to the second year of life were quantified in mesotrophic Lake Opinicon, Leeds County, Ontario, Canada (787 ha) during May through October 1998 and May 1999 (Fig. 1). This system contains populations of both bluegill Lepomis macrochirus and pumpkinseed L. gibbosus (e.g., Keast and Eadie 1985, Booth and Keast 1986, Cargnelli and Gross 1996, 1997), with adults reaching total lengths >200 mm (J. E. Garvey, unpublished data). The congeners have similar life histories, with protracted spawning, nest building, and parental care by males. Most adult male bluegills in Lake Opinicon mature late at about age 7 or 8 (Drake et al. 1997). Pumpkinseed are believed to mature at similar ages in this system. Bluegills produce nests in large colonies, whereas pumpkinseed build solitary nests (Jennings 1997, Fox and Crivelli 1998). Larvae of both species

FIG. 1. Study sites in Lake Opinicon, Ontario, Canada, where nesting adults (with the exception of site D), larval fish, and zooplankton were sampled during May through August 1998. (See Table 1 for additional site information.)
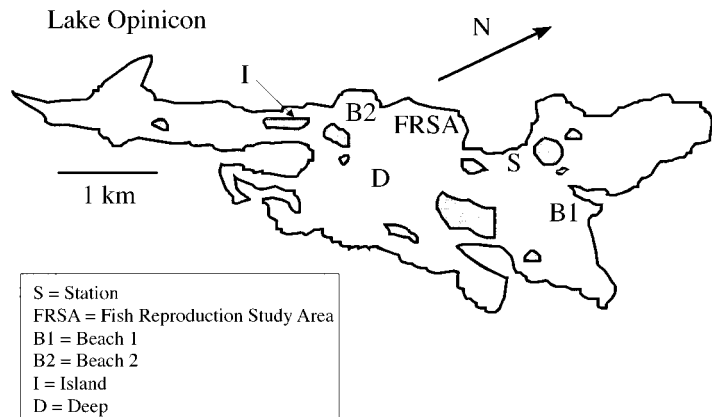
are obligate zooplanktivores, residing in the open water for 2–3 wk post-hatch before returning to the littoral zone as juveniles at about 20 mm total length (Werner and Hall 1988, Garvey and Stein 1998). During all of these early life stages, habitat and foraging characteristics are quite similar between species (Osenberg et al. 1992). And the larvae of these species are very similar morphologically (Auer 1982) and could not be readily distinguished in the field. Hence, we combined results for these two species to explore general relationships among the embryonic, larval, and juvenile stages.

Nesting survey

Weekly, we snorkeled to visually survey five sites for nesting adult bluegill and pumpkinseed males (Fig. 1). Sites were selected in shallow areas (<2 m depth) with substrates of sites representing those typically used by sunfish for spawning (Table 1; Fig. 1). The survey began when spawning started on 22 May 1998 and ceased on 20 July 1998 when spawning ended. During each weekly survey we swam transects searching for nesting adults until the designated area was completely covered (Table 1; Fig. 1). When a nest was

encountered, the adult was identified to species, and the status of offspring was recorded as (1) nest empty, (2) eggs present, (3) non-swimming embryos present (i.e., embryos did not have developed eyes or inflated swim bladders), or (4) swimming embryos present (i.e., embryos had well-developed, "golden" eyes and inflated swim bladders). Swimming golden-eye embryos were within one day of becoming free-swimming, exogenous-feeding larvae in the open water. To estimate the number of embryos produced on nests we removed all individuals from five pumpkinseed and five bluegill nests with a turkey baster (see Claussen 1991). Embryos were preserved in 95% ethanol and later measured (nearest millimeter standard length, SL) and counted. Standard length rather than total length (TL) was quantified for larvae because caudal fins were often damaged.

Open-water sampling

Limnetic sunfish larvae (<15 mm SL) were sampled twice weekly during 12 May through 6 August 1998 with two, 0.5-m diameter, 500-μm mesh conical nets. Nets were towed simultaneously at the surface. We sampled four shallow, inshore sites close to the nesting

TABLE 1. Location and dominant characteristics of sampling sites in Lake Opinicon, Ontario, Canada, during May through October 1998 and May 1999. All sites correspond to those in Fig. 1.

Site name	Characteristics	Area surveyed for nests (m²)	Nesting survey?	Ichthyoplankton survey?	Zooplankton survey?
Station	Sand/rock/silt/macrophyte	5 400	Y	Y	Y
FRSA	Sand/macrophyte	3 277	Y	Y	Y
Beach 1	Sand	1 120	Y	Y	Y
Beach 2	Macrophyte/silt	1 925	Y	N†	N†
Island	Macrophyte/silt	1 935	Y	Y	Y
Deep	Open water	NA	N	Y	Y

Notes: The Station site was located on the north shore near the Queen's University Biological Station (QUBS). The FRSA site is roughly the same as the Fish Reproduction Study Area described in Claussen (1991) and Cargnelli and Gross (1996). Beach 1 was a sandy bay located in the northeast portion of the lake. Beach 2 and Island were located in the northwest portion of the lake. The Deep site was in the center of the lake near one of the deepest areas (8 m). All other sites were ≤2.5 m depth. Y = yes, N = no; NA = not applicable.

† Because the Beach 2 site was close to the Island site, ichthyoplankton and zooplankton data corresponding to this site were derived from the Island site.

survey sites and one deep, offshore site (Table 1; Fig. 1). The volume of water sampled was quantified with an attached flowmeter. Larval fish were preserved in 95% ethanol, identified to genus, and counted to estimate number of larval sunfish per cubic meter (as per Stahl and Stein [1994]). At least five larvae per site were measured (millimeters SL). Larval densities at each site were averaged between the two tows.

During 6 May through 6 August 1998 we collected zooplankton twice weekly at the same five stations where larval fish were sampled (Table 1; Fig. 1). Zooplankton was collected with a 0.3-m diameter net (54-μm mesh) towed from the bottom to the surface, and preserved in 70% ethanol. To quantify densities of zooplankton, we identified cladocerans and rotifers to genus and copepods as calanoids, cyclopoids, or nauplii. For abundant taxa, a minimum of 50 individuals per sample were counted from a well-mixed subsample. For rare taxa, we counted one eighth of the sample. If we calculated that the total number within a sample was ≤25 individuals, we discontinued sampling. If we estimated >25 individuals/sample from that eighth, we continued counting until either 50 individuals or the entire sample was counted (Stahl and Stein 1994). Average daily water temperature data (1-m depth) were obtained from a continuous record maintained by the Queen's University Biological Station (QUBS; Elgin, Ontario, Canada).

Juveniles and otoliths

Juveniles were collected on two dates in fall 1998 (21 September and 6 October) and two dates in spring 1999 (11–12 May). In fall, inshore seining was ineffective at capturing juvenile sunfish. We used a small bottom trawl net (5-mm mesh) to capture sunfish in offshore vegetation at 1–3 m depth. In spring, we used a bag seine (10 m long, 3-mm mesh) to capture sunfish at the inshore sites where the nesting survey was conducted (Table 1; Fig. 1). All sunfish <80 mm TL (about 63 mm SL) were immediately preserved in 95% ethanol. Total length of juvenile fish rather than SL was quantified. Juveniles were identified to species in the laboratory using diagnostic morphological characteristics of gill rakers (Trautman 1981). Age (0 or 1) was initially determined by searching for annuli on scales with a dissecting scope (DeVries and Frie 1996). This method confirmed that no sunfish >60 mm TL (~47 mm SL) was age-0.

Otoliths were removed from a subsample of juvenile pumpkinseed and bluegill ≤60 mm TL collected on each date (September 1998, $N = 64$ fish; October 1998, $N = 39$ fish; May 1998, $N = 48$ fish). One sagittal otolith per fish was mounted on a glass slide with thermoplastic cement, and ground and polished with 12-μm and 3-μm lapping paper, respectively (see DeVries and Frie [1996] for a review). Sunfish from all three dates were identified as either age-0 or age-1 by the presence of an annual ring, determined using a com-

pound microscope. Daily rings of age-0 fish were read with a compound microscope for fish captured in fall 1998. A second reader verified ring counts of the initial reader. Ring counts for fish collected in spring 1999 were unreliable because increments between daily rings declined during winter and were impossible to differentiate.

Production of daily rings was verified with larvae of known ages reared in the laboratory. Non-swimming pumpkinseed and bluegill embryos were collected from nests on 26 June 1998. Larvae swam-up on the night of 28 June 1998 and were transferred to 100-mL beakers immersed in a bath of flowing water pumped from Lake Opinicon. Small zooplankton (<150 μm) were added to beakers daily after a water change. During a 25-d period a subsample of 1–5 larvae was removed every 1–2 d and preserved in ethanol. Larvae were then aged using otoliths (see above). An initial sample of embryos from nests was aged as well. Daily rings were not detected on any embryos from nests ($N = 40$ fish), suggesting that embryos had hatched within 24 h of collection (i.e., 25 June 1998). Counts of daily rings corresponded well to days post-removal from nests ($r^2 = 0.91$; slope = 1.2; $N = 21$ bluegill, $N = 58$ pumpkinseed). From this, we confirmed that ring counts corresponded to days post-hatching and that swim-up (the point that larvae become free swimming following inflation of their swim bladder) occurred approximately three days after the hatch date.

Analyses

Site-specific larval production.—Larvae produced inshore may be transported offshore by advection or remain inshore if advection is not important. For each sampling date, we used linear regression to compare density of sunfish larvae at the deep site to the average density of larvae produced at the four inshore sites. Failure to detect density differences among sites would indicate that advection transported larvae from inshore nesting areas into the open lake.

We assumed that if larvae sampled at the deep site represented survivors that had migrated to this area, then they would be older and larger than those sampled at the inshore sites. We used a one-way ANOVA, pooling larvae among dates for each site to determine whether larval sizes varied among sites. Alternatively, if larvae were not quickly transported from their nesting sites or if survival during the transition from the nests to the open water was relatively invariant, we expected close correspondence between embryo production on nests and associated site-specific larval densities. We tested the null hypothesis that golden-eye embryo production on nests (using our average estimate of embryos on nests per area surveyed) was unrelated to larval density at each site and date using a two-dimensional Kolmogorov-Smirnov (2-DKS) test. This test detects changes in variance within bivariate distributions, which is particularly useful if threshold

changes occur (Garvey et al. 1998*b*). Exact *P* values for the 2-DKS were generated by rerandomizing the original data 5000 times and comparing a randomly generated test statistic, *D,* to the *D* generated for the observed data pairs (Garvey et al. 1998*b*).

Survival and growth.—In all analyses, juveniles collected on 21 September and 6 October were treated separately. Age-specific survival was estimated by comparing the cumulative frequency distributions of swim-up dates for juveniles sampled on the two fall dates to the cumulative frequency distribution of open-water larvae produced in the spring. A traditional Kolmogorov-Smirnov (KS) test was used to test for the maximum difference between the distributions (SAS Institute 1990). To further characterize differences between the back-calculated and larval distributions, we calculated an index of survival (IS) for juveniles sampled on the two fall dates. This index was comprised of the proportion of individuals within each back-calculated hatch date divided by the proportion of larvae produced during that spring date. For dates on which larvae were not sampled in spring, we assumed that larval densities were the same as on the previous sampling date. An index value near 1 indicated equal representation of individuals in spring and fall distributions. Index values less than or greater than 1 were interpreted as representing lower than or higher than expected survival to the juvenile stage. We used the 2-DKS to explore relationships between individual IS and edible zooplankton densities and temperature on the back-calculated dates when larvae first swam-up from nests and fed exogenously (the hatch date plus 3 d). Edible zooplankters are defined as those small enough for recent swim-up larvae to consume (Bremigan and Stein 1994). Hence, we only included small taxa (i.e., copepod nauplii and rotifers) in this analysis (Bremigan and Stein 1994).

Age can influence fall size. We used an analysis of covariance (ANCOVA) to determine how juvenile lengths varied as a function of hatch date (the covariate) and fall sampling date (i.e., 21 September and 6 October). To further explore how growth varied as a function of age during fall, we regressed hatch date against the width (in micrometers) of the last 20 daily rings on otoliths from 21 September and 6 October. Increment width correlates positively with somatic growth (DeVries and Frie 1996). If size-selective mortality occurred during winter, the length frequency distribution would shift to one dominated by larger individuals (Garvey et al. 1998*c*). Hence, we used a KS test to compare cumulative length frequency distributions between the two fall dates and between 6 October and 11–12 May.

RESULTS

Time series

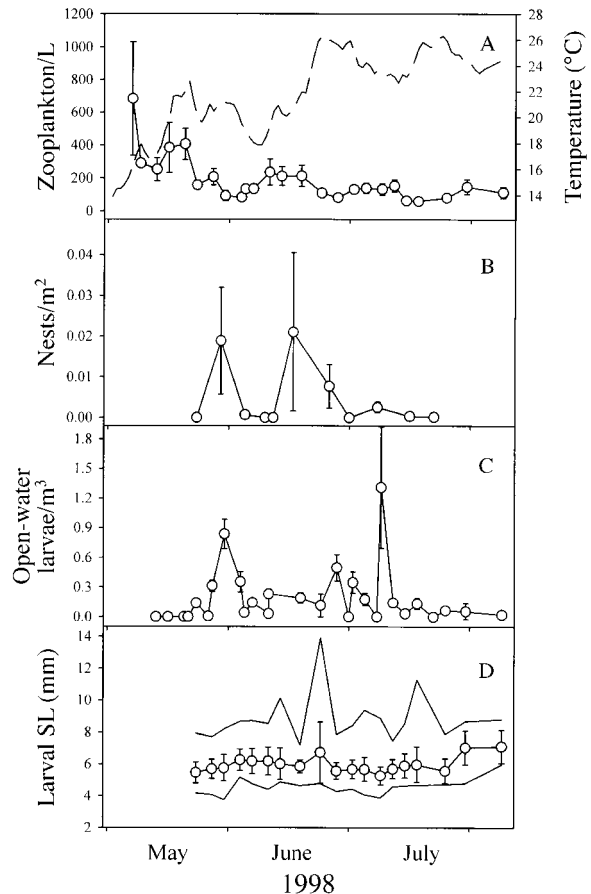Zooplankton densities across sites exceeded 600 zooplankters/L in May and declined to 60–100 zoo-

FIG. 2. Survey results. All data were collected in Lake Opinicon, Ontario, Canada, during May through August 1998. (A) Density of zooplankton (rotifers plus crustaceans, open symbols, left-hand vertical axis; data are means ± 1 SE; $N = 5$ sites per date) and mean daily water temperature (1-m depth; dashed line, right-hand vertical axis). (B) Density of bluegill and pumpkinseed nests with golden-eye larvae surveyed with snorkeling at five sites; data are means ± 1 SE. (C) Density of sunfish larvae sampled with paired 500-μm-mesh conical nets towed at the surface ($N = 4$ inshore sites per date). Densities of larvae at the deep-water site were only ~8% of average inshore densities on each date. Data are means ± 1 SE. (D) Larval standard lengths ($N = 25$ larvae total per date). Data are means ± 1 SD; solid lines above and below the symbols are the maximum and minimum larval fish lengths for each date.

plankters/L by late summer (Fig. 2A). Across all sampling dates, an average of 70% (by number) of the zooplankton was comprised of small copepod nauplii and rotifers edible to all sizes of bluegill.

Bluegill and pumpkinseed nests containing eggs and guarding males were first encountered on 22 May when water temperatures reached 19°C. Golden-eye embryos first occurred on surveyed bluegill and pumpkinseed nests on 28 May (Fig. 2B). Nesting activity peaked twice during summer. The number of golden-eye embryos on nests was 1133 ± 553 embryos and 576 ± 305 embryos (mean ± 1 SD) for bluegill and pump-
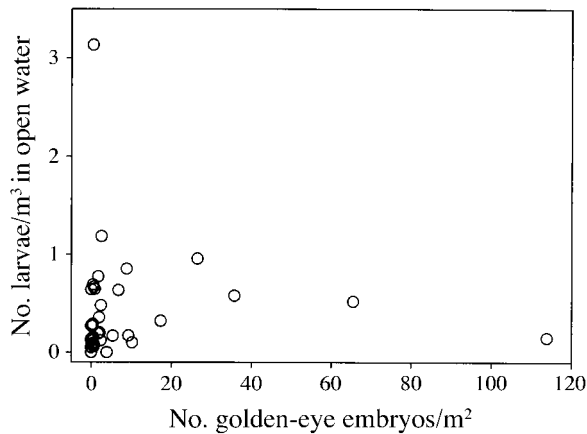
FIG. 3. Relationship between the density of golden-eye sunfish embryos surveyed weekly on nests and the density of sunfish larvae sampled in adjacent open-water sites 1–3 d following each nest survey (see Table 1 for description) for each site and date ($N = 38$) in Lake Opinicon, Ontario, Canada, during May through July 1998.

kinseed, respectively ($N = 5$ fish for each species). Between 22% and 32% of nests encountered on each date through 7 June were occupied by pumpkinseed males. For the remainder of the summer, pumpkinseed nests were more common than bluegill nests, comprising 51–100% of the nests encountered. The last dates on which males were observed guarding nests were 5 July and 13 July for bluegill and pumpkinseed, respectively.

Sunfish larvae first appeared in inshore ichthyoplankton tows on 22 May (Fig. 2C), the same date that guarding males (but not golden-eye embryos) were first encountered. Obviously, nests with golden-eye larvae were missed before the first date that open-water larvae were sampled. Larval densities between the paired net tows were positively correlated across all dates and sites (Pearson's correlation: $r = 0.93$; $N = 90$ tows), indicating that densities in nets corresponded closely during each tow. Although larval densities were fairly similar among the inshore sites on each date (Fig. 2C), larval densities at the deep, offshore site (Deep) were only weakly related to those inshore (linear regression: $r^2 = 0.15$, $P = 0.08$), reaching only ~8% of the inshore estimates. Inshore densities of larvae peaked once in late May and once in early July (Fig. 2C). The sizes of larvae were similar among all sites with standard lengths being 5.87 ± 0.84 mm, 5.78 ± 0.86 mm, 5.88 ± 0.93 mm, 5.77 ± 0.79 mm, and 6.00 ± 0.94 mm (mean ± 1 SD) for the Station, FRSA, Beach1, Beach2/Island, and Deep sites, respectively (ANOVA: $F_{4, 408} = 0.48$, NS). Mean larval sizes were similar among all dates, except during 28 July and 6 August when mean lengths increased (Fig. 2D). Apparently, fewer small, recently hatched larvae were contributing to length distributions by late summer as spawning ceased.

Stage-specific survival

Production of golden-eye embryos varied tremendously among sites and dates (Fig. 3). At each site and date, their production and site-specific larval density in the open water on the following sample date were unrelated (Fig. 3; 2DKS: $D = 0.09$, $P = 0.13$). Local spawning activity did not directly translate to temporal patterns of larval production in the open water.

Survival of open-water larvae to the juvenile stage varied among dates (Fig. 4). By 12 June, 40% of the larvae were produced. However, back-calculated swimup distributions indicated that most juveniles captured in the fall derived from larvae produced in late June or thereafter (Fig. 4; Kolmogorov-Smirnov [KS]: September, $D = 0.39$, $P = 0.01$; October, $D = 0.42$, $P = 0.006$). Older age-0 juveniles were not missed by our sampling gear in fall because larger age-1 individuals were readily sampled by the trawling gear. Of all the fish aged with otoliths, 23% (all >48 mm TL) were age-1. We conclude that most larvae hatched before mid-June did not survive to the juvenile stage.

Edible zooplankton density on the date of larval swim-up following hatching was related to the index of survival developed for juveniles collected in October but not in September (two-dimensional [2-D] KS: September, $D = 0.05$, $P = 0.75$; October, $D = 0.13$, $P = 0.01$). Contrary to expectations, the analysis suggested that larval survival of October juveniles was greater on dates when small zooplankton densities were <100 individuals/L. This pattern may be due to the decline in zooplankton densities in late June and July when larval survival was often high. The occurrence of warm temperatures during swim-up did influence survival from the larval to juvenile stage (Fig. 5; 2-DKS: September, $D = 0.11$, $P = 0.03$; October, $D = 0.19$, $P = 0.0004$). The 2-DKS detected the largest change in bi-
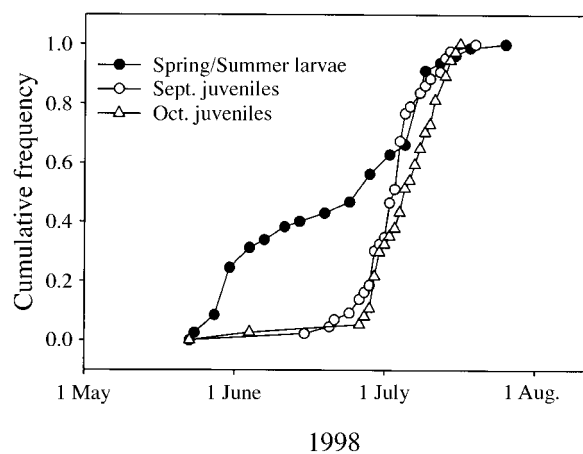

FIG. 4. Cumulative frequency distributions for sunfish larvae sampled in the open water in spring/summer and for back-calculated swim-up dates of sunfish juveniles collected on 21 September ($N = 43$) and 6 October 1998 ($N = 37$) in Lake Opinicon, Ontario, Canada.
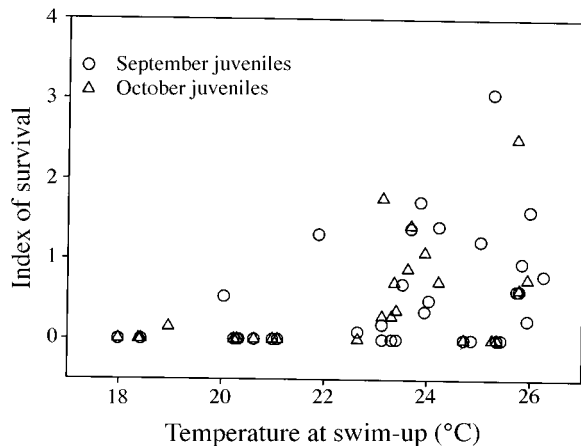
FIG. 5. Index of survival from the swim-up larval stage to the juvenile stage for sunfish juveniles as a function of mean daily water temperature on the date of swim-up. Juveniles were collected on 21 September ($N = 29$) and 6 October ($N = 28$) 1998 in Lake Opinicon, Ontario, Canada. The index of survival is the proportion of individuals within each swim-up date divided by the proportion of larvae produced during each spring date.
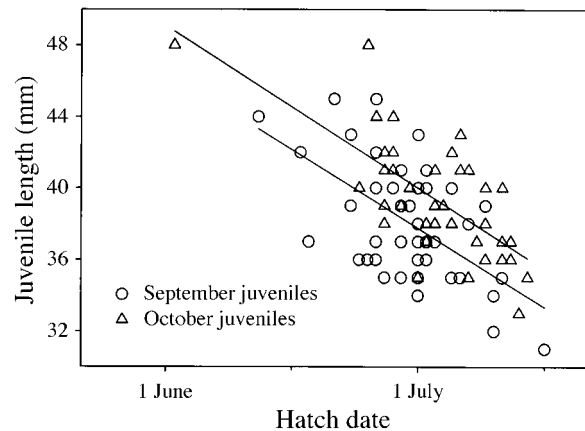

FIG. 6. Influence of back-calculated hatch date on fall total length of juvenile sunfish sampled on either 21 September ($N = 43$) or 6 October ($N = 36$) 1998 in Lake Opinicon, Ontario, Canada. Upper and lower regression lines correspond to October and September data, respectively.

variate distributions at 23.5°C for both the September and October juveniles. Below this apparent threshold temperature, survival was often low. At temperatures above this threshold, variation in survival increased and survival was frequently high.

Growth and survival

Length declined with hatch date (Fig. 6; ANCOVA: age, $F_{1,77} = 352.4$, $P = 0.0001$) and increased similarly for all ages between 21 September and 6 October (Fig. 6; ANCOVA: month, $F_{1,77} = 95.9$, $P = 0.0003$). Growth rates as estimated by the width of the last 20 daily rings on otoliths increased with hatch date in September (Fig. 7; linear regression, slope $= 1.24$, $r^2 = 0.55$), suggesting that younger fish grew more rapidly than older counterparts. By October, differences among the ages vanished (Fig. 7; linear regression, slope $= 0.16$, $r^2 = 0.01$), as growth of younger fish apparently declined.

Lengths of both bluegill and pumpkinseed captured in the fall were similar. Pumpkinseed comprised 26% of the sunfish catch. Cumulative size distributions of age-0 sunfish (<48 mm; as confirmed by otoliths) did not appear to differ between the September and October sampling dates (Fig. 8; KS: $D = 0.17$, $P = 0.58$), suggesting that no size-selective mortality occurred in the fall. From October through May, the length frequency distribution of sunfish in the 1998 cohort shifted to one dominated by large individuals (Fig. 8; KS: $D = 0.53$, $P = 0.0001$). Total length increased from 39.3 ± 3.3 mm to 44.5 ± 3.5 mm (mean $\pm$ 1 SD) between October 1998 and May 1999. This suggests the selective loss of small individuals during winter. Otoliths from the May 1999 sample revealed that some individuals as large as 51 mm TL derived from the

1998 cohort. Some growth may have occurred during fall through spring (Fig. 8).

DISCUSSION

Interdependent processes regulating growth and survival at multiple life stages drove recruitment of age-0 sunfish in Lake Opinicon in 1998. In contrast to previous findings in this system (Cargnelli and Gross 1996), the hypothesis that early hatching consistently conveys a survival advantage was unsupported. We argue below that protracted reproduction effectively increases expected lifetime fitness in the face of environmental variation, which has important implications for management of fish and other organisms with similar life histories.
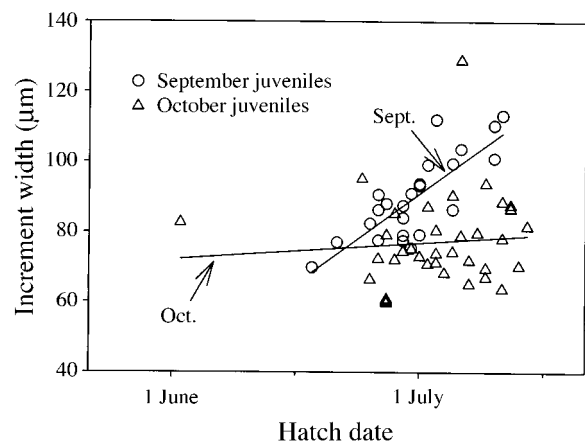

FIG. 7. Effect of hatch date on the width of the last 20 daily rings on otoliths from juveniles collected on 21 September ($N = 32$) and 6 October ($N = 36$) 1998. Increment width correlates positively with somatic growth.
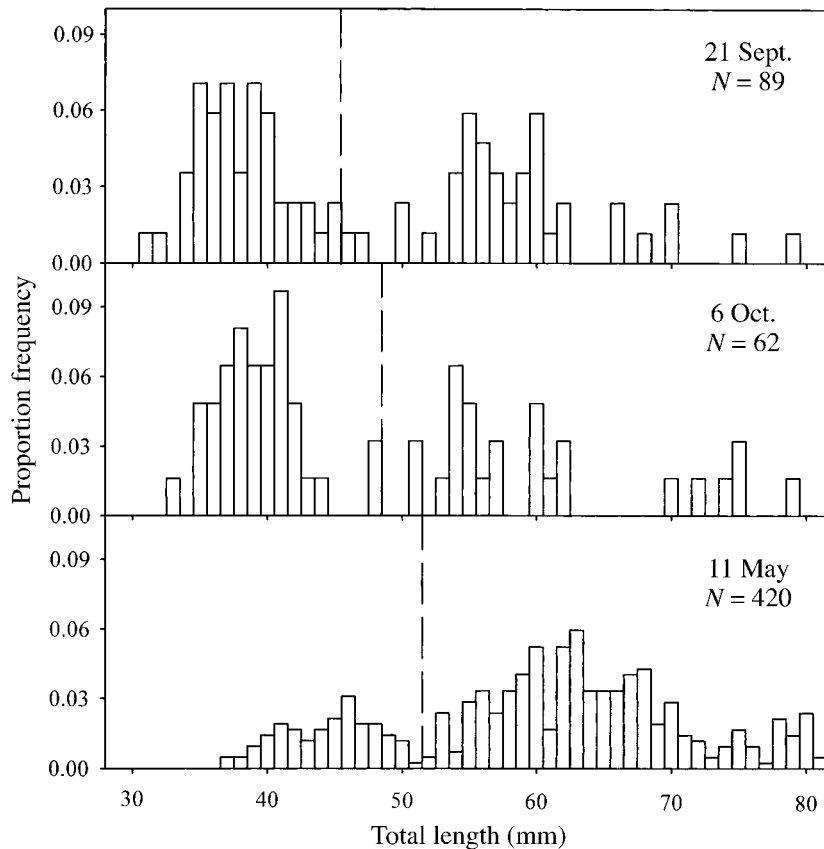
FIG. 8.   Length frequency distributions for sunfish collected on 21 September and 6 October 1998 and on 11 May 1999 in Lake Opinicon, Ontario, Canada. Otoliths were used to verify that sunfish at lengths to the left of the dashed line in each panel were members of the 1998 cohort. Fish at lengths to the right of the dashed line were produced in 1997 or earlier.

Interdependent life stages

Embryonic to larval stage.—Patterns of age-0 sunfish production must be regulated by temporal patterns of adult spawning. We found the presence of sunfish larvae in the open water to be closely linked temporally with the nesting activity of both species. While previous authors have reported that larval bluegill were grouped into discrete intra-annual cohorts as a function of colonial nesting events (Cargnelli and Gross 1996, Partridge and DeVries 1999), we observed the formation of bluegill colonies among sites within Lake Opinicon to be relatively asynchronous during May through July 1998. Solitary pumpkinseed nests were found throughout the spawning season at all sites.

Given that nests containing golden-eye embryos were encountered on most sampling dates, we conclude that larval production to the open water was continuous in both species through the season. The average density of free-swimming, golden-eye embryos on bluegill nests was about one order of magnitude lower than that quantified in previous, intensive nesting surveys in Lake Opinicon (Claussen 1991). This disparity may have arisen due to our relatively low sample size for nesting embryos ($N = 10$ nests total). Conversely, re-productive investment or survival of embryos from the egg stage to the free-swimming stage may have been relatively low during 1998. Densities on pumpkinseed nests were lower than those on bluegill nests, suggesting that average egg production per nest may be generally lower in this congener.

The densities of nesting embryos and open-water larvae were unrelated throughout the season. This lack of congruence may relate to our inability to sample the entire lake shoreline or to high mortality that occurred during larval dispersal. Elliott et al. (1997) reported high mortalities at this stage as a result of *Hydra* predation. Thus, site-specific variability in mortality may have translated to the variable relationship between nesting embryos and open-water larvae.

As expected (Post et al. 1995), the spatial distribution of open-water larvae was heterogeneous, with most larvae occurring in shallow-water areas near the nesting sites. This suggests that strong advection of larvae between inshore and offshore sites following swim-up was unlikely. Sizes of larvae were similar between inshore and offshore sites. We conclude that the few larvae sampled offshore did not represent older, larger survivors that had successfully migrated there. Rather,

a few larvae probably were transported to the offshore zone shortly following swim-up. While nesting activity was asynchronous among inshore sites, the variability in larval densities among sites within dates was less than that among dates. In particular, open-water larvae reached similar peak densities across all sites on two distinct dates. Based on our nesting survey results, we conclude that lake-wide congruence in production of larvae from nests was not an underlying mechanism. Lake-wide environmental conditions regulating the transition from nests to open water may have produced the synchronous appearance of open-water larvae among spatially distinct sites. Advective transport of larvae along the shoreline also may have contributed to the similarity among inshore sites, although some of the sites were well isolated from others (e.g., Beach 1 in Fig. 1).

Larval to juvenile stage.—A large proportion of early hatched sunfish larvae did not survive to the juvenile stage in Lake Opinicon. Intermediate- and late-hatched individuals experienced high survival to fall. Food availability or temperature during larval swim-up may have affected age-specific patterns of survival. Low food availability during the onset of exogenous feeding has been shown to influence survival in some systems, either by directly causing starvation or by reducing growth and increasing the time during which larvae are vulnerable to predators (Houde 1987, Leggett and DeBlois 1994, Letcher et al. 1996). Zooplankton density did not appear to influence survival to the juvenile stage in Lake Opinicon, suggesting that food availability was unimportant. Alternatively, warm temperatures >23.5°C appeared to greatly enhance survival to the juvenile stage. Water temperatures sharply declined from 21°C to about 18°C immediately following the peak of larval abundance in late May. Bioenergetics modeling using the generalized Wisconsin model (Hanson et al. 1997) revealed that declining spring temperatures are capable of reducing growth rates relative to those of larvae produced later during the summer (J. E. Garvey, *unpublished data*). If this temperature-induced delayed growth occurred, it is possible that the susceptibility of these larvae to predators was increased.

Cumulative mortality across the growing season may simply be higher for early spawned fish as a function of increasing duration of exposure to predators and other sources of mortality. However, Cargnelli and Gross (1996) reported that the earliest hatched individuals of the 1993 cohort of age-0 bluegill in Lake Opinicon were disproportionately abundant the following year. Further, rather than a *continuous* exponential increase in survival with declining age in 1998, as might be expected if mortality was cumulative, the cumulative hatch date distribution and index of survival of sunfish both suggested a marked *threshold* increase in survival of larvae produced following late June. Taken in combination, we conclude that early hatching

need not necessarily compromise first-summer survival through prolonged exposure to lethal factors.

Juvenile stage.—Early hatch of age-0 fish could extend their growing season and thereby increase fall body size (Phillips et al. 1995, Donovan et al. 1997). Large size often translates to improved winter survival in north-temperate systems (e.g., Post et al. 1998). Hence, relatively older (and larger) individuals may experience a higher probability of recruitment. In Lake Opinicon, fall size indeed increased with increasing age. Interestingly though, younger fish appeared to be growing more rapidly than older counterparts in early fall, perhaps due to some compensatory growth mechanism (Bertram et al. 1993). This difference vanished by late fall, perhaps as a function of declining fall temperatures. As expected, a higher proportion of large sunfish survived during winter 1998–1999 relative to their small counterparts. Some growth may also have contributed to the shift to larger sizes by spring.

Implications

Interdependent life stages.—Isolating single critical life stages in which variable mortality occurs may be insufficient for developing management strategies. This is particularly true for organisms undergoing complex ontogenetic changes during early life. For organisms with such unique life stages, events regulating growth and survival during both the larval and juvenile stages are important and interdependent (Ludsin and DeVries 1997). For sunfish in Lake Opinicon, early abiotic (i.e., temperature) conditions and biotic (i.e., predation) factors (Elliott et al. 1997) regulated survival during the larval stage. In turn, variations in growth of larvae surviving these effects translated into differential overwinter survival. Many species must contend with unpredictable early circumstances that have varying consequences for future life stages. To illustrate, abiotic characteristics of drying pools alter the development time and size at metamorphosis of amphibian larvae (Denver et al. 1998), thereby affecting future interactions during later terrestrial stages. A frustrating aspect of the amphibian system, however, is that ecological interactions following metamorphosis are often unknown because of the difficulty of sampling terrestrial stages. Important ecological mechanisms linked with early events in life may be missed, potentially weakening the ability to develop sound conservation or management strategies. Conversely, the sunfish system is ideal because of the ease with which interactions during all life stages can be assessed. Predicting population responses to environmental variation mandates an understanding of factors affecting growth and survival across multiple life stages. When possible, longitudinal, long-term studies are required to isolate important interactions and determine management options.

Variability, life histories, and management.—Management of populations requires a profound apprecia-

tion for the responses of life histories to uncertainty. To accomplish this, managers must understand long-term processes and subsequent responses of target populations. A popular view in fish ecology is that early spawning is better because it provides a survival advantage to offspring. Previous work in Lake Opinicon led to this conclusion (Cargnelli and Gross 1996). However, like our current study, this earlier study explored dynamics within only one cohort during one year, ignoring important variable environmental circumstances that confront this assemblage among years. Phenotypic variation in the timing of spawning may have important implications for responses to inter-annual variability. Combining results of this study with that of Cargnelli and Gross (1996) provides insight into long-term responses.

Phenotypic variation in reproductive timing may contribute to stable population structure across years. In one small Wisconsin lake, alternating sizes of small and large spawning smallmouth bass *Micropterus dolomieui* contribute to a relatively stable bimodal size distribution (Baylis et al. 1993, Wiegmann et al. 1997). Large adults compete effectively for nesting sites early in spring, producing offspring that mature early at small sizes. The resulting small adult offspring compete poorly for nesting sites and must spawn late in the spring, generating young that mature late and at large sizes. The cycle then repeats itself when these large adult offspring successfully compete for spawning sites in early spring. Because sunfish often compete in a size-specific fashion for nests, this mechanism may operate in Lake Opinicon, although it has yet to be explored.

In variable environments, variation in the timing of reproduction among individuals may provide survival insurance in the face of unpredictable spring conditions. During most years when spring conditions are amenable to larval survival, early spawning, large-bodied adults may indeed have very high reproductive success (Cargnelli and Gross 1996). However, during infrequent years when spring conditions reduce larval survival, late, small-bodied spawners have an advantage, although their reproductive output may still be lower than that of large counterparts during "good" years. Similar to diversified bet hedging (e.g., Philippi and Seger 1989), the phenotypic combination of early and late reproduction increases expected mean fitness through time. These life-history responses to environmental variation are common in many organisms, contributing to greater stability than expected if successful reproduction only occurred during typically favorable conditions.

To effectively manage populations, we must understand how life histories respond to environmental variation. If this is ignored, management strategies directed toward life stages or recruits that are believed to have the highest expected success given average conditions may inadvertently reduce population stability and resiliency. Several authors have proposed management strategies that protect early spawning adults from exploitation (e.g., Trebitz 1991). This argument is based on the assumption that early hatched individuals contribute strongly to cohort strength. Our data indicate that late-spawning adults can contribute significantly to year-class formation under specified environmental conditions. Given the potentially stochastic contribution of individual nests to larval production, spawning adults should be protected throughout the season.

Our research suggests that the size structure of populations and the temporal patterns of reproduction are important determinants of the responses of populations to environmental variation (see also Drake et al. 1997, Jennings 1997, Jennings et al. 1997). In fisheries, maintenance of age structure rather than size structure is often a key management focus (Hilborn and Walters 1992). Our results suggest that fisheries managers must also consider how size-specific regulations affect population stability under uncertain interannual conditions. Generally, conservationists and managers must identify the important interdependencies among life stages and determine how patterns of reproduction affect population dynamics through time. Only with a true grasp of this "temporal dimension in recruitment" may viable management options be developed.

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