EXPLORING MECHANISMS UNDERLYING RECRUITMENT OF WHITE CRAPPIE IN OHIO RESERVOIRS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

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* * * * *

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ABSTRACT

Organisms that produce many, small offspring generally exhibit variable population size, owing to variation in production and survival of offspring. Using a life-history approach, we focused on ecological mechanisms underlying the production and survival of white crappie *Pomoxis annularis*, a popular North American sport fish exhibiting high variability in recruitment to maturity (i.e., age-2).

Offspring production begins with adult energy allocation to reproduction. Female white crappies initiate ovary development during autumn, 6 months before spring spawning. To understand why females develop ovaries “early”, we used optimality and simulation models. Results revealed that early ovary development is an adaptation to uncertainty in spring feeding conditions.

To investigate how mean condition and egg production of the adult population influence larval density and age-2 catch per effort (CPE), we sampled white crappie from 14 reservoirs. Although mean condition influenced ovary characteristics, only population egg production influenced larval density and age-2 CPE. Thus, population egg production can limit recruitment success.

After larvae hatch, numerous mortality events occur before recruitment to age-2. We focused on two periods: between the larval and juvenile stage and during the first
winter of life. In reservoirs, we evaluated how zooplankton density, water temperature, and larval density influenced larval growth and survival. Growth increased with zooplankton density, whereas survival was unrelated to any measured variable. We then evaluated how food, fish size, and winter severity influenced winter survival in the lab. Winter severity regulated survival with only 47% of the juveniles surviving the severe winter, and 97% surviving the mild winter. Although temperatures < 4°C caused mortality in the lab, fish may occupy ≥ 4°C habitat during Ohio winters in the field.

Overall, white crappie recruitment is likely set by the egg or larval stage, though considerable winter mortality remains a possibility. With this caveat, we recommend that managers use catch restrictions to increase adult biomass and subsequent egg production to improve poor recruitment. Higher egg production should increase larval density and ultimately the number of fish recruiting to both maturity and the sport fishery.
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TABLE OF CONTENTS

Abstract ..................................................................................................................... ii

Acknowledgments ................................................................................................. iv

Vita ......................................................................................................................... vii

List of Tables ......................................................................................................... xi

List of Figures ....................................................................................................... xiv

Chapters:

1. Introduction ..................................................................................................... 1

   Overview of chapters ........................................................................................ 5
   Chapter 2 .......................................................................................................... 5
   Chapter 3 ......................................................................................................... 6
   Chapter 4 ......................................................................................................... 6
   Chapter 5 ......................................................................................................... 7
   Summary ............................................................................................................ 7

2. Optimal energy allocation: when should allocation to ovaries resume after
   spawning? ......................................................................................................... 10

   Introduction ..................................................................................................... 10
   Methods ........................................................................................................... 13
   White crappie life history ............................................................................... 13
   Modeling overview .......................................................................................... 14
   Dynamic programming model ....................................................................... 14
   Individual based model .................................................................................. 19
   Field sampling ................................................................................................. 21
   Results ............................................................................................................. 22
   Dynamic programming results ....................................................................... 22
   Individual-based model results ..................................................................... 24
   Field results ..................................................................................................... 26
Methods ................................................................................................. 112
Species life history ................................................................................ 112
Field and laboratory ............................................................................. 113
   Zooplankton sampling and estimation ............................................. 113
   Collection and aging of larvae ....................................................... 114
   Collection and aging of juveniles ..................................................... 115
Analyses .................................................................................................. 116
   Larval growth .................................................................................. 116
   Larval survival in 2000 .................................................................... 118
Results .................................................................................................... 121
   Zooplankton availability ............................................................... 121
   Larval growth ................................................................................ 122
   Larval survival in 2000 .................................................................. 123
Discussion .............................................................................................. 125
   Assumptions .................................................................................. 125
   Growth ............................................................................................ 127
   Survival ........................................................................................... 128
   Conclusions ................................................................................... 133
Literature Cited .................................................................................... 135

5. Winter temperatures influence survival of age-0 white crappie .. 153
   Introduction ..................................................................................... 153
   Methods .......................................................................................... 156
      Energy density of fish from Ohio reservoirs ................................ 156
      Experiment .................................................................................. 157
   Results ............................................................................................. 160
      Energy density of field fish ........................................................... 160
      Experiment .................................................................................. 160
   Discussion ........................................................................................ 163
      Implications for recruitment ......................................................... 166
   Literature Cited ............................................................................... 168

Bibliography .......................................................................................... 187
### LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Summary of seasonal water temperatures in 10 Ohio reservoirs during at least 2 years</td>
<td>38</td>
</tr>
<tr>
<td>2. Characteristics of 14 Ohio reservoirs that were differentially sampled for <em>Pomoxis</em> spp. larvae, adult white and black crappie, white crappie fecundity, and white crappie ovary energy density during 1998-2001. White crappie population is the mean percentage of adult white crappie (by number) of the total adult <em>Pomoxis</em> spp. populations (black and white crappie) across 4 years (1998-2001) of autumn trapnetting. Mean adult CPE (fish/net night) is the mean CPE of fish ≥ age-2 collected across 4 years of autumn trapnetting. CV is the coefficient of variation (σ/mean).</td>
<td>92</td>
</tr>
<tr>
<td>3. AICc model selection results to explain larval hatch ordered by Δi, where Δi is the difference between each model i and the model with the minimum AICc value (i.e., model 1). For each model, 17 observations (i.e., reservoir-years) were used. Parameter estimates for each independent variable, the residual sums of squares, and $r^2$ for each model also are provided.</td>
<td>93</td>
</tr>
<tr>
<td>4. Characteristics of Ohio reservoirs sampled for <em>Pomoxis</em> spp. larvae and zooplankton (i.e., crustacean and rotifer zooplankton) during 1998-2000. Juvenile white crappies also were sampled in five reservoirs. Mean chlorophyll a (µg/L) concentration is the grand mean of upstream- and downstream- integrated water samples collected weekly during May – June 2000. Trophic status is based on Wetzel (2002), where E represents eutrophic and M represents mesotrophic; greater or less than signs are used when concentrations fall between 2 trophic indicators. White crappie population is the percentage of adult white crappie (by number) of the total adult <em>Pomoxis</em> spp. populations (black crappie + white crappie) pooled over 4 years (1998-2001) of autumn trapnetting. Mean white and black crappie adult (age ≥ 2) CPE (fish/net night) provides a relative size of the adult populations during 1998 – 2001 (except for Knox, which is only from 1998).</td>
<td>140</td>
</tr>
<tr>
<td>5. Period-specific regression parameters ($b_0, b_1$) used to predict age from length for each reservoir for which larval hatch distributions were estimated in 2000. Data derive from larvae aged ≤ 11 d. Period divides the 9-week</td>
<td></td>
</tr>
</tbody>
</table>
sampling period by three: early (April 30 – May 20), middle (May 21 – June 10), and late (June 11 – July 1). Estimates were not made in the early and late period of Caesar Creek or in the late period of Burr Oak because of insufficient samples size (i.e., < 13 larvae collected per sample). Because we knew the larval hatch distribution in Acton would be inaccurate due to one missed week of sampling, we only estimated the middle period.

6. Pearson’s correlation coefficient and \( P \)-value (in parentheses) between \( \beta_i \), an index of *Pomoxis* spp. larval survival during 2000, and preferred crustacean zooplankton biomass (i.e., copepods and *Diaphanosoma* spp.), density of all fish larvae (i.e., gizzard shad, *Lepomis* spp., *Pomoxis* spp.), and temperature during the week of hatch for four Ohio reservoirs. Significant \( (P \leq 0.05) \) positive correlations are depicted in bold text. “N” is the number of weekly cohorts for which \( \beta_i \) was measured in each reservoir.

7. Characteristics of Ohio reservoirs from which age-0 white crappie were collected for bomb calorimetry during October 17 – 27, 2000, and ordered by latitude (south to north). Mean chlorophyll \( a \) (\( \mu \text{g/L} \)) concentration was the grand mean of upstream and downstream integrated water samples collected weekly during May – June 2000 (M. Vanni, Miami University, unpublished data). Mean and standard deviation (in parentheses) of age-2 white catch per effort (CPE) provide an index of recruitment success and variability. Age-2 CPE data result from 4 years of autumn trapnetting (Bunnell et al. in review). Total length (mm) range and N (number of individuals) describe the age-0 white crappie analyzed for bomb calorimetry.

8. Mean and standard deviation (in parentheses) of initial, final total length (TL, mm) and initial, final wet mass (g) for small (71 – 90 mm TL) and large (91 – 120 mm TL) age-0 white crappie held in the lab for 5-6 weeks and then subjected to simulated warm and cold Ohio winters. Eighteen fish were used per winter \( \times \) food \( \times \) size treatment.

9. Age-0 white crappie survival (%) through the experiment as a function of winter, food, and size. Within each winter, chi-square test determined whether differences in survival occurred between fish at different food levels, as well as between small and large fish. Chi-square statistic is shown for all tests and \( P > 0.5 \).

10. Results of a general linear model for the effects of simulated winter temperature, size, food treatment, possible two-way interactions, and tank on daily growth rate \([(\text{final mass} – \text{initial mass})/d \text{ in experiment}] \) of age-0 white crappie, collected from Pleasant Hill Reservoir, Ohio, in our lab experiment. Tank was nested within winter, size, and food as each tank had different food or size treatments, within a winter.
11. Mean energy density (kJ/g wet mass) of age-0 white crappie as a function of food treatment as well as whether they survived or died during the experiment. Degrees of freedom for both t-tests equaled 18.............................176
LIST OF FIGURES

Figure | Page
--- | ---
1. Linkages between life history stages of white crappie in Ohio reservoirs. Solid-lined arrows indicate transitions between life stages and dashed-line arrows indicate potential factors, evaluated within the dissertation, which could influence survival between stages. The timeline indicates the approximate dates in which life-history stages were sampled and the solid-lined arrows at the bottom of the figure indicate the life history stages that each dissertation chapter explored. In the timeline, y refers to any given calendar year. | 9
2. Functions used to describe ovary size in the models, derived from field data (Bunnell et al. 2000) collected from Ohio reservoirs. (A) Maximum ovary mass (g) as a function of fish length (cm) (Equation 6). (B) Gonadosomatic index (GSI) as a function of fish length (cm). (C) Proportion of ovaries remaining after spring spawning as a function of fish length (cm) (Equation 7). | 40
3. Optimal proportion of energy allocated to somatic growth, \( \sigma \), during autumn by a simulated age-3 white crappie as a function of fish length, when summer and spring levels of consumption are constant across years. Levels of spring and summer consumption are labeled on each figure panel. Ovary mass at the beginning of autumn was 0 g (open circles) or 25% of maximum ovary mass (closed circles). Data illustrated with closed circles were offset by 0.02 to allow all points to be seen. | 42
4. Optimal proportion of energy allocated to somatic growth, \( \sigma \), during autumn of a simulated age-3 white crappie as a function of fish length, when level of summer consumption was constant across years but level of spring consumption varied between years. Level of consumption and the probability that spring consumption is low (i.e., \( P = 0.2 \)) are labeled on each figure panel. Ovary mass at the beginning of autumn was 0 g (open circles) or 25% of maximum ovary mass (closed circles). Data illustrated with closed circles were offset by 0.02 to allow all points to be seen. | 44
5. Growth trajectories of white crappie, including both modeled fish and fish collected from three Ohio reservoirs, as a function of age and season. Modeled fish lengths are depicted with solid lines. Symbols indicate mean.
fish length (cm) sampled from reservoirs for the 1996 year class, during autumn 1998 (age-2), 1999 (age-3), and 2000 (age-4) (D. B. Bunnell, unpublished data). Dashed lines are interpolated growth trajectories of reservoir fish. ......................................................46

6. Mean GSI ± standard error of modeled white crappie as a function of constant spring consumption levels (spring $P$) when summer $P$ is 0.2 (circles) or 0.6 (triangles).  (A) Fish less than 28 cm in length, which represents the largest common length for all treatments of summer and spring $P$ values.  (B) Fish from all length classes in which greater than 50% of the replicates contained fish in that length class .............................................48

7. Mean GSI ± standard error of modeled white crappie as a function of the probability, $\rho_1$, that level of spring consumption was low (i.e., $P = 0.2$), which corresponds to the probability, $1-\rho_1$, that level of spring consumption was high (i.e., $P = 0.6$).  Circles represent fish that experienced a constant low level of summer consumption (i.e., $P = 0.2$), and triangles represent fish that experienced a constant high level of summer consumption (i.e., $P = 0.6$).  (A) Fish less than 28 cm in length, which represents the largest common length for all treatments.  (B) Fish from all length classes in which greater than 50% of the replicates contained fish in that length class ..................50

8. Autumn GSI of white crappie collected between the second week in October and the first week in November 1998 – 2000, from five Ohio reservoirs.  Horizontal lines inside the box represent the median GSI, box ends represent the 25th and 75th percentile, and error bars represent the 10th and 90th percentile.  Numbers above the error bars represent mean fish length (cm) sampled.  Vertical dashed lines separate reservoirs .........................52

9. Somatic energy density (kJ / g wet mass) as a function of individual condition during autumn 1999 (circles) and spring 2000 (triangles) of female white crappie collected from Alum Creek, Caesar Creek, and Pleasant Hill, OH reservoirs.  Individual condition is the residual from predicted mass of the total fish mass in autumn, and of the somatic mass, only, in spring (i.e., total mass – gonad), for a given total length .......................95

10. Ovary energy density (kJ / g wet mass) of pre-spawning white crappie collected from seven Ohio reservoirs during April 1999 and three Ohio reservoirs during April 2000 (see Table 2).  (a) Ovary energy density as a function of individual fish total length (TL).  The vertical line identifies length = 24.9 cm as the threshold total length identified by the two-dimensional Kolmogorov – Smirnov test (2-DKS; Garvey et al. 1998b).  In panels (a) and (b), triangles represent fish smaller than the length threshold (i.e., short fish) and squares represent fish larger than the length threshold (i.e., long fish).  (b) Ovary energy density as a function of individual spring
condition, where individual spring condition is the residual from spring predicted wet mass. Again, the vertical line identifies condition = -1.83 as the threshold condition index identified by 2-DKS. (c) Weighted mean ovary energy density for each reservoir-year as a function of population condition in the previous autumn. Weighted mean ovary energy density uses the proportion of the population above and below the 24.9 cm TL threshold (see panel (a)) to weight mean ovary energy density. Population condition uses the proportion of fish in each cm length class for each reservoir-year to weight the mean residual autumn wet mass for each cm length class. Symbols represent the last digit of the year that fish were collected (e.g., 9 = 1999), followed by the two-letter reservoir code found in Table 2. Note different scales in panel (c) compared to panels (a) and (b).

11. Mean egg diameter of pre-spawning white crappie that contained mature eggs. Fish were collected from seven Ohio reservoirs during April 1999 and five Ohio reservoirs during April 2000 (see Table 2). Between 38 – 240 (mean = 114.5) eggs were measured per fish, pooled across six different parts of the ovary. (a) Mean egg diameter as a function of individual fish total length (TL). (b) Mean egg diameter as a function of individual spring condition, where individual spring condition is the residual from spring predicted wet mass. (c) Mean egg diameter as a function of residual fecundity, the difference from predicted fecundity at a given total length.

12. (a) Total fecundity of pre-spawning white crappie collected from seven Ohio reservoirs during April 1999 and five Ohio reservoirs during April 2000 (see Table 2) as a function of total length (cm). The solid line is predicted fecundity using non-linear regression. (a) Fecundity as a function of individual fish total length (TL). (b) Residual fecundity, for a given length, as a function of individual spring condition, where individual spring condition is the residual from predicted wet somatic mass, for a given length. (c) Mean residual fecundity for 12 reservoir-years as a function of population condition the previous autumn. Population condition uses the proportion of fish in each cm length class for each reservoir-year to weight the mean residual autumn wet mass for each cm length class. Symbols represent the last digit of the year that fish were collected (e.g., 9 = 1999), followed by the two-letter reservoir code from Table 2. ANCOVA was used to determine the effects of population condition index (covariate) and year.

13. Ovarian development of white crappie sampled from Alum Creek during April 21 – 27 (a), May 25 – 27 (b), and June 25 (c) 1999 as a function of total length. Ovarian development is defined as the proportion of predicted April ovary mass attained for fish of a given length.
14. Linkages between life history stages of *Pomoxis* spp. Note the log\(_{10}\) scale on all y-axes. (a) Mean hatch density of white and black crappie larvae sampled during May – June 1999 (eight reservoirs) and 2000 (nine reservoirs) as a function of estimated egg production of white and black crappie for each respective year. White and black crappie were combined owing to our inability to visually distinguish species as larvae. Symbols represent the year of hatch (e.g., 9 = 1999) followed by the reservoir code (see Table 2). (b) Total CPE of age-2 black and white crappie sampled with trapnets during autumn 2000 and 2001 as a function of mean hatch density of black and white crappie larvae sampled during May – June 1998 (11 reservoirs) and 1999 (8 reservoirs). (c) Mean CPE of age-2 white crappie (i.e., the 1999 year-class) sampled during autumn 2001 with trapnets as a function of estimated white crappie egg production during spring 1999. The egg production index incorporates length frequency data from autumn 1998 into a length/fecundity relationship. On the y-axis, note the addition of 1 to all values to permit transformation of CPE values of 0.

15. Pathway by which adults influence recruitment (i.e., age-2 CPE) of white crappie in Ohio reservoirs. Arrows denote a positive relationship between life-history categories (e.g., adult, egg (ovary), larvae, and age-2); arrows with larger heads denote stronger linkages than those with smaller heads. Dashed arrow lines indicate that adult catch per effort and maternal length (i.e., population length) were used to estimate population egg production. Number letter combinations in parentheses, associated with each arrow, represent figures that depict each relationship. For maternal characteristics, including length and condition, individual (indiv) and population (pop’n) effects on ovary characteristics are noted.

16. Mean biomass (µg/L) of crustacean (filled bars) and rotifer (open bars) zooplankton from the upstream (A) and downstream (C) sites of five Ohio reservoirs during May – June 2000. Mean number of crustacean (filled bars) and rotifer (open bars) zooplankton per L from the upstream (B) and downstream (D) sites also is depicted. We calculated the mean of weekly upstream and downstream samples separately. The grand mean of upstream and downstream zooplankton samples are shown. Reservoirs are ordered from low to high productivity (see Table 4).

17. Daily growth rate \([(\text{mm (TL)} - 3.23)/\text{d}]\) of two age-classes of *Pomoxis* spp. larvae sampled from 19 Ohio reservoir-years as a function of zooplankton biomass. Age-class I represents fish aged between 3 and 9 d, whereas age-class II represents a group of fish aged between 10 and 16 d. Each data point represents the mean of larvae grouped as a function of reservoir, site, year, week of hatch, and week of collection (5 – 29 larvae per data point, mean = 12.2 larvae). In (a), total zooplankton biomass includes crustacean zooplankton and rotifers. In (b), preferred crustacean zooplankton biomass
includes calanoid and cyclopoid copepods, and *Diaphanosoma* spp. For both age-classes, only those individuals sufficiently small to be consumed were included and mean TL at time of capture for each group of larvae determined gape size.

18. **Time of peak density of Pomoxis spp. larvae relative to peak density of gizzard shad larvae.** Each data point (N = 42) represents the peak density of gizzard shad larvae at a particular site (upstream or downstream) across 21 Ohio reservoir years. On the x-axis, negative numbers (i.e., to the left of the dashed vertical line at 0) indicate how many weeks Pomoxis spp. peaked before gizzard shad; positive numbers indicate how many weeks Pomoxis spp. peak after gizzard shad. The dashed horizontal line at 10 gizzard shad larvae/m³ indicates the critical density above which gizzard shad larvae can compromise survival of bluegill larvae (Garvey et al. 1998). Closed triangles indicate the reservoir sites for which survival was estimated in 2000.

19. **Survival of white crappie larvae to the juvenile stage in five Ohio reservoirs during 2000, as a function of week of hatch.** The proportion of larvae hatching (sampled May – June 2000) from weekly cohorts is depicted as shaded, vertical bars on the left y-axis, whereas the proportion of juveniles collected during July 11-14, 2000 from weekly cohorts is depicted as solid circles on the right y-axis. The asterisk on the proportional distribution of larvae in Acton (panel a) indicates that the distribution likely underestimates the proportion of larvae hatched during the week of May 3 as a result of no larval samples collected during the week of May 10.

20. **The index of weekly cohort survival, β<sub>i</sub> (equation 17), as a function of (A) mean temperature, (B) preferred crustacean zooplankton biomass, and (C) density of fish larvae, during the week of hatch.** In all panels, the dashed horizontal line represents β<sub>i</sub> when the proportion of juvenile survivors equals the proportion of larvae hatched (i.e., log<sub>10</sub> = 2, see equation 17).

21. **Energy density (kJ/g wet mass) of age-0 white crappie increased with total length (mm).** Two-letter symbols represent four Ohio reservoirs from which fish were sampled during October 2000 (see Table 7 for details). Triangles represent energy density of age-0 white crappie at the beginning of the experiment, after spending 5 – 6 weeks in the laboratory.

22. **Mortality of age-0 white crappie in the cold winter experiment as a function of temperature (a) and total length (b).** Because only 2 of 72 warm water fish died, similar relationships are not depicted for the warm winter. Panel (a) depicts the number of fish that died (37 fish, vertical bars) during each day of the simulated winter, regardless of food level. A solid, horizontal line occurs at 4°C, the temperature below which mortality was frequent.
Panel (b) depicts total length of starved (open circles) and fed (closed circles) fish that died as a function of simulated day of winter. Neither number of days, food treatment, nor the days \( \times \) food interaction predicted the total length of fish that died. ................................................................. 180

23. Mean daily growth rate \([\frac{\text{(final mass} - \text{initial mass)}}{\text{d in experiment}}]\) of different size classes and feeding levels of age-0 white crappie as a function of winter treatment. The zero daily growth rate is indicated by a solid horizontal line. The initial sampling unit was a partition (i.e., the mean of three fish); each data point on the graph represents the grand mean of six partitions for each treatment................................................................. 182

24. Percent feeding by age-0 white crappie (vertical, filled bars) and the temperature regime (solid black line) for the cold (a) and warm (b) winters, as a function of simulated day of winter. Here, feeding represents the percent of all fish observed to eat in the first 5 min following food presentation, independent of size. 4°C is highlighted with a solid, horizontal line, the temperature below which feeding was infrequently observed in the cold winter................................................................. 184

25. Energy density (kJ/g wet mass) as a function of total length (TL) for age-0 white crappie that survived both experimental winters (a) and died during the cold winter (b). Because only two fish died in the warm winter (versus 37 fish in the cold winter), we did not quantify their energy density. The vertical line at 90.5 mm TL separates the small and large sizes of fish.............. 186
CHAPTER 1

INTRODUCTION

Understanding how population size is regulated remains a central goal of ecology (Murdoch 1994). Organisms that produce numerous offspring (e.g., plants, amphibians, fishes) typically are subject to population fluctuations, owing to variable survival of their offspring during their first year of life [e.g., tree seedlings (Buckley et al. 1998), frog tadpoles (Wilbur 1980), fish larvae (Houde 1987)]. Years of high offspring survival increase population sizes into the future, whereas years of poor survival reduce population sizes in later years. By understanding those mechanisms that regulate offspring survival, one can anticipate population changes through time.

Owing to their nutritional and economic value, substantial efforts have been made to understand variability in fish population size. Before the 20th century, migratory patterns of marine fishes were believed to drive differences in harvest (Sinclair 1997). Hjort (1914), however, challenged conventional wisdom by hypothesizing that the time following yolk-sac absorption by larvae drove the “highly irregular” pattern of the “renewal process”, i.e., first-feeding larvae will survive only if they overlap spatially and temporally with sufficient prey resources. The outcome of this critical period was hypothesized to drive the relative abundance of recruits, which then affected future adult densities. Some 40 years later, Ricker (1954) and Beverton and Holt (1957) postulated
that spawning stock biomass drove differences in recruitment success, which again
served to diversify research in fish recruitment. Their models predicted that number of
recruits increases with total spawning biomass, until the number of recruits either
asymptotically approaches a maximum (Beverton and Holt 1957) or declines (Ricker
1954) owing to density-dependent survival (e.g., competition, cannibalism). Thus, their
models focused research on adults, and resultant production of eggs and embryos,
whereas Hjort (1914), and later, Cushing (1968), drew attention to the importance of
factors occurring after embryos became larvae (i.e., after their yolk-sac was absorbed).
These two paradigms set the direction of recruitment research that remains today.

With regard to adults influencing recruitment, the conventional models relating
adult biomass to recruitment often failed (Shepherd and Cushing 1990). However, recent
improvements in quantifying spawning stock as well as recruit abundance, and the
subsequent accumulation of long time series of data likely facilitated the positive
relationships that have emerged recently (Hilborn and Walters 1992; Myers and
Barrowman 1996). In fact, the realization that too few adults have led to poor
recruitment and eventual collapse of some marine fisheries (e.g., Atlantic cod, Myers et
al. 1996) provides additional evidence that spawning stock biomass likely contributes to
recruitment success. Adults also may influence recruitment via “maternal effects”. Here,
both egg and embryo are influenced by non-genetic energetic contributions from the
mother including her condition or size (Bernardo 1996; Solemdal 1997). To elaborate,
avaries from fish in high energetic condition produce larger eggs (Chambers and
Waiwood 1996), more eggs (Marshall et al. 1999), and larger embryos (McCormick
1998) than those in low energetic condition. Similarly, fish length also positively
influences egg (Beacham and Murray 1985) and embryo (Heyer et al. 2001) size. Thus, condition or length distribution of a population can positively influence recruitment success (e.g., Marshall et al. 1999). Consequently, both spawning stock biomass and maternal effects of adult populations can influence fish recruitment.

After yolk-sacs are absorbed and larvae begin feeding, they must navigate a gauntlet of potential sources of mortality to survive beyond the first year of life. Because fishes are highly fecund, small changes in percent survival of larvae and juveniles can translate into dramatic effects on populations (Houde 1987). Hjort (1914) and, later Cushing (1968) focused on the role of starvation after yolk-sac absorption, a mortality source that continues to be pursued (e.g., Werner and Blaxter 1980; Leggett and Deblois 1994; Letcher et al. 1996; Garvey and Stein 1998a). Predation is now also recognized as a key source of mortality (Mills et al. 1987; Leggett and Deblois 1994; Mason and Brandt 1996). Finally, abiotic factors, including water temperature and flow patterns, influence recruitment of both marine (Cushing 1982; Leggett et al. 1984; Koslow et al. 1987) and freshwater fishes (Clady 1976; Mion et al. 1998). However, not one abiotic or biotic factor, nor one critical life-history stage, can be identified to regulate fish recruitment across taxa (Leggett and Dublois 1994). In specific populations, however, a life-history stage can be identified from which recruitment success can be predicted (e.g., Forney 1976; Mion et al. 1998; Sammons and Bettoli 1998). In these cases, biologists then seek to understand the mechanisms driving survival to that critical life-history stage.

Herein, I have focused on evaluating the relative contributions of the two major paradigms driving recruitment research in fishes: 1) adult impacts (e.g., maternal effects and spawning stock biomass) and 2) sources of mortality for age-0 fishes. White crappie
is a model species to evaluate these paradigms given their highly variable recruitment throughout reservoirs and lakes in North America (Beam 1983; McDonough and Buchanan 1991; Sammons and Bettoli 1998) and Ohio (D. B. Bunnell, unpublished data). Previous work on recruitment has centered on the role of water elevation during the spawning season (e.g., Mitzner 1981), as well as starvation during the larval period (e.g., Pope and DeVries 1994). I will consider both of these hypotheses, as well as new ones, including the role of maternal effects and spawning stock biomass. I also will explore how seasonal energy allocation patterns in mature female white crappie are influenced by prey availability, which has implications for when ovary development begins. Because I have considered such a wide range of competing hypotheses to explain variable recruitment, the implications of this work should go beyond white crappie, to other fish species and perhaps to other highly fecund taxa.

In addition to the contribution that this research will make to the basic understanding of population dynamics, these results also can be applied to fishery management. White crappie is a popular sportfish, often ranked among the top three species in North America, based on biomass harvested by anglers (Allen and Miranda 1998). The variability in white crappie recruitment affects angler catch-rates both within and across fisheries (Mitzner 1984; Hooe 1991; Allen and Miranda 1998). If the life history stage from which recruitment can be predicted is identified, then fishery managers will be able to anticipate fluctuations in population abundance. In addition, if factors critical to recruitment can be manipulated (i.e., spring water level, spawning stock biomass, prey availability, nutrient input), managers could do so, thereby improving recruitment success and population density. If the critical factors are either impervious to
modification (i.e., spring warming rate, reservoir draw-down in the fall) or unpopular (i.e., reduction of predator biomass), managers still have the capacity to predict years of poor recruitment and reduce angler expectations via education.

**Overview of chapters**

In Chapters 2 – 5, we take a life history approach to understand how potential mechanisms influence recruitment of white crappie in Ohio reservoirs (Figure 1). First, we define recruitment as the catch per effort (CPE) of age-2 white crappie. By age-2, white crappies are fully vulnerable to our sampling gear (Colvin 1991), and in most cases, have matured and have reached a size to make them attractive to anglers. Below, the basic questions and approach of each chapter are described.

**Chapter 2. Energy allocation:** This chapter seeks to explain the seasonal energy allocation pattern observed by adult (i.e., ≥ age-2) female white crappie in Ohio reservoirs. Specifically, we used dynamic-programming to determine the optimal proportion of energy allocated to growth and reproduction in each season. Our primary goal was to understand why white crappie begin allocating energy to reproduction during autumn, more than 6 months before spawning. Allocating energy to reproduction in autumn may increase the probability that ovaries will be developed by spring. However, if allocation to growth, rather than reproduction, occurs during autumn, then females will attain a larger size by spring enabling them to accommodate and produce larger ovaries. The basic trade off is one of potential fecundity, as size and fecundity are positively related. Ultimately, this chapter provides insight into how the seasonal feeding
environment, which may vary across populations, will influence energy allocation decisions that will affect both individual growth rates and reproductive success of white crappie.

**Chapter 3. Adult impacts:** This chapter focuses on the two means by which adult white crappie contribute to recruitment success: maternal effects (i.e., female length and condition) and spawning stock biomass (i.e., population egg production). The chapter relies upon 4 years of field collections during which we characterized the population of adults in 14 Ohio reservoirs, and then related their characteristics to recruitment success (i.e., age-2 catch per effort). On a smaller subset of six reservoirs, we also explore how maternal length and condition influence ovary characteristics (e.g., fecundity, egg size, ovary energy density), providing additional insight into how maternal characteristics could influence recruitment. In doing so, we quantify the relative contribution of maternal effects and spawning stock biomass to recruitment of white crappie in Ohio reservoirs.

**Chapter 4. Age-0 growth and survival:** We use field data to explicitly test the hypothesis put forth by Hjort (1914), that the ability of first-feeding larvae (i.e., after yolk-sac is absorbed) to begin feeding on zooplankton will regulate recruitment. Here, we focus on five reservoirs sampled during 2000 and determine whether survival from the larval (i.e., age 1-week) to the juvenile stage (i.e., age 4 – 10 weeks) is related to zooplankton prey biomass during the first week of life. Alternative hypotheses evaluated include density of fish larvae, water elevation, and temperature in the reservoir during that critical first week. In addition, we also explore factors influencing growth of black and white crappie larvae.
Chapter 5. Age-0 survival- impact of winter: This chapter expands upon the paradigm explored in Chapter 4, that critical periods during the first year of life regulate recruitment success. Here, the critical period is winter, when size-dependent processes including starvation, predation, or susceptibility to cold winter temperatures can influence survival and ultimately, recruitment. A laboratory factorial experiment evaluates how size (large vs. small fish length), level of food (starved vs. fed), and winter (mild vs. severe) influence growth and survival of age-0 white crappie.

Summary. The focus of this research is to understand mechanisms underlying the recruitment of white crappie in Ohio reservoirs. We considered multiple hypotheses. First, we explored the impact of adults: 1) through their energy allocation decisions, 2) through offspring contributions attributed to maternal phenotype, and 3) whether numbers of adults relate to number of offspring. Next, we focused on the larval and juvenile stages, and tested explicit hypotheses regarding the role of zooplankton, density of competitors, as well as abiotic factors (e.g., temperature and water elevation) in governing the growth of larval and their survival to the juvenile stage. Finally, we evaluated whether survival during the first winter of life regulates year-class strength. Our approach to addressing these questions also was diverse, as we used modeling (Chapter 2), experiments (Chapter 5), and field sampling (all Chapters). Our findings should contribute to the basic understanding of fisheries population dynamics and may provide tools for managers to improve crappie fisheries.
Figure 1. Linkages between life history stages of white crappie in Ohio reservoirs. Solid-lined arrows indicate transitions between life stages and dashed-line arrows indicate potential factors, evaluated within the dissertation, which could influence survival between stages. The timeline indicates the approximate dates in which life-history stages were sampled and the solid-lined arrows at the bottom of the figure indicate the life history stages that each dissertation chapter explored. In the timeline, \( y \) refers to any given calendar year.
Figure 1

Potential factors:
- Length distribution of adults
- Water elevation
- Condition factor of adults

Life stages:
- Adults (> age-2)
- Eggs
- Larvae
- Juveniles
- Age-1
- Age-2(+) only

Timeline:
- October_y
- April_{y+1}
- May_{y+1}
- July_{y+1}
- May_{y+2}
- October_{y+3}

Coverage in dissertation:
- Chapter 2
- Chapter 3
- Chapter 4
- Chapter 5
CHAPTER 2

OPTIMAL ENERGY ALLOCATION: WHEN SHOULD ALLOCATION TO OVARIATES RESUME AFTER SPAWNING?

Introduction

When energy resources are limited, how an organism partitions energy between somatic (storage or growth) and reproductive tissue will influence its lifetime fitness. For iteroparous organisms, optimal energy allocation will be a response to the trade-off between current reproductive development and somatic growth toward future reproductive development (Williams 1966). This trade-off is most pronounced in organisms for which body size is positively related to fecundity because energy allocated to somatic rather than reproductive growth can actually enhance future potential fecundity. Over the reproductive life of an organism, this trade-off can influence a number of life history patterns, including age at first reproduction, whether an organism allocates energy to somatic growth after reproduction (as in indeterminate growers) or ceases somatic growth after reproduction (determinate growth), and when, in indeterminately growing organisms, allocation to reproduction begins after the previous reproductive event. Variability in food (Gurney and Middleton 1996; Shertzer and Ellner 2002) or length of growing season (Hom 1987; Kozlowski and Teriokhin 1999) as well as mortality (Pugliese 1987; Kozlowski and Uchmanski 1987; Pugliese and Kozlowski
1990; Engen and Saether 1994; Heino and Kaitala 1996; Kozlowski and Teriokhin 1999) are predicted to influence both age at first reproduction and whether an organism grows determinately or indeterminately. We suggest that similar factors may be influencing when indeterminately growing organisms begin allocation to reproduction, following a reproductive event.

Our modeling efforts centered on energy allocation between reproductive events for indeterminately growing organisms in which body size is positively related to fecundity, and determined how soon allocation to reproduction should begin, given the costs to potential fecundity. Consider two contrasting strategies. An “early” strategy allocates energy to somatic growth for a relatively short period before beginning energy allocation to gonads. This strategy maximizes the chance that an individual has developed gonads by the next reproductive opportunity, but compromises somatic body size, limiting potential fecundity for the next reproductive event. Alternatively, a “late” strategy increases body size and maximizes potential fecundity by allocating energy to somatic growth for a relatively long period, before beginning energy allocation to gonads. In this case, however, the organism risks not having sufficient time or energy to maximize gonad size before the reproductive opportunity arises.

Iteroparous fish provide an excellent model to explore this trade-off as they generally exhibit indeterminate growth. In addition, many fish species follow a summer of growth by beginning allocation to reproduction (i.e., ovaries) during autumn, six months before reproduction in the following spring (largemouth bass Micropterus salmoides, Adams 1982a; walleye Stizostedion vitreum, Henderson and Nepszy 1994; yellow perch Perca flavescens, Henderson et al. 2000). We also observed autumn
allocation to ovaries in white crappie; the level of early allocation varied between years within systems. Using white crappie as a model, we used dynamic programming to explore why allocation of energy to reproduction, rather than somatic growth, might be optimal during autumn and why they would allocate more in some years than others. We thought this “early” allocation could be in response to either one or both of the following: a plastic response to recent high consumption during summer or an evolutionary response to the probability of low consumption during the coming reproductive season. If summer consumption was very high, then an individual may be in a position to begin allocating energy to ovaries as early as autumn. In this scenario, early energy allocation to ovaries is a plastic response to recent good feeding conditions. Alternatively, early allocation may be an evolutionary response to the likelihood of low consumption just prior to reproduction. If feeding conditions are either poor or highly variable during the reproductive season (in this case, spring), then an individual must begin allocating energy to ovaries well before reproduction. While either of these may explain the general occurrence of early allocation to ovaries, only the first of these (i.e., a plastic response to recent feeding conditions) can explain year-to-year differences in timing of allocation to ovaries.

Dynamic programming is perfectly equipped to explore these two scenarios simultaneously, as it can provide state (e.g., length, ovary size, current level of consumption)-dependent energy allocation decisions (where state dependence can be thought of as a response to past conditions) that optimize lifetime reproductive fitness in a framework that considers expected future fitness (which can be thought of as an expression of “evolutionary experience”). In the dynamic programming model, optimal
allocation decisions were made by fish exposed to different levels of summer and spring consumption, as well as different probabilities of experiencing different levels of spring consumption.

To allow us to compare allocation decisions arising from the optimality model with data collected from white crappie in Ohio reservoirs, we embedded the output from the dynamic programming model within an individual-based simulation model. Growth and gonadal investments of the simulated cohort of “optimal” fish were then compared to populations of Ohio fish to gain insight into whether level of summer or spring food availability influence energy allocation decisions of white crappie in Ohio reservoirs.

**Methods**

*White crappie life history*

White crappie are native to lakes and low-gradient rivers east of the Rocky Mountains (Trautman 1957), but have been introduced as far west as California (Goodson 1966). As an economically important sportfish in North America, white crappie growth and reproduction are fairly well-described. White crappie growth is generally fastest during early summer (Gabelhouse 1991; Guy and Willis 1995), when prey are abundant and water temperatures are increasing. In Ohio, white crappies typically mature by age-2, although slow growth may delay maturity (Bunnell et al. 2000). Reproduction begins when water temperatures rise to near 14°C in the late spring or early summer (Siefert 1968) and typically lasts 6 - 8 weeks, which generally is early May to mid June in Ohio (Bunnell et al. 2000).
Modeling overview

We used dynamic programming to find optimal energy allocation decisions under a variety of consumption levels. First, we determined state-dependent, optimal allocation to somatic growth (length) or ovaries, under a variety of different levels of summer and spring consumptions. In each case, level of food was constant within a season. Next, we determined state-dependent, optimal allocation level when spring consumption randomly varied between years. These state- and feeding environment (both amount and certainty of food)- dependent, optimal allocation decisions were then used by simulated fish in an individual-based model. This allowed us to translate optimal energy allocation decisions into seasonal growth dynamics of somatic and reproductive tissue which, in turn, could be compared to seasonal growth of somatic and reproductive tissue of white crappie from Ohio reservoirs.

Dynamic programming model:

The objective of this model was to determine how fish length \(L\), ovary size \(G\), and level of consumption \(I\) influence optimal allocation of energy between somatic and ovarian growth during each season \(t\) for female white crappie. For each season \(t\), the modeled fish chose the allocation strategy that maximized expected fitness from \(t\) to terminal time \(T\), given its current states \(L, G,\) and \(P\) (\(P\) represents proportion of maximum consumption achieved in a given season). We made \(t = 1\) correspond to summer for an age-2 fish. Seasons were defined as summer (June through August), autumn (September through November), winter (December through February), and spring (March through May). We assumed spawning occurred at the end of spring; thus,
ovary size at the end of spring, immediately before spawning, was the maximum ovary size attained. Fitness was measured in terms of expected number of larvae produced. Number of larvae produced in a given year was a function of ovary mass at the end of spring. We assumed that there were 10,000 mature ova per g of ovary (Bunnell et al. 2000) and that 10% of fertilized eggs successfully hatched.

\[
\text{larvae}(G) = 10,000 \cdot (0.1)G
\]  
(1)

Modeled individuals chose the proportion \( \sigma \) of available energy to allocate to somatic growth such that expected lifetime larval production was maximized. We used backward iteration (Mangel and Clark 1988) to find the optimal solution. We calculated

\[
F(L, G, P, t) = \max_{t} \left[ \rho_1 F(L', G', P_1, t + 1) + \rho_2 F(L', G', P_2, t + 1) \right],
\]  
(2)

where \( \beta \) is the probability of surviving the current season. In a spawning season \( t \) (i.e., spring), maximum expected future fitness is

\[
F(L, G, P, t) = \beta \max_{t} \left[ (\rho_1 F(L', G', P_1, t + 1) + (\rho_2 F(L', G', P_2, t + 1) + \text{larvae}(G')) \right].
\]

Because \( T \) corresponds to a summer time-step, \( F(L, G, P, T) = 0 \).

Seasonal survival, \( \beta \), equaled 0.86 which corresponds to an annual probability of survival of 0.55, falling within the range (0.37-0.88) of annual survival estimates of white crappie in Ohio reservoirs (D. B. Bunnell, unpublished data). Because lifespan
varies between fish and to avoid the effects of an artificially constant lifespan, our model simulated uncertain terminal time for fish by defining $T$ as 49. We have no reason to believe that seasonal survival rate changes with age. Under this assumption, the probability of a fish surviving from time $t = 1$ to $t = T$ is 0.0007. Because white crappie rarely live to age-6, we used output only from $t = 1$ to 16 (corresponding to summer of an age-2 fish through spring of an age-5 fish), though optimal solutions took into account the possibility of these fish living beyond age 5. The range of lengths of fish evaluated in the model was 115-445 mm. Although fish less than 185 mm could have small (<0.5 g) ovaries, we never observed age-2 white crappie less than 185 mm to have conspicuous ovaries during field sampling. Thus, we set $\sigma = 1$ (i.e., allocate all energy to somatic growth) for all fish less than 185 mm.

Proportion of maximum consumption, $P$, was used to vary seasonal consumption. For all seasons, consumption $I$ was defined as:

$$I = P I_{\text{max}}(t, L),$$

where $I_{\text{max}}$ (maximum consumption) is a function of both season ($t$) and fish length ($L$). We set 3.8% of body mass per day as the mass-standardized, maximum daily consumption rate (g prey g$^{-1}$ day$^{-1}$) for white crappie at optimal temperature (24°C; Hayward and Arnold 1996). To model the effects of temperature, we first determined mean seasonal water temperatures of 10 Ohio reservoirs, varying in latitude, from at least 2 years per reservoir (Table 1). We then used the temperature dependence function from a preliminary bioenergetics model for white crappie (Zweifel 2000) to determine the maximum consumption values for each season: summer was 3.8% of body mass per day, autumn was 1.46% of body mass per day, winter was 0.26% of body mass per day,
and spring was 0.82% of body mass per day. Although $P$ has not been measured for white crappie, $P$ varies both within and between seasons for other fish. During summer, $P$ for largemouth bass *Micropterus salmoides* varied between 0.0 - 0.8 in Wisconsin lakes during summer (Rice and Cochran 1984; Essington et al. 2000). In a review of 18 fish species, Schindler and Eby (1997) found measured fish growth rate was only 26% of the maximum potential bioenergetic growth rate.

At the end of each season, $L'$ and $G'$ are the new lengths and ovary masses arising from optimal allocation. We modeled seasonal somatic and ovarian growth as a function of consumption and a general growth efficiency function for poikilotherms (Peters 1983). Body mass was modeled as a direct function of length, $M = aL^b$. We used length and mass data from white crappie collected in Ohio reservoirs to set $a = 2.28 \times 10^{-6}$ and $b = 3.332$ (Bunnell et al. 2000). Length at the end of each season $t$ ($L'$) was then calculated as:

$$L' = \left( \frac{aL^b + \sigma k(aL^b)^h}{a} \right)^{1/b}$$  \hspace{1cm} (4)

and ovary mass at the end of each non-spawning season ($G'$) was calculated as:

$$G' = G + j(1 - \sigma)lk(aL^b)^h$$  \hspace{1cm} (5)

(see Appendix for derivations), where $j$ represents a correction coefficient for building ovarian tissue (see Appendix), $k = 0.21$ and $h = -0.05$ (Peters 1983). For fish, maximum ovary size is limited by fish length. Using data from white crappie collected from Ohio reservoirs (Figure 2; Bunnell et al. 2000), we set maximum ovary size as

$$G_{\text{max}} = 1.8197^{-14} (L)^{6.09257}$$  \hspace{1cm} (6)
After spawning in the beginning of summer, ovary mass was reduced to $\psi(L)$ of the pre-spawning ovary mass (at the end of spring), where $\psi(L)$ was estimated as

$$\psi(L) = \left( \frac{10^{(7.8568+3.3236\times \log(L))}}{10^{(13.74+6.09257\times \log(L))}} \right)$$  \hspace{1cm} (7)

(Figure 2). This relationship was determined from monthly field sampling of adult female white crappie during April through August in one Ohio reservoir (Bunnell et al. 2000).

We used the dynamic programming model to assess how level of consumption (a function of water temperature and prey availability) and uncertainty of level of future consumption affected patterns of optimal allocation. We expected that allocation might depend on both the current quality of the environment, as reflected in the current level of consumption, as well as probabilities regarding future levels of consumption.

**Effect of constant level of seasonal consumption across years**

We varied levels of spring and summer consumption to explore how $\sigma$, the optimal proportion of energy allocated to somatic growth, varied between seasons. We completed a $2 \times 10$ factorial design of model runs including two levels within the summer consumption treatment ($P = 0.2$ and $P = 0.6$) and ten levels within the spring consumption treatment ($P = 0.1, 0.2, 0.3, \ldots, 1.0$). In all treatments, $P = 0.4$ for autumn and winter seasons, and $\rho = 1.0$ in all seasons.
Effect of variable level of spring consumption across years

We varied level of summer consumption and allowed spring consumption levels to vary randomly between years to explore how uncertainty about spring consumption, the season leading up to reproduction, might influence $\sigma$. In a given year, the spring consumption treatment was either low ($P_1$), with probability $\rho_1$, or high ($P_2$), with probability $\rho_2 = 1 - \rho_1$. The level of summer consumption was constant across years within each treatment. We completed a $2 \times 9$ factorial design of model runs including two levels within the summer consumption treatment (summer $P = 0.2$ or 0.6) and nine levels within the spring consumption treatment ($\rho_1 = 0.0, 0.01, 0.05, 0.1, 0.2, 0.4, 0.6, 0.8,$ and 1.0) with $P_1 = 0.2$ and $P_2 = 0.6$. Again, we set $P = 0.4$ for autumn and winter, and $\rho = 1.0$ for all seasons except spring.

Individual-Based Model:

In this model, we used the optimal state- and time-dependent energy allocation decisions ($\sigma$) from the dynamic programming model output to determine seasonal growth (somatic and ovary) for individuals in a cohort of white crappie. At the initiation of each model run ($t = 1$, corresponding to summer), 1000 fish were drawn from a normal distribution of lengths (mean = 193 mm, S.D. = 15.5), which represents a typical length distribution of age-2 white crappie in the summer in Ohio (D. B. Bunnell unpublished data). We assumed that white crappie reached maximum ovary size by the end of spring, and then spawned at the beginning of summer. Thus, the first season of the simulation, pre-spawning ovary size was drawn from a normal distribution (mean = length-specific $G_{\text{max}}$ from equation (6); S.D. = 0.5), which was then immediately reduced, due to
spawning, according to Equation 7, as in the dynamic programming model. For each of
the 16 seasons (time-steps), fish grew according to equations (4) and (5), as in the
dynamic programming model. All other parameters and functions, including survival
probability $\beta$, consumption rate (Equation 3), maximum ovary size (Equation 6), and
probability of maximum consumption ($\rho$) occurring also were identical to those used in
the dynamic programming model. For each dynamic programming treatment (20
resulting from the constant consumption factorial, and 18 resulting from the variable
spring consumption factorial), we ran 10 simulations of 1000 fish each. We then were
able to monitor the somatic growth and ovarian investments of these modeled fish.
Because field data on ovary mass are often expressed as gonadosomatic index, $GSI =
(\text{ovary mass (g)/total body mass (g)})100\%$, we expressed our simulation results in this
form. Within each simulation, we first calculated the mean GSI for each mm length class
of fish. Across each 1-cm length class, we then calculated a grand mean GSI for each
simulation. Across the 10 simulations, we finally calculated the mean GSI for each cm
length class. Because GSI increased with fish size (Figure 2A), we used only fish less
than or equal to 28 cm to ensure common size comparisons for analyses in which we
compared across treatments of differing levels of consumption; 28 cm was the largest
length attained in the lowest-consumption treatment. To determine whether growth rates
of modeled fish were similar to growth rates of fish captured in the field, we calculated
the mean fish length in each season for each simulation. We then calculated the mean
fish length across all simulations for each treatment.
**Field sampling**

We sampled adult white crappie during autumn from Ohio reservoirs to explore how GSI compared to autumn GSI from simulated white crappie experiencing varying summer and spring food levels. Adult white crappies were captured in trapnets (Colvin and Vasey 1986) in the autumn in two Ohio reservoirs during 1998, and in at least four Ohio reservoirs during 1999-2000. Ovaries were collected from fish between the second week in October and the first week in November. During 1998, white crappies were not systematically collected from all sizes of fish from each reservoir. During 1999-2000, however, all sizes of fish sampled were sacrificed for removal of ovaries; no more than six ovaries were collected per centimeter size class (across all cm size class in all reservoir years, range = 1 – 6 fish and median = 2 fish). All fish were placed on ice upon capture and then returned to the laboratory and identified to sex, weighed (nearest g), and measured (TL, nearest mm). From females, ovaries were removed and weighed.

To explore whether reproductive investment of individuals differed across reservoirs or years in which different sizes of white crappie were sampled, we first calculated ovary mass residuals from the linear relationship between ovary mass and total mass. We then used a general linear model (PROC GLM; SAS Institute 1999) with residual ovary mass as the dependent variable, reservoir, year, and the reservoir×year interaction as class variables.
Results

Dynamic programming results

The optimal allocation of energy to somatic growth, $\sigma$, was much more sensitive to spring than summer consumption levels. To illustrate this general result, we focus on age-3 fish that experienced varying levels of summer and spring consumption. All fish larger than 20 cm initiated allocation to reproduction during autumn, and the level of allocation was dependent on consumption in the coming spring. Across all possible treatments of summer and spring consumption, optimal autumn $\sigma$ varied among fish of similar lengths (Figure 3). Small differences (e.g., < 0.2%) between the $\sigma$ with the highest and second or third highest expected fitness values led to variability in optimal $\sigma$. Thus, in some cases, between two and four different $\sigma$ values yielded very similar expected fitness values. Despite this variability, general trends were apparent for all treatments. When spring consumption was always high ($P = 0.6$), small white crappie allocated nearly all of their energy to somatic growth during autumn, whereas larger fish allocated up to 70% of resources to ovary development (Figure 3A,B). Size of ovary coming into autumn had a predictable effect: those fish without ovary mass allocated more energy to reproduction than those with about 25% of their maximum ovary mass already achieved. In addition, constant high summer consumption (Figure 3B) did not increase energy allocation to ovaries during autumn, compared to constant low summer consumption (Figure 3A). When spring consumption was always low ($P = 0.2$, Figure 3C,D), all sizes of white crappie allocated more energy to ovaries (i.e., smaller $\sigma$) during autumn than when spring consumption was always high (compare Figures 3C,D to
Figures 3A,B). Again, summer consumption had no observable impact on $\sigma$, and fish entering autumn with larger ovaries allocated less energy to reproduction than those entering with smaller ovaries.

When uncertainty in level of spring consumption was introduced, autumn $\sigma$ decreased as the probability of low consumption (i.e., $P = 0.2$) during spring increased. When the probability of low spring consumption was extremely low ($\rho = 0.01$, corresponding to a 99% probability that consumption will be high in spring; Figure 4A,B), the allocation pattern did not differ considerably from a system in which level of spring consumption was always high (Figure 3A,B). However, when the probability of a low consumption spring was increased from 1% to just 10% (i.e., $\rho$ increased from 0.01 to 0.10), then the allocation pattern (Figure 4C,D) closely resembled one that occurs when low consumption during spring always occurs (Figure 3C,D). Similar to the results when spring consumption was constant, summer consumption did not influence $\sigma$, and fish entering autumn without ovary mass allocated more energy to reproduction than those entering with ovaries that were 25% of maximum mass.

Again focusing on age-3 fish, we looked at allocation to reproduction during summer. During summer, nearly all energy was allocated to somatic growth. In fact, energy was never allocated to reproduction during summer for fish less than 32 cm in length. Larger fish allocated between 10 and 30% of energy to reproduction, depending on the probability of low consumption during spring, at least nine months later. In model runs in which high spring consumption ($P = 0.6$) occurred in 99-100% of the years, only fish greater than 36 cm in length allocated energy ($\sigma = 0.1$) to reproduction in summer. When low spring consumption ($P = 0.2$) occurred in 10-100% of the years, fish greater
than 32 cm in length allocated up to 30% of energy to reproduction. Percent allocated to reproduction increased with fish length and decreased with increasing mass of ovary entering the summer. Level of summer consumption did not directly influence allocation patterns. Thus, summer allocation to reproduction occurs only for large fish.

**Individual-Based Model results**

We present results only from autumn, as allocation to reproduction occurred at nearly all sizes of fish and we could compare ovary growth of modeled fish to that of fish sampled in the field during autumn. First, to ensure that our model grew white crappie at reasonable rates, we compared the growth rates of modeled fish at various consumption rates (i.e., $P$-values) to growth rates of fish captured in Ohio reservoirs. From modeled fish, we estimated the mean length of fish at the end of each season from six treatments, where $\rho = 1.0$ in all seasons: three levels of spring feeding ($P = 0.2, 0.6, 1.0$) when summer consumption was low (i.e., $P = 0.2$), and then three levels of spring feeding ($P = 0.2, 0.6, 1.0$) when summer was high (i.e., $P = 0.6$). We compared those lengths to lengths of fish collected from three reservoirs and found considerable overlap (Figure 5). Hence, the $P$-values used in our model seem to be reasonable estimates of consumption for white crappie in Ohio reservoirs. We also calculated GSI at the end of the spring (just before spawning) to assess whether modeled fish maximized ovary size. When levels of summer and spring consumption were constant, all simulated fish attained the maximum GSI possible. With uncertainty regarding level of spring consumption, fish still attained near maximum GSI (greater than 96% of maximum size) in spring.
When consumption levels were constant within seasons across years, autumn GSI was driven by level of spring consumption (Figure 6). When comparing fish of similar sizes (e.g., less than 28 cm in length) across treatments of different feeding levels (Figure 6A), mean autumn GSI always was less than 1.0 when spring \( P > 0.3 \). Mean autumn GSI exceeded 1.0 only when spring \( P \leq 0.3 \). When mean GSI was calculated using fish of all lengths (Figure 6B), the general pattern of decreasing mean autumn GSI with increasing levels of spring consumption remained. However, both mean GSI and standard errors were higher when all sizes were included, likely because GSI increases with fish size (Figure 2B). When comparing the effects of summer feeding level, mean autumn GSI differed little between high- and low-consumption summer treatments at similar fish lengths (Figure 6A). However, across all fish lengths, the high-consumption summer treatment produced larger fish than the low-consumption treatment. With the inclusion of larger fish, higher mean autumn GSI occurred in the high-consumption summer compared to the low-consumption summers (Figure 6B) because of the higher GSI associated with larger fish.

To explore how uncertainty in spring consumption influenced somatic and reproductive growth, we varied the probability, \( \rho_1 \), that spring consumption level was low (i.e., \( P = 0.2 \)). When \( \rho_1 \) exceeded 0.10, mean GSI was at least 1.4 when using fish of similar sizes (Figure 7A), and at least 2.0 when all sizes of fish were included (Figure 7B). Only when \( \rho_1 < 0.05 \) was mean GSI less than 1.0. Thus, mean GSI was remarkably similar whether low consumption in spring always occurred or whether it occurred with probability equal to 0.10 (i.e., which equals a probability of 0.90 that a high consumption
in spring will occur). The inclusion of larger fish, either through high summer consumption or by including all sizes of fish in calculating the mean (Figure 7B), increased autumn GSI.

**Field results**

During autumn, we collected ovaries from 238 white crappie across three reservoirs in 1998, four reservoirs in 1999, and five reservoirs in 2000. Conspicuous, yellow ovaries were observed in all white crappie, but autumn GSI varied between reservoir-years (Figure 8). Across reservoir-years, mean autumn GSI ranged from 1.0 to 3.1, and GSI measured from fish in Alum Creek in 1998 were noticeably higher than all others. The mean autumn GSI of all fish collected was 1.4. In late April, about 2 weeks before spawning, a white crappie 25 cm in length (about the average fish size sampled in autumn) has an average GSI of 4.0 (D. B. Bunnell, unpublished data). Thus, by autumn, the average fish had developed at least 30% of its ovary mass for the following spring.

Residual ovary mass (residuals from the linear relationship between ovary mass and body mass) was used to determine whether ovary size, a measure of energy allocation available from fishes sampled in the field, differed between years or reservoirs. Residual ovary mass was influenced by reservoir ($F_{4,226} = 13.70; P < 0.0001$), year ($F_{2,226} = 45.13; P < 0.0001$), and the reservoir×year interaction ($F_{5,226} = 23.88; P < 0.0001$). Because we were interested in whether the large ovaries measured in Alum Creek in 1998 drove these results, we removed all Alum Creek observations from the data set and repeated the analysis. The reservoir×year interaction remained significant ($F_{3,190} =$
11.62; \( P < 0.0001 \), but the \( P \)-values associated with reservoir \( (F_{3,190} = 1.48; P = 0.22) \) and year \( (F_{2,190} = 2.81; P = 0.06) \) increased. Within all reservoirs, ovary size during autumn varied between years.

**Discussion**

For spring-spawning fish that grow indeterminately, our model described the optimal time to begin allocating energy to reproduction following a reproductive event, given the trade-off between current reproductive development and somatic growth toward future reproductive development, under different levels of summer and spring feeding. We focused on autumn because many spring-spawning fish begin energy allocation to reproduction during this season (Adams 1982a; Henderson and Nepszy 1994; Henderson et al. 2000) which, in turn, reduces the length and commensurate fecundity that could have been attained by spring. In addition, results of our model revealed considerable allocation to reproduction to occur during autumn for nearly all sizes of fish (i.e., fish greater than 20 cm in length). Only very large fish (i.e., length > 32 cm) allocated energy to reproduction during summer, and then only a small amount. The model evaluated whether early allocation to reproduction was a plastic response to recent high consumption during summer or an evolutionary response to the probability of low consumption during the coming reproductive season. The possibility of low consumption during the reproductive season (spring) regulated autumn allocation to reproduction; level of summer consumption had no discernible impact. Autumn GSI of modeled white crappie making optimal decisions matched that of white crappie sampled from Ohio reservoirs when modeled white crappies were faced with probabilities of low
consumption during spring that ranged from 10 to 100%. When spring food levels were always high or when low levels occurred with a probability of less than or equal to 5%, GSI of “modeled” white crappie was less than that of white crappies sampled from Ohio reservoirs. In our view, the risk that the coming spring might not provide enough food to build ovaries to their maximum size has selected for white crappies to begin allocating energy to ovaries, rather than to somatic growth, during autumn.

In our model, white crappies were permitted to allocate energy only to somatic growth or ovaries; allocation to energy storage was not permitted. Although white crappie do accumulate visceral lipid stores, our model assumed that gonads are developed directly from prey resources, a strategy referred to as “income” breeding (Stearns 1992). Other organisms, including some fish, frogs, lizards, and birds (Henderson and Nepsety 1994; Chastel et al. 1995; Doughty and Shine 1998; Bonnet et al. 2001), are “capital” breeders in that they rely more upon energy stores than on incoming food to fuel development of reproductive tissue (Stearns 1992). Although the reproductive strategy of white crappie is unknown, we assume white crappie to be “income” breeders (i.e., permitting allocation only to somatic growth or ovaries) in this model. From a reproductive perspective, storage of energy in ovaries is somewhat analogous to storage of energy in visceral fats, except that energetic losses associated with converting stored energy to gonadal tissue are omitted (Jönsson 1997; but see Bonnet et al. 1998). Thus, relative to a model in which fish were permitted to store energy viscerally, our model may be biased toward more allocation to ovaries in autumn. Energy stores may also be important in supplementing energetic needs during times of low food availability, such as winter. In our model, only energy available for growth, i.e. after basic energetic
maintenance needs have been met, could be allocated to somatic growth or reproduction. Despite not including energy storage, our model still expresses the basic trade-off between immediate reproductive development (allocating to gonads or energy stores) and somatic growth toward future reproductive development (allocating to somatic growth).

*Is autumn energy allocation a plastic response to summer feeding levels?*

Phenotypic plasticity in energy allocation suggests that energy allocation decisions can respond to changes in the environment (e.g., changes in food level). Experimental work reveals that organisms can either increase or decrease reproductive allocation in response to significant changes in food levels (e.g., Aronson et al. 1992; Cheung and Lam 1999; Stelzer 2001). In building this model, we hypothesized that allocation to ovaries during autumn would be high following summers of high consumption. Specifically, we thought white crappie would capitalize on abundant summer prey by beginning ovary development during autumn in preparation for reproduction 6-7 months later.

Interannual variability in early ovary development can be explained by a plastic response to recent (summer) feeding conditions. For the field data, we were able to assess autumn energy allocation only through ovary mass. Here, we found support for plasticity in energy allocation decisions with a significant interaction occurring between reservoir and year indicating that ovary size (using residual ovary mass as an index) differed across years within a reservoir. The model results, however, suggested that summer consumption does not directly influence optimal energy allocation. Dynamic programming revealed that autumn allocation of energy to ovaries for a fish of a given
size was not higher following summers of high consumption than following summers of
low consumption. Similarly, optimal allocation during summer was not influenced by
consumption during that season. Level of summer consumption, however, will have a
considerable impact on fish size. Because fish size influences energy allocation in all
combinations of summer and spring consumption, summer consumption will indirectly
influence energy allocation through its effect on fish size.

Initial support for the hypothesis that early energy allocation to ovaries would
follow summers of high consumption derived largely from observations of capital
breeding organisms. For many of these taxa, the months preceding commencement of
gonadal development influence later reproductive output. For example, summer feeding
is critical to determining the percent of mature walleye that ultimately will spawn the
following spring (Henderson and Nepszy 1994; Henderson et al. 1996). High levels of
summer feeding lead to high-energy stores, upon which walleye rely to fuel reproductive
development (Henderson et al. 1996). Prey resources during seasons well before
reproduction have been shown to influence the reproductive output of other taxa,
including female aspic vipers *Vipera aspis* (Bonnet et al. 2001), southern water skink
*Eulamprus tympanum* (Doughty and Shine 1998), and guppies *Poecilia reticulata*
(Reznick and Yang 1993). However, high consumption during pre-reproductive seasons
for “capital” breeding taxa do not necessarily directly influence energy allocation to
reproduction, but rather have a greater impact on energy stores. These higher energy
stores, in turn, influence energy allocation decisions regarding reproduction. Thus for
both modeled white crappie and some capital-breeding taxa, success of feeding in
seasons before commencement of reproductive allocation, directly influences the state (e.g., length, energy stores) of an organism which, in turn, may later influence energy allocation decisions regarding gonadal tissue.

Is autumn energy allocation an evolutionary response to spring feeding levels?

Our second hypothesis was that consumption during spring, the season leading to reproduction, would influence allocation decisions in the previous autumn. Of course, white crappie cannot predict level of consumption six months later. Thus if modeled white crappie are responding to probabilities of future spring consumption (e.g., constant or randomly varying levels of consumption), then this can be viewed as an evolutionary adaptation to an environment. In our model, fish allocated energy to ovaries during autumn in response to probabilities of spring consumption. First, when low consumption (i.e., $P < 0.2$) during spring always occurred, some allocation to ovaries during autumn was generally optimal. The more surprising result was that significant allocation to ovaries occurred when low consumption during spring had only a 10% probability of occurring (i.e., spring $P = 0.2; \rho \geq 0.1$). Thus, the model suggests that the consistent autumn allocation to ovaries observed by white crappie in Ohio reservoirs is a response to the possibility of low feeding levels in the coming spring.

In addition to matching our field data, the model results match energy allocation field data from fish sympatric with white crappie. In general, those fish reproducing before or at the same time as white crappie also begin allocating energy to ovaries during fall, whereas those fish reproducing later in summer wait until spring or early summer to begin allocating energy to ovaries, when high consumption likely occurs with a higher
probability. Walleye (Henderson and Nepszy 1994), yellow perch (Henderson et al.
2000), northern pike *Esox lucius* (Diana and Mackay 1979), and largemouth bass (Adams
et al. 1982a) all reproduce during early or late spring (Amundrud et al. 1974; Auer 1982),
before or during white crappie reproduction, and begin building ovary mass during
autumn. Bluegill *Lepomis macrochirus*, conversely, reproduces later in summer and
waits until late spring or early summer to initiate ovary development (Morgan 1951). It
would be interesting to document autumn energy allocation patterns of white crappie in
the more southern extent of their range. If feeding opportunities are greater both during
winter and spring in the southeastern United States than in Ohio, more southerly white
crappie populations may wait until spring to begin allocating energy to ovaries.

Spring feeding conditions in Ohio can be uncertain for a number of reasons. First,
consumption in poikilotherms is a function of temperature (Jobling 1994) and spring
temperatures are quite variable across years. Second, gizzard shad *Dorosoma
cepedianum*, the primary prey of adult white crappie in Ohio reservoirs, are susceptible to
high mortality during long, cold winters (Adams et al. 1982b); thus, variability in winter
severity causes variability in potential spring consumption. Finally, white crappie
population densities are quite variable between years (McDonough and Buchanan 1991).
If intraspecific competition affects consumption, variable population densities can lead to
variable success in spring feeding.

Uncertainty in future feeding opportunities (i.e., prey availability, length of
growing season) results in theoretical predictions of simultaneous or “intermediate”
allocation of energy to growth and reproduction. In previous models, this pattern
provided evidence for optimality of indeterminate growth over determinate growth (e.g.,
King and Roughgarden 1982; Gurney and Middleton 1996; Kozlowski and Teriokhin 1999). In our model in which indeterminate growth was expected, the timing of this “intermediate” allocation was our focus. As the probability of low consumption in spring reached 10%, earlier allocation to reproduction became optimal. Thus, even a small probability of an unfavorable spring resulted in a “bet-hedging” strategy where somatic growth and future fecundity were compromised in favor of early reproductive development in autumn. Analogous to previous models (e.g., King and Roughgarden 1982), a “bang-bang” strategy of 100% energy allocation to somatic growth followed by a switch to 100% allocation of energy to reproduction was no longer optimal when uncertainty in future growth opportunities was introduced.

**Summary**

For indeterminately growing organisms such as white crappie, in which fecundity is related to body size, a trade-off exists during autumn, between immediate reproductive development and growth toward future reproductive development. Dynamic programming models revealed initiation of allocation to reproduction to be regulated by probabilities of spring consumption levels rather than consumption levels during summer. When optimal, “modeled” white crappies were faced with a 10 - 100% probability of low food levels during spring, their autumn reproductive investment (GSI) was similar to fish collected from Ohio reservoirs. Thus, uncertainty regarding future feeding opportunities, which predicts indeterminate growth in previous models, also predicts that reproductive development will begin early, at the expense of continued somatic growth that could increase later potential fecundity.
Appendix

Derivation of seasonal growth equations for length and ovaries.

Peters (1983) estimated change in tissue mass (i.e., growth, $\Delta M$, in grams) per mass of food ingested $I$ (in grams) for a variety of types of animals:

$$\frac{\Delta M}{I} = kM^h$$  \hspace{1cm} (A1)

For poikilotherms, $k = 0.21$ and $h = -0.05$ (Peters 1983).

Given $M' = M + \Delta M$ we can substitute into equation (A1):

$$M' = M + IkM^h$$  \hspace{1cm} (A2)

Because ovarian tissue has approximately 1.33 times the caloric density (calories per g of tissue) of somatic tissue (D. B. Bunnell, unpublished data), we assumed ovaries required more energy per gram of growth; thus $G' = G + jIkW^h$, where $j = 0.75$. Because we are monitoring length ($L$), rather than body mass ($M$) of fish in our models, we transform $M'$ in equation (A2) to $L'$. Given $M = aL^b$,

$$L = \left(\frac{M}{a}\right)^{1/b}$$  \hspace{1cm} (A3)

Substituting equation (A3) into equation (A2),

$$L' = \left(\frac{aL^b + Ik(aL^b)^h}{a}\right)^{1/b}.$$
Literature Cited


Trautman, M. B. 1957. The fishes of Ohio. The Ohio State University Press, Columbus, Ohio.


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Table 1. Summary of seasonal water temperatures in 10 Ohio reservoirs during at least 2 years.
Figure 2. Functions used to describe ovary size in the models, derived from field data (Bunnell et al. 2000) collected from Ohio reservoirs. (A) Maximum ovary mass (g) as a function of fish length (cm) (Equation 6). (B) Gonadosomatic index (GSI) as a function of fish length (cm). (C) Proportion of ovaries remaining after spring spawning as a function of fish length (cm) (Equation 7).
Figure 2
Figure 3. Optimal proportion of energy allocated to somatic growth, $\sigma$, during autumn by a simulated age-3 white crappie as a function of fish length, when summer and spring levels of consumption are constant across years. Levels of spring and summer consumption are labeled on each figure panel. Ovary mass at the beginning of autumn was 0 g (open circles) or 25% of maximum ovary mass (closed circles). Data illustrated with closed circles were offset by 0.02 to allow all points to be seen.
Figure 3

Autumn σ (proportion of energy to growth)

Fish length (cm)

(A) Summer P = 0.2, Spring P = 0.6
(Gonad = 25% of max, Open circles: Gonad = 0 g)

(B) Summer P = 0.6, Spring P = 0.6

(C) Summer P = 0.2, Spring P = 0.2

(D) Summer P = 0.6, Spring P = 0.2
Figure 4. Optimal proportion of energy allocated to somatic growth, $\sigma$, during autumn of a simulated age-3 white crappie as a function of fish length, when level of summer consumption was constant across years but level of spring consumption varied between years. Level of consumption and the probability that spring consumption is low (i.e., $P = 0.2$) are labeled on each figure panel. Ovary mass at the beginning of autumn was 0 g (open circles) or 25% of maximum ovary mass (closed circles). Data illustrated with closed circles were offset by 0.02 to allow all points to be seen.
Figure 4:

- **A**: Summer $P = 0.2$, $Pr(poor\ spring) = 0.01$
- **B**: Summer $P = 0.6$, $Pr(poor\ spring) = 0.01$
- **C**: Summer $P = 0.2$, $Pr(poor\ spring) = 0.1$
- **D**: Summer $P = 0.6$, $Pr(poor\ spring) = 0.1$
Figure 5. Growth trajectories of white crappie, including both modeled fish and fish collected from three Ohio reservoirs, as a function of age and season. Modeled fish lengths are depicted with solid lines. Symbols indicate mean fish length (cm) sampled from reservoirs for the 1996 year class, during autumn 1998 (age-2), 1999 (age-3), and 2000 (age-4) (D. B. Bunnell, unpublished data). Dashed lines are interpolated growth trajectories of reservoir fish.
Field Growth Rates

- Caesar Creek
- Acton
- Pleasant Hill

Figure 5
Figure 6. Mean GSI ± standard error of modeled white crappie as a function of constant spring consumption levels (spring $P$) when summer $P$ is 0.2 (circles) or 0.6 (triangles). (A) Fish less than 28 cm in length, which represents the largest common length for all treatments of summer and spring $P$ values. (B) Fish from all length classes in which greater than 50% of the replicates contained fish in that length class.
Figure 6

(A) Fish < 28 cm

- Summer $P = 0.2$
- Summer $P = 0.6$

(B) All possible fish lengths
Figure 7. Mean GSI ± standard error of modeled white crappie as a function of the probability, $\rho_1$, that level of spring consumption was low (i.e., $P = 0.2$), which corresponds to the probability, $1-\rho_1$, that level of spring consumption was high (i.e., $P = 0.6$). Circles represent fish that experienced a constant low level of summer consumption (i.e., $P = 0.2$), and triangles represent fish that experienced a constant high level of summer consumption (i.e., $P = 0.6$). (A) Fish less than 28 cm in length, which represents the largest common length for all treatments. (B) Fish from all length classes in which greater than 50% of the replicates contained fish in that length class.
Figure 7

(a) Fish < 28 cm

- Summer $P = 0.2$
- Summer $P = 0.6$

(b) All possible fish lengths

Mean autumn "field" GSI
Figure 8. Autumn GSI of white crappie collected between the second week in October and the first week in November 1998 – 2000, from five Ohio reservoirs. Horizontal lines inside the box represent the median GSI, box ends represent the 25th and 75th percentile, and error bars represent the 10th and 90th percentile. Numbers above the error bars represent mean fish length (cm) sampled. Vertical dashed lines separate reservoirs.
Figure 8

Autumn GSI

Alum Creek
Acton
Berlin
Caesar Creek
Pleasant Hill

1998
1999
2000
CHAPTER 3

ADULT CONTRIBUTIONS TO RECRUITMENT
VARIABILITY IN WHITE CRAPPIE

Introduction

A variety of organisms, including plants, amphibians, and fishes, produce large numbers of small offspring. The survival of these offspring can be quite unpredictable which, in turn, will influence adult population size in later years (e.g., tree seedlings (Buckley et al. 1998), frog tadpoles (Wilbur 1980), fish larvae (Houde 1987)). Thus, understanding mechanisms underlying the number of offspring that survive to a later life stage (i.e., recruitment) is central to understanding their population fluctuations. For sport fishes, understanding recruitment variability is critical to successful management, given that recruitment can vary up to ten orders of magnitude among years within systems (Forney 1976; Sissenwine 1984), as well as among systems within a year (Garvey et al. 1998a; Myers et al. 1997). This variability presents two major problems for managers. First, interannual variability can frustrate anglers, especially in years when few fish recruit to the fishery, compromising catch rates. Fishery managers who are able to forecast these poor years by understanding the mechanisms driving this variability, can reduce angler expectation in poor fishing years and, in the best scenario, identify underlying causes of poor recruitment. A second related problem is not one of variability but, rather, consistently poor recruitment, perhaps following years when recruitment was
higher. Consistently poor recruitment is typically a result of overexploitation that reduces spawning stock to levels from which recovery is extremely slow (Hutchings 2000).

To understand recruitment variability, research historically has centered on two major processes: 1) variability in spawning stock (e.g., Ricker 1954; Beverton and Holt 1957), and 2) variability in age-0 fish survival, owing to starvation (e.g., Hjort 1914; Cushing 1968), predation (e.g., Mills et al. 1987), or unfavorable abiotic factors (e.g., Leggett et al. 1984; Mion et al. 1998). The perceived importance of these two factors as regulators of recruitment variability has shifted over the past century, from starvation during early life (Hjort 1914), to spawning stock (Ricker 1954; Beverton and Holt 1957), and then back to factors influencing survival of age-0 fishes (e.g., Leggett and DeBlois 1994). More recently, however, the role of adults in explaining recruitment variability is again being recognized (see Myers and Barrowman 1996; Solemdal 1997). Stock/recruit models recently have been documented for a variety of taxa, owing to improved techniques for measuring both spawning stock and recruit numbers (Hilborn and Walters 1992), improved temporal and spatial description of egg production (Kjesbu et al. 1998; Marshall et al. 1998; Kraus et al. 2000; Marteinsdottir et al. 2000), and years of data accumulation and archiving which has permitted meta-analyses (Myers and Barrowman 1996). From a management perspective, this return to an emphasis on adults is helpful because adult populations are easier to manage than abiotic or biotic factors regulating survival of age-0 fishes (Hilborn and Walters 1992). In addition, researchers are understanding how traits of individual mothers influence traits of offspring, owing to nutritive and hormonal links between mother and embryo. Coined “maternal effects”,

54
these maternal characteristics, including age, condition, or length, can influence offspring survival by affecting egg or larval size at hatch (see Bernardo 1996; Solemdal 1997). If maternal effects can be characterized at the population level, then they can be used with conventional stock/recruit models to increase our understanding of adult impact on recruitment (Solemdal 1997).

Length and condition are the maternal characteristics most commonly related to eggs and larvae. Maternal condition has been correlated positively with fecundity (Atlantic cod *Gadus morhua* Kjesbu et al. 1991; Marshall et al. 1999), egg size (Atlantic cod, Chambers and Waiwood 1996; Marteinsdottir and Steinarsson 1998), hatching success (Baltic herring *Clupea harengus membras* Laine and Rajasila 1999), larval body size (damselfish *Pomacentrus amboinensis* McCormick 1998), and even larval feeding success and growth (Atlantic cod, Marteinsdottir and Steinarsson 1998) for a variety of fish taxa. Similarly, maternal length has been correlated positively with egg size (Atlantic cod, Kjesbu 1989, Marteinsdottir and Steinarsson 1998; chum salmon *Oncorhynchus keta* Beacham and Murray 1985) and larval body size (chum salmon, Beacham and Murray 1985; yellow perch *Perca flavescens* Heyer et al. 2001). Despite these relationships between individual mothers and eggs or embryos, studies rarely link maternal effects to recruitment success at the population level. Marshall et al. (1999), however, were able to characterize condition of Atlantic cod populations using a population index of liver size and, in turn, discovered that population liver index was positively related to recruitment success (Marshall et al. 1999).

In this paper, we sought to gain a more complete understanding of how adult population characteristics influence recruitment success of white crappie *Pomoxis*
annularis, a popular, North American freshwater sportfish. Across North America, white crappie and conspecific black crappie Pomoxis nigromaculatus exhibit variable recruitment success both temporally within reservoirs (Beam 1983; McDonough and Buchanan 1991; Sammons and Bettoli 1998) and spatially across reservoirs (Colvin 1991a), thus causing highly variable fishing success for anglers (Hooe 1991). Previous white crappie recruitment research has focused on the positive effects of water elevation (Mitzner 1981; Beam 1983; McDonough and Buchanan 1991; Maceina and Stimpert 1998) and competitive interactions at the larval stage (Guest et al. 1990; Pope and DeVries 1994; Slipke et al. 1998). In our view, the role of adults in explaining recruitment variability has generally been overlooked, although adult biomass accounted for 9 - 44% of white crappie recruitment variability in four southeastern United States reservoirs (Allen and Miranda 1998). The impact of maternal effects is unknown, although poor white crappie condition during summer has been predicted with recently developed bioenergetic models (Hayward and Arnold 1996; Zweifel 2000). Specifically, when temperatures exceed 27°C, low consumption coupled with high basal metabolism compromises growth and condition (Hayward and Arnold 1996; Zweifel 2000). White crappie can be exposed to temperatures exceeding 27°C as far north as Missouri (Hayward and Arnold 1996) and Ohio (D. B. Bunnell unpublished data). Because they naturally occur as far south as eastern Texas (Trautman 1957), summer condition of
white crappie may be compromised throughout much of its range. If maternal condition influences eggs and larvae, then maternal effects would contribute to recruitment variability.

We evaluated how white crappie recruitment (defined as catch per effort (CPE) of age-2 fish) varied as a function of 1) egg production of the population, a function of spawning stock, the conventional mechanism by which adults putatively influence recruitment, and 2) maternal characteristics, the more recently proposed mechanism by which adults can influence survival of offspring and, in turn, recruitment success. Our approach was a 4-year, tiered sampling scheme in which adults and recruits were sampled from all 14 study reservoirs, and then ovaries and larvae were sampled from a smaller subset (Table 2). We determined whether individual maternal characteristics (condition and length) influenced characteristics of the ovary (e.g., fecundity, mean egg diameter, gonadosomatic index, and energy density (kJ/g wet mass)). We then constructed population measures of condition and egg production, and related them to larval density, and recruitment to age-2.

Methods

*Field and laboratory*

Reservoirs were selected to span three gradients: 1) latitude, which may influence summer water temperature and, in turn, adult condition, 2) productivity, which may influence abundance of prey fish and, in turn, adult condition, and 3) spawning stock, which is hypothesized to influence recruitment, and which indirectly should influence level of intraspecific competition which, in turn, may influence maternal characteristics (e.g., length, condition). To estimate productivity, we used historical total phosphorus
concentrations (Bremigan and Stein 2001). To estimate spawning stock of white crappie, we used historical creel data (1988 - 1995) collected from anglers by Ohio Division of Wildlife (R. S. Hale, Ohio Department of Natural Resources, Inland Fisheries Research Unit, Hebron, OH) as a surrogate.

Autumn adult sampling

Adult white and black crappies (where they occurred- see Table 2) were sampled with Missouri-style trapnets (Colvin and Vasey 1986) (1.27 cm mesh, with two 0.91 m by 1.82 m square frames, four 0.76 m diameter hoops, and a 21.3 m lead) during autumn 1998 – 2001 from 14 reservoir populations per year (Table 2). Pomoxis spp. recruit fully to the trapnets by age-2 (Colvin and Vasey 1986), and thus we used age-2 CPE as our index of recruitment. Our goal was twofold: 1) to estimate age-specific, species-specific, mean catch per effort (CPE; fish/net nights) and 2) to use length and wet mass to provide indices of maternal condition and length for each population in each year.

For each reservoir-year, 10 nets were set at fixed locations within the reservoir over 4 nights (i.e., 40 net nights), except for Pymatuning for which we used 20 nets per night, owing to its large area (i.e., Pymatuning = 59.29 km², range of other reservoirs = 2.53 – 14.20 km²). Locations were stratified across three major areas of the reservoir (upper reach, middle reach, and lower reach near the dam), and within each reach, we selected sites 2 – 4 m deep on the slope of the channel, through which Pomoxis spp. move during autumn. All fish collected were identified to species, and measured (nearest mm, total length, TL). We measured the wet mass (nearest 0.5 g) of up to 10 fish per cm length class per species. To determine fish age, we used otoliths, which required killing
the fish. Otoliths were collected from a minimum of 220 fish per species greater than 12 cm TL (assumed to be at least age 1). All fish from at least 50% of the nets per day (selected randomly before sampling) were harvested for later age estimation. Fish not harvested for later aging were released after their left pectoral fin was clipped to prevent recaptured fish from being counted on later days. In dense populations of black or white crappie, fish in all nets were returned to the reservoir later in the week (i.e., after 220 otoliths had been collected). In sparsely populated reservoirs, however, we determined early in the week that fish in all nets had to be collected to obtain 220 otoliths. In addition, we removed otoliths from the first 20 fish less than or equal to 12 cm TL encountered per species to verify they were age-0. Finally, in three reservoirs during 1999 (Alum Creek, Caesar Creek, Pleasant Hill), at least two fish per cm length class randomly were selected and frozen whole in water for later estimation of somatic energy density.

Our goal in estimating somatic energy density was to determine whether somatic energy density, a time-consuming measure of energetic condition (e.g., Hartman and Brandt 1995), was related to residuals of wet mass, predicted by total length, which is easier to measure. To estimate energy density, frozen-in-water fish were thawed at room temperature and the tissue was dried following Rand et al. (1994). Dried tissue was ground with dry ice using a Retsch ZM 100 electric tissue grinder, and dried again for 3 d at 65-70°C. At least two ~ 1-g composite pellets were made for each fish and burned in an oxygen calorimeter (Parr Instruments, Model 1341). A third pellet was burned if the two estimates differed more than 2% (~ 100 cal/g), which occurred in fewer than 10% of
our burns. Initial energy density was corrected for liberated H$_2$SO$_4$ (using a base titration), sulfur content (using a fixed average), and fuse combustion (Parr Institute Co. 1993). Mean energy density was calculated for each fish.

To determine age, whole otoliths were bathed in glycerol and annular rings were counted with 10 - 20x magnification. Some older otoliths needed to be cracked in half to facilitate age estimation. Age distributions for each reservoir-year were constructed using an age-length key (DeVries and Frie 1996), where the proportion of ages that comprised each cm length group made up the “key” which, in turn, was applied to the population length distribution. For each net night, we then estimated CPE for each age-class. Across the 40 net-nights, we determined mean CPE of age-2 fish, our index of year-class strength.

**Spring adult sampling**

Using the same trapnets as used in autumn, we collected adult white crappie from seven reservoirs during April 19 - 28, 1999 and five reservoirs during April 17 – 21, 2000 (Table 2). Our goal was to collect adult females we presumed would begin spawning in the next 1 – 2 weeks; from these females, we extracted ovaries to count and measure mature eggs, estimate energy density, and calculate gonadosomatic index [GSI= (mass of gonads / somatic mass)100]. Because white crappie reproduction is likely regulated by photoperiod (Siefert 1968), we assumed that populations across Ohio latitudes were at similar developmental stages. In addition, ova never were expelled during handling, suggesting that fish were not actively reproducing in late April.
In each reservoir, 4 – 6 trapnets were set for 3 – 4 nights to collect at least four female fish per cm length class to ensure a broad distribution of ages and lengths of crappie. Upon capture, white crappie were placed on wet ice and returned to the lab to be identified to sex, weighed (nearest g), and measured (TL, nearest mm). Fish in each cm length class were alternately preserved for either fecundity and egg diameter measures or ovary energy density estimation.

We estimated potential fecundity (i.e., count of the most developed oocytes in female fish before spawning, Kjesbu et al. 1991) from 122 white crappie sampled across 12 reservoir-years. Herein, potential fecundity will be referred to as fecundity. Ovaries were removed and weighed (nearest 0.1 g) before being preserved in 5% buffered formalin for at least 6 mo. From each reservoir, we estimated fecundity from 7 – 13 fish, typically one per cm length class. From each of six 4-mm diameter cores (three from each ovary lobe; Henderson and Nepszy 1994), mature oocytes were counted and their diameter was measured (first 20 eggs encountered, nearest 0.01 mm). As in previous studies (Barwick 1981), we documented three stages of oocytes within each mature ovary: 1) primary (translucent color and 0.01 - 0.20 mm diameter), 2) secondary (partially opaque, 0.20 - 0.55 mm diameter), and 3) mature (completely opaque, fully-yolked, 0.40 – 1.0 mm diameter). Only fully yolked oocytes were considered mature and used in our fecundity estimates. After counting, the individual cores and the remaining ovary were dried at 60°C to a constant mass. We estimated ova density for each core (eggs/g), and then estimated mean ova density across cores. We multiplied mean ova density by the total dry mass of the ovary (remaining ovary + mass of six individual cores) to estimate fecundity for each fish.
In addition to egg diameter, we quantified energy density (kJ/g wet mass) of whole ovaries as a metric of ovary quality. We estimated ovary energy density from 156 white crappie sampled across seven reservoirs in 1999 and three reservoirs in 2000 (Table 2). Fish selected for later estimation of ovary energy density were frozen whole after initial measurements in the lab (i.e., identifying sex and measuring length and mass). Estimation of ovary energy density was identical to previously described methods for estimating energy density of somatic tissue, except that we used a micro-calorimeter (Parr Instruments Model 1425), which allowed us to use 0.1 g samples of dried ovary tissue. The mean of two samples was used to characterized the energy density of each ovary. To explore relationships between somatic energy density and individual condition of white crappie during spring, we also estimated energy density of somatic tissue (N = 47 fish) from three reservoirs in 2000. Methods of somatic energy density estimation in spring were identical to methods used for fish sampled in autumn.

To explore gonadal changes after white crappie were presumed to have begun spawning, we also sampled adult white crappie with trapnets during late May and June, 1999 from Alum Creek reservoir. From these fish, we estimated GSI, which indicates the degree of gonadal development (Strange 1996). We then could evaluate how GSI of white crappie changed between late April and late June.

*Spring sampling for larvae*

Limnetic larvae were sampled weekly during May-June from 12 reservoirs during 1998 and 8-9 reservoirs during 1999-2000 (Table 2). Two replicate 5-min tows were completed at fixed upstream and downstream sites during the day with a 1 × 2 m
neuston net (0.5 mm mesh) along the top meter of the water. A flowmeter mounted at the mouth of the net estimated distance traveled, which enabled us to calculate volume sampled. Samples were preserved in 95% ethanol; *Pomoxis* spp. were later separated in the laboratory from walleye *Stizostedion vitreum*, yellow perch, *Morone* spp., gizzard shad *Dorosoma cepedianum*, and *Lepomis* spp. larvae, and then counted. The two species of *Pomoxis* larvae cannot be distinguished visually with any reliability owing to their similar number of myomeres (Siefert 1969).

When *Pomoxis* spp. larvae were extremely abundant, at least 200 individuals were counted from a known percentage of the sample, then extrapolated to a total estimate. All individuals were counted when fewer than 200 individuals occurred. In some samples, however, larvae were extremely rare (i.e., less than four individuals in at least 25% of the sample). To save processing time, we determined how well extrapolating from 25% predicted the complete count. For 36 estimates in 1998, we found the extrapolated estimate to be a strong predictor of the complete count ($r^2 = 0.69; F_{1,34} = 77.3; P < 0.0001$). Hence, we used the extrapolated estimate when fewer than four individuals were counted in at least 25% of the sample for the samples processed in 1999-2000.

To determine larval density, we sought to include only fish that hatched in the week between the previous and current sampling event to eliminate biasing larval density higher when larval survivorship was high, as those larvae could be sampled during multiple weeks. Previous analyses suggest fish larger than 9 mm TL should have been captured in earlier weeks of sampling, and thus were excluded when estimating larval density for each sample (Bunnell et al. In preparation). Herein, larval hatch density refers
to the density of larvae smaller than 9 mm TL, rather than density of all larvae captured. Mean larval hatch density was calculated at each site and then a reservoir-wide, mean density of hatch was calculated for each week of sampling.

**Analyses**

*Characterizing maternal characteristics*

We characterized maternal length and condition at the individual and population levels. Season-specific, individual condition was estimated as the residual from predicted wet mass using the relationship

\[ M = aL^b \]  

(8)

where \( M \) is mass (g) and \( L \) is cm length class. The autumn relationship pooled 4 years of trapnetting data, whereas 2 years of data were pooled for spring. During spring, somatic (i.e., total mass minus ovary mass), rather than total mass (as was used in autumn), was used to remove the effects of ovary mass, which can be large for long fish in spring. Because wet mass can be a poor predictor of energetic condition (Hartman and Brandt 1995), we also evaluated whether individual condition was positively related to somatic energy density (kJ/g wet mass) of 79 white crappie using Pearson’s correlation.

Population condition of adults (i.e., fish larger than 18 cm TL) was estimated only in autumn. We used condition of fish in autumn, rather than spring, to characterize population condition because our autumn sampling was more extensive than spring and produced a less biased length distribution of adults. Using autumn condition to explore maternal effects on reproduction also is useful because white crappie begin reproductive development during autumn (Bunnell and Marschall in review). To characterize
population condition, we estimated the mean residual for each cm length class for each species and reservoir-year. We then used the length distribution from each reservoir-year to produce a weighted mean residual across cm length classes, where the proportion in each cm length class for each species weighted the mean residual for each cm length class.

**Impact of maternal characteristics on ovary quality**

We used mean diameter of mature eggs and whole ovary energy density as metrics of ovary quality, and determined whether these metrics were related to maternal condition or length. To determine whether maternal length, condition, and the length × condition interaction of individual white crappie were related to mean egg diameter of mature eggs, we used a general linear model (Proc GLM; SAS Institute 1999). For this and subsequent general linear models, response variables were log transformed when necessary to meet assumptions of normality and homogeneity of variance.

We explored the effects of maternal characteristics on ovary energy density at both the individual and population level. At the individual level, we first regressed both individual condition and TL of spring fish against ovary energy density. However, we observed the impact of condition and TL on ovary energy density to change over the range of both independent variables. Because we did not interpret the relationships to be linear, we used a two-dimensional Kolmogorov–Smirnov test (2-DKS) to determine whether a threshold relationship existed, i.e., is there some condition or length value beyond which the variance in ovary density was constrained (Garvey et al. 1998b)?
Characterizing ovary quality at the population level required multiple steps given the threshold relationships between length, condition, and ovary energy density. For each reservoir-year, we first estimated the mean ovary energy density of fish above and below the length threshold. We then calculated a weighted grand mean energy density where length threshold means were weighted by the proportion of the population that was above and below the length threshold during sampling the previous autumn. To determine how weighted mean ovary quality varied as a function of population condition from the previous autumn and year, we then used analyses of covariance (Proc GLM; SAS Institute 1999) with population condition as the covariate.

Impact of maternal characteristics on fecundity

To determine whether fecundity was influenced by individual condition, we first standardized fecundity across different lengths of fish by calculating a residual from predicted fecundity, from the relationship:

\[ F = aL^b \]  \hspace{1cm} (9)

where \( F \) is total number of mature eggs and \( L \) is fish length (cm) (Blaxter 1969). We then used a general linear model (Proc GLM; SAS Institute 1999) to determine whether spring individual condition was related to residual fecundity. At the population level, we used analysis of covariance (Proc GLM; SAS Institute 1999) to determine how year and population condition (the covariate) influenced mean residual fecundity for each reservoir year.
Impact of maternal length on rate of ovarian development

To explore how ovarian development was influenced by fish length, we sampled white crappie in the last week of April, May, and June 1999 from Alum Creek. We could not evaluate the effect of maternal condition on ovarian development because we had no predicted mass for fish of a given length in May or June. We used ovary mass to assess maturation. Because ovary mass covaries with fish length, we estimated predicted April ovary mass as a function of length with 354 white crappie sampled over 13 reservoir-years using the same relationship as equation (9), except $F$ was replaced by ovary mass (g). We then compared female ovary mass in any given month to predicted April ovary mass for a given length as an index of ovarian development.

Impact of egg production, maternal characteristics, and water elevation on larval hatch density

We wanted to determine how population condition from the previous autumn, population egg production, and reservoir water elevation during the spawning season influenced larval hatch density. We did not use population length, our other maternal characteristic, as a separate variable because it was used in our estimate of egg production. Because both black and white crappie larvae are included in larval hatch density, we considered both black and white crappie adult populations when characterizing population condition and egg production. The mean population condition of both species used the percent species composition from each reservoir year to weight the species-specific population condition. Predicted egg production, $E$, was estimated as

$$E = \sum_{i=18}^{n} F_i (CPE_i \times 200 \times 0.5),$$

(10)

67
where \( i = \) cm length classes 18 to \( n \), \( F_i \) is the predicted fecundity in length class \( i \), \( CPE_i \) is CPE for each cm length class \( i \) from the previous autumn of sampling, 200 is a constant to assure that all CPE values greater than 1, and 0.5 represents the proportion of females. Although sex ratio was not measured, we assumed it to be 1:1. Predicted fecundity \( F \) was estimated using all 122 white crappie for which fecundity was estimated as

\[
F = (0.0941)L^{4.0785}
\]

where \( L \) is length in cm. Here, we assumed that only the eggs we characterized as mature would be spawned in that year. No evidence exists that suggests female white crappies are fractional spawners (i.e., that the smaller, partially opaque eggs will mature and be expelled later that year). Also, we assumed that white crappie and black crappie have similar length/fecundity relationships.

During 1995 – 2000, daily water elevation (m above sea level) was acquired either from the United States Army Corps of Engineers (for Alum Creek, Berlin, Burr Oak, Caesar Creek, Deer Creek, Delaware, Piedmont, Pleasant Hill, Seneca, Tappan), Pymatuning State Park (Pymatuning), the City of Akron, Ohio (for LaDue), or Miami Conservancy District (for Acton Lake). We focused on water elevation during May – June, the period when \( Pomoxis \) spp. are spawning. We first determined the average May – June water elevation for each reservoir across all years, and then characterized water elevation during spawning, \( W \), as

\[
W = \frac{E_{V_{yr}} - E_{V_{avg}}}{E_{V_{avg}}}
\]

where \( E_{V_{yr}} \) is the mean water elevation during spawning for a given year and \( E_{V_{avg}} \) is the average water elevation during the 1995 - 2000 spawning seasons.
To estimate total density of larvae hatched, we used the mean density across all sampling weeks. Although the total density across weeks would have been best, weather or boat problems prevented sampling during in 1 week in Delaware in 1998 and 1 week in Acton and Berlin in 2000. Because the mean across sampling weeks was a strong predictor of total hatch density ($F_{1,26} = 1992.3; P < 0.0001; r^2 = 0.99$), the mean was an excellent surrogate for total hatch density.

Owing to the use of three independent variables (i.e., weighted population condition, *Pomoxis* spp. egg production, $E$, and spawning water elevation, $W$) to explain only 17 reservoir-years of larval hatch density, we used Akaike’s Information Criterion (AIC) to choose the suite of models that best described our data set, rather than an iterative multiple regression which selects only the “best” model. We used least-squares regression (Proc REG; SAS Institute) to estimate parameters and residual sums of squares, and then calculated AIC (Burnham and Anderson 1998) for each of the eight possible models (including a null model with only an intercept). Because our ratio of parameters to observations was less than 40, we then calculated second-order AIC ($AIC_c$) as

$$AIC_c = AIC + \frac{2K(K+1)}{n-K-1}$$

(13)

where $K$ is the number of parameters and $n$ is the number of observations, (Burnham and Anderson 1998). For each model, $\Delta_i$ was reported as

$$\Delta_i = AIC_c - \min(AIC_c)$$

(14)
where min(AICc) is the smallest AICc value among the models. Models for which $\Delta_i \leq 2$ provided “substantial” support in explaining variation in the data (Burnham and Anderson 1998).

Impact of egg production, maternal condition, and larval hatch density on recruitment

We used two general linear models (Proc GLM; SAS Institute 1999) to determine 1) whether larval hatch density related to recruitment (i.e., age-2 CPE) of white and black crappies, and 2) how adults (i.e., population condition and predicted population egg production) related to white crappie recruitment. The first analysis included both species because we could not separate them as larvae, whereas the second analysis focused only on white crappie. Although path analysis would have permitted us to analyze the independent variables simultaneously, we lacked the recommended minimum of 10 observations per variable (Mitchell 1993). Hence we used two separate linear models to determine the life history stage at which recruitment could be predicted.

Results

Characterizing maternal characteristics

The relationship $M = aL^b$ fit length and mass data well for both white (total wet mass = 0.00483(TL)$^{3.288}$) and black crappie (total wet mass = 0.00277(TL)$^{3.5214}$) during autumn and white crappie during spring (somatic wet mass = 0.00318(TL)$^{3.4228}$). Using residuals of predicted somatic mass, for a given length, individual condition was positively correlated with somatic energetic density (kJ/g wet mass) for fish in both
autumn and spring (Figure 9; $r = 0.62; P < 0.0001; N = 79$ fish). Thus, individual condition provided an appropriate surrogate for energetic condition of white crappie across Ohio reservoirs.

**Impact of maternal characteristics on ovary quality**

We explored how maternal characteristics related to both energy density and mean egg diameter of ovaries collected from white crappie during April, at least 1 week before spawning. Using 154 white crappie collected across seven reservoirs in spring 1999 and three reservoirs in spring 2000, 2-DKS detected a significant threshold relationship between both TL (Figure 10a; $D_{BKS} = 0.164, P = 0.0002$) and individual condition (Figure 10b; $D_{BKS} = 0.114, P = 0.0002$) versus ovary energy density (kJ/ g wet mass). The threshold TL was 24.9 cm; fish smaller than 24.9 cm TL exhibited highly variable ovary energy density, whereas larger fish were relatively less variable and ovary energy density was always greater than 6 kJ/g wet mass. The threshold individual condition was -2.0, suggesting that the threshold condition was nearly “average” mass for a given length (Figure 10b). The relationship between individual condition and energy density also suggested an interaction between length and condition. Most all fish larger than 24.9 cm TL (i.e., long fish), independent of condition, generally had calorie-rich ovaries (i.e., > 6 kJ/g wet mass). Conversely, fish smaller than 24.9 cm TL (i.e., short fish), ovary energy density generally increased with condition.

At the population level, condition also was positively related to ovary energy density. Weighted mean ovary energy density for each reservoir was strongly related to population condition from the previous autumn (ANCOVA: population condition, $F_{1,7} =$
18.64; \( P = 0.001 \)), but did not differ among years (ANCOVA: year, \( F_{1,7} = 0.00; P = 0.99 \)).

We then pooled years and used linear regression to determine that population condition strongly predicted weighted mean ovary energy density at the population level (Figure 10c; \( F_{1,8} = 29.17; P < 0.0001; r^2 = 0.78 \)). Those populations in better condition during autumn possessed more calorie-rich, pre-spawn ovaries the following spring.

Sufficient (at least 30 eggs per fish) eggs were measured for 104 white crappies, for which fecundity was estimated. Mean egg diameter increased with TL (Figure 11a; \( F_{1,100} = 11.05; P < 0.001 \)), but not with individual condition (Figure 11b; \( F_{1,100} = 0.67; P = 0.41 \)). The length \( \times \) condition interaction also was not significant (\( F_{1,100} = 0.71; P = 0.40 \)). Thus, fish length was positively related to both energy density and mean diameter of mature eggs.

**Impact of maternal characteristics on fecundity**

Nearly 80% of the variability in total fecundity was explained by total length (Figure 12a; \( F_{1,120} = 547.5; r^2 = 0.79; P < 0.001 \)). All 122 white crappie sampled across 12 reservoir years had conspicuous, yellow ovaries during late April. However, 10% (12 / 122) had no mature ova; these fish always were smaller than 24 cm TL, which closely corresponded to the threshold size observed in the ovary energy density analyses (i.e., 24.9 cm TL). Residual fecundity, for a given length, was used to compare the effects of maternal condition across fish of different lengths. Residual fecundity increased slightly with individual condition (Figure 12b; \( F_{1,120} = 5.65; r^2 = 0.05; P = 0.02 \)). At the population level, mean residual fecundity was influenced by both population condition (Figure 12c; ANCOVA: \( F_{1,9} = 5.75; P = 0.04 \)) and year (Figure 12c; ANCOVA: \( F_{1,9} = \)
6.99; \( P = 0.03 \). Effects of condition were driven by the 1999 year-class, in which linkage between population condition and mean residual fecundity was stronger than for the 2000 year-class. Finally, we evaluated whether a trade-off existed between mean egg diameter and residual fecundity. Mean egg diameter was weakly positively related to residual fecundity (Figure 11c; \( F_{1,106} = 7.41; r^2 = 0.07; P = 0.01 \)). Nonetheless, egg diameter does not appear to be compromised by increasing fecundity.

**Impact of maternal characteristics on rate of ovarian development**

From fish collected in April (at least 1 week before spawning), ovary mass was highly related to maternal length (\( F_{2,352} = 1615.58; r^2 = 0.90; P < 0.0001 \)). During April – June 1999, we used the proportion of predicted April ovary mass of a given length that each fish had attained to determine the level of ovarian development. Fish size influenced development. As in the ovary energy density analyses, \( \sim 25 \) cm appeared to separate the development dynamics of short and long fish. For fish longer than 25 cm, ovarian development was much higher in April than in May or June, suggesting spawning occurred in early May. Conversely, for fish shorter than 25 cm, ovarian development increased from April to May and values in June were similar to May, suggesting spawning occurred in late May or June. Thus, long fish likely spawned before short fish in Alum Creek in 1999.

**Impact of egg production, maternal characteristics, and water elevation on larval hatch density**

We explored how population condition from the previous autumn, predicted population egg production, and reservoir water elevation during spawning influenced
larval hatch density in eight reservoirs in 1999 and nine reservoirs in 2000. The smallest AICc value (i.e., \( \Delta_i = 0 \)) occurred for the null model, which included only the intercept (Table 3). However, the next smallest \( \Delta_i \) was 2.82, which suggests that the model that includes population egg production (Figure 14a; \( F_{1,15} = 3.40; r^2 = 0.18; P = 0.09 \)) also provides support for explaining the data (Burnham and Anderson 1998). In addition, the parameter values for population egg production and water elevation during spawning were positive in all models, implying both may increase larval hatch density. The parameter for weighted condition of the population was negative, which was opposite from our hypothesis. Although variance in larval hatch density was largely unexplained, of the factors that were measured, population egg production likely had the greatest impact on larval hatch density owing to its small AICc.

**Impact of egg production, maternal condition, and larval hatch density on recruitment**

Both larval hatch density and population egg production were related to age-2 CPE, our index of recruitment success. Age-2 CPE of white and black crappies increased with larval hatch density of white and black crappie (Figure 14b) across 11 reservoirs in the 1998 year-class and 8 reservoirs from the 1999 year-class. Despite high variability at low densities of larvae, age-2 CPE generally increased with larval density. Next, we omitted the larval stage, and evaluated whether population egg production and population condition were related to white crappie age-2 CPE (+1, then \( \log_{10} \) transformed). Here, we were able to use 14 reservoirs from only the 1999 year-class, as population egg production and condition were not estimated for the 1998 year-class (i.e., we did not sample in autumn 1997). Egg production (\( t = 2.99; P = 0.01 \)) was useful in explaining
age-2 CPE, but population condition ($t = -0.53; P = 0.61$) was not. Thus, when the model was reduced to simple linear regression, egg production explained 46% of the variability in age-2 white crappie CPE (Figure 14c; $F_{1,12} = 10.42; r^2 = 0.47; P = 0.008$).

**Discussion**

Adults strongly influenced recruitment success of white crappie (Figure 15). Population egg production, which was estimated by using both adult CPE and population length, explained 47% of the variability in recruitment (i.e., age-2 CPE) of the 1999 white crappie year-class across 14 Ohio reservoirs. Recruitment also increased with density of larval hatch. Finally, because recruitment increased with population egg production, linkages between multiply life history stages indicate that conventional stock/recruit dynamics are the mechanism underlying recruitment of white crappie in Ohio reservoirs. Maternal characteristics, including length and condition, influenced ovary characteristics (e.g., energy density, egg diameter, GSI, see Figure 15), which, in turn, could influence timing of spawning. Specifically, long fish and short fish in higher condition may spawn earlier than short fish in poorer condition. Although population condition of females was unrelated to recruitment, the length distribution of the adult females will influence the population egg production. Because egg production was a strong predictor of recruitment, maternal characteristics indirectly influence recruitment by affecting the number of eggs produced in each population.
Impacts of maternal characteristics on recruitment

For female fishes, length and condition have been linked to characteristics of eggs and offspring. For example, egg size (i.e., diameter, volume) increases with maternal condition (Chambers and Waiwood 1996; Marteinsdottir and Steinarsson 1998) and length (Beacham and Murray 1985; Kjesbu 1989). Although we expect these maternal effects on eggs to be translated to offspring phenotypes, few studies have linked maternal effects to offspring, perhaps due to interacting environmental factors such as temperature (Bengtson et al. 1987; Benoit and Pepin 1999; but see Beacham and Murray 1985; Heyer et al. 2001). Hence, detecting maternal impacts on recruitment success may be extremely difficult (but see Marshall et al. 1999). In our study, maternal characteristics did not directly explain variability in recruitment for white crappie. Rather, egg production appeared to overwhelm maternal effects, as populations producing more eggs enjoyed greater recruitment success than those producing fewer eggs. In fact, because populations with low egg production (e.g., Piedmont, Pymatuning) were comprised of fishes in excellent condition, population condition was negatively related to larval hatch density and recruitment success across all reservoirs. Even so, maternal effects did influence ovary characteristics.

For white crappie sampled in the 1 – 2 weeks before spawning, ovary energy density, egg diameter, and GSI all increased with maternal length. Individual condition of white crappie influenced only short fish (i.e., < 24 cm TL); positive condition females had higher energy density and GSI values than negative condition ones. However, condition influenced residual fecundity and energy density at the population level, as high population condition in autumn was strongly positively correlated with ovary energy density.
density the following spring across 10 reservoir-years, and related to residual fecundity across seven reservoirs in the spring of 1999 (but not for five reservoirs in 2000).

Finally, maternal length also influences when ovary mass peaks for fish of a given size, which likely affects ovarian development and timing of spawning. Sampling in Alum Creek in 1999 revealed fish longer than 25 cm to exhibit maximum ovary size by early May, whereas fish shorter than 25 cm attained their largest ovary size in late May and June.

In our view, the ultimate impact of maternal characteristics depends on how these April results are interpreted. Are the maternal effects on ovaries due to 1) differences in rate of ovarian development or 2) differences in the quality and quantity ovary “end product”, i.e., are we comparing ovaries at the same stage of ovary development? These interpretations are not mutually exclusive. For example, short fish in poor condition may spawn later (interpretation #1) but these fish also may never achieve the energy density and egg diameter of either long fish or short fish in good condition during April (interpretation #2). Because we did not sample ovary quality or fecundity through the spawning season, our data cannot evaluate the second interpretation. Our results do, however, suggest that maternal characteristics influence ovarian development which, in turn, influences the timing of reproduction. Given that larvae hatch from early May through late June and that crappies spawn only once per season, as generally believed, then individuals must be spawning at different times. As previously mentioned, measures of ovary size in Alum Creek in 1999 indicated that long fish reproduce earlier than short fish. Fish length has been correlated with earlier spawning for a number of taxa including herring *Clupea harengus* (Ware and Tanasichuk 1989; Slotte et al. 2000),
capelin *Mallotus villosus* (Carscadden et al. 1997), and largemouth bass *Micropterus salmoides* (Goodgame and Miranda 1993). As an explanation, long fish may develop their gonads at a faster rate (e.g., Ware and Tanasichuk 1989; but see Slotte et al. 2000) or they may initiate vitellogenesis earlier than shorter ones (sensu Slotte et al. 2000), owing to their higher energy stores (Stewart et al. 1983; Slotte 1999).

If maternal effects influence the timing of reproduction, then maternal effects could indirectly influence recruitment success. Timing of larval hatch can be critical to recruitment for both marine (Narimatsu and Munehara 1999) and freshwater (Cargnelli and Gross 1996) fishes. Early hatching larvae can gain length advantages over later-hatched ones (e.g., Cargnelli and Gross 1996), which may provide survival advantages to those early-hatching larvae (Miller et al. 1988). However, late-hatching fishes also can gain survival advantages should abiotic factors (e.g., water temperature, hydrology) be improved later in the season, relative to early in the season (e.g., Narimatsu and Munehara 1999). When timing of hatch is critical to larval survival and recruitment success, maternal characteristics, through their impact on reproductive timing, could play a large role in shaping recruitment success.

*Impacts of egg production on recruitment*

Egg production, alone, explained 47% of the variability in age-2 CPE, strongly suggesting that conventional stock/recruit dynamics regulate recruitment of white crappie in Ohio reservoir populations. Because we also sampled larvae, we were in the unique position to evaluate predictions associated with the egg production mechanism: if the total number of eggs limit recruitment to age-2, then egg production should be related to
larval hatch density and, in turn, larval hatch density should be related to age-2 CPE. These predictions were generally met. For the relationship between population egg production and density of larval hatch, higher than predicted hatch in Acton Reservoir in 2000 (see AT in Figure 14a) reduced the $r^2$ from 0.41 to 0.18. In our view, realizing the effect of this one data point increases confidence that higher egg production does increase larval density. The relationship between larval density and recruitment was not linear. Rather, recruitment increased at low densities of larvae with high variability and recruitment remained high at higher densities of larvae (i.e., 0.15/m$^3$). Nonetheless, high density of larval hatch generally led to higher recruitment. Thus, these positive associations between life history stages (i.e., egg, larvae, age-2) reinforce our interpretation that egg production underlies recruitment variation of white crappie in Ohio reservoirs.

In addition to including three life history stages, our approach differed from conventional stock/recruit studies in that our data were replicated spatially, rather than temporally. Simply put, we chose reservoirs that varied in spawning stock biomass, then evaluated how their predicted egg production related to recruitment success. As such, we could complete our study in a relatively short time as well as avoid problems associated with auto-correlated time series data when stock/recruit models replicate across years within a single system (Walters 1985). One caveat to our approach is that a correlation between egg production and recruitment could be spurious should processes occurring after larvae hatch regulate recruitment to age-2 (e.g., predation, starvation, overwinter mortality) rather than egg production. In this case, few recruits (and adults) would not result from too few eggs and larvae, but from poor survival of larvae to age-2. Again,
because eggs and larvae, and larvae and age-2 abundance all were positively correlated, we believe that egg production limits recruitment in Ohio reservoirs.

The importance of stock size (i.e., egg production) in influencing recruitment success has become better appreciated in recent years for both freshwater and marine fish systems. In a meta-analysis, Myers and Barrowman (1996) found spawner abundance to be generally positively related to recruitment across 364 spawner recruitment time series for 10 orders of freshwater and marine fishes. This relationship was best revealed when a broad range of spawner abundance occurred, particularly when low spawner abundance occurred, often due to overfishing. In freshwater fish populations, however, individual stock/recruit relationships are not frequently documented (LeCren et al. 1977; Myers and Barrowman 1996; Post et al. 1998; Gillooly et al. 2000; but see Chadwick 1982, Schram et al. 1995, Madenjian et al. 1996, Allen and Miranda 1998, Hansen et al. 1998 for varying degrees of success). Myers and Barrowman (1996) argued that the freshwater species for which they analyzed lacked sufficient variation in spawner abundance to detect stock/recruit patterns, perhaps because those species were less subject to extreme overexploitation than marine species.

Comparisons of white crappie adult CPE in Ohio reservoirs to other United States reservoir populations suggest that Ohio populations do contain relatively low spawner abundance, which likely increases the probability of detecting a stock/recruit relationship (sensu Myers and Barrowman 1996). Mean CPE of adult (≥ age-2) white crappie in Ohio reservoirs ranged 0.04 – 5.14 per net night across 4 years of sampling, whereas mean CPE of adults among four Missouri reservoirs ranged 10.8 – 25.8 per net night (sampled with the same gear; Colvin 1991a). Clearly, Ohio white crappie populations may well be
limited by egg production. Low spawning stock, even in our most white-crappie abundant systems, may explain why our stock recruit relationship was linear, i.e., why we failed to detect density-dependent reductions in recruitment predicted in conventional models (e.g., Ricker 1954; Beverton and Holt 1957).

Even when linkages between spawning stock biomass and egg or larval production occur in freshwater systems, linkages to later life stages often do not exist, owing to post-larval processes such as predation, competition, or overwinter survival (e.g., Post et al. 1998; Gillooly et al. 2000). For white crappie, high water level during the previous winter (Maceina and Stimpert 1998) and during the spawning season (Mitzner 1981) is related to strong recruitment, implying that high water levels facilitate survival to the larval stage and beyond. Larval hatch density of freshwater fishes, in turn, also can be unrelated to recruitment owing to a host of abiotic (e.g., overwinter mortality, Ludsin and DeVries 1997; Post et al. 1998) and biotic (e.g., predation, Post et al. 1998; starvation, Partridge and DeVries 1999) factors. However, Pomoxis spp. larvae in Normandy reservoir, Tennessee were strongly related to density of age-1 fish over 5 years (Sammons and Bettoli 1998), providing another example (in addition to ours) that white crappie recruitment is set by the larval stage.

**Management implications**

Our primary finding that egg production drives recruitment provides Ohio fishery managers with tools to predict and improve recruitment of white crappie, and a new perspective from which to explain the success, failure, and variability of crappie fisheries to constituent groups. Predicting recruitment success could be achieved by sampling
adult populations with trapnets during autumn to estimate length distribution and CPE, which can be used to predict egg production for the following spring via our length fecundity relations. Because recruitment increased with egg production, managers could increase the size distribution or number of adults to improve recruitment. At least three catch restrictions could increase egg production: 1) length limits, which set the minimum length of fish legally harvested, 2) creel limits, which limit the number of fish harvested by an angler each day, and 3) a closed fishing season during April – May, i.e., preventing fishing for crappies during the spawning season when the fish are on the nest, ensuring that all mature adults can attempt to reproduce each year. To our knowledge, only length (Colvin 1991b; Webb and Ott 1991; Hale et al. 1999) and creel limits (Colvin 1991b; Webb and Ott 1991) have been used to manage crappie fisheries in the United States. Their goal is to increase the average size of fish harvested in systems where growth rates are high. A closed season would be the last option for managers because the spring spawning season is traditionally the best fishing season for crappies, and enforcement of species-specific fishing bans would be very difficult.

With these recommendations come a few caveats. First, this scenario implies a positive feedback where increasing spawning stock will continue to increase recruitment. Certainly, at some higher levels of spawning stock, age-2 CPE will either level off (sensu Beverton and Holt 1957) or decrease (sensu Ricker 1954), owing to density-dependent factors influencing either adults (e.g., reduced per capita egg production) or age-0 fishes (starvation, predation). In fact, at higher densities maternal effects may have a greater impact on recruitment. With our data, however, we cannot estimate when the spawning stock threshold would occur. Rather, our results suggest that within our ranges of
spawning stock (i.e., 0.1 – 5.1 mean CPE of adults), increasing spawning stock should increase recruitment success. Second, we assume that catch restrictions will increase spawning stock by reducing total mortality. If management regulations are to increase spawning stock, fishing mortality must comprise the majority of total mortality (where total equals fishing plus natural). Across the United States, fishing mortality in white and black crappie fisheries range from 20% in Alabama (Reed and Davies 1991) to 40 – 68 % in Georgia reservoirs (Larson et al. 1991) to >50% in Missouri reservoirs (Colvin 1991a). We have no data for Ohio reservoirs, but hypothesize that the low spawning stock (especially relative to Missouri) is due to overexploitation by anglers or predation. Indicting predation on adult white crappie (i.e., > 18 cm TL) as the factor limiting spawning stock size would require high densities of large-gaped predators, which is possible but not likely in Ohio reservoirs. Regardless, in Ohio and elsewhere, fishing mortality should be quantified before catch restrictions are implemented, to ensure that total mortality would be reduced sufficiently to improve spawning stock and resultant egg production.

Although adult impacts on recruitment are becoming more recognized in marine taxa (Myers and Barrowman 1996; Solemdal 1997), few studies have demonstrated that adults influence recruitment in freshwater systems. We demonstrated that egg production limits recruitment success, strongly justifying a management program that restricts catch and increases spawning stock of white crappie. However, we also found evidence of maternal characteristics influencing ovaries at the individual level. Although maternal effects did not influence population dynamics in our relative low-density Ohio reservoirs (relative to Missouri reservoirs), condition or length of the adult population may be more
likely to influence recruitment in reservoirs with higher adult densities. If density-dependent growth limits maternal length or condition in a high-density adult population, then quality of individual ovaries (e.g., energy density, egg diameter) may be compromised, which may influence recruitment at the population level.


Trautman, M. B. 1957. The fishes of Ohio. The Ohio State University Press, Columbus, Ohio.


Table 2. Characteristics of 14 Ohio reservoirs that were differentially sampled for *Pomoxis* spp. larvae, adult white and black crappie, white crappie fecundity, and white crappie ovary energy density during 1998-2001. White crappie population is the mean percentage of adult white crappie (by number) of the total adult *Pomoxis* spp. populations (black and white crappie) across 4 years (1998-2001) of autumn trapnetting. Mean adult CPE (fish/net night) is the mean CPE of fish ≥ age-2 collected across 4 years of autumn trapnetting. CV is the coefficient of variation (σ/mean).
<table>
<thead>
<tr>
<th>Reservoir Name</th>
<th>Code</th>
<th>County</th>
<th>Surface Area km²</th>
<th>Years Pomoxis spp. larvae sampled</th>
<th>Years fecundity of white crappie estimated</th>
<th>Years ovary energy density of white crappie estimated</th>
<th>White crappie population % (range)</th>
<th>Mean white crappie adult CPE Fish/net night (CV)</th>
<th>Mean black crappie adult CPE Fish/net night (CV)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acton</td>
<td>AT</td>
<td>Butler</td>
<td>2.53</td>
<td>1998-2000</td>
<td>1999-2000</td>
<td>1999</td>
<td>100.0 (100.0-100.0)</td>
<td>3.13 (0.95)</td>
<td>0</td>
</tr>
<tr>
<td>Alum Creek</td>
<td>AM</td>
<td>Delaware</td>
<td>13.71</td>
<td>1998-2000</td>
<td>1999-2000</td>
<td>1999 - 2000</td>
<td>65.0 (48.5-82.0)</td>
<td>0.78 (0.36)</td>
<td>0.77 (0.76)</td>
</tr>
<tr>
<td>Berlin</td>
<td>BR</td>
<td>Portage</td>
<td>13.44</td>
<td>1998-2000</td>
<td>1999-2000</td>
<td>1999</td>
<td>68.8 (57.5-76.0)</td>
<td>0.90 (0.43)</td>
<td>0.96 (0.80)</td>
</tr>
<tr>
<td>Burr Oak</td>
<td>BO</td>
<td>Morgan</td>
<td>2.69</td>
<td>1998-2000</td>
<td>1999</td>
<td>1999</td>
<td>98.2 (96.2-99.7)</td>
<td>0.92 (0.38)</td>
<td>0.05 (0.40)</td>
</tr>
<tr>
<td>Caesar Creek</td>
<td>CC</td>
<td>Warren</td>
<td>10.55</td>
<td>1998-2000</td>
<td>1999-2000</td>
<td>1999 - 2000</td>
<td>84.9 (71.2-95.2)</td>
<td>1.41 (1.43)</td>
<td>0.39 (0.94)</td>
</tr>
<tr>
<td>Cowan</td>
<td>CW</td>
<td>Clinton</td>
<td>2.76</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>100.0 (100.0-100.0)</td>
<td>0.48 (0.33)</td>
<td>0</td>
</tr>
<tr>
<td>Deer Creek</td>
<td>DC</td>
<td>Pickaway</td>
<td>5.17</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>100.0 (100.0-100.0)</td>
<td>2.42 (1.53)</td>
<td>0</td>
</tr>
<tr>
<td>Delaware</td>
<td>DW</td>
<td>Delaware</td>
<td>5.26</td>
<td>1998, 2000</td>
<td>-</td>
<td>-</td>
<td>52.2 (33.3-71.9)</td>
<td>0.78 (0.70)</td>
<td>1.86 (0.96)</td>
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<tr>
<td>LaDue</td>
<td>LD</td>
<td>Geauga</td>
<td>6.07</td>
<td>1998-2000</td>
<td>1999-2000</td>
<td>1999</td>
<td>88.9 (83.1-96.0)</td>
<td>1.92 (0.38)</td>
<td>0.36 (0.57)</td>
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<tr>
<td>Piedmont</td>
<td>PD</td>
<td>Belmont</td>
<td>9.20</td>
<td>1998</td>
<td>-</td>
<td>-</td>
<td>91.2 (66.7-100)</td>
<td>0.11 (0.65)</td>
<td>0.03 (0.00)</td>
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<tr>
<td>Pleasant Hill</td>
<td>PH</td>
<td>Richland</td>
<td>3.16</td>
<td>1998-2000</td>
<td>1999-2000</td>
<td>1999 - 2000</td>
<td>97.4 (94.6-98.7)</td>
<td>5.14 (0.60)</td>
<td>0.34 (1.50)</td>
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<tr>
<td>Pymatuning</td>
<td>PY</td>
<td>Ashtabula</td>
<td>59.29</td>
<td>1998-2000</td>
<td>-</td>
<td>-</td>
<td>19.3 (15.2-24.3)</td>
<td>0.94 (0.49)</td>
<td>0.25 (0.54)</td>
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<tr>
<td>Seneca</td>
<td>SC</td>
<td>Noble</td>
<td>14.20</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>100.0 (100.0-100.0)</td>
<td>2.66 (0.59)</td>
<td>0</td>
</tr>
<tr>
<td>Tappan</td>
<td>TP</td>
<td>Harrison</td>
<td>8.62</td>
<td>1998</td>
<td>-</td>
<td>-</td>
<td>100.0 (100.0-100.0)</td>
<td>0.99 (0.59)</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 3. AICc model selection results to explain larval hatch ordered by $\Delta_i$, where $\Delta_i$ is the difference between each model $i$ and the model with the minimum AICc value (i.e., model 1). For each model, 17 observations (i.e., reservoir-years) were used. Parameter estimates for each independent variable, the residual sums of squares, and $r^2$ for each model also are provided.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\Delta_i$</th>
<th>Residual sums of squares</th>
<th>Intercept</th>
<th>Population egg production</th>
<th>Water elevation during spawning</th>
<th>Weighted population condition</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.00</td>
<td>4.50</td>
<td>-1.19</td>
<td></td>
<td></td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>2.82</td>
<td>3.67</td>
<td>-1.45</td>
<td>1.14$^8$</td>
<td></td>
<td></td>
<td>0.18</td>
</tr>
<tr>
<td>3</td>
<td>3.28</td>
<td>3.77</td>
<td>-1.19</td>
<td></td>
<td></td>
<td>-0.02</td>
<td>0.16</td>
</tr>
<tr>
<td>4</td>
<td>4.50</td>
<td>3.06</td>
<td>-1.44</td>
<td>1.05$^8$</td>
<td></td>
<td>-0.02</td>
<td>0.32</td>
</tr>
<tr>
<td>5</td>
<td>5.24</td>
<td>3.20</td>
<td>-1.39</td>
<td>1.31$^8$</td>
<td>2.39</td>
<td></td>
<td>0.29</td>
</tr>
<tr>
<td>6</td>
<td>5.35</td>
<td>4.26</td>
<td>-1.11</td>
<td></td>
<td>1.68</td>
<td></td>
<td>0.05</td>
</tr>
<tr>
<td>7</td>
<td>7.10</td>
<td>3.57</td>
<td>-1.12</td>
<td></td>
<td>1.53</td>
<td>-0.02</td>
<td>0.21</td>
</tr>
<tr>
<td>8</td>
<td>7.62</td>
<td>2.66</td>
<td>-1.38</td>
<td>1.22$^8$</td>
<td>2.20</td>
<td>-0.02</td>
<td>0.41</td>
</tr>
</tbody>
</table>

Table 3. AICc model selection results to explain larval hatch ordered by $\Delta_i$, where $\Delta_i$ is the difference between each model $i$ and the model with the minimum AICc value (i.e., model 1). For each model, 17 observations (i.e., reservoir-years) were used. Parameter estimates for each independent variable, the residual sums of squares, and $r^2$ for each model also are provided.
Figure 9. Somatic energy density (kJ / g wet mass) as a function of individual condition during autumn 1999 (circles) and spring 2000 (triangles) of female white crappie collected from Alum Creek, Caesar Creek, and Pleasant Hill, OH reservoirs. Individual condition is the residual from predicted mass of the total fish mass in autumn, and of the somatic mass, only, in spring (i.e., total mass – gonad), for a given total length.
Figure 9

\[ r = 0.62 \]
\[ P < 0.0001 \]
\[ N = 79 \]
Figure 10. Ovary energy density (kJ / g wet mass) of pre-spawning white crappie collected from seven Ohio reservoirs during April 1999 and three Ohio reservoirs during April 2000 (see Table 2). (a) Ovary energy density as a function of individual fish total length (TL). The vertical line identifies length = 24.9 cm as the threshold total length identified by the two-dimensional Kolmogorov – Smirnov test (2-DKS; Garvey et al. 1998b). In panels (a) and (b), triangles represent fish smaller than the length threshold (i.e., short fish) and squares represent fish larger than the length threshold (i.e., long fish). (b) Ovary energy density as a function of individual spring condition, where individual spring condition is the residual from spring predicted wet mass. Again, the vertical line identifies condition = -1.83 as the threshold condition index identified by 2-DKS. (c) Weighted mean ovary energy density for each reservoir-year as a function of population condition in the previous autumn. Weighted mean ovary energy density uses the proportion of the population above and below the 24.9 cm TL threshold (see panel (a)) to weight mean ovary energy density. Population condition uses the proportion of fish in each cm length class for each reservoir-year to weight the mean residual autumn wet mass for each cm length class. Symbols represent the last digit of the year that fish were collected (e.g., 9 = 1999), followed by the two-letter reservoir code found in Table 2. Note different scales in panel (c) compared to panels (a) and (b).
Ovary energy density of white crappie before spawning (kJ/g wet mass)

Spring 1999-2000

$D_{BKS} = 0.18$

$P = 0.0002$

$N_{ry} = 10$ reservoir-years

$N_f = 156$ fish

Individual spring condition of white crappie

Population condition of white crappie during previous autumn

$r^2 = 0.78$

$F = 29.71$

$P < 0.0001$

$N = 10$ reservoir-years
Figure 11. Mean egg diameter of pre-spawning white crappie that contained mature eggs. Fish were collected from seven Ohio reservoirs during April 1999 and five Ohio reservoirs during April 2000 (see Table 2). Between 38 – 240 (mean = 114.5) eggs were measured per fish, pooled across six different parts of the ovary. (a) Mean egg diameter as a function of individual fish total length (TL). (b) Mean egg diameter as a function of individual spring condition, where individual spring condition is the residual from spring predicted wet mass. (c) Mean egg diameter as a function of residual fecundity, the difference from predicted fecundity at a given total length.
Total Length of white crappie (cm)

Individual spring condition of white crappie

Mean egg diameter (mm)

Residual fecundity (*1000)

Figure 11
Figure 12. (a) Total fecundity of pre-spawning white crappie collected from seven Ohio reservoirs during April 1999 and five Ohio reservoirs during April 2000 (see Table 2) as a function of total length (cm). The solid line is predicted fecundity using non-linear regression. (a) Fecundity as a function of individual fish total length (TL). (b) Residual fecundity, for a given length, as a function of individual spring condition, where individual spring condition is the residual from predicted wet somatic mass, for a given length. (c) Mean residual fecundity for 12 reservoir-years as a function of population condition the previous autumn. Population condition uses the proportion of fish in each cm length class for each reservoir-year to weight the mean residual autumn wet mass for each cm length class. Symbols represent the last digit of the year that fish were collected (e.g., 9 = 1999), followed by the two-letter reservoir code from Table 2. ANCOVA was used to determine the effects of population condition index (covariate) and year.
(a) Fecundity = 0.0941*\(L^{4.0785}\)
\(r^2 = 0.79\)
\(F = 547.5\)
\(P < 0.001\)
\(N = 122\) fish

(b) \(F = 5.65\)
\(r^2 = 0.05\)
\(P = 0.02\)
\(N = 122\) fish

(c) \(F_{\text{cond}} = 5.75\)
\(P_{\text{cond}} = 0.04\)
\(F_{\text{yr}} = 6.99\)
\(P_{\text{yr}} = 0.03\)
\(N = 12\) reservoir-years

Figure 12
Population condition of white crappie during previous autumn
Figure 13. Ovarian development of white crappie sampled from Alum Creek during April 21 – 27 (a), May 25 – 27 (b), and June 25 (c) 1999 as a function of total length. Ovarian development is defined as the proportion of predicted April ovary mass attained for fish of a given length.
Figure 13

(a) April
N = 24 fish

(b) May
N = 22 fish

(c) June
N = 13 fish

Proportion of predicted April ovary mass attained versus White crappie total length (cm)

103
Figure 14. Linkages between life history stages of *Pomoxis* spp. Note the log$_{10}$ scale on all y-axes. (a) Mean hatch density of white and black crappie larvae sampled during May – June 1999 (eight reservoirs) and 2000 (nine reservoirs) as a function of estimated egg production of white and black crappie for each respective year. White and black crappie were combined owing to our inability to visually distinguish species as larvae. Symbols represent the year of hatch (e.g., 9 = 1999) followed by the reservoir code (see Table 2). (b) Total CPE of age-2 black and white crappie sampled with trapnets during autumn 2000 and 2001 as a function of mean hatch density of black and white crappie larvae sampled during May – June 1998 (11 reservoirs) and 1999 (8 reservoirs). (c) Mean CPE of age-2 white crappie (i.e., the 1999 year-class) sampled during autumn 2001 with trapnets as a function of estimated white crappie egg production during spring 1999. The egg production index incorporates length frequency data from autumn 1998 into a length/fecundity relationship. On the y-axis, note the addition of 1 to all values to permit transformation of CPE values of 0.
Figure 14

(a) Mean hatch density of Pomoxis spp. (x 10^6)

F = 3.40
r^2 = 0.18
P = 0.09
N = 17 reservoir-years

(b) Mean hatch density of Pomoxis spp. (#/m³)

N = 19 reservoir-years

(c) Mean CPE (+1) of age-2 white crappie (fish/net night + standard error)

F = 10.42
r^2 = 0.47
P = 0.008
N = 14 reservoirs

White crappie egg production (x 1,000,000)
Figure 15. Pathway by which adults influence recruitment (i.e., age-2 CPE) of white crappie in Ohio reservoirs. Arrows denote a positive relationship between life-history categories (e.g., adult, egg (ovary), larvae, and age-2); arrows with larger heads denote stronger linkages than those with smaller heads. Dashed arrow lines indicate that adult catch per effort and maternal length (i.e., population length) were used to estimate population egg production. Number letter combinations in parentheses, associated with each arrow, represent figures that depict each relationship. For maternal characteristics, including length and condition, individual (indiv) and population (pop’n) effects on ovary characteristics are noted.
Figure 15

Adults (≥ age-2)
- Catch per Effort (CPE)
- Maternal length
  - Maternal condition
- Ovary
  - Population egg production
  - Energy density
  - Egg diameter
  - Ovary development
- Larvae
  - Hatch density
- Age-2
  - Catch per Effort (CPE)

(10a, 10b, 10c, 11a, 11b, 12a, 12b, 12c, 13, 14a, 14b, 14c)
CHAPTER 4

EXPLORING FACTORS INFLUENCING GROWTH AND SURVIVAL OF WHITE CRAPPIE LARVAE

Introduction

Variable survival of young fish can drive population fluctuations (Sissenwine 1984; Houde 1987). To explain variable offspring survival of fishes, early marine studies focused on the role of starvation, during the period when larvae shift from feeding endogenously on yolk-sacs to exogenously on zooplankton (Hjort 1914). This transition became known as a “critical period” as Hjort (1914) argued that poor year-classes could be explained by the failure of first-feeding larvae to procure zooplankton prey. This hypothesis later was extended to freshwater environments. In experiments, survival of freshwater larvae generally increases with zooplankton density (e.g., Li and Mathias 1982; Hart and Werner 1987; Welker et al. 1994; Bestgen 1996). Similar to marine larvae, starved freshwater larvae also will reach a point of irreversible starvation (i.e., point of no return, Bestgen 1996). Despite experimental support for the hypothesis, zooplankton prey is generally unrelated to survival in freshwater field studies (e.g., Welker et al. 1994; Betsill and Van Den Avyle 1997; Garvey et al. 2002). The positive relationship between fish size and resistance to starvation (Hunter 1981; Miller et al. 1988) may help explain these opposite results. Because freshwater larvae are generally
larger at hatch than marine larvae, Houde (1994) predicted that larval starvation would be less likely to occur in freshwater larvae. Thus, starvation during the larval stage may be rare for freshwater larvae.

Beyond the direct effects of starvation, low zooplankton densities also can influence larval survival via indirect effects. First, starved larvae swim more slowly than better-fed counterparts (Mesa et al. 1994; Rice et al. 1987a; Chick and Van Den Avyle 2000), which may increase their vulnerability to predators (but see Elliott and Leggett 1998). Second, low zooplankton densities and resultant slow growth increase the length of vulnerability to gape-limited predators (Crowder et al. 1987; Rice et al. 1987b; Miller et al. 1988). Third, small size resulting from slow growth will reduce the proportion of zooplankton prey available to gape-limited larvae (e.g., Schael et al. 1991; Bremigan and Stein 1994; DeVries et al. 1998), which could perpetuate slow growth. Finally, the frequently observed pattern of size-dependent overwinter mortality (Oliver et al. 1979; Nielson 1980; Johnson and Evans 1996) may place slow-growing larvae at a distinct disadvantage later, should they survive the larval period. Faster growth and resultant larger size likely confers a host of survival advantages to age-0 fishes (Miller et al. 1988).

We evaluated Hjort’s (1914) critical period hypothesis with white crappie *Pomoxis annularis*, a popular freshwater sport fish that frequently exhibits variable recruitment. We had two reasons to hypothesize that low zooplankton densities would influence larval survival. First, its relatively small size among freshwater species should make white crappie vulnerable to starvation. With an egg diameter of 0.75 mm (Bunnell et al. in review), its eggs are among the smallest 10% of freshwater species (Winemiller
and Rose 1992). Owing to the positive relationship between egg diameter, larval size at hatch, and resistance to starvation (Hunter 1981), first-feeding white crappie larvae are likely more vulnerable to starvation than most freshwater larvae.

A second reason to expect low zooplankton densities to influence larval survival is explained within an Ohio reservoir food web context. Specifically, interspecific competition with gizzard shad may reduce available zooplankton densities for white crappie larvae. Previous research in hypereutrophic Ohio reservoirs has documented bluegill survival to be compromised by competitive interactions with gizzard shad (reviewed by Stein et al. 1995). High densities of gizzard shad larvae (e.g., > 10/m$^3$; DeVries and Stein 1992; Garvey and Stein 1998; Garvey et al. 1998) and surviving juvenile gizzard shad (>25 mm) reduce survival of bluegill larvae (DeVries and Stein 1992; Garvey et al. 1998; Garvey and Stein 1998) by depleting crustacean zooplankton densities (Dettmers and Stein 1992; DeVries and Stein 1992; Dettmers and Stein 1996). Timing of larval hatch is critical: larvae hatching after the peak of larval gizzard shad abundance survive poorly owing to either the direct effects of starvation or the indirect effects of slow-growth (DeVries and Stein 1992, Garvey and Stein 1998). The peak of bluegill larval density is at the same time (36%) or after (40%) the peak of gizzard shad (Garvey and Stein 1998), whereas white crappie larvae typically peak before bluegill larvae (Post et al. 1995) but at about the same time as gizzard shad larvae (Pope and DeVries 1994). As a result, white crappie larvae are likely less vulnerable to competitive interactions with gizzard shad than bluegill. Nonetheless, the temporal, spatial, and diet (DeVries et al. 1998) overlap of first feeding gizzard shad and white crappie larvae may facilitate competition.
Previous research into mechanisms underlying white crappie recruitment has included both biotic and abiotic factors. In Ohio reservoirs, population egg production (i.e., an index of stock size) explained nearly 50% of white crappie recruitment variability (Bunnell et al. in review), which supports stock/recruit models in the southeastern United States (Allen and Miranda 1998). With this paper, we are evaluating whether additional variability can be understood by exploring factors influencing larval survival. Beyond Ohio, evidence of competition between age-0 gizzard shad and white crappie is equivocal. Both a pond experiment (Guest et al. 1990) and field sampling (Slipke et al. 1998) revealed negative correlations between gizzard shad and white crappie abundance. However, another pond experiment revealed no impact of gizzard shad on white crappie larvae (Pope and DeVries 1994). Abiotic factors also may influence recruitment. Abundance of age-0 crappies increases with spring water level (Mitzner 1981; McDonough and Buchanan 1991) in midwestern United States reservoirs, and winter hydrology is strongly correlated with year-class strength (Maceina and Stimpert 1998) in southeastern United States reservoirs. For each of these correlations, however, the mechanisms underlying increased recruitment are unclear. Finally, recent experimental work suggests that prolonged exposure to water temperatures < 4°C can cause considerable mortality during the first winter of life (McCollum et al. in review).

In this paper, we used otoliths to understand how zooplankton density, water temperature, and density of fish larvae (i.e., mostly gizzard shad) influenced the growth of white and black crappie Pomoxis nigromaculatus larvae and survival of white crappie larvae in Ohio reservoirs. By providing fish age, otoliths can estimate both growth rate and hatch date. To estimate survival, we compared a distribution of when all weekly
cohorts were hatched to a distribution of when surviving juveniles were hatched. To evaluate whether a critical period existed, we then related that weekly cohort survival to the aforementioned factors that were measured during each cohort’s first two weeks of life.

Methods

Species life history

White and black crappies are popular sport fishes (Hooe 1991), having been introduced to the western United States (Goodson 1966) and south to Mexico and Panama (Welcomme 1988). These two species co-occur, with white crappies occurring more often in turbid waters than black crappies (Trautman 1957), though exceptions arise. Among our study reservoirs, white crappies generally predominate, especially in populations for which survival was estimated (Table 4). Adults of both species spawn for 6 – 8 weeks in late spring through early summer (Pope and Willis 1998; D. B. Bunnell unpublished data) and exhibit similar reproductive strategies as males build nests in the littoral zone (0.2 – 0.8 m depth, Siefert 1968; Pope and Willis 1997) and then provide nest defense to incubating eggs (2 – 4 d) and embryos (i.e., yolk-sac larvae, 2 – 6 d; Siefert 1968). Larvae depart the nest at about the time of yolk-sac absorption (Siefert 1968), migrating to the limnetic zone where exogenous feeding begins. As larvae grow and recruit to the juvenile stage, both species migrate to the benthos of the limnetic zone, and zooplankton remains their primary prey (Pine and Allen 2001; D. B. Bunnell unpublished data). Species can first be visually distinguished by the juvenile stage.
Zooplankton were sampled weekly during May-June from 12 reservoirs during 1998 and 9 reservoirs during 1999-2000 (Table 4). With a conical, 54 µm-mesh net, we sampled crustacean zooplankton and rotifers from 1 m above the reservoir bottom to its surface at fixed upstream and downstream sites. Upon collection, zooplankton were preserved in 70% ethanol. Crustacean zooplankton were estimated for 29 reservoir-years, whereas rotifer estimates were available for 19 reservoir-years. In the laboratory, cladoceran zooplankters were identified to genus (e.g., Daphnia, Bosmina, Eubosmina, Ceriodaphnia, Chydorus, Diaphanosoma, and Moina spp.), and copepod zooplankters were classified as calanoid, cyclopoid, or nauplii, using Balcer et al. (1984). Rotifers were counted and identified (Stemberger 1979) to genus using a compound microscope. Crustacean zooplankton were counted following Stahl and Stein (1994). We measured crustacean total length (excluding spines on cladocerans, but including up to the base of the caudal rami on copepods) to the nearest 0.01 mm of the first 22 individual crustaceans encountered in each taxon, using a Sigma Scan digitizing system. We then used taxon-specific, length/dry weight equations (Dumont et al. 1975; Bottrell et al. 1976; Rosen 1981; Culver et al. 1985) to convert length to biomass. We measured up to 25 individuals from each rotifer genus to the nearest 0.1 mm using the ocular micrometer on a compound microscope. Rotifer biomass was calculated using geometric formulas that approximate the volume of individuals (Ruttner-Kolinsko 1977). Volume was converted to wet weight assuming a specific gravity of 1. Dry weight was estimated as 0.1 times wet weight (Doohan 1973).
Collection and aging of larvae

Limnetic larvae were sampled weekly in the top meter of water with neuston nets (1×2 m wide mouth, 0.5-mm mesh) during May-June from 12 reservoirs during 1998 and 9 reservoirs during 1999-2000 (Table 4) at the same fixed upstream and downstream sites as zooplankton were collected. Each of two replicates was a 5 min tow at 1 m/s, except when high zooplankton densities necessitated shorter tows. A flowmeter mounted at the mouth of net permitted estimates of volume sample. Sampling was completed during the day in all reservoirs. Across a productivity gradient of Ohio reservoirs, *Pomoxis* spp. larvae are evenly distributed across the top 3 m of water in the day (Arend 2002). Thus, our sampling should provide an appropriate representation of larval densities in the epilimnion. Larvae were identified as gizzard shad, *Lepomis* spp., or *Pomoxis* spp. Similar numbers of myomeres prevented us from visually separating *Pomoxis* (Siefert 1969) or *Lepomis* genera to species. Details of estimating density (m⁻³) are presented in Bunnell et al. (In review). The 9-week sampling period was divided into three, 3-week periods: early, middle, and late. We measured total length (nearest 0.01 mm) of up to the first 50 *Pomoxis* spp. larvae encountered in all replicate samples. Because mean percent species composition of adult white and black crappie ranged 4.5% to 100% across reservoirs (Table 4), we likely had both black and white crappie larvae. Thus, growth of larvae was characterized at the genus level.

For all reservoir-years, we quantified age of *Pomoxis* spp. larvae during 1 week in the middle period (between late May and early June) because larvae generally were captured at the highest density and widest length distribution during this middle period. For a subset of reservoirs in 2000, we also estimated ages of larvae sampled during the
early and late periods (see “Analyses: Larval survival in 2000” for more details). Thirty fish per site were selected for age estimation, such that the length distribution of those to be aged mirrored the length distribution of previously measured fish (Ludsin and DeVries 1997). Right and left sagittal otoliths were removed and mounted on glass slides with Canada balsam. White crappie larvae lay their first ring at hatch, and subsequent rings are formed daily (Sweatman and Kohler 1991); we assumed that black crappie larvae also lay daily rings (sensu Pine and Allen 2001). Daily rings were counted at 100-200x magnification; number of rings estimated of age in days. From a subset of 100 aged otoliths, readers disagreed no more than 2 d on 97% of the otoliths with age estimates less than 11 d. Disagreements on the remaining 3% of otoliths were 3 d. Thus, all otoliths that had an initial age estimate less than 11 d were not aged by a second reader. Those initially aged to be at least 11 d were aged by a second reader. In this case, a mean of the two age estimates was used when the estimates differed by 3 or fewer days. When the age estimates differed by more than 3 d (occurred ~ 10% of otoliths), a third “consensus” read occurred (Welker et al. 1994). In about 3% of consensus reads, the otolith was determined to be unreadable.

Collection and aging of juveniles

During 2000, we collected juvenile white crappies (15 – 70 mm TL) to explore factors relating to early survival of Pomoxis spp. larvae. By focusing on five reservoirs (Acton, Burr Oak, Caesar Creek, LaDue, and Pleasant Hill) in which white crappie made up greater than 85% of the adult (age ≥ 2 years) population (Table 4), we assumed that nearly all Pomoxis spp. larvae sampled were white crappie larvae. White crappie
juveniles were sampled with a bottom trawl (mouth width = 3.7 m; body length = 4.6 m; bar mesh body = 8.4 mm; bar mesh bag = 6.4-mm; same as Pine and Allen 2001) during July 11-14, 2000. At each reservoir, we pulled four to seven trawls for a minimum of 3 min, at depths 3 – 6 m in both upstream and mid-reservoir sites. Trawling at deeper downstream sites, near the dam, yielded no juvenile white crappie. Within each reservoir, white crappie (N= 76-250 per reservoir) were measured (nearest mm TL) and then pooled across sites. As for aging of larvae, we used the length distribution to sub-sample a similarly distributed length distribution of 60 juveniles to be aged. Otoliths were prepared as described for larvae, except otoliths older than 20 d were ground with 1-9 µm wet-dry sandpaper owing to their highly convex shape and opaque color.

**Analyses**

**Larval growth**

For all fish that were aged, daily growth rate (DGR, mm/d) was estimated as

\[
DGR = (TL – 3.23) / \text{age},
\]

where TL (mm) represents total length at capture, 3.23 is TL at hatch and age is the number of days since hatch. Length at hatch was the y-intercept in the age versus length regression for all larvae aged (\(TL = 3.23 + 0.46(\text{age}), F_{1,1720} = 10896; r^2 = 0.86, P < 0.0001\)), and was more than some previous measures (2.56 mm TL, Siefert 1969) and less than others (4 mm TL, Chatry and Conner 1980). Larvae aged younger than 17 d were grouped as a function of reservoir, year, site, week of hatch, week of collection, and age-class (age-class I: 3 – 9 d; age-class II: 10 – 16 d) to estimate a mean daily growth rate of fishes that experienced similar conditions. Only those groups with at least five larvae were used. Across all reservoirs but within each age-class, we evaluated whether
variability in mean DGR was explained by some measure of zooplankton (see below),
density of all fish larvae (gizzard shad + *Pomoxis* spp. + *Lepomis* spp.), and temperature
using a general linear model (Proc GLM; SAS Institute 1999), with reservoir as a class
variable. For each group of larvae, the independent variables were the average value
from week of hatch until week of capture. All variables were measured weekly, except
temperature for which remote data loggers measured temperature every 4 hours at 1 m
depth at fixed upstream and downstream sampling sites. We hypothesized that two
measures of zooplankton could relate to growth: total zooplankton biomass (rotifer +
crustacean zooplankton; *Pomoxis* spp. larvae do consume rotifers (Arend 2002; D. B.
Bunnell unpublished data) or simply preferred crustacean zooplankton biomass (calanoid
and cyclopoid copepods, nauplii, and *Diaphanosoma* spp., DeVries et al. 1998; Pope and
Willis 1998; D. B. Bunnell unpublished data). Because they are related, we used
Pearson’s correlation to determine which zooplankton variable to include in the general
linear model, i.e., which was most positively correlated to growth within each age class.

Because *Pomoxis* spp. larvae are gape-limited (Schael et al. 1991; DeVries et al.
1998), we estimated biomass of only those zooplankters sufficiently small to be eaten.
Using mean TL of each age-class group, we estimated gape size with a TL / gape size
regression (DeVries et al. 1998). We used the length measurements for each zooplankton
taxon at each site per sampling week to estimate weekly “available” biomass of all
zooplankton taxa as

\[ B = \sum p_i (A_i)(B_i), \]  

(16)
where \( p_i \) is proportion of individuals in taxa \( i \) that are sufficiently small to eat, \( A_i \) is the total zooplankton abundance (#/L) for taxa \( i \), and \( B_i \) is the mean biomass of individuals in taxa \( i \) that are small enough to eat. For all rotifer taxa, \( p_i = 1.0 \), except for \textit{Asplanchna} spp. which can exceed the gape of \textit{Pomoxis} spp. larvae larger than 8 mm TL.

\textit{Larval survival in 2000}

Collecting a sample of juvenile survivors from five reservoirs in 2000 enabled us to use otoliths to calculate hatch dates (day of capture – estimated age) and compare proportional cohort distributions of juvenile survivors with proportional cohort distributions of recently hatched larvae. For each juvenile aged, we calculated a hatch date and assigned a weekly cohort. We then calculated a proportional distribution of weekly cohorts for each reservoir. To estimate a proportional distribution of weekly cohorts for larvae, we used larvae sampled with neuston nets. Hence, we evaluated whether the proportional distribution of weekly larval cohorts was similar to the proportional distribution of weekly cohorts that survived to be juveniles. For larvae, we sought to include only fish that had arrived to the limnetic zone of the reservoir since our previous sampling event. This approach eliminated biasing the distribution toward weekly cohorts in which larvae were surviving well, as those cohorts could be sampled during multiple weeks. Larvae collected in our nets were aged as young as 4 d, corroborating when \textit{Pomoxis} spp. larvae depart the nest and begin to feed exogenously (Siefert 1968). We then assumed that all larvae recruited to the limnetic zone by age 5 d; in our weekly sampling schedule, the oldest fish that could have recruited to the limnetic
zone between weekly sampling events would be age 11 d. Fish older than 11 d should have been captured in earlier sampling efforts, and thus, were not included in our later analyses.

Rather than use otoliths to estimate age of all larvae sampled, we used period-specific, system-specific, length vs. age regressions (Table 5) to construct proportional cohort distributions of larvae. Owing to low numbers of larvae collected, we did not estimate age of larvae sampled from the early and late periods of Caesar Creek or from the late period of Burr Oak. Because larvae were not sampled one week in the early period of Acton, we focused only on aging larvae from the middle period of Acton. In these instances, we used the regression generated from the middle sampling period to estimate ages of larvae sampled in all periods. Recalling that up to the first 50 larvae encountered per replicate were measured (if less than 50 larvae were collected, then all larvae were measured), ages and hatch dates were estimated using the appropriate regression, and weekly cohorts were assigned for each individual. We then generated a proportional distribution of cohorts for each site, and multiplied the proportion that were estimated to be 11 d or younger by the total mean density for each site to estimate the total “hatch” density. Multiplying the cohort proportion by the total hatch density estimated the cohort-specific hatch density for each site/sampling day combination. Because we could not link surviving juveniles to a specific site, we pooled across sites and sampling days by summing cohort hatch densities to generate a total reservoir hatch density which, in turn, permitted us to determine a proportional distribution of weekly cohorts that were hatched for each reservoir.
With distributions of weekly cohorts for both larvae and juveniles, we calculated an index of weekly cohort, larval survival, $\beta_i$, as

$$\beta_i = \log\left(\frac{J_i}{H_i}\right) + 1,$$

(17)

where $i$ represents weekly cohorts 1 through 9, $J_i$ is the proportion of all juvenile white crappie sampled that were hatched in weekly cohort $i$, and $H_i$ is the proportion of all larvae hatched that hatched in weekly cohort $i$. We evaluated how $\beta_i$ related to characteristics measured during hatch week. We also evaluated how characteristics measured during the first 2 weeks of life related to $\beta_i$, as larvae that hatch late during their hatch week would not begin exogenouss feeding until the second week (i.e., ~ 4 d of life, Siefert 1968). Measured characteristics used in the analyses are the same as used in the growth analyses: density of all fish larvae, temperature, and one measure of zooplankton (i.e., total zooplankton biomass or preferred crustacean biomass). Pearson’s correlation was used to determine which zooplankton measure to include. For all zooplankton biomass measures, we used 8.3 mm TL (i.e., predicted length for age 11 d larva) to determine the gape size (DeVries et al. 1998) and biomass (see equation 16) of zooplankton sufficiently small for consumption by each cohort during each respective period. Because we could not determine whether juvenile survivors came from upstream or downstream sites, and zooplankton (Bremigan and Stein 2001; this paper) and temperature can vary between sites within Ohio reservoirs, we used the proportion hatching from each site to weight all mean variables. For zooplankton estimates for LaDue on May 10, when a sample was not collected downstream, we applied the average zooplankton biomass ratio of upstream : downstream to the known upstream biomass.
We first included $\beta_i$ from all reservoirs and used multiple linear regression (Proc REG; SAS Institute 1999) to explore whether general patterns would emerge across reservoirs. Condition indices and variance inflation factors (Hair et al. 1995) were used to evaluate multicollinearity. Within each reservoir, we then used Pearson’s correlation to relate $\beta_i$ to our measured variables.

**Results**

**Zooplankton availability**

Densities and composition of zooplankton varied across reservoirs, as well as between upstream and downstream sites within reservoirs. We describe zooplankton collected May - June 2000 from reservoirs for which juvenile survivors were sampled (i.e., Acton, Burr Oak, Caesar Creek, LaDue, Pleasant Hill, Figure 16) because they illustrate these general trends. Crustacean biomass was higher that rotifer biomass in all sites except upstream Pleasant Hill and both sites at Acton Reservoir (Figure 16). One week of high *Asplanchna* spp. density drove the high mean rotifer biomass estimated upstream in Pleasant Hill; the mean of the other 8 weeks was 13.95 µg/L. In Acton Reservoir, however, rotifer biomass was nearly always greater than crustacean zooplankton biomass. With regard to number of zooplankton, rotifer density exceeded crustacean zooplankton density at both sites of all reservoirs. In fact, mean crustacean density was less than < 50/L for all reservoirs. Across all reservoir sites between May and June 2000, the highest crustacean zooplankton density observed was 78/L and the
median density was 13/L. Mean total density of all zooplankters exceeded 150/L at all upstream sites and 60/L at all downstream ones. Thus, fish larvae were faced with a prey environment that varied both in composition and density across sites and reservoirs.

Larval growth

Mean growth rates of larvae ranged 0.27 – 0.57 mm/d across all reservoir-years. Among measures of zooplankton biomass, total zooplankton \((r = 0.53; N = 42 \text{ groups}; P = 0.0003)\) and preferred crustacean zooplankton \((r = 0.52; N = 42 \text{ groups}; P = 0.0005)\) were highly correlated with growth rate of age-class I fishes (i.e., those larvae younger than 9 days), whereas only preferred crustacean zooplankton \((r = 0.42; N = 36 \text{ groups}; P = 0.01)\) was correlated with growth rate of age-class II fishes (i.e., those larvae aged between 10 and 16 days). In the general linear model, reservoir was not a significant factor in either the age-class I \(F_{6,32} = 1.21; P = 0.33\) or II \(F_{7,25} = 1.15; P = 0.37\) model. Without the reservoir variable, only total zooplankton biomass \(t_{1,38} = 4.01; P = 0.003\) explained variation in growth of age-class I fishes (Figure 17a); densities of fish larvae \(t_{1,38} = -1.63; P = 0.11\) and temperature \(t_{1,38} = -0.65; P = 0.52\) were not significant. For these young, gape-limited larvae, growth rate was highly variable when total zooplankton biomass was < 10 µg/L (Figure 17a). Biomass of preferred crustacean zooplankton small enough to eat improved some of the variability as faster growth generally occurred only when biomass exceeded 1.5 µg/L. Among age-class II fishes, which are much less gape-limited than age-class I fishes by the time they are captured,
growth increased linearly with preferred crustacean zooplankton biomass (Figure 17b;\( t_{1,32} = 2.46; P = 0.02 \)); temperature (\( t_{1,32} = 1.68; P = 0.10 \)) and density of fish larvae (\( t_{1,32} = -0.34; P = 0.74 \)) were not important.

**Larval survival in 2000**

To estimate our index of survival, \( \beta \), we used proportional distributions of weekly cohorts of recently hatched larvae and surviving juveniles. Construction of proportional distributions of larvae used period-specific (i.e., early, middle, and late) length vs. age regressions in all periods for which sample sizes were sufficient; we substituted the regression from the middle sampling period in Acton, Burr Oak, and Caesar Creek (see Table 5). Using length vs. age regressions from the middle sampling period did not differ from those that used period-specific length vs. age regressions in Pleasant Hill and LaDue reservoirs (Kolmogorov – Smirnov test: LaDue: \( K = 0.007, D = 0.01, P = 1.00 \); Pleasant Hill: \( K = 0.004, D = 0.008, P = 1.00 \)), indicating that using the middle period as a substitute for all periods in the other three reservoirs was reasonable.

Of the 42 reservoir sites sampled during 1998 – 2000, white crappie larvae peaked in density before gizzard shad in 38% of sites, at the same time in 21% of sites, and after gizzard shad larvae in the remaining 41% (Figure 18). We could not determine the peak density of bluegill larvae because ichthyoplankton sampling stopped in July, when bluegill continued to hatch. Peak densities of gizzard shad larvae exceeded 10/m\(^3\) in 48% of the sites. However, the worst possible scenario for white crappie larvae, where gizzard shad larvae exceed 10/m\(^3\) and peak density of white crappie larvae occurred either at the same time or after the peak of gizzard shad larvae (Garvey and Stein 1998), was observed
in only 31% of all sites (Figure 18). In the four reservoirs for which larval survival was estimated in 2000, peak density of white crappie larvae was at the same time or after the peak of gizzard shad larvae in 6/8 sites (Figure 18). Among those sites, however, gizzard shad densities exceeded 10/m³ in only one.

In reservoirs from which juveniles were sampled and aged, later-hatched weekly cohorts survived better than earlier-hatched ones in Caesar Creek, LaDue, and Pleasant Hill reservoirs (Figure 19). Earlier-hatched fish fared better than later-hatched ones in Burr Oak. In Acton, most of the surviving juveniles derived from earlier cohorts. We explored how characteristics of two periods, hatch week and the mean of hatch week and the following week, related to survival, β, of white crappie larvae. We did not estimate βi for Acton because no larval samples were collected in the second week of May, when 2% of the surviving juveniles were hatched. Because results were similar between the two time periods, we present only the results relating βi to hatch week.

When cohort weekly survival from all reservoirs was combined, preferred crustacean zooplankton biomass was the only variable positively correlated with survival (r = 0.21; N = 31 weekly cohorts; P = 0.26), though it was not significant. In the multiple regression model, only temperature was marginally related to βi (Figure 20A; t1,27 = 1.83; P = 0.08), suggesting that warmer temperatures increased survival of larvae; preferred crustacean zooplankton biomass (Figure 20B; t1,27 = 0.79; P = 0.43), density of fish larvae (Figure 20C; t1,27 = 1.47; P = 0.15) were not significant in the overall general linear model (F3,27 = 2.48; r² = 0.22; P = 0.08). Within reservoirs, correlations between survival and biotic and abiotic characteristics during hatch week revealed few significant correlations (Table 6). In Burr Oak, both preferred crustacean zooplankton biomass and
density of fish larvae were positively related to \( \beta \). Temperature and \( \beta \) were positively related in Caesar Creek. All other correlations were non-significant. Overall, our measured variables failed to reveal evidence that zooplankton biomass or number of larval competitors influenced survival to the juvenile stage.

**Discussion**

We hypothesized that low zooplankton densities would influence growth of *Pomoxis* spp. larvae, and, in turn, survival of white crappie larvae to the juvenile stage. Growth of *Pomoxis* spp. larvae increased with zooplankton biomass across 19 Ohio reservoir-years. However, zooplankton biomass was correlated with survival in only one of four study reservoirs, and was unrelated to survival across all reservoirs. Across all four reservoirs, only temperature was positively related to survival. Densities of fish larvae and zooplankton densities during the week of hatch were unrelated to larval survival.

**Assumptions**

To explore factors influencing survival of white crappie larvae, we made assumptions regarding the effectiveness of the bottom trawl as well as the construction of our proportional distributions of larvae and juvenile cohorts. One potential bias with bottom trawl is its restriction to sampling areas devoid of major benthic structure. Thus, to assume that we have a random sample of juvenile survivors, we assumed that juvenile habitat use was similar across sizes and ages. Although we cannot know whether this assumption was violated, the bottom trawl did collect a wide range of sizes within each
reservoir (minimum range = 29 mm; maximum range = 42 mm). In addition, one interpretation of sampling either all earlier- or all later- hatched cohorts in all reservoirs would have been a size-bias in the bottom trawl. We did not find a consistent pattern of all earlier- or all later-hatched cohorts across reservoirs.

With regard to constructing the proportional distributions, we made two major assumptions for the larvae. First, we assumed that our sample of limnetic larvae was an appropriate representation of all those larvae that initially recruited to the limnetic zone from the nest. If our sampling schedule had failed to capture larvae before they starved, then this assumption would have been violated. Given our weekly sampling schedule, starved Pomoxis spp. larvae would have to survive a minimum of 1 and maximum of 6 d before being collected. Although mortality of starved Pomoxis spp. larvae has not been measured in the laboratory, their size at hatch predicts that 50% of starved larvae will survive 14 d (Miller et al. 1988). Thus, we are confident that larvae did not die from starvation before we sampled them. Second, we assumed that putative differences in growth rate between fish that hatched early and late in the spawning season would not influence the proportional distributions of weekly cohorts. Because distributions constructed using period-specific, length vs. age regressions did not differ from those that applied only the length vs. age regression from the middle period to all periods, this assumption was justified in LaDue and Pleasant Hill reservoirs. This result occurred because the difference in predicted age across periods was generally about 1 d (e.g., for an 8 mm fish: range of Pleasant Hill predicted ages = 7.9 – 9.1 d, range of LaDue predicted ages = 8.9 – 9.2 d), which would rarely affect the assignment of a fish to a
weekly cohort. Larval hatch distributions in Caesar Creek and Burr Oak also likely would not have been influenced by the use of period-specific length vs. age regressions.

**Growth**

We expected temperature and zooplankton biomass to positively influence growth, whereas density of fish larvae was expected to reduce growth. Previous work exploring factors influencing growth of *Pomoxis* spp. larvae has been somewhat different from these expectations. In Illinois reservoirs, growth was negatively correlated with crustacean zooplankton density and temperature and positively correlated with copepod nauplii density and percent of water volume occupied by littoral habitat (Claramunt and Wahl 2000). To explore how zooplankton could influence growth of *Pomoxis* spp. in Ohio reservoirs, we considered the limited gape of larvae by calculating the biomass of only those zooplankton small enough for the average larvae in each group, a step omitted in most studies (but see Michaletz 1997). One caveat to our method is a higher inaccuracy with older larvae (i.e., age-class II): because the gape is based on the size at capture, our method does not incorporate the more restrictive gape limitation previously experienced by larvae in their first week.

As expected, growth increased with zooplankton biomass across all Ohio reservoir-years. Both temperature and density of all fish larvae, however, were unrelated to growth rates of larvae. We are unsure why warmer temperatures did not increase growth (sensu Houde 1997), but other freshwater field studies also have failed to find a positive relationship between growth and temperature (Welker et al. 1994; Claramunt and Wahl 2000; but see Betsill and Van Den Avyle 1997). For larvae younger than 9 d (i.e.,
age-class I), total zooplankton biomass best explained daily growth rate, suggesting rotifers and other small non-preferred prey (i.e., genera Bosmina, Chydorus, Eubosmina, Asplanchna, Brachionus etc.) improve growth of gape-limited larvae. However, growth was highly variable at low densities of total zooplankton biomass. Here, high densities of preferred (i.e., copepods and Diaphanosoma spp.; DeVries et al. 1998; Pope and Willis 1998; D. B. Bunnell unpublished data) crustacean zooplankton appeared to increase growth. Thus, all zooplankton seemingly are important for growth of recently hatched larvae, but higher densities of preferred taxa also can yield faster growth. As larvae grew older (i.e., age-class II) and became less limited by gape, biomass of preferred crustacean zooplankton was the only zooplankton measure to influence growth. Comparisons with previous studies revealed growth rates of Pomoxis spp. larvae in Ohio reservoirs (range = 0.26 – 0.57 mm/d, mean = 0.47 mm/d) to be somewhat lower than those measured in Illinois (range = 0.26 – 1.00 mm/d, mean = 0.58 mm/d, Claramunt and Wahl 2000) but higher than those measured in Alabama (range = 0.25 – 0.35 mm/d, Dubuc and DeVries 2002).

Survival

We hypothesized that higher zooplankton densities would improve larval survival. In Ohio reservoirs, low zooplankton densities, which result from high densities of gizzard shad, likely reduce survival of bluegill larvae (see Stein et al. 1995; Garvey et al. 1998). As relatively small freshwater larvae that co-occur with gizzard shad, we expected white crappie larvae to be vulnerable to starvation following yolk-sac absorption (sensu Hunter 1981; Miller et al. 1988). We evaluated our hypothesis by linking survival directly to
zooplankton prey, the presumed mechanism to underlie gizzard shad and bluegill competitive interactions. In addition, we expected that survival would decrease with increasing densities of larval competitors and increase with temperature, as similar studies using otoliths revealed positive correlations between temperature and larval survival (American shad *Alosa sapidissima*, Crecco and Savoy 1985; *Lepomis* spp., Garvey et al. 2002).

Analysis that included weekly cohort survival of all reservoirs indicates that our measured factors did not strongly influence larval survival. Only temperature was marginally related to survival. Given our inability to detect temperature effects on larval growth, we are unsure how warmer temperature could increase survival. Rather, temperature may be a spurious correlation because temperature increased from May to June and later-hatched cohorts generally survived better than earlier ones. Within reservoirs, survival increased with zooplankton biomass only in Burr Oak. Burr Oak is the least productive of our study reservoirs, but crustacean zooplankton densities were comparable to other reservoirs in 2000. Thus, poor survival resulting from slow growth or starvation in Burr Oak seems no more likely than in other reservoirs.

Given the small size at hatch of white crappie larvae, this species presented an ideal scenario for detecting low zooplankton effects on larval survival among freshwater species. Indeed, many experiments predict that survival of freshwater larvae should increase with zooplankton (Li and Mathias 1982; Hart and Werner 1987; Welker et al. 1994) and reviews indicate that resistance to starvation increases with length at hatch (Hunter 1981; Miller et al. 1988). However, our freshwater field study joins other that have failed to relate higher zooplankton to increased survival (e.g., Welker et al. 1994;
Betsill and Van Den Avyle 1997; Garvey et al. 2002). How can these seemingly opposite field and laboratory results be reconciled? Laboratory evidence clearly demonstrates a positive effect of zooplankton, but it also demonstrates the hardiness of first-feeding larvae. Although no starvation experiments have been conducted on white crappie, time to 50% survival was about 7 days after first feeding had begun for pumpkinseed (Hart and Warner 1987), which is in the same family and is similar in size (egg size = 0.8 – 1.2 mm; length at hatch = 2 – 3 mm TL; Auer 1982) to white crappie. The length at hatch versus time to 50% mortality regression generated in the review paper by Miller et al. (1988) predicts that the majority of starved white crappie larvae could survive between 5 and 10 days (assuming TL at hatch ranges 2.6 to 4 mm). Of course in nature, spatial patchiness of zooplankton or low visibility by a larva could lead to a short-term, zero prey environment, i.e., approximating the laboratory starvation experiments. In our view, however, starvation for several consecutive days is unlikely. Thus, starvation alone is unlikely to regulate survival of white crappie or other freshwater larvae.

In addition to preventing starvation, high zooplankton densities can provide numerous indirect positive effects on survival. Larvae that are feeding well likely avoid predators better than their starved counterparts (Mesa et al. 1994; Rice et al. 1987a; Chick and Van Den Avyle 2000). Other positive indirect effects are due to size advantages that can be attained in a high zooplankton environment. Faster growth to a larger size reduces the window of vulnerability to gape-limited predators (Crowder et al. 1987; Rice et al. 1987b; Miller et al. 1988), although large size can lead to higher predation risk in some cases (Litvak and Leggett 1992; Gleason and Bengston 1996). Despite detecting a positive effect of zooplankton density on growth of white crappie larvae, zooplankton
had no positive effect on survival. One potential explanation is that zooplankton effects on size were not dramatic. For a fish aged 12 d (i.e., age-class II larvae), the average fish is predicted to grow to a length of 9 mm in a low zooplankton environment (i.e., 5 µg/L) but only to 9.35 mm in a relatively high zooplankton environment (i.e., 20 µg/L). As these fish increase in age, the size differences will become magnified. Nonetheless, at the larval stage, a high zooplankton environment may not translate into positive indirect effects on survival because it may not have a sufficiently large effect on fish size. [At later stages in other fishes, size also has been positively linked to overwinter survival (Oliver et al. 1979; Nielson 1980; Johnson and Evans 1996). For white crappie, however, larger size does not improve overwinter survival (McCollum et al. in review).]

Finally, previous research in hypereutrophic Ohio reservoirs suggested that high densities of gizzard shad larvae would reduce survival of white crappie larvae (Stein et al. 1995). We evaluated this hypothesis in four Ohio reservoirs that were mesotrophic and eutrophic and found survival to be unrelated to densities of larval gizzard shad. In fact, later-hatched cohorts that had a higher probability of co-occurring with gizzard shad larvae, survived better than earlier ones in three of four reservoirs. Of course, this result is consistent with the result that zooplankton did not influence survival, as zooplankton is the mechanism underlying competitive larval interactions in hypereutrophic reservoirs. Unfortunately, we could not quantify survival in Acton, the most eutrophic reservoir in which juvenile white crappie were sampled in 2000, because larvae were not sampled 1 week in early May. If $\beta_t$ had been calculated for Acton, might a general relationship between zooplankton biomass and larval survival been revealed? Although we cannot know, it is notable that 80% of the juvenile survivors were hatched May 7 – May 27,
when densities ranged 2 – 6 crustaceans/L and 34 – 315 rotifers/L. Because recently hatched *Pomoxis* spp. larvae select small crustaceans including copepods and *Diaphanosoma* spp. (DeVries et al. 1998; Pope and Willis 1998; D. B. Bunnell unpublished data), such a low density of crustaceans during that time period seemingly would have resulted in poor survival. But because such a high proportion of the juveniles were hatched during that time period, the high densities of rotifers must have enabled those larvae to grow and survive. Overall, our inability to detect a relationship between survival and zooplankton biomass across reservoirs, coupled with the high proportion of juveniles that survived a low prey environment in Acton Reservoir, strongly indicate that zooplankton biomass during the first few weeks of life does not directly influence survival of white crappie larvae.

Our failure to link survival of white crappie larvae to gizzard shad, via low zooplankton densities, supports previous experimental work (Pope and DeVries 1994). Complementary research in these same Ohio reservoirs indicates that densities of adults and subsequent larvae limit recruitment to age-2 (Bunnell et al. in review). If white crappie year-class strength is set by the larval stage (Sammons and Bettoli 1998; Bunnell et al in review), then processes governing mortality between the larval period and age-2 should be similar across Ohio reservoirs. This work does not reject that prediction insofar as mortality of larvae was not related to variables that are known to vary across reservoirs, such as temperature and densities of larvae and zooplankton.

With survival of larval cohorts unrelated to zooplankton density, temperature, water elevation, and larval fish density, what potential hypotheses remain regarding mechanisms regulating larval survival? In terms of abiotic factors, the impact of wave
action resulting from strong winds during late spring / early summer storms may influence survival of limnetic larvae. However, we know of no supporting evidence for this hypothesis. Predation remains a viable hypothesis (e.g., Forney 1976; Mason and Brandt 1996). Potential predators of larvae are numerous, including earlier-hatched larvae such as cannibalistic *Pomoxis* spp. larvae, or limnetic walleye and yellow perch, as well as other limnetic adults such as white crappie (Kim and DeVries 2001). Support for the hypothesis that multiple factors likely interact to regulate survival of larvae

**Conclusions**

As expected, increasing densities of zooplankton increased growth rates of *Pomoxis* spp. larvae. With this result, we expected to document higher survival of white crappie larvae when zooplankton densities were high, owing to avoiding the direct effect of starvation as well as the indirect effects of size or condition-dependent mortality (Miller et al. 1988). However, zooplankton was positively correlated with survival in only one of four study reservoirs; this correlation is dubious owing to the lack of correlation between zooplankton and growth. When survival of weekly larval cohorts was pooled across reservoirs, only temperature was marginally related to survival. Survival did not increase with zooplankton density or decrease with increasing densities of limnetic fish larvae (i.e., gizzard shad). Given their relatively small size at hatch, white crappie should be more vulnerable to starvation at first feeding than most freshwater larvae. Conversely, we documented *Pomoxis* spp. larvae to survive despite low densities of crustacean zooplankton (< 50/L) across the productivity gradient. In our view, these results cast doubt on the importance of zooplankton to explaining survival of
freshwater larvae. This work joins previous studies in failing to link survival of larvae to zooplankton biomass, despite countering experimental evidence that low zooplankton densities should both directly (through starvation, Werner and Blaxter 1980; Li and Mathias 1982; Hart and Werner 1987; Welker et al. 1994; Bestgen 1996) or indirectly (through slow growth and small body size, Rice et al. 1987a; Miller et al. 1988; Chick and Van Den Avyle 2000) compromise larval survival.
Literature Cited


Trautman, M. B. 1957. The fishes of Ohio. The Ohio State University Press, Columbus, Ohio.


<table>
<thead>
<tr>
<th>Reservoir</th>
<th>County</th>
<th>Code</th>
<th>Surface Area (km²)</th>
<th>Mean Chlorophyll (µg/L)</th>
<th>Trophic status</th>
<th>White Crappie Population (%)</th>
<th>Mean white and black crappie adult CPE (fish/net night)</th>
<th>Years larvae and zooplankton estimated</th>
<th>Years juvenile white crappie estimated</th>
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<td>88.9</td>
<td>2.28</td>
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Table 4. Characteristics of Ohio reservoirs sampled for *Pomoxis* spp. larvae and zooplankton (i.e., crustacean and rotifer zooplankton) during 1998-2000. Juvenile white crappies also were sampled in five reservoirs. Mean chlorophyll a (µg/L) concentration is the grand mean of upstream- and downstream - integrated water samples collected weekly during May – June 2000. Trophic status is based on Wetzel (2002), where E represents eutrophic and M represents mesotrophic; greater or less than signs are used when concentrations fall between 2 trophic indicators. White crappie population is the percentage of adult white crappie (by number) of the total adult *Pomoxis* spp. populations (black crappie + white crappie) pooled over 4 years (1998-2001) of autumn trapnetting. Mean white and black crappie adult (age ≥ 2) CPE (fish/net night) provides a relative size of the adult populations during 1998 – 2001 (except for Knox, which is only from 1998).
<table>
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<td></td>
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Table 5. Period-specific regression parameters ($b_0$, $b_1$) used to predict age from length for each reservoir for which larval hatch distributions were estimated in 2000. Data derive from larvae aged ≤ 11 d. Period divides the 9-week sampling period by three: early (April 30 – May 20), middle (May 21 – June 10), and late (June 11 – July 1). Estimates were not made in the early and late period of Caesar Creek or in the late period of Burr Oak because of insufficient samples size (i.e., < 13 larvae collected per sample). Because we knew the larval hatch distribution in Acton would be inaccurate due to one missed week of sampling, we only estimated the middle period.
<table>
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<tr>
<th>Reservoir</th>
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<th>Preferred crustacean zooplankton biomass</th>
<th>Density of all fish larvae</th>
<th>Temperature</th>
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<td><strong>0.80</strong> (0.03)</td>
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<td>7</td>
<td>-0.69 (0.08)</td>
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<td>0.66 (0.07)</td>
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Table 6. Pearson’s correlation coefficient and $P$-value (in parentheses) between $\beta_i$, an index of $Pomoxis$ spp. larval survival during 2000, and preferred crustacean zooplankton biomass (i.e., copepods and $Diaphanosoma$ spp.), density of all fish larvae (i.e., gizzard shad, $Lepomis$ spp., $Pomoxis$ spp.), and temperature during the week of hatch for four Ohio reservoirs. Significant ($P \leq 0.05$) positive correlations are depicted in bold text. “N” is the number of weekly cohorts for which $\beta_i$ was measured in each reservoir.
Figure 16. Mean biomass (µg/L) of crustacean (filled bars) and rotifer (open bars) zooplankton from the upstream (A) and downstream (C) sites of five Ohio reservoirs during May – June 2000. Mean number of crustacean (filled bars) and rotifer (open bars) zooplankton per L from the upstream (B) and downstream (D) sites also is depicted. We calculated the mean of weekly upstream and downstream samples separately. The grand mean of upstream and downstream zooplankton samples are shown. Reservoirs are ordered from low to high productivity (see Table 4).
Figure 16

(A) Upstream

(B) Upstream

(C) Downstream

(D) Downstream

Zooplankton biomass (µg/L)

Zooplankton abundance (no/L)

Crustacean

Rotifer

LaDue

LaPleasant Hill Caesar Creek Burr Oak

0 20 40 60 80

0 100 200 300 400

0 100 200 300 400 500

0 100 200 300 400 500

Figure 16
Figure 17. Growth rate [(mm (TL) – 3.23)/d] of two age-classes of *Pomoxis* spp. larvae sampled from 19 Ohio reservoir-years as a function of zooplankton biomass. Age-class I represents fish aged between 3 and 9 d, whereas age-class II represents a group of fish aged between 10 and 16 d. Each data point represents the mean of larvae grouped as a function of reservoir, site, year, week of hatch, and week of collection (5 – 29 larvae per data point, mean = 12.2 larvae). In (a), total zooplankton biomass includes crustacean zooplankton and rotifers. In (b), preferred crustacean zooplankton biomass includes calanoid and cyclopoid copepods, and *Diaphanosoma* spp. For both age-classes, only those individuals sufficiently small to be consumed were included and mean TL at time of capture for each group of larvae determined gape size.
(a) Age-class I

Total zooplankton biomass (µg/L)

0 20 40 60 80 100 120

0.25 0.30 0.35 0.40 0.45 0.50 0.55 0.60

Preferred crust. ZP < 1.5 µg/L

Preferred crust. ZP > 1.5 µg/L

(b) Age-class II

DGR = 0.47 + 0.0022x(ZP)

\( R^2 = 0.18 \)

\( P = 0.01 \)

N = 36 groups of larvae

Figure 17
Figure 18. Time of peak density of *Pomoxis* spp. larvae relative to peak density of gizzard shad larvae. Each data point (N = 42) represents the peak density of gizzard shad larvae at a particular site (upstream or downstream) across 21 Ohio reservoir years. On the x-axis, negative numbers (i.e., to the left of the dashed vertical line at 0) indicate how many weeks *Pomoxis* spp. peaked before gizzard shad; positive numbers indicate how many weeks *Pomoxis* spp. peak after gizzard shad. The dashed horizontal line at 10 gizzard shad larvae/m³ indicates the critical density above which gizzard shad larvae can compromise survival of bluegill larvae (Garvey et al. 1998). Closed triangles indicate the reservoir sites for which survival was estimated in 2000.
Figure 18

(Week of peak *Pomoxis* spp. density) - (Week of peak gizzard shad density)

Peak density of gizzard shad (#/m$^3$)

*Pomoxis* spp.

before shad

after shad
Figure 19. Survival of white crappie larvae to the juvenile stage in five Ohio reservoirs during 2000, as a function of week of hatch. The proportion of larvae hatching (sampled May – June 2000) from weekly cohorts is depicted as shaded, vertical bars on the left y-axis, whereas the proportion of juveniles collected during July 11-14, 2000 from weekly cohorts is depicted as solid circles on the right y-axis. The asterisk on the proportional distribution of larvae in Acton (panel a) indicates that the distribution likely underestimates the proportion of larvae hatched during the week of May 3 as a result of no larval samples collected during the week of May 10.
Figure 19

Week of hatch

Proportion of larval hatch

Proportion of juvenile survivors

(A) Acton

(B) Burr Oak

(C) Caesar Creek

(D) LaDue

(E) Pleasant Hill

May 3  May 10  May 17  May 24  May 31  June 7  June 14  June 21  June 28
Figure 20. The index of weekly cohort survival, \( \beta_i \) (equation 17), as a function of (A) mean temperature, (B) preferred crustacean zooplankton biomass, and (C) density of fish larvae, during the week of hatch. In all panels, the dashed horizontal line represents \( \beta_i \) when the proportion of juvenile survivors equals the proportion of larvae hatched (i.e., \( \log_{10} = 2 \), see equation 17).
Figure 20

(A) Temperature (°C) vs. proportion of larval = proportion of juvenile

(B) Preferred crustacean zooplankton biomass (µg/L) vs. Survival (β)

(C) Larval fish density (no./m³) vs. Survival (β)

152
CHAPTER 5

WINTER TEMPERATURES INFLUENCE SURVIVAL OF AGE-0 WHITE CRAPPIE

Introduction

Owing to high potential mortality, the first winter of life can be critical to setting year-class strength for both freshwater and marine fishes (Adams et al. 1982; Henderson et al. 1988; Ludsin and DeVries 1997; Malloy and Targett 1991; Hurst and Conover 1998; Lankford and Targett 2001). For sport fishes, understanding mechanisms underlying winter mortality, as well as characteristics of fishes that increase their probability of survival is essential for successful fishery management. Among characteristics of age-0 fishes, size influences most sources of mortality (Sogard 1997). Starvation, particularly for small age-0 fishes, frequently has been documented as the mechanism underlying winter mortality (Oliver et al. 1979; Johnson and Evans 1990; Miranda and Hubbard 1994a, Ludsin and DeVries 1997). Size-dependent predation also has been hypothesized to regulate winter mortality (see Nielsen 1980; Miranda and Hubbard 1994b; Kristiansen et al. 2000), as small fish are more vulnerable to gape-limited predators than large ones (Werner and Gilliam 1984). Finally, smaller fishes appear more vulnerable to osmoregulatory failure that can result from extreme winter
temperatures (Johnson and Evans 1996; but see Lankford and Targett 2001). Relative to starvation and predation, osmoregulatory failure that has received less attention (but see Bodensteiner and Lewis 1992; Johnson and Evans 1996).

During winter, age-0 fishes are presumed to rely upon energy stores, rather than energy intake, to meet metabolic demands (Shuter et al. 1980). Large fish are less likely than small fish to exhaust energy stores for two reasons: large fish have 1) a lower mass-specific metabolism (Peters 1983), and 2) frequently have a higher energy density (e.g., Ludsin and DeVries 1997, Post and Parkinson 2001) than small fish. As a result, size-dependent winter starvation has been documented for many taxa in both the field (Miranda and Hubbard 1994a; Post et al. 1998; Sutton and Ney 2001) and in experiments (Oliver et al. 1979; Post and Evans 1989; Johnson and Evans 1990; Thompson et al. 1991; Ludsin and DeVries 1997; Kirjasniemi and Valtonen 1997; Schultz et al. 1998). However, size-dependent overwinter mortality does not always occur in the field (see Kohler et al. 1993; Jackson and Noble 2000) or in experiments (Toneys and Coble 1979; Isely 1981; Garvey et al. 1998; Jonas and Wahl 1998). In these cases, food may be abundant resulting in small and large fish having similar energy densities going into winter.

Exposure to extreme winter temperatures also can contribute to mortality owing to osmoregulatory failure (Bodensteiner and Lewis 1992; Johnson and Evans 1996; Lankford and Targett 2001). At cold temperatures (i.e., < 4°C), membrane permeability can be changed, compromising ion transport mechanisms, and resulting in a net loss of critical ions (e.g., Na⁺) (Wikgren 1953; Morris and Bull 1968), and death (Johnson and Evans 1996). Size also has been hypothesized to influence susceptibility to
osmoregulatory failure (Johnson and Evans 1996), because small fish have a larger gill area, on a per gram basis, than large fish (Hughes 1984). However, large age-0 Atlantic croakers *Micropogonias undulatus* are more susceptible to lower temperatures than small ones (Lankford and Targett 2001), suggesting the mechanism underlying size-dependent mortality from cold temperatures requires improved understanding.

In this paper, we explore how different winter conditions influence growth and survival of age-0 white crappie, *Pomoxis annularis*. White crappie are native to lakes and low-gradient rivers in an area bounded by the Appalachian mountains to the east, the Rocky mountains to the west, southern Ontario to the north, and eastern Texas to the south (Trautman 1957), being introduced as far west as California (Goodson 1966) and as far south as Mexico and Panama (Welcomme 1988). Thus, Ohio represents the northern extent of their native and introduced range. Throughout North America, including Ohio, white crappie exhibit variable recruitment success (McDonough and Buchanan 1991, Sammons and Bettoli 1998; Maceina and Stimpert 1998; Bunnell et al. in review). To evaluate how level of food (starved, fed), winter severity (duration and temperature), and fish length (≤ 90 mm, > 90 mm total length (TL)) influence winter survival of age-0 white crappie, we ran an experiment in temperature-controlled rooms in the laboratory.

To place our experimental results into a natural context, we also sampled age-0 white crappie from four Ohio reservoirs during October, and quantified whole fish energy density (kJ/g wet mass). In estimating pre-winter energy density we sought to 1) compare energy density of Ohio reservoir fish to experimental fish, 2) quantify whether energy density increased with fish size within a reservoir, and 3) quantify whether mean energy density of fishes varied between reservoirs. If large fishes had greater energy...
density than small fishes, then size-dependent overwinter starvation could be occurring in Ohio reservoirs. Reservoirs were selected to span gradients of latitude, productivity, and recruitment success (Table 7). Latitude influences the duration of winter, as well as littoral water temperature. Productivity likely influences food availability which, in turn, could influence pre-winter energy density. Historical recruitment success provided a comparison for predictions generated from the experimental results. For example, should fish from reservoirs with historically high recruitment (e.g., Pleasant Hill) be more energetically dense than fish from reservoirs with historically poor recruitment (e.g., Pymatuning), then we would have additional support that overwinter starvation influenced recruitment.

Methods

Energy density of fish from Ohio reservoirs

Age-0 white crappies were collected from four Ohio reservoirs during October 17 - 27, 2000 (Table 7), using Missouri-style trapnets (Colvin and Vasey 1986). Placed on ice in the field, and then frozen in water upon return to the laboratory, fish (selected along a length gradient) were bombed with an oxygen calorimeter to quantify energy density (Parr Instruments, Model 1425). After fish were thawed, stomachs were cleared and fish were individually dried at 65-70°C to constant mass (Rand et al. 1994), which was usually 3 d. Dried tissue then was ground to a powder and re-dried for 3 d at 65-70°C. We burned at least two 0.01-g composite pellets from each fish. A third pellet was burned if kJ/g differed by > 10% of the mean, which occurred in < 10% of samples.
Initial energy density was corrected for liberated H₂SO₄ (using a base titration), sulfur content (using a fixed average), and fuse combustion (Parr Institute Co. 1993). Mean energy density (kJ/g wet mass) was calculated for each fish.

**Experiment**

We captured ~ 200 age-0 white crappie with bottom trawls and Missouri-style trapnets from Pleasant Hill during October 18 – 27, 2000. Fish were transported to the laboratory in a 600-L hauling tank containing aerated, salted water (0.5% NaCl by mass) to reduce physiological stress. Transport mortality was 0%. Upon arrival, individuals were transferred to two 1200-L circular tanks (15-17°C), and held for 5 – 6 weeks, during which we provided *ad libitum* blackworms *Lumbriculus variegates* and maintained a ~12 hour dark / light photoperiod.

We evaluated how winter temperature (long, cold or short, warm), fish size (≤ 90 mm or > 90 mm TL), and food availability (starved or fed) influenced age-0 white crappie growth and survival in two temperature-controlled rooms which simulated extreme warm and cold winters in Ohio (temperature data from 11 reservoirs during 1994 through 2000; D. B. Bunnell unpublished data; J. E. Garvey, Southern Illinois University, Carbondale, Illinois, unpublished data). Winter was defined as the period between 10°C in the autumn and 10°C in the spring; thus winter treatments differed in duration (cold = 173 d; warm = 133 d) and temperature (days temperature < 4°C = 114 in cold winter and 6 in warm winter). Two remote temperature loggers per room recorded air temperatures four times per day; water temperature was recorded once per day. In each room, air temperatures began at 15°C, and were adjusted to decline at a rate of ≤ 0.5°C per d,
depending on temperature treatment. Twelve 25 W bulbs per room provided light; “photoperiod” mimicked an Ohio winter. Each room housed eight 55 L tanks (four each of fed and starved). Each tank was divided into three compartments, each housing three fish. Eight treatments derived from two winters × two food treatments × two size classes.

The experiment began on November 29, 2001; herein, date will refer to simulated date as we used photoperiod regimes and temperature to simulate extreme Ohio winters. The cold winter was October 22, 2000 – April 12, 2001, whereas the warm winter was November 16, 2000 – March 28, 2001. 144 fish were weighed (nearest 0.1 g) and measured (nearest mm TL), and large (91 – 120 mm TL) and small (70 – 90 mm TL) fish were placed randomly into food and winter treatments (N = 18 fish per treatment; Table 8). Fish not used in the experiment (N = 17) were euthanized for later determination of energy density of pre-experiment fish. Within each compartment, individuals were identified by size, coloration, and fin markings. For the food treatment, white crappies were either fed live blackworms (30% maximum consumption, estimated from a bluegill Lepomis macrochirus bioenergetics model, Kitchell et al. 1974) or starved. Fed fish were observed for 5 min following feeding. Within each winter treatment, all sizes of fish were pooled to determine percent of fish feeding (noting the change in the denominator when mortalities occurred). To maintain water quality, feces were removed and one-third of the water replaced daily in all treatments. Ammonia (NH₄⁺) was monitored daily and never approached 0.50 ppm. Fish that died during the experiment were identified,
weighed, measured, and frozen in water for later estimates of energy density. At the end
of each winter, surviving fish were euthanized and then also identified, weighed,
measured, and frozen in water.

Differences in percent survival of individual fish per treatment were evaluated
using chi-square analyses. To account for the differences in days that fish were in the
experiment (owing to either mortality or winter treatment), daily growth rate \([(\text{final mass } – \text{ initial mass})/ \text{ d in experiment}]\) was calculated for each fish. For growth, each
compartment was a sampling unit; thus, we determined the mean daily growth within
each compartment. A general linear model (Proc GLM; SAS Institute 1999) determined
whether variability in growth rate was explained by class variables winter, size, and food,
potential two-way interactions, as well as tank effects nested within the three treatments.

For analyses of energy density, we also used general linear models (Proc GLM;
SAS Institute 1999). From autumn fish collected from Ohio reservoirs, we set reservoir
as a class variable and used fish TL as a covariate. For post-hoc comparisons of least-
squares mean energy density across reservoirs, we used Tukey-Kramer adjusted multiple
comparisons. For experimental fish, we estimated energy density from five fish that
survived and five fish that died for each treatment. Here, winter, food, and size were set
as class variables; number of days in the experiment was a covariate in analyses that
included fish that died.
Results

Energy density of field fish

Energy density (kJ/g wet mass) of 65 age-0 white crappie collected from four Ohio reservoirs during autumn 2000 increased with TL (Figure 20; $F_{1,60} = 78.71; P < 0.0001$). Thus large fish had an energetic advantage over small fish approaching winter in Ohio. Using TL as a covariate, the least-squares mean energy density of fishes differed among reservoirs (Figure 20; $F_{3,60} = 32.21; P < 0.0001$). Tukey-Kramer adjusted multiple comparisons of least-squares means ordered energy density of age-0 white crappie as [Delaware = Caesar Creek] > [Pleasant Hill = Pymatuning]. Thus, the reservoir from which our experimental fish were collected (Pleasant Hill) contained age-0 white crappie that possessed relatively low energy density relative to Delaware and Caesar Creek reservoirs.

Experiment

When the experiment began, energy density (kJ/g wet mass) of 17 age-0 white crappie increased with length ($F_{1,15} = 10.72; P = 0.005$), indicating that large fish had an energetic advantage over small fish. However, energy density of fish from Pleasant Hill declined (Figure 20) since the 5 weeks from their capture in October ($F_{1,36} = 15.98; P = 0.0003$, using TL as covariate). Compared to age-0 white crappie entering winter in Ohio reservoirs, our experimental fish were in an extremely poor energetic state.

Comparing fish lengths across winter treatments, mean initial TL of large fish in the warm winter exceeded mean initial TL of large fish in the cold winter ($t_{70} = 2.48; P = 0.02$); among small fish, no difference in mean initial TL existed between winters ($t_{70} = 0.84; P = 0.40$). In food treatments, mean initial TL of starved, large and small sizes of
fish was similar to mean initial TL of fed, large and small sizes of fish, respectively (large: $t_{70} = 0.24$, $P = 0.81$; small: $t_{70} = 0.12$, $P = 0.91$). Thus, aside from differences between sizes of large fish between the winters, our random placement of fish into treatments was successful.

Winter treatment greatly influenced age-0 white crappie survival, as 97% of fish survived the warm winter, whereas only 47% of fish survived the cold winter ($\chi^2 = 595.0; P < 0.0001$). Within each winter, neither food treatment nor size influenced survival (Table 9). In the cold winter, mortality began when water temperatures approached $2^\circ C$; peak mortality occurred when water temperatures fell to $1^\circ C$ (Figure 21a). Small fish did not die earlier than large fish, as length of fish that died did not increase with days in the experiment (Figure 21b, $F_{1,30} = 0.29; P = 0.60$). In addition, food treatment ($F_{1,30} = 0.21; P = 0.65$) and the food $\times$ days in the experiment interaction ($F_{1,30} = 0.16; P = 0.69$) did not influence length of fish that died.

Both food and size influenced daily growth rate, as small and fed fish had higher daily growth rates than large and starved fish, respectively (Table 10; Figure 22). No tank effects were detected. The food level $\times$ winter treatment was the only significant interaction as starved fish in the cold winter had higher daily growth rates than those in the warm winter, whereas fed fish in the cold winter had lower daily growth rates than those in the warm winter (Table 10; Figure 22). In terms of mass gained or loss during the experiment, 34% of all fed fish gained mass (mean mass gained = 0.30 g); the remainder either lost or maintained mass (mean mass lost or maintained = 0.55 g). Of the starved fish, 99% lost mass (mean mass lost = 1.33 g) and 1% gained mass (mass gained = 0.30 g). This latter gain was likely due to a measuring error.
Feeding during the cold winter was less frequent than during the warm one (Figure 23). In the cold winter, percent feeding fell below 10 on November 3, and remained consistently low (including many 0%) through April 5 (Figure 23a). As temperatures increased to 10°C in the cold winter, percentage of fish feeding did not concomitantly increase. Conversely, in the warm winter temperatures percent feeding generally ranged 5 – 15% throughout the coldest period (i.e., December 22 – March 11) during mid-December through mid-March (Figure 23b). As temperatures increased to 10°C, percentage of fish feeding in the warm winter increased, greatly exceeding the percentage feeding in the cold winter. If feeding during the first 5 min reflects feeding for the remainder of the day, then higher daily growth rates among fed fish in the warm winter, compared to fed fish in the cold winter, could be attributed to low consumption, especially during the second half of winter.

Similar to daily growth, both food and size treatments influenced energy density (kJ/g wet mass) of age-0 white crappie. Winter ($F_{1,36} = 1.51; P = 0.23$) did not influence energy density of survivors. Among survivors, fed fish were more energetically dense than their starved counterparts (Figure 24a; $F_{1,36} = 46.11; P < 0.0001$) and large fish had a higher energy density than small fishes ($F_{1,36} = 6.23; P = 0.02$). Because only two fish died during the warm winter, we focused on fish from the cold winter to explore energy density of fish that died during the experiment. Here, variability in energy density was best explained by food as fed fish that died had marginally greater energy density than starved fish that died (Figure 24b; $F_{1,16} = 4.03; P = 0.06$). Neither size ($F_{1,16} = 2.27; P = 0.15$), nor days in the experiment ($F_{1,16} = 0.33; P = 0.58$), influenced energy density of fish that died.
To determine whether energy density influenced mortality in the cold winter, we compared energy density between fish that died and survived within each food treatment using a $t$-test. Pooling across size treatments, energy density was similar between both fed fish that died and survived, as well as starved fish that died and survived (Table 16). We have no evidence that energy density, alone, caused mortality in the cold winter.

**Discussion**

Pre-winter energy density of age-0 white crappie increased with length in four Ohio reservoirs. With lower energy density than their larger counterparts, small age-0 white crappie could lose an amount of energy overwinter sufficient to cause mortality. In our experiment, cold-winter mortality (53%) exceeded warm-winter mortality (3%) by a substantial margin. In the cold winter, fish size and feeding treatment were unrelated to mortality, as both large and small fish died and energetic density of fish that died versus those that survived did not differ within a feeding treatment. In fact, energy density of cold-winter fish that died was higher than warm-winter fish that survived. Our experimental results suggest that significant, size-independent mortality only should occur in nature when age-0 white crappie are exposed to water $< 4^\circ$C. Simply put, energetic deficiencies did not cause mortality.

We hypothesized that winter survival would increase with fish length, as has been documented with several other fish species (white perch *Morone americana* and yellow perch *Perca flavescens*: Johnson and Evans 1991; freshwater drum *Aplodinotus grunniens*: Bodensteiner and Lewis 1992; coho salmon *Oncorhynchus kisutch*: Quinn and
Peterson 1996; largemouth bass *Micropterus salmoides*: Ludsin and DeVries 1997, Fullerton et al. 2000; roach *Rutilus rutilus* Kirjasniemi and Valtonen 1997; Atlantic silverside *Menidia menidia*: Schultz et al. 1998; striped bass *Morone saxatilis* Sutton and Ney 2001). Large fish should have a survival advantage over small fish because mass-specific metabolism declines with size (Peters 1983) and energy reserves typically increase with size (Ludsin and DeVries 1997; Garvey et al. 1998; Post and Parkinson 2001; Sutton and Ney 2001). In many winter experiments, small fish die earlier than the large fish, due to starvation (Post and Evans 1989; Johnson and Evans 1991; Hales and Able 2001).

Size offered few advantages in our experiment. In the beginning, large fish were more energetically dense than small fish, but this difference did not translate into higher survival or daily growth rate. Large fish died just as early as small fish. Small fish actually had a higher daily growth rate across all feeding treatments. However, the difference was most pronounced in starved fishes, which is not surprising given that small fish have lower total metabolic costs than large ones (Peters 1983).

In nature, large fish also are presumed to survive better than small fish, owing to size-dependent predation (Nielson 1980; Miranda and Hubbard 1994b; Kristiansen et al. 2000), i.e., small fish are more vulnerable to gape-limited predators (Werner and Gilliam 1984). In our experiment, fish did not increase in length during winter, suggesting that autumn length determines spring length. In addition to length, however, end-of-winter energetic condition could influence age-0 white crappie vulnerability to predation; fish in high energetic condition could avoid predators more adeptly, and also may be able to resume foraging earlier in spring. In our experiment, food availability regulated energetic
condition at the end of experiment. Thus, zooplankton prey during winter likely dictates
ergetic condition entering spring which, in turn, may influence predation risk as
piscivores become more active. In addition, our feeding observations suggest that cold-
winter fish were less willing than warm-winter ones to begin feeding as temperatures
warmed in late winter which, in turn, could reduce their energetic condition. Thus, both
zooplankton prey and winter temperatures could contribute to end-of-winter condition.

To our surprise, all sizes of age-0 white crappie can survive winter without food,
as evidenced by starved fish that survived 133 d in the warm winter and 173 d in the cold
winter. Adding support to the hardiness of these fish, their energetic condition at the
beginning of the experiment was considerably lower than the energetic condition of fish
in Ohio reservoirs. Thus, the age-0 white crappie entered our experiment in an
unrealistically poor condition. Yet, these fish were still able to survive 6 mo without
food.

Exposure to temperatures < 4°C caused mortality of age-0 white crappie.
Because warm-winter temperatures were < 4°C for only 6 d, we do not know how long
age-0 white crappie can survive < 4°C. The first cold-winter mortality occurred after 18
consecutive days of < 4°C. On the following day, the cooling system in the cold winter,
temperature-controlled room broke down, resulting in the warm-temperature spike
observed around the first of December. Although the occurrence of mortalities resumed
11 d following the break-down, we attribute these mortalities to prolonged exposure to
cold temperatures, rather than the abrupt temperature change around the first of
December. In fact, our highest mortality (3 died) occurred on the coldest day (1°C), 27 d
after the breakdown.
Exposure to extremely cold temperatures during winter does influence survival of other age-0 fishes (summer flounder *Paralichthys dentatus*: Malloy and Targett 1991; freshwater drum: Bodensteiner and Lewis 1992; white perch: Johnson and Evans 1996; Atlantic croakers: Lankford and Targett 2001). Osmoregulatory failure is presumed to be the mechanism as membrane permeability changes during colder temperatures, compromising ion transport, and resulting in too few critical ions (Morris and Bull 1968). Because small fish have a larger gill area per unit mass (Hughes 1984), they are hypothesized to be more susceptible to osmoregulatory failure than large fish (Johnson and Evans 1996). In our study, mortality was unrelated to size which suggests that potential differences in gill area likely were inconsequential for large and small age-0 white crappie. When water temperature remained < 4°C, osmoregulatory failure was likely the mechanism driving overwinter mortality of age-0 white.

**Implications for recruitment**

Our experiment has eliminated the hypothesis that winter starvation via energy depletion regulates recruitment of white crappie to age-1. Rather, prolonged exposure to water temperatures < 4°C, likely regulates their survival. However, age-0 white crappie could avoid the lethal thermal habitat that occurs in shallow Ohio reservoir waters during winter (D. B. Bunnell, unpublished data) by occupying the benthic, limnetic zones of the reservoir, where 4°C water always will be present because water is most dense at 4°C (Wetzel 1983). In fact, during summer and autumn, age-0 white crappie are captured in greater densities in the benthic, limnetic habitat of Ohio reservoirs than in the shallow, littoral habitat (D. B. Bunnell, unpublished data). Based on our experiment, age-0 white
crappie should remain benthic through winter, as well. The only caveat to warmer, benthic habitat is the possibility of low oxygen concentrations. During long, cold Ohio winters, when ice covers reservoirs, low oxygen concentrations could occur, thus squeezing crappie into cooler, more-oxygenated shallow waters that could offer temperatures $< 4^\circ\text{C}$.

Among the four Ohio reservoirs sampled, the system with the lowest index of recruitment, Pymatuning, also is the most northern system (Table 7). Although our experimental results predict that cold winters should lead to poor recruitment in northern Ohio systems, we cannot conclude that cold winters explain variability in recruitment among Ohio reservoirs. At a minimum, we would need extensive vertical dissolved oxygen temperature profiles documenting low oxygen concentrations in the benthic limnetic habitat. Because water flows both in (from tributaries) and out (through the dam) of most Ohio reservoirs during winter, low dissolved oxygen concentrations may never occur during winter. Moving farther south, winter water temperatures may become less important in regulating recruitment. Even so, exposure to water temperature $< 4^\circ\text{C}$ causes considerable size-independent mortality of age-0 individuals, providing a potential mechanism by which winter may regulate recruitment of white crappie.
Literature Cited


Trautman, M. B. 1957. The fishes of Ohio. The Ohio State University Press, Columbus, Ohio.


Table 7. Characteristics of Ohio reservoirs from which age-0 white crappie were collected for bomb calorimetry during October 17 – 27, 2000, and ordered by latitude (south to north). Mean chlorophyll $a$ (µg/L) concentration was the grand mean of upstream and downstream integrated water samples collected weekly during May – June 2000 (M. Vanni, Miami University, unpublished data). Mean and standard deviation (in parentheses) of age-2 white catch per effort (CPE) provide an index of recruitment success and variability. Age-2 CPE data result from 4 years of autumn trapnetting (Bunnell et al. in review). Total length (mm) range and N (number of individuals) describe the age-0 white crappie analyzed for bomb calorimetry.
<table>
<thead>
<tr>
<th>Winter</th>
<th>Food</th>
<th>Small age-0 white crappie</th>
<th>Large age-0 white crappie</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>TL mm</td>
<td>Mass g</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Begin</td>
<td>End</td>
</tr>
<tr>
<td>Warm</td>
<td>Fed</td>
<td>83.1</td>
<td>83.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(7.0)</td>
<td>(7.0)</td>
</tr>
<tr>
<td>Warm</td>
<td>Starved</td>
<td>83.6</td>
<td>82.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(4.5)</td>
<td>(4.6)</td>
</tr>
<tr>
<td>Cold</td>
<td>Fed</td>
<td>82.2</td>
<td>83.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(6.1)</td>
<td>(6.8)</td>
</tr>
<tr>
<td>Cold</td>
<td>Starved</td>
<td>82.1</td>
<td>81.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(6.0)</td>
<td>(5.5)</td>
</tr>
</tbody>
</table>

Table 8. Mean and standard deviation (in parentheses) of initial, final total length (TL, mm) and initial, final wet mass (g) for small (71 – 90 mm TL) and large (91 – 120 mm TL) age-0 white crappie held in the lab for 5–6 weeks and then subjected to simulated warm and cold Ohio winters. Eighteen fish were used per winter × food × size treatment.
Table 9. Age-0 white crappie survival (%) through the experiment as a function of winter, food, and size. Within each winter, chi-square test determined whether differences in survival occurred between fish at different food levels, as well as between small and large fish. Chi-square statistic is shown for all tests and $P > 0.5$. 

<table>
<thead>
<tr>
<th>Winter temperature</th>
<th>Food level</th>
<th>Size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fed</td>
<td>Starved</td>
</tr>
<tr>
<td>Warm</td>
<td>100.0</td>
<td>94.2</td>
</tr>
<tr>
<td>$\chi^2$</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>Cold</td>
<td>50.0</td>
<td>48.4</td>
</tr>
<tr>
<td>$\chi^2$</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>Factor</td>
<td>Relative effect</td>
<td>Degrees of Freedom</td>
</tr>
<tr>
<td>-----------------</td>
<td>--------------------------</td>
<td>--------------------</td>
</tr>
<tr>
<td>Winter</td>
<td>Cold = Warm</td>
<td>1</td>
</tr>
<tr>
<td>Size</td>
<td>Large &lt; Small</td>
<td>1</td>
</tr>
<tr>
<td>Food</td>
<td>Fed &gt; Starved</td>
<td>1</td>
</tr>
<tr>
<td>Size × food</td>
<td>-</td>
<td>1</td>
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<tr>
<td>Size × winter</td>
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<td>1</td>
</tr>
<tr>
<td>Feed × winter</td>
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<td>1</td>
</tr>
<tr>
<td>Tank</td>
<td>-</td>
<td>25</td>
</tr>
<tr>
<td>Error</td>
<td>-</td>
<td>16</td>
</tr>
</tbody>
</table>

Table 10. Results of a general linear model for the effects of simulated winter temperature, size, food treatment, possible two-way interactions, and tank on daily growth rate [(final mass – initial mass)/d in experiment] of age-0 white crappie, collected from Pleasant Hill Reservoir, Ohio, in our lab experiment. Tank was nested within winter, size, and food as each tank had different food or size treatments, within a winter.
<table>
<thead>
<tr>
<th>Food treatment</th>
<th>Fate of fish</th>
<th>Mean energy density (standard deviation)</th>
<th>$t$-statistic ($P$-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fed</td>
<td>Survived</td>
<td>3.35 (0.42)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Died</td>
<td>3.22 (0.14)</td>
<td>0.94 (0.37)</td>
</tr>
<tr>
<td>Starved</td>
<td>Survived</td>
<td>2.78 (0.44)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Died</td>
<td>3.04 (0.28)</td>
<td>1.54 (0.14)</td>
</tr>
</tbody>
</table>

Table 11. Mean energy density (kJ/g wet mass) of age-0 white crappie as a function of food treatment as well as whether they survived or died during the experiment. Degrees of freedom for both $t$-tests equaled 18.
Figure 21. Energy density (kJ/g wet mass) of age-0 white crappie increased with total length (mm). Two-letter symbols represent four Ohio reservoirs from which fish were sampled during October 2000 (see Table 7 for details). Triangles represent energy density of age-0 white crappie at the beginning of the experiment, after spending 5 – 6 weeks in the laboratory.
Figure 21
Figure 22. Mortality of age-0 white crappie in the cold winter experiment as a function of temperature (a) and total length (b). Because only 2 of 72 warm water fish died, similar relationships are not depicted for the warm winter. Panel (a) depicts the number of fish that died (37 fish, vertical bars) during each day of the simulated winter, regardless of food level. A solid, horizontal line occurs at 4°C, the temperature below which mortality was frequent. Panel (b) depicts total length of starved (open circles) and fed (closed circles) fish that died as a function of simulated day of winter. Neither number of days, food treatment, nor the days × food interaction predicted the total length of fish that died.
Simulated Dates
Oct 1  Nov 1  Dec 1  Jan 1  Feb 1  Mar 1  Apr 1  May 1

Total length (mm) at start of experiment

Fed
Starved

Figure 22
Figure 23. Mean daily growth rate [(final mass – initial mass)/d in experiment] of different size classes and feeding levels of age-0 white crappie as a function of winter treatment. The zero daily growth rate is indicated by a solid horizontal line. The initial sampling unit was a partition (i.e., the mean of three fish); each data point on the graph represents the grand mean of six partitions for each treatment.
Figure 23

Mean daily growth (g/d) +/- standard error

-0.016
-0.012
-0.008
-0.004
0.000
0.004
0.008

Cold
Warm

Winter treatment

Growth = 0

Large, fed
Small, fed
Larger, starved
Small, starved
Figure 24. Percent feeding by age-0 white crappie (vertical, filled bars) and the temperature regime (solid black line) for the cold (a) and warm (b) winters, as a function of simulated day of winter. Here, feeding represents the percent of all fish observed to eat in the first 5 min following food presentation, independent of size. 4°C is highlighted with a solid, horizontal line, the temperature below which feeding was infrequently observed in the cold winter.
Figure 24

Simulated Dates

Percent of age-0 white crappie feeding in first 5 min

(a) Cold winter

(b) Warm winter

Water Temperature (°C)

Percent Feeding

4°C
Figure 25. Energy density (kJ/g wet mass) as a function of total length (TL) for age-0 white crappie that survived both experimental winters (a) and died during the cold winter (b). Because only two fish died in the warm winter (versus 37 fish in the cold winter), we did not quantify their energy density. The vertical line at 90.5 mm TL separates the small and large sizes of fish.
Fish that died during cold winter

Total length of age-0 white crappie (mm)

Energy density (kJ/g wet mass)

(a) Fish that survived both cold and warm winters

(b) Fish that died during cold winter

N = 40 fish

N = 20 fish

Cold, fed
Warm, fed
Cold, starved
Warm, starved

Small fish
Large fish

Figure 25
BIBLIOGRAPHY


Trautman, M. B. 1957. The fishes of Ohio. The Ohio State University Press, Columbus, Ohio.


