

North American Journal of Fisheries Management 2006 v.26, n.1, p.1-12

ISSN: (Print 0275-5947) (Online 1548-8675)

DOI: 10.1577/M04-207.1

<http://afsjournals.org/>

<http://afsjournals.org/loi/fima>

<http://afsjournals.org/doi/pdf/10.1577/M04-207.1>

© Copyright by the American Fisheries Society 2006

Predicting Crappie Recruitment in Ohio Reservoirs with Spawning Stock Size, Larval Density, and Chlorophyll Concentrations

DAVID B. BUNNELL*¹

Aquatic Ecology Laboratory, Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 1314 Kinnear Road, Columbus, Ohio 43212-1156, USA

R. SCOTT HALE

Ohio Department of Natural Resources, Division of Wildlife, Inland Fish Research Unit, 10517 Canal Road SE, Hebron, Ohio 43025, USA

MICHAEL J. VANNI

Department of Zoology, Miami University, 212 Pearson Hall, Oxford, Ohio 45069, USA

ROY A. STEIN

Aquatic Ecology Laboratory, Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 1314 Kinnear Road, Columbus, Ohio 43212-1156, USA

Abstract.—Stock–recruit models typically use only spawning stock size as a predictor of recruitment to a fishery. In this paper, however, we used spawning stock size as well as larval density and key environmental variables to predict recruitment of white crappies *Pomoxis annularis* and black crappies *P. nigromaculatus*, a genus notorious for variable recruitment. We sampled adults and recruits from 11 Ohio reservoirs and larvae from 9 reservoirs during 1998–2001. We sampled chlorophyll as an index of reservoir productivity and obtained daily estimates of water elevation to determine the impact of hydrology on recruitment. Akaike’s information criterion (AIC) revealed that Ricker and Beverton–Holt stock–recruit models that included chlorophyll best explained the variation in larval density and age-2 recruits. Specifically, spawning stock catch per effort (CPE) and chlorophyll explained 63–64% of the variation in larval density. In turn, larval density and chlorophyll explained 43–49% of the variation in age-2 recruit CPE. Finally, spawning stock CPE and chlorophyll were the best predictors of recruit CPE (i.e., 74–86%). Although larval density and recruitment increased with chlorophyll, neither was related to seasonal water elevation. Also, the AIC generally did not distinguish between Ricker and Beverton–Holt models. From these relationships, we concluded that crappie recruitment can be limited by spawning stock CPE and larval production when spawning stock sizes are low (i.e., CPE < 5 crappies/net-night). At higher levels of spawning stock sizes, spawning stock CPE and recruitment were less clearly related. To predict recruitment in Ohio reservoirs, managers should assess spawning stock CPE with trap nets and estimate chlorophyll concentrations. To increase crappie recruitment in reservoirs where recruitment is consistently poor, managers should use regulations to increase spawning stock size, which, in turn, should increase larval production and recruits to the fishery.

Because fish recruitment can vary up to 10 orders of magnitude within (Forney 1976; Sissenwine 1984) and among systems (Myers et al. 1997; Garvey et al. 1998), the ability to understand the mechanisms underlying recruitment and to predict recruitment variability is a central goal of fisheries management. If factors critical to recruitment success can be manipulated (e.g.,

reservoir productivity or water elevations), then managers can potentially modify those factors to improve recruitment success. Conversely, if these factors cannot be manipulated (e.g., climate), managers can at least inform anglers before a poor year-class recruits to the fishery in an attempt to manage angler expectations.

Several mechanisms can influence fish recruitment. First, population biology predicts that the number of recruits should be related to the number or biomass of adults (Hilborn and Walters 1992). Several different models for this relationship have been proposed, but the Ricker and Beverton–Holt models have been the

* Corresponding author: dbunnell@usgs.gov

¹ Present address: U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan 48105, USA.

Received December 9, 2004; accepted July 28, 2005
Published online December 19, 2005

most commonly evaluated. Second, environmental factors, such as concentrations of zooplankton prey (Hjort 1914; Cushing 1968), densities of predators (Mills et al. 1987), climate (Leggett et al. 1984), or flow (Mion et al. 1998), can explain variation in recruitment. Most investigators now agree, however, that a combination of spawning stock size and environmental factors probably provides the best insight into recruitment variability. In fact, both factors can be integrated in a modified Ricker or Beverton–Holt stock–recruit model that incorporates environmental variables (Hilborn and Walters 1992).

Studies that have applied the stock–recruit relationship to multiple life history stages (e.g., adult stock, larvae, and recruits; for examples, see Elliott 1985; Post et al. 1998) have several advantages over those that use only two life history stages (e.g., adult stock and recruits). First, including an intermediate life history stage, such as larvae, between adult stock and recruits can serve as a validation of the stock–recruit relationship. If recruitment is related to spawning stock size, then recruitment also should be related to larval density. Second, evaluating the relationships with multiple life history stages can help determine the stage at which recruitment can be predicted. For example, if the number of recruits is unrelated to spawning stock size but related to larval density, then the critical period must occur sometime between the spawning of eggs and hatching of embryos. Conversely, if recruitment is unrelated to both spawning stock size and larval density, then factors beyond the larval stage (e.g., juvenile competition, predation, overwinter mortality) must determine the ultimate number of recruits.

Crappies *Pomoxis* spp. are notorious for their high recruitment variability (Beam 1983; McDonough and Buchanan 1991; Sammons and Bettoli 1998), which then drives highly variable angling success (Hooe 1991). Several lines of research indicate that crappie recruitment is influenced by environmental variables. Via modeling, Allen and Miranda (2001) demonstrated that environmental fluctuation modulates density-dependent recruitment responses. In empirical studies, recruitment to age 1 has been strongly correlated with reservoir hydrology (i.e., discharge, retention) either before (Maceina and Stimpert 1998; Sammons and Bettoli 2000; Sammons et al. 2002; Maceina 2003) or during (Mitzner 1981; Beam 1983; McDonough and Buchanan 1991) spawning. High discharge and short retention before spawning are hypothesized to either cue enhanced crappie reproduction or spur primary production to enhance food resources for young crappies (Maceina and Stimpert 1998; Maceina 2003). Reservoir productivity also has been positively correlated with aspects of age-0 crappie success. First-

year growth of black crappies *P. nigromaculatus* in Minnesota lakes increases with chlorophyll concentrations up to 100 $\mu\text{g/L}$ (McInerney and Cross 1999), and juvenile crappie catch per effort (CPE) generally increases with productivity in Alabama (Dubuc and DeVries 2002) and Florida (Allen et al. 1998) systems. Evidence for recruitment to be related to spawning stock size is limited to a set of four reservoirs in Arkansas and Mississippi, where spawning stock density explained 9–44% of crappie recruitment to age 1 (Allen and Miranda 1998). Another study, however, found recruitment to age 1 to be linearly related to the density of larvae produced (Sammons and Bettoli 1998). Hence, two studies have found recruitment to age 1 to be related to other crappie life history stages. Despite evidence that environmental factors, spawning stock biomass, and larval density all relate to crappie recruitment, we are unaware of any analysis that has integrated these environmental and population variables into the modified Ricker or Beverton–Holt stock–recruit model.

In this study, we used a tiered sampling design to sample adult white crappies *P. annularis* and black crappies and age-2 crappie recruits from 11 reservoirs and crappie larvae from only a subset of those reservoirs (Table 1). We also measured two environmental variables, reservoir water elevation and chlorophyll (i.e., reservoir productivity), which we hypothesized could influence crappie recruitment. We then considered several different combinations of stock–recruit models, with and without environmental variables, to address the following questions: (1) Does larval density relate to spawning stock size, reservoir productivity, reservoir water elevation, or some combination of these variables ($N = 8$ reservoirs from the 1999 year-class and 9 reservoirs from the 2000 year-class)? (2) Does the number of age-2 recruits relate to larval density, reservoir productivity, reservoir water elevation, or some combination of these variables ($N = 11$ reservoirs from the 1998 year-class and 8 reservoirs from the 1999 year-class)? (3) Does the number of age-2 recruits relate to spawning stock size, reservoir productivity, reservoir water elevation, or some combination of these variables ($N = 11$ reservoirs from the 1999 year-class)? Hence, we had two overall objectives: (1) We sought to determine whether stock–recruit models (with or without environmental variables) explain variation in crappie recruitment; and (2) we sought to determine the life history stage(s) at which recruitment to the fishery could be best predicted.

Methods

We combined white and black crappies in our study for three reasons. First, these two species are managed

TABLE 1.—Characteristics of 11 Ohio reservoirs sampled for white and black crappies. Chlorophyll equals the mean of the annual chlorophyll-*a* concentrations during May–June 1998–2000 (although Piedmont and Tappan reservoirs were sampled only in 1998). These chlorophyll estimates differ slightly from those of Knoll et al. (2003) because they used data from April through October (rather than May through June) to calculate the mean. Water fluctuation equals the difference between the regulated winter and summer elevations. Retention time (volume divided by discharge) was estimated daily. Because of extremely low discharge events (even zero discharge) in some reservoirs, we calculated the median annual retention time and present the mean of the median annual retention times for 1996–2000. Autumn trap-netting occurred on each reservoir during 1998–2001. Percent composition of white crappies is the mean percentage of adult white crappies (by number) of the total adult black and white crappie populations sampled by autumn trap-netting across those same years.

Reservoir	Code	Surface area (ha)	Chlorophyll ($\mu\text{g/L}$)	Water fluctuation (m)	Retention time (d)	Mean depth (m)	Percent composition of white crappies	Years of larval sampling
Alum Creek	AM	1,371	13.08	0.9	3,056	7.3	65.0	1998–2000
Acton Lake	AT	253	53.77	0.3		3.9	100.0	1998–2000
Burr Oak	BO	269	11.74	0	485	4.5	98.2	1998–2000
Berlin	BR	1,344	16.09	2.9	153	4.5	68.8	1998–2000
Caesar Creek	CC	1,055	18.51	0.9	1,196	11.6	84.9	1998–2000
Delaware	DW	526	34.80	1.5	87	3.5	52.2	1998, 2000
LaDue	LD	607	16.00	1.3	473	6.1	88.9	1998–2000
Piedmont	PD	920	9.50	1.5	336	4.5	91.2	1998
Pleasant Hill	PH	316	23.37	1.8	62	4.8	97.4	1998–2000
Pymatuning	PY	5,929	6.81	0.5	^a	4.6	19.3	1998–2000
Tappan	TP	862	20.90	1.5	774	3.3	100.0	1998

^a Not available.

as one in Ohio reservoirs. Second, this approach has validity from an ecological perspective. White and black crappie spawning times and habitat largely overlap (Siefert 1968; McNerny and Held 1995) and both species share similar diets through at least the juvenile life stage (Ellison 1984). Finally, these two species cannot be visually distinguished as larvae, owing to overlap in the number of myomeres (Siefert 1969). As a result, any analyses involving larvae in reservoirs with both species must involve both species at other life history stages as well.

Our 11 Ohio study reservoirs varied in their composition of white and black crappies (Table 1), although white crappies predominated in 10 reservoirs. Reservoir size ranged between 253 and 1,371 ha, except for Pymatuning Lake at 5,929 ha (Table 1). Mean reservoir depth ranged between 3.3 and 7.3 m, except for Caesar Creek Reservoir at nearly 12 m. Annual retention times ranged between 2 months and several years, but annual water level fluctuations were more similar among reservoirs (range, 0–2.9 m). Chlorophyll concentrations ranged from 6.8 (oligotrophic–mesotrophic) to 53.8 (eutrophic) $\mu\text{g/L}$ (Wetzel 1983).

Autumn sampling of spawning adult and age-2 recruits.—During October through mid-November 1998–2001, we estimated CPE of adults and age-2 recruits with Missouri-style trap nets (1.27-cm mesh with two 0.91-m \times 1.82-m rectangular frames, four 0.76-m diameter hoops, and a 21.3-m lead; Colvin and Vasey 1986). Within each reservoir each autumn, 10 nets were set at fixed locations over 4 nights (i.e., 40 net-nights). We selected sites such that nets were

stratified across three major areas of the reservoir (upper reach, middle reach, and lower reach). Sites were typically 2–4 m deep; nets were set on the slope of the channel (through which white crappies move during autumn). Crappies were identified to species and measured (nearest mm, total length [TL]). We used otoliths to estimate age. When a particular species was abundant (i.e., >200 crappies sampled during a week), all fish from at least 50% of the nets per day (selected randomly a priori) were harvested for age estimation. In reservoirs with lower densities, we took otoliths from fishes in all nets. On average, we aged 157 (SD = 75) white crappies and 70 (SD = 61) black crappies per reservoir. Fish not harvested for aging were released after their left pectoral fin was clipped to prevent them from being counted later.

We classified adults as crappies age 2 and older, which generally corresponds to sizes larger than 180 mm TL. Spawning stock CPE (fish per net-night) was calculated as mean CPE of crappies age 2 and older captured in the autumn prior to spawning. Hence, we assumed that overwinter mortality rates did not differ across reservoirs. We set age 2 as our index of recruitment because age-2 crappies had fully recruited to our trap nets, similar to the results of Colvin and Vasey (1986) in Missouri reservoirs. Age-2 crappie CPE was estimated with a length–age key (DeVries and Frie 1996) from otolith-derived age estimates. Under 10–20 \times magnification, we counted annular rings of whole otoliths immersed in glycerol. To facilitate aging of old fish (i.e., >4 years), we cracked otoliths into two sections with a knife. For each reservoir and

species combination, we calculated the proportion of ages that comprised each centimeter length-class. This “key” then was applied to the population length distribution to estimate ages of all captured fish. For each reservoir, we calculated the mean CPE of age-2 crappies across net-nights.

Spring sampling of larvae.—To generate estimates of larval density, we sampled ichthyoplankton weekly during May–June from 11 reservoirs during 1998, 8 reservoirs during 1999, and 9 reservoirs during 2000. At a fixed speed (1 m/s), two replicate 5-min tows were completed at fixed upstream and downstream sites during the day with a 1-m \times 2-m neuston net (0.5-mm mesh) along the top meter of the water. A flowmeter in the net mouth estimated distance traveled, from which sample volume was calculated. Because crappie larvae sampled in the top 3 m of water during the day are evenly distributed in Ohio reservoirs (Arend 2002), our sampling estimated larval densities in the epilimnion. Samples were preserved in 95% ethanol upon capture and crappies were later counted in the laboratory. When high densities of larvae were collected, we subsampled by volume or by weight (see Bunnell et al. 2003 for details).

To determine larval density, we sought to include only larvae that were newly arrived to the limnetic zone of the reservoir. By doing so, we avoided biasing larval density to higher estimates in the reservoirs or years in which larvae were surviving well, as those larvae could be sampled during multiple weeks. Using relationships between larval age and size, we determined that larvae longer than 8 mm were available for capture at smaller sizes in earlier weeks of sampling (Bunnell et al. 2003). Thus, these longer fish were excluded when estimating larval density. Herein, “larval density” refers to the density of larvae less than or equal to 8 mm, rather than density of all larvae captured. Mean larval density was calculated for each site and then for each week of sampling (across sites) in each reservoir. To characterize larval density for a particular year, we calculated the average density across weeks.

Environmental variables.—For 1998–2000, we acquired daily water elevation levels (meters above sea level) from the U.S. Army Corps of Engineers (for Alum Creek, Berlin, Burr Oak, Caesar Creek, Delaware, Piedmont, Pleasant Hill, and Tappan reservoirs), from the Pymatuning State Park (for Pymatuning Reservoir), from the City of Akron (for LaDue Reservoir), and from the Miami Conservancy District (for Acton Lake Reservoir). We focused on water elevation during three seasons: winter (January–March), spring (April–May), and summer (June–September). For each year, we calculated the mean daily water elevation in each season and in each

reservoir. To make the data comparable across reservoirs, we calculated the percent deviation from standard summer pool elevation in each reservoir as [(mean seasonal elevation – summer pool elevation)/(summer pool elevation)] \times 100%.

We used chlorophyll *a* (hereafter “chlorophyll”) as a measure of reservoir productivity. At least twice during each summer of ichthyoplankton collection, we collected integrated water samples from the euphotic zone at upstream and downstream sites of each reservoir. Samples were immediately placed on ice and stored inside a cooler. Upon returning to the laboratory, a known sample of water (50–100 mL) was passed through a Gelman type A/E glass fiber filter; the filter was placed in either foil or a film canister and frozen for later extraction. Chlorophyll was extracted later with acetone and quantified with a fluorometer (Turner BioSystems, Inc., Sunnyvale, California; Model TD-700) calibrated with commercial standards. For each year, we calculated the average chlorophyll concentration at each site in each reservoir. We then averaged the two sites to characterize the chlorophyll for each reservoir in each year.

Analyses.—For each of the three relationships among the life history stages (i.e., larval density versus spawning stock CPE, age-2 recruits versus larval density, and age-2 recruits versus spawning stock CPE), we considered several different stock–recruit models. First, we considered simple stock–recruit models without environmental variables; that is, Ricker ($R = Se^{[a - bS]}e^\varepsilon$) and Beverton–Holt ($R = [aS/\{b + S\}]e^\varepsilon$) models, where e^ε is the lognormal error term and the variables for R and S are a function of the relationship evaluated. For example, when evaluating larval density relative to spawning stock CPE, R represents larval density and S represents spawning stock CPE. For both models, we \log_e transformed both sides of each equation (Ricker: $\log_e[R] = \log_e[S] + a - bS + \varepsilon$; Beverton–Holt: $\log_e[R] = \log_e[aS] - \log_e[b + S] + \varepsilon$) and used nonlinear regression (Proc NLIN; SAS Institute 1999) to estimate the parameters. We report r^2 values as the model sum of squares divided by the corrected total sum of squares.

We also modified the Ricker and Beverton–Holt models to include environmental variables (Hilborn and Walters 1992). We modified the Ricker model as $R = Se^{(a - bS + c_1X_1 + c_2X_2)}e^\varepsilon$ and the Beverton–Holt model as $R = \frac{aS}{b+S}e^{c_1X_1 + c_2X_2}e^\varepsilon$, where X_1 and X_2 are environmental variables (either chlorophyll or one of the seasonal water elevations) and c_1 and c_2 are the respective parameters for environmental variables. Again, we \log_e transformed both sides of each equation (Ricker: $\log_e[R] = \log_e[S] + a - bS + c_1X_1 + c_2X_2 + \varepsilon$; Beverton–Holt: $\log_e[R] = \log_e[aS] - \log_e[b + S] + c_1X_1$

+ $c_2X_2 + \varepsilon$) and used nonlinear regression to estimate the parameters. We used second-order Akaike's information criterion (AIC_c ; Burnham and Anderson 2002) to determine which model(s) provided the most support for the data. For each of the three relationships, we compared 16 different candidate models: two different model structures (Ricker and Beverton–Holt) \times eight different combinations of environmental variables ([1] no environmental variables, [2] chlorophyll, [3] summer water elevation, [4] winter water elevation, [5] spring water elevation, [6] summer water elevation and chlorophyll, [7] winter water elevation and chlorophyll, and [8] spring water elevation and chlorophyll).

Results

Catch rates of age-2 crappie recruits in trap nets varied widely across reservoirs and years (Figure 1). Within a reservoir and year combination, the relative standard error ($RSE = [SE/mean] \times 100$) of age-2 crappies ranged from 10% to 49%, with a mean RSE of 22% across all reservoirs and years ($N = 44$). Catch rates of larval crappies generally peaked the last week of May or the first week of June, but crappie larvae were collected over an average of 40 d (range = 20–53 d) across all reservoirs and years. Mean larval density varied across reservoirs within a year and across years within a reservoir (Figure 1).

The first stock–recruit models that we evaluated explored whether larval density was related to spawning stock CPE. Of the 16 candidate models, the 2 models with chlorophyll as the sole environmental variable (i.e., Ricker model and Beverton–Holt model) provided equally “substantial” support as the model that best supported the data because their respective Δ_i values (difference between each model and the model with the minimum AIC_c) were less than 2 (Table 2; Burnham and Anderson 2002). The r^2 values of these two models ranged from 0.63 to 0.64 (Table 2). In the Beverton–Holt version, each of the estimated slope parameters were positive ($a = 0.064$, $SE = 0.032$; $b = 3.017$, $SE = 2.647$; $c_1 = 0.035$, $SE = 0.012$), which revealed that larval density increased with chlorophyll or reservoir productivity (Figure 2). In the Ricker version, the signs of the slope parameters were variable ($a = -4.23$, $SE = 0.344$; $b = 0.093$, $SE = 0.034$; $c_1 = 0.034$, $SE = 0.012$), but larval density again increased with chlorophyll (Figure 2). All models that included a seasonal water elevation variable had Δ_i values of 4 or greater, indicating “considerably less” support as the best model to explain variation in larval density (Burnham and Anderson 2002). Larval densities appeared to reach an asymptote at higher densities of

spawning stock CPE (Figure 2). This asymptotic relationship is generally associated with the Beverton–Holt curve, whereas the Ricker curve is typically more dome-shaped (Quinn and Deriso 1999). However, AIC_c found both curves supported the data equally well.

Using 11 reservoirs from the 1998 year-class and 8 reservoirs from the 1999 year-class, we next evaluated whether the CPE of age-2 crappies (i.e., recruitment) was related to larval density. In this case, 4 of the 16 candidate models provided “substantial” support as the best model (Table 2). Two of these four models were simple Beverton–Holt ($a = 8.662$, $SE = 5.217$; $b = 0.097$, $SE = 0.087$) and Ricker ($a = 4.336$, $SE = 0.251$; $b = 4.350$, $SE = 1.977$) models without any environmental variables. The other two models included chlorophyll as an environmental variable in the Beverton–Holt ($a = 6.807$, $SE = 4.33$; $b = 0.104$, $SE = 0.093$; $c_1 = 0.015$, $SE = 0.012$) and Ricker ($a = 4.033$, $SE = 0.349$; $b = 4.055$, $SE = 1.961$; $c_1 = 0.014$, $SE = 0.012$) models. Recruitment of crappies to age 2 increased with chlorophyll and appeared to reach an asymptote with increasing larval densities (Figure 3). In general, however, variation in age-2 recruits explained by the top models was relatively low ($r^2 = 0.43$ – 0.49 ; Table 2) compared with the models explaining variation in larval density ($r^2 = 0.63$ – 0.64 ; Table 2).

Finally, we evaluated one of the most commonly analyzed stock–recruit relationships, namely, whether spawning stock CPE predict the number of age-2 recruits. Two Ricker models were identified as most supportive of the data, explaining 86% and 74% of the variance (Table 2). The first included only chlorophyll ($a = -0.638$, $SE = 0.280$; $b = 0.086$, $SE = 0.023$; $c_1 = 0.047$, $SE = 0.018$) and the second included no environmental variables ($a = -0.323$, $SE = 0.322$; $b = 0.572$, $SE = 0.026$). As found in the other relationships, chlorophyll had a positive effect in the first model (Figure 4). Perhaps owing to the relatively low recruitment event observed at the highest spawning stock size (Figure 4), the Ricker model was slightly favored over the Beverton–Holt model. However, the Beverton–Holt model without environmental variables and the Beverton–Holt model that included chlorophyll ranked 3rd and 4th with Δ_i values of 2.8 and 4.0, respectively. Although these Δ_i values do not have the same level of support of the data as the top-ranked Ricker models (Burnham and Anderson 2002), the differences between the Ricker and Beverton–Holt models were relatively small and these Beverton–Holt models still explained 71–80% of the variation in recruitment (Table 2).

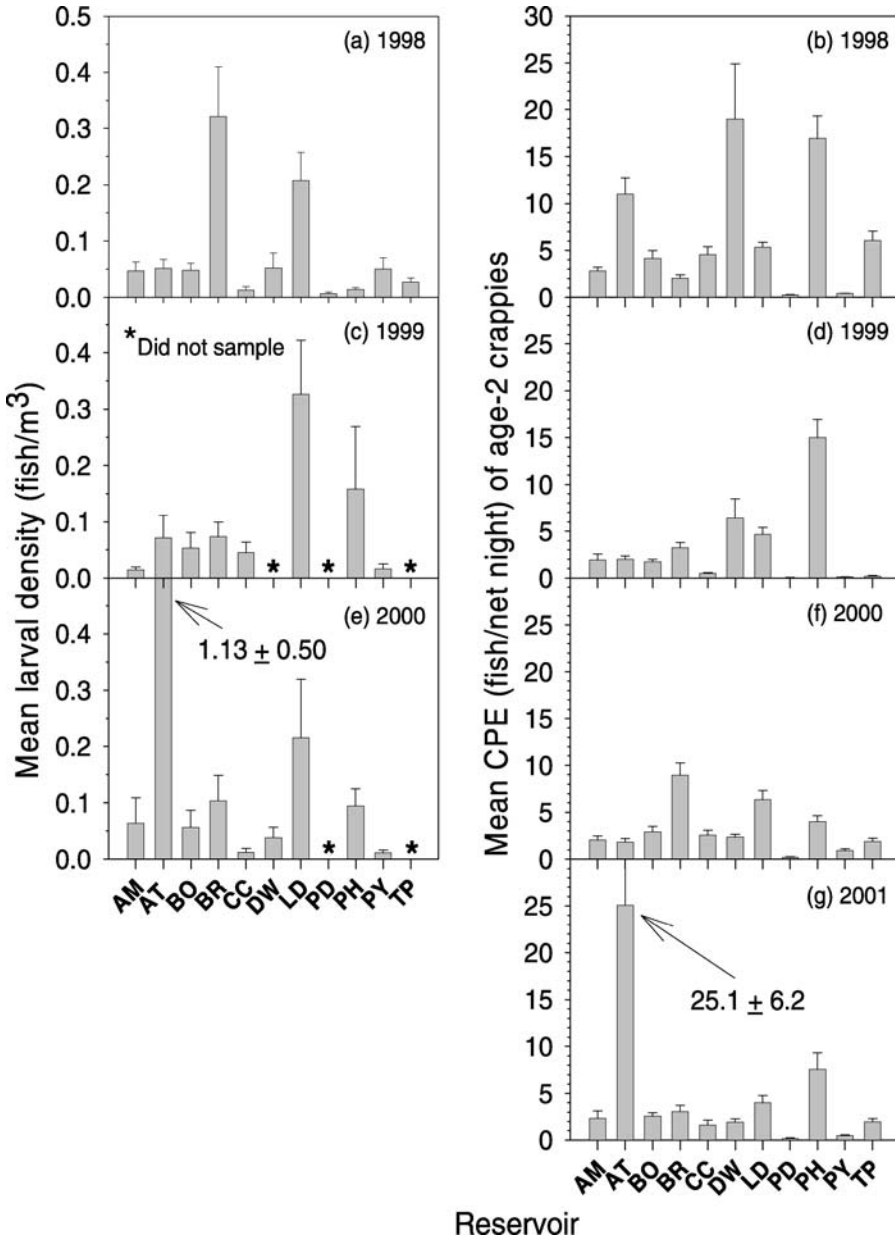


FIGURE 1.—Interannual variation of larval densities and the number of age-2 white and black crappie recruits in 11 Ohio reservoirs (see Table 1 for reservoir codes). Panels (a), (c), and (e) depict the mean density of white and black crappie larvae sampled with neuston nets during May and June 1998–2000. To keep all y-axes of equal size, the larval density of Acton Lake Reservoir (AT) in 2000 was truncated and the mean and SE indicated. Panels (b), (d), (f), and (g) depict the catch per effort (CPE) ± SE of white and black crappies age 2 and older sampled by autumn trap-netting during 1998–2001. To keep all y-axes of equal size, the CPE of Acton Lake Reservoir in 2001 was truncated and the mean and SE indicated.

Discussion

Density of crappie larvae and the CPE of age-2 crappie recruits in Ohio reservoirs were explained best by either Ricker or Beverton–Holt stock–recruit models that included chlorophyll, an indicator of

reservoir productivity. Higher productivity appeared to enhance production of crappie larvae and age-2 recruits. The inclusion of seasonal water elevation variables in the models was not helpful in explaining crappie recruitment. In terms of predicting recruitment

TABLE 2.—Rankings of models to explain the variation in white and black crappie larval density or catch per effort (CPE) of age-2 crappies sampled in 11 Ohio reservoirs between 1998 and 2001. Only the five highest-ranking models in each group are displayed. Rank was determined by the corrected Akaike information criterion (AIC_c) value (smallest value equals highest rank). All models included the parameters a , b , and ϵ from either the Ricker (R) or Beverton–Holt (BH) models. Some models also included one or more of the following environmental variables: chlorophyll (CHL), winter water elevation (WI), spring water elevation (SP), and summer water elevation (SU). Data include K (the number of parameters estimated), σ^2 (the residual sum of squares divided by N), Δ_i (the difference between each model and the model with the minimum AIC_c), and r^2 (the proportion of variance explained by the model).

Environmental parameters and variables	K	σ^2	AIC_c	Δ_i	r^2
Models to explain variation in larval density with adult CPE					
CHL (BH)	4	0.502	-0.378	0.00	0.64
CHL (R)	4	0.518	0.152	0.53	0.63
SU, CHL (BH)	5	0.497	3.554	3.93	0.65
SP, CHL (BH)	5	0.499	3.626	4.00	0.64
WI, CHL (BH)	5	0.502	3.735	4.11	0.64
Models to explain variation in CPE with larval density					
None (BH)	3	0.602	-2.029	0.00	0.44
None (R)	3	0.604	-1.969	0.06	0.43
CHL (BH)	4	0.546	-0.649	1.38	0.49
CHL (R)	4	0.552	-0.445	1.58	0.48
SP (R)	4	0.583	0.620	2.65	0.45
Models to explain variation in age-2 CPE with adult CPE					
CHL (R)	4	0.219	-2.039	0.00	0.86
None (R)	3	0.402	-0.595	1.44	0.74
None (BH)	3	0.454	0.733	2.77	0.71
CHL (BH)	4	0.314	1.937	3.98	0.80
WI (R)	4	0.354	3.236	5.28	0.78

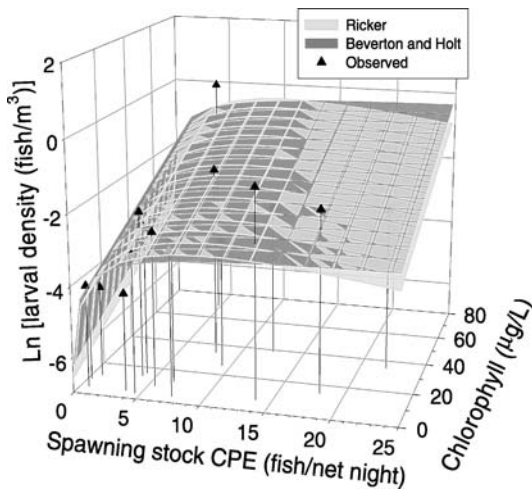


FIGURE 2.—Predicted crappie larval density as a function of crappie spawning stock CPE (mean number of crappies age 2 and older sampled with trap nets during autumn 1998–2001) and chlorophyll concentration in 11 Ohio reservoirs. The light gray surface represents the predictions of the Ricker model, whereas the dark gray panels represent the predictions of the Beverton–Holt model. Observed larval density (larvae were sampled with neuston nets during May and June 1998–2000) is represented by triangles with drop lines and includes data from 8 reservoirs from the 1999 year-class and 9 reservoirs from the 2000 year-class.

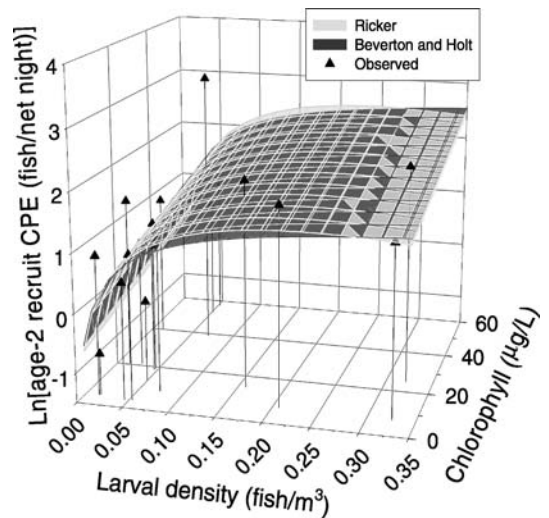


FIGURE 3.—Predicted CPE of age-2 crappie recruits as a function of crappie larval density and chlorophyll concentration in 11 Ohio reservoirs. The light gray surface represents the predictions of the Ricker model, whereas the dark gray panels represent the predictions of the Beverton–Holt model. Observed CPE of age-2 crappie recruits (sampled with trap nets during autumn 1998–2001) is represented by triangles with drop lines and includes data from 11 reservoirs from the 1998 year-class and 8 reservoirs from the 1999 year-class.

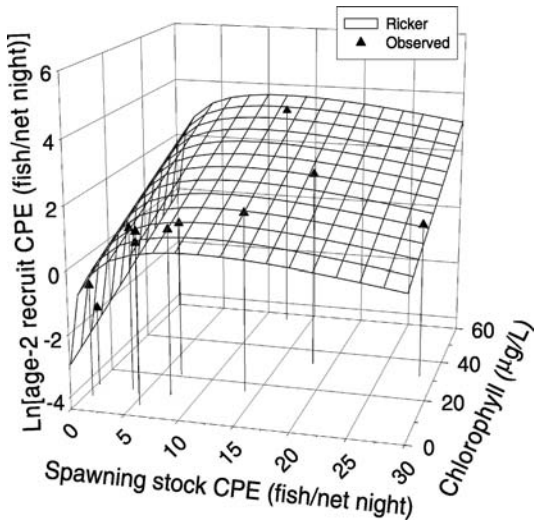


FIGURE 4.—Catch per effort (CPE) of age-2 crappie recruits predicted by the Ricker model as a function of crappie spawning stock CPE (mean number of crappies age 2 and older sampled with trap nets during autumn 1998–2001) and chlorophyll concentration in 11 Ohio reservoirs. Observed CPE of age-2 crappie recruits (sampled with trap nets during autumn) are represented by triangles with drop lines and include data from 11 reservoirs from the 1999 year-class.

to age 2 (i.e., the fishery), spawning stock CPE and chlorophyll had considerably higher r^2 values (0.74–0.86) than larval density and chlorophyll (0.43–0.49). As a result, managers seeking to predict recruitment would be better served by sampling adults rather than larvae. Including larval density data in stock–recruit models was helpful, however, in confirming the mechanism of the stock–recruit relationship. Larval density was extremely low at low spawning stock sizes and low larval density led to generally low CPE of age-2 crappies. Taken together, these relationships provide strong evidence that crappie recruitment is indeed regulated by spawning stock, especially when spawning stock size is low. Similarly, in Normandy Reservoir, Tennessee, the number of age-1 recruits is limited by the number of larvae produced (Sammons and Bettoli 1998). Hence, managers seeking to increase recruitment in systems with historically poor recruitment should focus on increasing spawning stock sizes.

A few caveats to our approach should be noted. First, unlike conventional stock–recruit studies, our sampling units were multiple populations in a particular year rather than one population across several years (but see Beard et al. 2003), an approach with advantages and disadvantages. Conventional stock–recruit analyses potentially suffer from autocorrelation within the time series (Walters 1985). This concern was

minimized with our approach and altogether was eliminated in our age-2 CPE versus spawning stock CPE analyses, where each data point (i.e., reservoir) was truly independent because multiple years within a reservoir were not included. The primary disadvantage of this approach, however, was that each reservoir population probably was exposed to different abiotic (i.e., temperature, reservoir hydrology) and biotic (i.e., density of predators, competitors, and prey) factors and these interreservoir differences probably were greater than the interannual differences within a single population. Hence, given these potential differences across reservoirs, our approach may be less likely to detect a stock–recruit relationship than one that has several years of data from one reservoir. In our view, however, we were able to detect a stock–recruit relationship because we sampled a wide range of spawning stock sizes, including those with low numbers of adults where the stock–recruit relationship should be best revealed (Hilborn and Walters 1992).

Second, our analyses assumed no measurement error in our independent variables, which was violated when spawning stock CPE and larval density were used. Although this is a common phenomenon for stock–recruit models, it can introduce bias to the estimated parameters (Walters and Ludwig 1981). Recent simulations and meta-analyses by Kehler et al. (2002) indicated that the magnitude and direction of the bias in Ricker models depend on the range of spawning stock sizes as well as the magnitude of the measurement error. For example, analyzing a data set of an unexploited fish population (where the spawning stock sizes are near equilibrium) will lead to greater bias in parameter estimation than analyzing one of an exploited fish population that includes low spawning stock sizes (Kehler et al. 2002). Although we do not know the magnitude of our measurement error, we can be somewhat reassured that our model included low spawning stock sizes.

Our study is one of a few recruitment studies that have estimated spawning stock size as well as larval abundance. Sampling multiple life history stages allows for determination and confirmation of when year-class strength is set and, in turn, allows for hypothesis generation of the important mechanisms. For largemouth bass *Micropterus salmoides*, the number of spawning adults, nests, newly hatched larvae, juveniles, and recruits were sampled for 12 years in Paul Lake, Michigan (Post et al. 1998). Larval density was correlated with the number of spawning adults (Post et al. 1998), a result similar to our study. Different from our study, however, the number of recruits was unrelated to larval density (Post et al. 1998); rather, spawning date and growth rate influ-

enced the probability of predation and overwinter mortality, and these processes interacted to regulate first-year survival (Post et al. 1998). Another study sampled several life history stages of brown trout *Salmo trutta* and found egg density to be a strong predictor of the number of survivors in five subsequent life history stages (Elliott 1985). Hence, this study was similar to ours in that a measure of spawning stock predicted the abundance of multiple life history stages.

Our data did not provide much distinction between the Beverton–Holt and Ricker stock–recruit models. From a biological perspective, we had insufficient information regarding juvenile survival to determine a priori which model would be appropriate. Only two other studies have described stock–recruit relationships for crappies. Allen and Miranda (1998) used the Ricker model with rotenone-derived density estimates of adults (age 1 and older) and recruits (age 0) from two Arkansas and two Mississippi reservoirs. The models explained 9–44% of the variation in recruitment across reservoirs; they did not mention attempts to fit a Beverton–Holt model (Allen and Miranda 1998). Bunnell et al. (2005) also estimated Ricker and Beverton–Holt models for white crappies in a paper that focused on the role of maternal effects. Although their study included a subset of the reservoirs that were in this study ($N = 7$), those stock–recruit models explained less than 5% of the variation in recruitment, probably owing to (1) a much smaller sample size and (2) use of an index of population fecundity rather than spawning stock CPE. Curiously, however, population fecundity should better estimate spawning stock size than stock abundance (Hilborn and Walters 1992). In this paper, we did not estimate crappie population fecundity because black crappie fecundity was unavailable. Given that we could not distinguish one stock–recruit model over the other and that processes that govern juvenile survival probably differ across systems and regions, we recommend that future crappie studies continue to consider both stock–recruit models.

Crappie recruitment studies commonly have focused on hydrological factors rather than stock–recruit analyses. In Iowa and Kansas reservoirs, high water levels during late spring through summer (i.e., while crappies are spawning inshore and larvae move offshore) have been positively correlated with recruitment success (Mitzner 1981; Beam 1983). Higher water levels may increase access to spawning habitat and afford greater protection for embryos on the nest (Beam 1983). More recently, hydrological factors (both pre- and postspawning) have been linked to recruitment in southeastern reservoirs. Strong year-classes are associated with years with short retention time or high

discharge before spawning (Maceina and Stimpert 1998; Sammons and Bettoli 2000; Sammons et al. 2002; Maceina 2003) or years with long retention time after spawning (Maceina and Stimpert 1998; Maceina 2003). Speculation regarding the mechanism centers on the possibility that increased precipitation (and resultant short retention time) during winter may increase primary production and food for first-feeding crappies (Maceina 2003). In addition, high precipitation and short retention times after spawning may reduce recruitment by increasing turbidity and reducing feeding efficiency for age-0 crappies (Maceina 2003). None of these hypotheses has empirical support, however.

The inclusion of seasonal water elevation data was not helpful in explaining recruitment variation in Ohio reservoirs. Because we did not have retention data for Acton Lake and Pymatuning reservoirs, we did not evaluate this variable within our formal analyses. However, post hoc analyses that included seasonal retention variables (and, subsequently, reduced our sample size) revealed that retention was as ineffective as seasonal water elevation in explaining recruitment variation. Despite the overall inability of reservoir hydrology to explain recruitment variation in our analyses, we note that multiple years of data on a particular reservoir or on a suite of reservoirs in the same basin (Maceina 2003) would be a better test of the impact of hydrology than we were able to offer. Comparing the hydrology of Alabama and Ohio reservoirs reveals differences that may limit the potential impact of hydrology on crappie recruitment in Ohio. The annual regulated change in water elevation is largely similar between the systems (Alabama range: 0.3–4.6 m; Maceina and Stimpert 1998; Maceina 2003; Ohio range: 0.0–2.9 m), but retention times are at least an order of magnitude longer in most of our Ohio study reservoirs (Alabama range: 2–55 d; Maceina and Stimpert 1998; Maceina 2003; Ohio range: 62–3,056 d). Hence, a more lotic-like environment in Alabama reservoirs may cause hydrology to more greatly influence crappie recruitment success than in the more lacustrine-like environment in Ohio reservoirs.

Reservoir chlorophyll concentrations were positively associated with larval density and crappie recruitment to age 2. Higher reservoir productivity typically positively influences crappie recruitment. Across 60 lakes in Florida, age-0 black crappie density increased with chlorophyll (Allen et al. 1998). Likewise, across 42 Minnesota lakes, first-year black crappie growth increased with chlorophyll as long as concentrations were less than 100 $\mu\text{g/L}$; at higher chlorophyll concentrations, first-year growth declined (McInerney

and Cross 1999). Finally, in three Alabama reservoirs, densities of postlarval juveniles were highest in the most productive ones, despite larval densities being highest in the least productive one (Dubuc and DeVries 2002). The most plausible explanation for higher chlorophyll concentrations enhancing crappie recruitment is through increased zooplankton biomass (Pace 1986), which should enhance crappie growth and reduce the probability of starvation. Age-0 crappies prefer calanoid and cyclopoid copepods and *Diaphanosoma* spp. (DeVries et al. 1998; D. B. Bunnell, unpublished data). The biomass of these preferred zooplankton taxa does not always increase with chlorophyll concentrations (Bremigan and Stein 2001; Bunnell et al. 2003; Pinto-Coelho et al. 2005). In fact, rotifers can dominate the zooplankton biomass of the most productive Ohio reservoirs, such as Acton Lake (Bunnell et al. 2003). Hence, if chlorophyll truly enhances crappie recruitment in Ohio reservoirs, it is probably through higher concentrations of smaller, nonpreferred zooplankton taxa, such as copepod nauplii and rotifers.

Management Implications

Because of the clear contributions of spawning stock size to crappie recruitment, Ohio managers can predict recruitment through autumn trap-netting and potentially strengthen annual recruitment through regulations. In systems where low spawning stock sizes limit production of larvae and age-2 fish, managers could improve recruitment by implementing catch restrictions to increase spawning stock sizes (Noble and Jones 1993). Options for catch restrictions include (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 season during April–May (i.e., preventing angling during the spawning season to ensure more adults will spawn). A closed season would probably be unacceptable to anglers because crappie catches are traditionally greatest during spring. To our knowledge, catch restrictions (i.e., creel or length limits) to increase spawning stock size have not been used to increase crappie recruitment; rather, length (Colvin 1991; Webb and Ott 1991; Hale et al. 1999) and creel limits (Colvin 1991; Webb and Ott 1991) are typically used to increase the average size of fish harvested or buffer the effects of weak year-classes.

With these recommendations come caveats. First, this scenario implies a positive feedback, where increasing spawning stock will continue to increase recruitment. As our results revealed, at higher levels of spawning stock size, age-2 CPE will stabilize (Beverton–Holt model), owing to density-dependent factors

influencing either adults (e.g., maternal effects on ovaries) or age-0 fishes (e.g., starvation, predation, cannibalism). Second, we assume that catch restrictions will increase the number of spawning adults by reducing total mortality. This scenario works only if fishing mortality (F) comprises a large portion of total mortality (Z ; equal to the sum of F and natural mortality M). With an estimate of exploitation rate (from tagging studies) and total annual mortality rate, the proportion of total deaths caused by fishing (i.e., F/Z , the exploitation ratio) can be calculated. We do not have estimates of exploitation ratios for these Ohio study reservoirs during our study period. In southeastern reservoirs, however, exploitation ratios have been estimated at more than 50% (Weiss Reservoir, Alabama; Reed and Davies 1991) and 43–83% (three Georgia reservoirs; Larson et al. 1991). Our concern is that if exploitation ratios are low, then implementing harvest restrictions would have a limited impact on the building of spawning stocks and subsequent increases in recruitment. As a result, before considering catch restrictions, managers in Ohio and elsewhere should quantify the exploitation ratio to ensure that reducing fishing mortality would sufficiently reduce total mortality to allow for spawning stock enhancement.

Acknowledgments

J. Fricke, J. Pyzoha, S. Thomas, J. Denlinger, D. Glover, R. Ginsberg, D. Gloeckner, M. Haugen, A. Iarussi, C. Hutt, E. Kohagen, B. Lutmerding, H. McLean, S. Miehl, A. Peer, J. Ritchie, M. Schmidt, A. Spencer, M. Thomas, M. Tomasi, J. Williams, and Ohio Department of Natural Resources, Division of Wildlife, provided assistance with fieldwork and laboratory processing. We thank Bill Renwick for providing water elevation data from Acton Lake. We thank Chuck Madenjian and three anonymous reviewers for helpful comments on the manuscript. This research was funded by Federal Aid in Sport Fish Restoration Project F-69-P, administered jointly by the U.S. Fish and Wildlife Service and Ohio Department of Natural Resources, Division of Wildlife, and the Department of Evolution, Ecology, and Organismal Biology at Ohio State University.

References

- Allen, M. S., M. V. Hoyer, and D. E. Canfield. 1998. Factors related to black crappie occurrence, density, and growth in Florida lakes. *North American Journal of Fisheries Management* 18:864–871.
- Allen, M. S., and L. E. Miranda. 1998. An age-structured model for erratic crappie fisheries. *Ecological Modelling* 107:289–303.
- Allen, M. S., and L. E. Miranda. 2001. Quasicycles in crappie populations are forced by interactions among population

- characteristics and environment. *Canadian Journal of Fisheries and Aquatic Sciences* 58:594–601.
- Arend, K. K. 2002. Do vertical gradients affect larval fish depth distribution and prey electivity among reservoirs that vary in productivity? Master's thesis. Ohio State University, Columbus.
- Beam, J. H. 1983. The effect of annual water level management on population trends of white crappie in Elk City Reservoir, Kansas. *North American Journal of Fisheries Management* 3:34–40.
- Beard, T. D., M. J. Hansen, and S. R. Carpenter. 2003. Development of a regional stock–recruitment model for understanding factors affecting walleye recruitment in northern Wisconsin Lakes. *Transactions of the American Fisheries Society* 132:382–391.
- Bremigan, M. T., and R. A. Stein. 2001. Variable gizzard shad recruitment with reservoir productivity: causes and implications for classifying systems. *Ecological Applications* 11:1425–1437.
- Bunnell, D. B., M. J. Gonzalez, and R. A. Stein. 2003. Zooplankton biomass enhances growth, but not survival, of first-feeding *Pomoxis* spp. larvae. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1314–1323.
- Bunnell, D. B., M. A. Scantland, and R. A. Stein. 2005. Testing for evidence of maternal effects among individuals and populations of white crappie. *Transactions of the American Fisheries Society* 134:607–619.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference*. Springer-Verlag, New York.
- Colvin, M. A. 1991. Evaluation of minimum-size limits and reduced daily limits on the crappie populations and fisheries in five large Missouri reservoirs. *North American Journal of Fisheries Management* 11:585–597.
- Colvin, M. A., and F. W. Vasey. 1986. A method of qualitatively assessing white crappie populations in Missouri reservoirs. Pages 79–85 in G. E. Hall and M. J. Van Den Avyle, editors. *Reservoir fisheries management: strategies for the 80s*. American Fisheries Society, Southern Division, Reservoir Committee, Bethesda, Maryland.
- Cushing, D. H. 1968. *Fisheries biology: a study in population dynamics*. University of Wisconsin Press, Madison.
- DeVries, D. R., M. T. Bremigan, and R. A. Stein. 1998. Prey selection by larval fishes as influenced by available zooplankton and gape limitation. *Transactions of the American Fisheries Society* 127:1040–1050.
- DeVries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483–512 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Dubuc, R. A., and D. R. DeVries. 2002. An exploration of factors influencing crappie early life history in three Alabama impoundments. *Transactions of the American Fisheries Society* 131:476–491.
- Elliott, J. M. 1985. Population regulation for different life stages of migratory trout *Salmo trutta* in a lake district stream, 1966–83. *Journal of Animal Ecology* 54:617–638.
- Ellison, D. G. 1984. Trophic dynamics of a Nebraska black crappie and white crappie population. *North American Journal of Fisheries Management* 4:355–364.
- Forney, J. L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966–1973. *Journal of the Fisheries Research Board of Canada* 33:783–792.
- Garvey, J. E., N. A. Dingledine, N. S. Donovan, and R. A. Stein. 1998. Exploring spatial and temporal variation within reservoir food webs: predictions for fish assemblages. *Ecological Applications* 8:104–120.
- Hale, R. S., M. E. Lundquist, R. L. Miller, and R. W. Petering. 1999. Evaluation of a 254-mm minimum length limit on crappies in Delaware Reservoir, Ohio. *North American Journal of Fisheries Management* 19:804–814.
- Hilborn, R., and C. J. Walters. 1992. *Quantitative fisheries stock assessment: choice, dynamics, and uncertainty*. Chapman and Hall, New York.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. *Rapports et Procès-verbaux des Réunions, Conseil Permanent International pour l'Exploration de la Mer* 20:1–228.
- Hooe, M. L. 1991. Crappie biology and management. *North American Journal of Fisheries Management* 11:483.
- Kehler, D. G., R. A. Myers, and C. A. Field. 2002. Measurement error and bias in the maximum reproductive rate for the Ricker model. *Canadian Journal of Fisheries and Aquatic Sciences* 59:854–864.
- Knoll, L. B., M. J. Vanni, and W. H. Renwick. 2003. Phytoplankton primary production and photosynthetic parameters in reservoirs along a gradient of watershed land use. *Limnology and Oceanography* 48:608–617.
- Larson, S. C., B. Saul, and S. Schleiger. 1991. Exploitation and survival of black crappies in three Georgia reservoirs. *North American Journal of Fisheries Management* 11:604–613.
- Leggett, W. C., K. T. Frank, and J. E. Carscadden. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences* 41:1193–1201.
- Maceina, M. J. 2003. Verification of the influence of hydrologic factors on crappie recruitment in Alabama reservoirs. *North American Journal of Fisheries Management* 23:470–480.
- Maceina, M. J., and M. R. Stimpert. 1998. Relations between reservoir hydrology and crappie recruitment in Alabama. *North American Journal of Fisheries Management* 18:104–113.
- McDonough, T. A., and J. P. Buchanan. 1991. Factors affecting abundance of white crappies in Chickamauga Reservoir, Tennessee, 1970–1989. *North American Journal of Fisheries Management* 11:513–524.
- McInerney, M. C., and T. K. Cross. 1999. Effects of lake productivity, climate warming, and intraspecific density on growth and growth patterns of black crappie in southern Minnesota lakes. *Journal of Freshwater Ecology* 14:255–264.
- McInerney, M. C., and J. W. Held. 1995. First-year growth of seven co-occurring fish species of Navigation Pool 9 of the Mississippi River. *Journal of Freshwater Ecology* 10:33–41.
- Mills, E. L., J. L. Forney, and K. J. Wagner. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. Pages 118–131 in W. C. Kerfoot and A. Sih, editors. *Predation: direct and indirect impacts on aquatic*

- communities. University Press of New England, Hanover, New Hampshire.
- Mion, J. B., R. A. Stein, and E. A. Marschall. 1998. River discharge drives differential survival of larval walleye. *Ecological Applications* 8:88–103.
- Mitzner, L. 1981. Influence of floodwater storage on abundance of juvenile crappie and subsequent harvest at Lake Rathbun, Iowa. *North American Journal of Fisheries Management* 1:46–50.
- Myers, R. A., G. Mertz, and J. Bridson. 1997. Spatial scales of interannual recruitment variations in marine, anadromous, and freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1400–1407.
- Noble, R. L., and T. W. Jones. 1993. Managing fisheries with regulations. Pages 383–402 in C. C. Kohler and W. A. Hubert, editors. *Inland fisheries management in North America*. American Fisheries Society, Bethesda, Maryland.
- Pace, M. L. 1986. An empirical analysis of zooplankton community size structure across lake trophic gradients. *Limnology and Oceanography* 31:45–55.
- Pinto-Coelho, R., B. Pinel-Alloul, G. Methot, and K. E. Havens. 2005. Crustacean zooplankton in lakes and reservoirs of temperate and tropical regions: variation with trophic status. *Canadian Journal of Fisheries and Aquatic Sciences* 62:348–361.
- Post, D. M., J. F. Kitchell, and J. R. Hodgson. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2588–2600.
- Quinn, T.J., and R.B. Deriso. 1999. *Quantitative fish dynamics*. Oxford University Press, New York.
- Reed, J. R., and W. D. Davies. 1991. Population dynamics of black crappies and white crappies in Weiss Reservoir, Alabama: implications for the implementation of harvest restrictions. *North American Journal of Fisheries Management* 11:598–603.
- Sammons, S. M., and P. W. Bettoli. 1998. Larval sampling as a fisheries management tool: early detection of year-class strength. *North American Journal of Fisheries Management* 18:137–143.
- Sammons, S. M., and P. W. Bettoli. 2000. Population dynamics of a reservoir sport fish community in response to hydrology. *North American Journal of Fisheries Management* 20:791–800.
- Sammons, S. M., P. W. Bettoli, D. A. Isermann, and T. N. Churchill. 2002. Recruitment variation of crappies in response to hydrology in Tennessee reservoirs. *North American Journal of Fisheries Management* 22:1393–1398.
- SAS Institute. 1999. *SAS/STAT user's guide*, version 8. SAS Institute, Inc., Cary, North Carolina.
- Siefert, R. E. 1968. Reproductive behavior, incubation, and mortality of eggs and post-larval food selection in the white crappie. *Transactions of the American Fisheries Society* 97:252–259.
- Siefert, R. E. 1969. Characteristics for separation of white and black crappie larvae. *Transactions of the American Fisheries Society* 98:326–328.
- Sissenwine, M. P. 1984. Why do fish populations vary? Pages 59–94 in R. M. May editor. *Exploitation of marine communities*. Springer-Verlag, Berlin.
- Walters, C. J. 1985. Bias in the estimation of functional relationships from time series data. *Canadian Journal of Fisheries and Aquatic Sciences* 42:147–149.
- Walters, C. J., and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock–recruitment relationships. *Canadian Journal of Fisheries and Aquatic Sciences* 38:704–710.
- Webb, M. A., and R. A. Ott. 1991. Effects of length and bag limits on population structure and harvest of white crappies in three Texas reservoirs. *North American Journal of Fisheries Management* 11:614–622.
- Wetzel, R. G. 1983. *Limnology*, 2nd edition. Saunders College Publishing, Fort Worth, Texas.