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Factors Related to Crappie Indices of Abundance in a Large, Fluctuating Canyon Reservoir in Idaho

Abstract

Crappie (*Pomoxis* spp.) populations are challenging to manage due to highly variable year-class strength; however, such variability has rarely been investigated in western North America, where crappie often occupy large, steep-sided reservoirs prone to severe drawdown. We investigated the influence that various factors had on crappie abundance, as indexed by long-term trawling for larval fish and long-term electrofishing for older fish. Our primary findings were that: 1) autumn age-0 crappie abundance was higher in years when larval abundance and reservoir flow were higher in the summer; 2) spring age-1 crappie abundance was higher in years when fish were larger and more abundant entering their first winter, when hydraulic residence time was reduced and the reservoir volume was higher during the winter, and when predatory-sized smallmouth bass (*Micropterus dolomieu*) were more abundant in the spring (though the latter relationship was likely not causative but rather a parallel response to mutually advantageous environmental conditions in the reservoir); and 3) age-0 crappie entering their first winter were larger in years with lower summer larval crappie abundance and warmer summer water temperature. We recommend autumn electrofishing to monitor crappie populations in large canyon reservoirs, where shorelines are often too steep to sample fish with trap nets, because it provides an index of age-0 crappie abundance and size at the onset of their first winter as well as data on older crappie year classes and sympatric species; it also requires less sampling effort than summer trawling.

Keywords: crappie, year-class strength, larval fish, large reservoirs

Introduction

Black crappie (*Pomoxis nigromaculatus*) and white crappie (*P. annularis*) fisheries can be challenging to manage because crappie populations can exhibit both cyclic and erratic fluctuations in recruitment (Allen 1997, Boxrucker and Irwin 2002, Maceina 2003, Martin and Maceina 2004). If crappie year-class strength is determined by the abundance and success of spawning adults, egg survival, and early larval survival, then summer larval sampling would offer a reliable method of detecting strong and weak year classes of crappie and perhaps allow managers some predictive ability in terms of the expected quality of a fishery in upcoming years.

For example, Sammons and Bettoli (1998) found that peak larval crappie density from Neuston net trawling was highly correlated with the number of age-1 crappie captured in coves with rotenone the following year. However, if mortality is substantial and highly variable for age-0 crappie during the first winter (e.g., McCollum et al. 2003) or for age-1 crappie (McInerny and Degan 1991), then year-class strength indices based on summer larval sampling may be unreliable as a predictor of the resulting fisheries they create.

Crappie recruitment has often been characterized as being cyclic, with strong year classes recurring every 2 to 5 years (Swingle and Swingle 1967, Guy and Willis 1995, Allen and Miranda 2001). Recurring fluctuations suggest that recruitment is being controlled by density-dependent factors such as fish growth, competition, or predation. Others

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have observed fluctuations in crappie year-class strength to be more erratic, and in such instances, the variation has been more commonly attributed to environmental conditions such as water temperature, water quality, lake/reservoir bathymetry, and hydrology (Mitzner 1991, Maceina 2003, Pope et al. 2004). Allen and Miranda (2001) argue that crappie populations do not exhibit true cycles in abundance, but may show quasi-cycles depending on the interaction between density-dependent and density-independent mechanisms. As pointed out by Clark et al. (2008), the complex mix of factors that can affect centrarchid recruitment tend to make conclusions derived from field studies highly site specific.

While recruitment variability and other characteristics of crappie populations have been investigated frequently in central and eastern North America, comparatively little research has been conducted on crappie populations in western North America, where they have been introduced. In the Intermountain West, canyon reservoirs are often larger, steeper, and deeper than waters that crappie typically occupy in other portions of the continent. For example, at full pool, Brownlee Reservoir in southwestern Idaho is nearly 100 km long, with an average depth of 32 m and a maximum depth of nearly 100 m, and it supports a popular multi-species fishery where anglers frequently target crappie, among other taxa. The reservoir has been monitored for larval crappie year-class strength and general fish abundance for decades, providing a unique opportunity to evaluate density-dependent and density-independent factors affecting crappie abundance in a large, steep-sided canyon reservoir. Our objectives were to: 1) determine whether summer larval trawling or autumn age-0 electrofishing was a better indicator of subsequent year-class strength of crappie; 2) determine what environmental factors contributed to strong and weak year classes of young crappie; and 3) evaluate whether strong year classes of young crappie persisted into later age classes of crappie.

Methods

Study Area

Brownlee Reservoir is the uppermost reservoir of three impoundments known as the Hells Canyon Complex. Brownlee Dam was completed in 1958 and impounds 92 km of the Snake River along the Idaho-Oregon state border; the dam is located at river kilometer 460. The reservoir is confined within a deep, narrow canyon, thus the reservoir is narrow (300 to 900 m wide) and steep-sided, with shorelines typically consisting of bedrock or mixtures of boulders, sand, and gravel substrate. Reservoir volume peaks at about 1.74×10^9 m³ of water, and it has a surface area of 6,100 ha. The elevation of the reservoir is 633 m above sea level at full pool. Large spring and autumn reservoir drawdowns are common and can reach 30 m. Reservoir refill periods are typically May to June following flood control operations, and October to November following summer flow augmentation for anadromous smolt outmigration and fall flow stability for Chinook salmon (*Oncorhynchus tshawytscha*) spawning in the Snake River below the Hells Canyon Complex. Operational guidelines for Brownlee Dam are also designed to minimize reservoir drafting during peak crappie and smallmouth bass (*Micropterus dolomieu*) spawning periods (see below).

The fish community in Brownlee Reservoir is dominated by nonnative warmwater sport fishes, including smallmouth bass, black crappie and white crappie, bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*), and channel catfish (*Ictalurus punctatus*) (Richter 2003, Richter et al. 2010). Black crappie are slightly more abundant than white crappie in the reservoir. Both reach a harvestable size of 200 mm (Miranda and Frese 1991) in Brownlee Reservoir at about age 2 (Lamansky 2011), and angler exploitation of harvestable-sized crappie in the reservoir typically ranges from 20 to 30% (Meyer and Schill 2014). Crappie in Brownlee Reservoir reach maximum ages of about 7, and feed almost exclusively on insects and zooplankton (Lamansky 2011). Although water temperature profiles within the reservoir were generally lacking for most of the

study, water temperature for the Snake River where it meets Brownlee Reservoir is regularly monitored (see below) and generally exceeds 25 °C in summer months, and often approaches 30 °C.

Larval Crappie Sampling

Larval crappie were sampled from 1993 to 1998 and again from 2005 to 2015. Early in the study, samples were collected approximately weekly from early to mid-May through mid-August. However, after several years of sampling it became apparent that, regardless of annual variation in environmental conditions, appreciable numbers of larval fish were only reliably captured from about 10 Jun to 31 Jul of each year. Thus all larval crappie data were summarized only between these two dates each year.

From 1993 to 1998, larval fish were collected by Idaho Power Company staff. Nine sampling sites were established somewhat systematically (i.e., about every 7 km moving upstream from the dam), and they remained fixed throughout the sampling period. At each location, one or two circular (0.5-m diameter) ichthyoplankton nets with 0.75-mm bar mesh were attached to the sides of the boat (opposite sides when two nets were towed). Tows were made at five depths (0 to 4 m) for one minute at each depth for a total of five minutes at a speed of about 1.3 m s⁻¹. Nets were towed approximately 12 m behind the boat. All tows at a particular location were combined for a single sample. The volume of water sampled was estimated using a flow meter attached within the net opening, and averaged 166 m³ for each location sampled each night. All larval samples were immediately chilled.

From 2005 to 2015, larval samples were collected by Idaho Department of Fish and Game staff. Eleven sampling sites were established somewhat systematically (i.e., about every 6 km moving upstream from the dam), and they remained fixed throughout the sampling period. At each location, a rectangular, 1-m by 2-m, Neuston net with 1-mm bar mesh was towed at the surface for five minutes at a boat speed of about 2.6 m s⁻¹. The volume of water sampled at each location was determined from a flow meter mounted

within the net opening; mean tow volume was 362 m³. In contrast to the smaller circular nets, which were attached off the sides of the boat, the Neuston net was attached by rope to a boom in the center of the boat, so tows were made by driving the boat in a circular fashion to keep the net out of the wake and in undisturbed water. The net was towed approximately 20 m behind the boat. Samples from each location were immediately preserved in a 10% formalin solution and later transferred to ethanol.

For both time periods, samples were collected at night from about 2200 to 0200 hr. Larval fish were identified in the laboratory using meristic features described by Auer (1982). While larval fish of multiple species were collected, only crappie were enumerated and measured for total length (TL) to the nearest mm. Larval crappie were not identified to species because the differences in meristic characteristics at that size are unreliable (Sammons and Bettoli 1998). An index of larval crappie abundance (i.e., catch per unit effort, or CPUE) was calculated by dividing the number of larval crappie captured in a net tow by the volume of water sampled (i.e., fish m⁻³) and averaging those values for each date. Mean and peak larval abundance was calculated for each year from the means for each sample date within a year, but annual mean and peak abundance was highly correlated (Pearson's correlation coefficient, $r = 0.91$), so peak abundance was removed from further consideration.

Electrofishing Surveys

While trap nets are considered the gear of choice for sampling crappie in large lentic systems (Miranda and Boxrucker 2009), at Brownlee Reservoir trap nets are largely ineffective because the shorelines are generally too steep. Therefore, the abundance of juvenile and adult crappie was indexed by spring and autumn nighttime boat electrofishing from 1993 to 2018. The boat electrofisher consisted of a Smith-Root GPP Model 5.0 (Smith-Root Inc., Vancouver, WA) powered by an on-board 5000 W generator, with two anode booms and with the boat serving as the cathode. The GPP electrofisher settings were held relatively constant throughout

the study, at 60 Hz, 40 to 60 % of power, and using the low range selector setting. These settings consistently produced 4 to 6 amps of average power output (depending on shoreline depth). Spring sampling across all years occurred from early April to late May but primarily from mid-April to early May, whereas autumn sampling occurred from early September to mid-October but primarily from mid- to late September.

For each sampling night, randomly selected 100-m shoreline electrofishing reaches (an average of 24 per year) were delineated before dark with reflective posts that were clearly visible after dark by the boat electrofishing lights. Electrofishing occurred from about 2200 to 0200 hr each night. One electrofishing netter was used while another person operated the boat and electrofishing equipment. All stunned fish (not just crappie) were netted and placed in a live well until the reach was completely sampled. Fish were released at the site once species, total length (mm), and weight (g) were recorded for each captured fish. Black crappie and white crappie captured during electrofishing were pooled for data analyses because crappie captured during larval trawling were pooled (since they could not be accurately distinguished to species), and anglers do not distinguish between the two species.

The average number of crappie caught electrofishing for each 100-m reach of shoreline was calculated for each year and sampling period for particular age classes. Age classes were determined from a combination of length-frequency analyses, prior growth analyses at Brownlee Reservoir, and the literature. For example, length-frequency analyses indicated that during autumn electrofishing, age-0 crappie consistently reached a maximum size of about 120 mm (Figure 1). Length-frequency analyses also revealed that age-1 crappie captured the following spring had grown slightly, with a more appropriate size cutoff consistently being about 140 mm (Figure 1). The latter cutoff was also consistent with an earlier study by Lamansky (2011), who produced back-calculated length-at-age for age-1 and age-2 Brownlee Reservoir crappie for the years 1995 to 2008, and found that

fish ≤ 145 mm TL in the spring (i.e., at annulus formation) were age 1.

Across all years, the average maximum length of crappie captured annually was 299 mm TL (mean sample size of 430 fish for each year). It has been well established that size at first maturity in fishes is typically about 0.6 times the maximum size in a population (see Pauly 1984, Charnov 1993, Froese and Binohlan 2000). Consequently, ≥ 179 mm was used as the size cutoff for crappie spawners in our study; such a cutoff is consistent with published accounts of crappie length and age at maturity (e.g., Thomas and Kilambi 1981, Scott and Crossman 1998, Michaletz 2013).

Environmental Conditions

Based on previous studies, we expected that the reservoir environmental conditions most likely to affect crappie abundance at different age classes and different time periods of the year would be reservoir storage and flow conditions, as well as water temperature (Mitzner 1991, McDonough and Buchanan 1991, Sammons and Bettoli 1998, Maceina 2003, Pope et al. 2004). Reservoir elevation was recorded daily by Idaho Power Company, from which we calculated daily reservoir volume (m^3 ; Table 1). Change in reservoir volume was calculated as the highest volume minus the lowest volume during a given time period. Mean daily inflow into Brownlee Reservoir ($\text{m}^3 \text{ s}^{-1}$) was obtained from the US Geological Survey (USGS) stream gage on the Snake River near Weiser, Idaho (USGS 2021). Mean daily outflow from the reservoir ($\text{m}^3 \text{ s}^{-1}$) was measured at Brownlee Dam by Idaho Power Company. Daily estimates of hydraulic residence time were calculated following the method of Quinn (1992) by setting inflow to zero and estimating the number of days needed to completely drain the reservoir based on estimates of daily volume and outflow.

Mean daily temperature ($^{\circ}\text{C}$) of water flowing into Brownlee Reservoir was recorded from June 1996 through the end of 2017 using a HOBO temperature logger (HOBO TidbiT v2 Water Temperature Data Logger UTBI-001, Onset Computer Corp. Bourne, MA) stationed at river kilometer 559. Due to gaps in data recording or

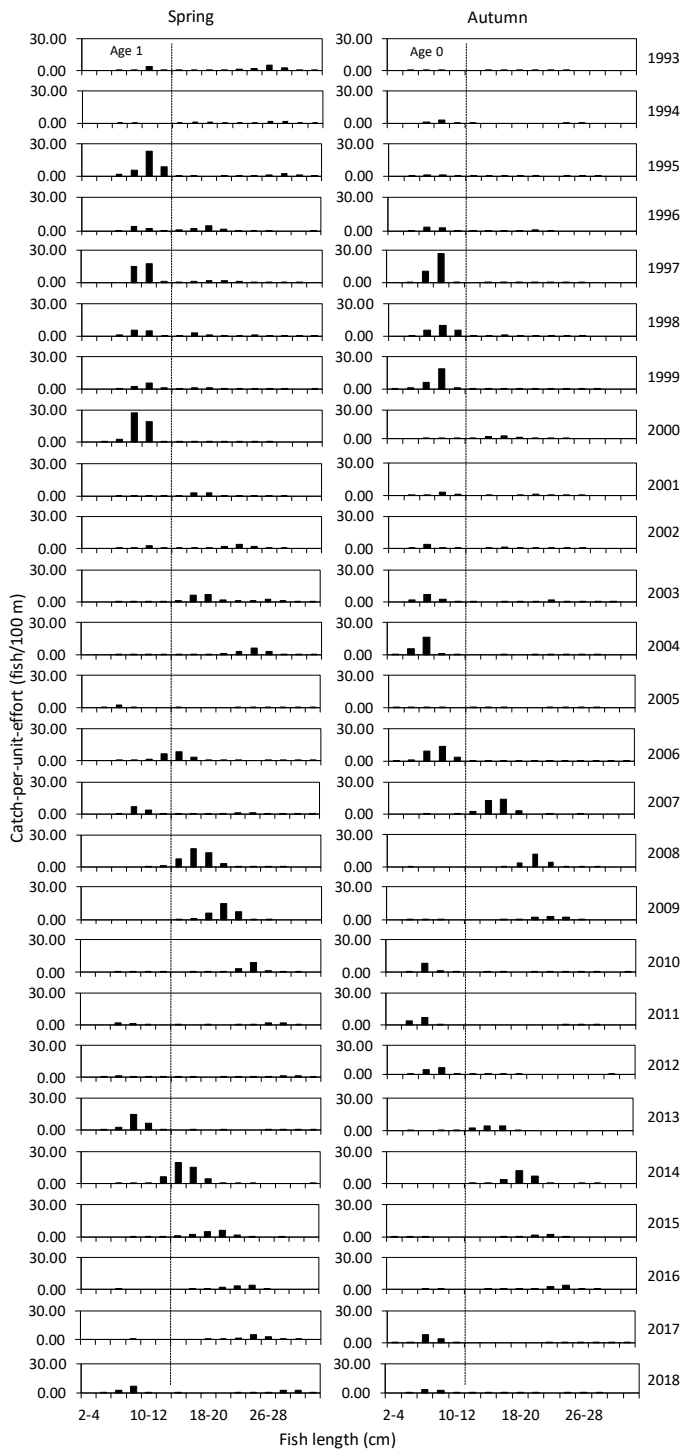


Figure 1. Length frequency of crappie captured with nighttime spring and autumn boat electrofishing from 1993 to 2018 in Brownlee Reservoir, Idaho.

equipment malfunction, no water temperature data were available for 1,874 of the 9,131 days from the beginning of 1993 to the end of 2017. Daily water inflow (obtained as described above) and nearby daily air temperature, obtained from the National Centers for Environmental Information (NOAA 2021) for the nearby station GHCND:USR0000ISNA were used to predict missing water temperature data using multiple linear regression; adjusted R^2 was 0.87 for this relationship.

Data Analyses

The same environmental conditions were summarized (i.e., averaged, except for the change in reservoir volume) for each time period (as described below), with metrics representing reservoir storage and flow conditions as well as water temperature. Reservoir flow metrics included mean daily inflow, outflow, and hydraulic residence time. Reservoir storage metrics included mean daily volume as well as the maximum change in volume for a particular time period. Water temperature was summarized as mean daily temperature for a particular time period.

We used general linear models to evaluate the influence of biotic and abiotic factors on crappie abundance. First, we investigated whether summer larval crappie abundance (as indexed by mean summer larval trawl CPUE) was affected by the abundance of spawning-sized crappie during the spawning season (as indexed by spring electrofishing CPUE), as well as reservoir flow, volume,

TABLE 1. Reservoir conditions during several time periods from 1993 to 2018 in Brownlee Reservoir, Idaho.

Parameter	Spawning period (01 May to 20 Jun)		Summer period (04 Jul to 15 Sep)		Winter period (10 Dec to 15 Apr)		Annual (01 Jan to 31 Dec)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Reservoir volume (billion m ³)	1.560	0.560–1.744	1.491	1.120–1.740	1.471	0.689–1.740	1.466	0.560–1.744
Change in reservoir volume (billion m ³)	0.401	0.019–1.131	0.371	0.266–0.620	0.471	0.128–1.053	0.635	0.343–1.178
Reservoir inflow (m ³ s ⁻¹)	689	193–2,200	291	167–844	494	220–2,322	452	167–2,322
Reservoir outflow (m ³ s ⁻¹)	712	178–2,645	371	153–968	585	238–2,778	505	153–2,778
Hydraulic residence time (days)	36	4–112	51	19–110	38	5–80	44	4–114
Water temperature (°C)	16.7	7.0–25.4	22.9	12.3–28.7	5.9	0–17.5	12.9	0–28.7

and water temperature conditions the spawning adults and resulting larvae experienced during the spawning period. Crappie spawn in the spring when water temperature is between 14 and 23 °C, and peak spawning generally occurs between 16 and 20 °C (Scott and Crossman 1998). This has been corroborated at Brownlee Reservoir, where over an 8-year period in the 1990s, crappie spawning on average lasted 48 days and ceased on 30 Jun (Richter 2003); water temperature during those spawning periods ranged from 12 to 22 °C, with peak spawning occurring at 18 to 20 °C. As mentioned above, Brownlee Reservoir generally starts refilling (after a spring flood control release period) on 01 May, and refill usually extends to about 20 Jun. Based on this combined information, we considered 01 May to 20 Jun to be the annual crappie spawning period. To evaluate whether the two different trawl nets influenced larval CPUE, trawl type (i.e., circular ichthyoplankton nets or rectangular neuston net) was included as a categorical predictor variable.

Next, we investigated whether electrofishing CPUE of age-0 crappie in autumn (i.e., crappie \leq 120 mm) was a function of summer larval trawl CPUE as well as the environmental conditions the larval fish experienced over the summer as they transitioned out of the larval stage. Brownlee Reservoir generally reaches full pool by 20 Jun and is held stable through 04 Jul, after which the reservoir begins a long period of summer drawdown that extends through September. However, since autumn electrofishing usually occurred in mid-September, we used 04 Jul to 15 Sep to represent the summer time period to avoid including environmental data collected after the electrofishing data were already collected. We also investigated (with a separate model) whether the mean size of age-0 crappie in autumn was a function of these same conditions; this model included age-0 crappie CPUE to evaluate a density-dependent effect on their growth.

Smallmouth bass was the most numerous species captured while electrofishing, and they are well known as piscivorous (MacRae and Jackson 2001, Weidel et al. 2007). To account for this potential predation impact on autumn age-0 crappie

CPUE, we included (as a predictor variable in the model) the autumn CPUE of smallmouth bass that were large enough to consume crappie up to the aforementioned age-0 cutoff of 120 mm; based on Fernando et al. (2018), this equated to a size of 291 mm and larger for potential smallmouth bass predators of age-0 crappie.

Finally, we examined whether electrofishing CPUE of age-1 crappie in the spring (i.e., ≤ 140 mm) was a function of the environmental conditions those fish experienced during winter as well as the abundance and size of age-0 fish entering their first winter. Again, rather than using strict winter calendar dates, we considered reservoir operation prior to and during winter. After the summer/autumn drawdown, the reservoir is refilled by 10 December, and then is drawn down again through the end of April for flood control. Considering that spring electrofishing generally occurred in mid-April, we used 10 December to 15 April to represent the winter time period. A potential predation effect was accounted for as described above, using the aforementioned spring age-1 crappie size cutoff of 140 mm; based on Fernando et al. (2018), this equated to a size of 344 mm and larger for potential smallmouth bass predators of spring age-1 crappie.

Prior to model construction, collinearity between the environmental predictor variables was assessed using correlation analysis. For each of the four time periods described above, flow into and out of Brownlee Reservoir were highly correlated ($r \geq 0.98$), and estimates of variance inflation factors for outflow exceeded 10 in all models, indicating excessive collinearity (Neter et al. 1985), thus outflow was discarded from further analyses. While other environmental variables were also somewhat correlated, variance inflation factors during model development were < 10 in all instances, and therefore no other variables were excluded from any models.

All parameter combinations were considered during general linear model construction, and models were ranked using Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002). Interaction terms were not considered due to the small sample size of

our overall dataset. We considered the most plausible models to be those with AIC_c scores within 2.0 of the best model (Burnham and Anderson 2004), and used AIC_c weights (w_i) to assess the relative plausibility of each of the most plausible models. Coefficient of determination (r^2) was also reported to describe the amount of variation in CPUE that was explained by the parameters in the most plausible models. Parameter estimates were reported only for the most plausible model, and only those parameter estimates with 95% confidence intervals (CIs) that did not overlap zero were interpreted as influential. All CPUE data were \log_{10} transformed prior to data analyses to better meet the assumptions of normality, linearity, and homogeneity of variance. Electrofishing catch was zero in two instances, so we added one fish to each summary of electrofishing catch prior to estimating electrofishing CPUE to remove zeros from the response variables. All analyses were conducted using the SAS statistical software package (SAS Institute 2009).

Results

Crappie Population Characteristics

On average, a total of over 5,000 larval crappie were captured each summer in night trawls conducted between 10 Jun and 31 Jul. Mean annual larval crappie CPUE in Brownlee Reservoir trawls was 0.38 fish m^{-3} ($SE = 0.11$) and varied over two orders of magnitude, from a low of 0.01 fish m^{-3} in 2007 to a high of 1.62 fish m^{-3} in 2010 (Figure 2). Among individual trawling days, the minimum and maximum CPUE for larval crappie ranged from 0.00 to 4.12 fish m^{-3} .

On average, 531 and 470 crappie were captured each year in spring and autumn night electrofishing, respectively. Crappie captured with electrofishing ranged in size from 41 to 375 mm in the spring and from 20 to 340 mm in the autumn (Figure 1). Crappie electrofishing CPUE for all sizes combined was highly variable through time, with a mean of $21.1 \text{ fish } 100 \text{ m}^{-1}$ of shoreline across all years ($SE = 2.2$). Mean total length of age-0 crappie in autumn electrofishing catch averaged 78.4 mm ($SE = 2.7$) across years, and ranged from a low of 52.8 mm in 2016 to a high of 108.9 mm

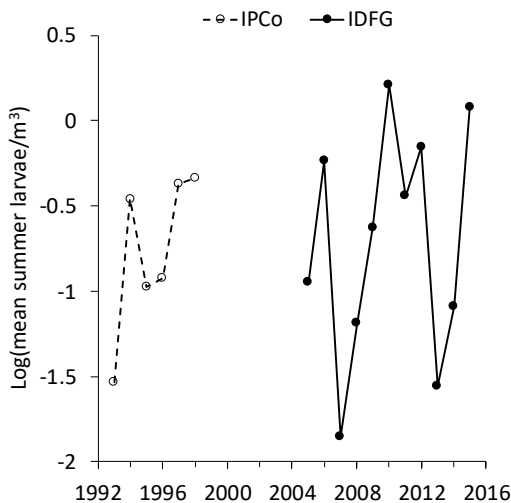


Figure 2. Crappie larval catch-per-unit effort (CPUE) (expressed in \log_{10}) from summer larval trawls through time at Brownlee Reservoir, Idaho, conducted by Idaho Power Company (IPCo) and Idaho Department of Fish and Game (IDFG) staff.

in 2014. In the autumn, catch of smallmouth bass large enough to prey on age-0 crappie (i.e., bass ≥ 291 mm) averaged 2.91 fish 100 m^{-1} (SE = 0.44), whereas in the spring, catch of smallmouth bass large enough to prey on age-1 crappie (i.e., bass ≥ 344 mm) averaged 1.32 fish 100 m^{-1} (SE = 0.20).

The \log_{10} CPUE of summer larval and autumn age-0 crappie age classes were positively related to the same age class in the subsequent sampling period (Figure 3). There was also a positive relationship between the length of age-0 crappie entering their first winter and the \log_{10} of age-1 CPUE the following spring.

Factors Affecting Crappie CPUE

None of the environmental conditions during the crappie spawning time period explained much of the variation in summer larval crappie CPUE, nor did the abundance of spawning-sized crappie (Tables 2 and 3). Seven of the 10 plausible models were single-factor models that individually included each of the biotic and abiotic predictor variables, but the best model (which included water temperature during the spawning period) only explained 11% of the variation in summer

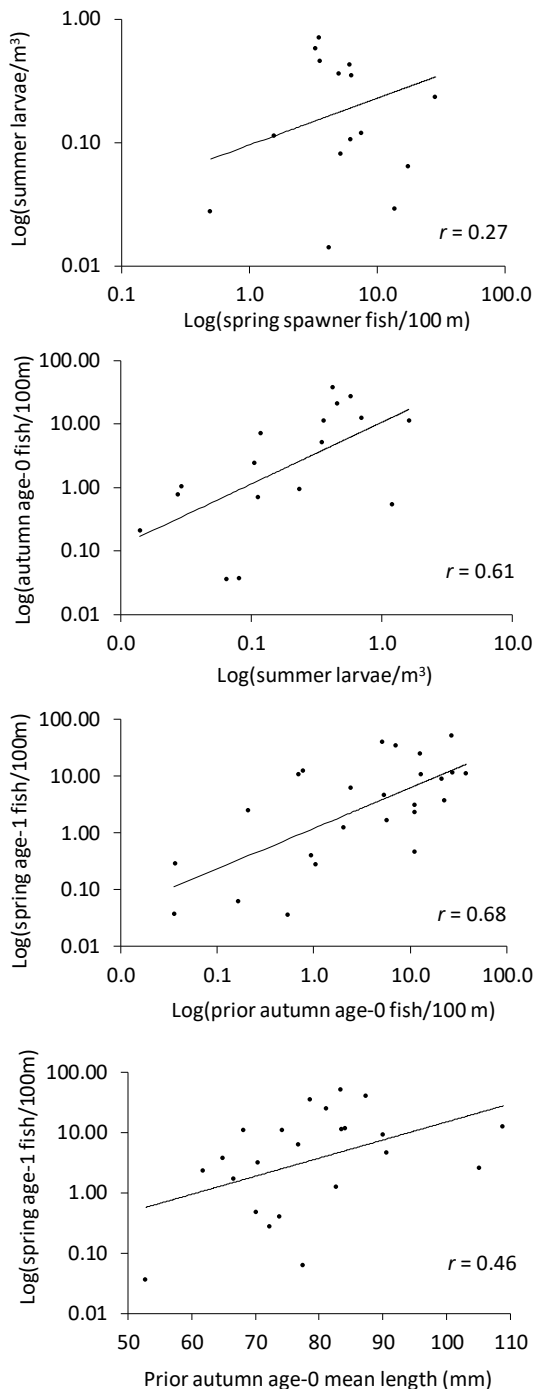


Figure 3. Relationships between crappie catch-per-unit effort (expressed in \log_{10}) in successive age classes from 1993 to 2018 in Brownlee Reservoir, Idaho, including Pearson correlation coefficients (r) and linear trendlines fitted to the data.

TABLE 2. Generalized linear model results used to relate biotic and abiotic factors to crappie catch-per-unit effort (CPUE) for various age classes in Brownlee Reservoir, Idaho. Only the most plausible models, with AIC_c scores within 2.0 of the top model, are shown. Akaike weights (w_i) demonstrate the relative plausibility of all the models, and the coefficient of determination (r^2) displays the amount of variation in CPUE that was explained by each model. For multi-parameter models, the parameters appear in order of their predictive ability (i.e., tighter confidence intervals around the parameter estimates). Top model for each age class section is highlighted.

Model	AIC_c	ΔAIC_c	w_i	r^2
Log(summer larval)				
Spawning temperature	2.49	0.00	0.09	0.11
Spawning volume	3.06	0.57	0.07	0.08
Spawning inflow	3.08	0.59	0.07	0.08
Spawning change in volume	3.43	0.94	0.06	0.06
Spawning residence time	3.69	1.20	0.05	0.05
Spring log(spawner CPUE)	3.77	1.28	0.05	0.07
Spawning temperature + Spring log(spawner CPUE)	4.36	1.87	0.04	0.03
Spawning volume + Spring log(spawner CPUE)	4.44	1.95	0.03	0.02
Trawl type	4.47	1.98	0.03	0.00
Spawning volume + Spawning temperature	4.48	1.99	0.03	0.02
Log(autumn age-0 CPUE)				
Log(summer larval CPUE) + summer inflow + Log(autumn bass predator CPUE)	-13.97	0.00	0.12	0.60
Log(summer larval CPUE) + summer inflow	-13.15	0.82	0.08	0.54
Log(summer larval CPUE) + Log(autumn bass predator CPUE)	-12.12	1.85	0.05	0.51
Autumn age-0 mean length				
Summer log(larval CPUE) + summer temperature	75.01	0.00	0.34	0.46
Log(spring age-1 CPUE)				
Prior autumn age-0 length + prior autumn log(age-0 CPUE) + winter hydraulic residence time + winter volume + Log(autumn bass predator CPUE)	-25.95	0.00	0.11	0.68
Prior autumn age-0 length + prior autumn log(age-0 CPUE) + winter inflow + Log(autumn bass predator CPUE)	-25.54	0.41	0.09	0.64
Prior autumn age-0 length + prior autumn log(age-0 CPUE) + winter inflow + Log(autumn bass predator CPUE) + winter volume	-25.13	0.82	0.08	0.66
Prior autumn age-0 length + prior autumn log(age-0 CPUE) + winter hydraulic residence time + winter volume	-24.55	1.40	0.06	0.62
Prior autumn age-0 length + prior autumn log(age-0 CPUE) + winter inflow	-24.25	1.70	0.05	0.58

larval crappie CPUE (Table 2); the parameter estimate overlapped zero (Table 3), indicating a non-influential association with summer larval crappie CPUE.

The best model (considered 50% more plausible than competing models, based on w_i) for predicting autumn age-0 crappie CPUE included summer larval crappie CPUE, mean daily summer inflow, and the CPUE of smallmouth bass large enough to prey on age-0 crappie (Table 2). Parameter estimates (and their CIs) indicated that age-0 crappie CPUE was higher in the autumn when larval catch and inflow were higher in the summer (Table 3); for predatory-sized smallmouth bass CPUE, the 95% CI around the

parameter estimate overlapped zero, indicating a non-influential association with autumn age-0 crappie CPUE. There was also support for models containing other combinations of these three predictor variables, but the parameter estimates differed little for the top model. Each of the most plausible models explained more than 50% of the variation in autumn age-0 crappie CPUE.

For spring age-1 crappie CPUE, the best model included terms for the size and abundance of age-0 crappie the previous autumn, as well as winter hydraulic residence time and reservoir volume, and the spring CPUE of predatory-sized smallmouth bass (Table 2). This model explained 68% of the variation in spring age-1 crappie CPUE, and none

TABLE 3. Coefficient estimates and 95% confidence limits (CLs) for the top general linear model (identified in Table 2) relating biotic and abiotic factors to crappie catch-per-unit effort (CPUE) or size in Brownlee Reservoir, Idaho.

Coefficient	Estimate	95% CLs	
		Lower	Upper
Log(summer larval CPUE)			
Intercept	1.330	-1.622	4.283
Spawning temperature	-0.124	-0.301	0.053
Log(autumn age-0 CPUE)			
Intercept	-0.788	-2.125	0.549
Log(summer larval CPUE)	0.594	0.067	1.120
Summer inflow	0.005	0.000	0.009
Log(autumn bass predator CPUE)	0.856	-0.072	1.784
Autumn age-0 mean length			
Intercept	-54.770	-152.107	42.568
Log(summer larval CPUE)	-15.149	-24.551	-5.748
Summer temperature	5.450	1.239	9.661
Log(spring age-1 CPUE)			
Intercept	-5.758	-9.701	-1.814
Prior autumn age-0 mean length	0.032	0.016	0.047
Log(prior fall age-0 CPUE)	0.422	0.088	0.756
Winter residence time	-0.038	-0.062	-0.014
Log(autumn bass predator CPUE)	0.449	0.003	0.895
Winter volume	3.42×10^{-9}	0.52×10^{-9}	6.32×10^{-9}

of the 95% CIs around the parameter estimates overlapped zero, indicating that they were all influentially associated with age-1 crappie CPUE (Table 3). These estimates indicated that spring age-1 crappie abundance was higher in years when they were larger and more abundant entering their first winter, when hydraulic residence time was reduced and the reservoir was fuller during winter, and when predatory-sized smallmouth bass were more abundant in the spring. There was similar model support (based on w_i) for several other competing models that explained similar amounts of variation in spring age-1 crappie CPUE (Table 2), which included various combinations of these same predictor variables, as well as winter inflow, which was positively associated with spring age-1 crappie CPUE (Table 2).

The most plausible model explaining the variation in mean length of age-0 crappie captured in autumn included terms for summer larval crappie CPUE and water temperature (Table 2). This model explained 46% of the variation in mean length

of age-0 crappie captured in the autumn, and parameter estimates indicated that age-0 crappie going into their first winter were larger in years with lower summer larval crappie CPUE and warmer summer water temperature (Table 3). Other competing models were at least 4 times less plausible (based on w_i).

Discussion

In a large, fluctuating, steep-sided reservoir, conditions common for water storage facilities built throughout the arid western US, we observed the same variability in larval and age-0 crappie abundance that has been observed elsewhere in North America (Mitzner 1991, McDonough and Buchanan 1991, Sammons and Bettoli

1998). Crappie recruitment fluctuations were apparent in CPUE data from both summer larval trawling and autumn age-0 electrofishing, and summer larval CPUE was a good indicator of autumn age-0 CPUE, as has been observed in earlier studies (McDonough and Buchanan 1991, Sammons and Bettoli 1998, St. John and Black 2004). However, while prior studies have found that various biotic and abiotic factors influence larval abundance, including spawner abundance, water storage levels, and reservoir flow (McDonough and Buchanan 1991, Mitzner 1991, Dockendorff and Allen 2005, Bunnell et al. 2006), we found no such relationships. A potential limitation in our study design was the use of two different larval trawl nets, although this also appeared to have little influence on summer larval crappie CPUE. In Brownlee Reservoir, it appears that other factors we did not measure, potentially including such conditions as water clarity, prevailing winds, and the abundance of other centrarchids (that could potentially compete for nesting sites and larval food, or prey upon larval

crappie), may have had more influence on larval crappie abundance (McDonough and Buchanan 1991, Mitzner 1991). Whether the lack of abiotic impacts on larval crappie abundance that we observed is common for such large, steep-sided reservoirs often found in western North America warrants further research. Nevertheless, there were reasonably strong relationships for CPUE between each subsequent crappie age class in Brownlee Reservoir, suggesting that once conditions permitted a strong year-class of larval crappie to materialize, that year-class generally persisted through time. The length-frequency plots through time (Figure 1) corroborate that conclusion for older age classes.

The highest CPUE of autumn age-0 crappie in Brownlee Reservoir occurred in years when larval abundance was higher, but also when summer inflow (or outflow) into the reservoir was higher; considering the high correlation between inflow and outflow, these two factors cannot be decoupled. Larval crappie are susceptible to entrainment through dams (Sorenson et al. 1998, Fryda et al. 2006) because their pelagic behavior extends from the time of hatching through much of their first summer (Post et al. 1995, Dockendorf and Allen 2005), thus it was surprising that increased reservoir flow in the summer was positively related to autumn age 0 crappie CPUE. However, because Brownlee Reservoir is almost 100 km in length, higher summer reservoir flow may have little impact on annual levels of crappie larval entrainment. With summer hydraulic residence time averaging 51 days over the course of the present study and rarely (4 of 25 years) dropping below 40 days, water retention time in Brownlee Reservoir is not particularly short compared to other reservoirs where crappie year-class strength investigations have been conducted (e.g., Maceina and Stimpert 1998, Sammons et al. 2002). Several studies have found higher larval crappie abundance in years with longer hydraulic residence time and higher water levels either before, during, or after spawning (e.g., McDonough and Buchanan 1991, Sammons and Bettoli 1998, Sammons et al. 2002, Maceina 2003), but these studies occurred in reservoirs with vastly different hydrologic and morphologic characteristics than Brownlee Reser-

voir. We speculate that higher summer flow into Brownlee Reservoir may improve water quality in the reservoir (Nürnberg 2002), including dissolved oxygen concentrations at the surface where larval crappie reside for much of the summer. Indeed, Botelho and Imberger (2007) discovered that the surface layer in the upper reaches of Brownlee Reservoir becomes hypoxic during the summer, an unusual condition known as an “oxygen block”, and higher summer inflow likely minimizes this condition. Higher summer inflow may also increase turbidity and therefore reduce predation on larval crappie (Kim and DeVries 2001), and may provide more organic and inorganic material and nutrients, increasing primary and secondary production during the growing season and thus boosting the survival of larval crappie.

Our results suggest that, while the number of age-1 crappie caught in the spring depended in part on how strong the age-0 cohort was the prior autumn, the size that age-0 crappie reached by the end of their first growing season also influenced age-1 crappie abundance the following spring. Numerous studies have highlighted centrarchid susceptibility to size-related winter mortality (e.g., Chang 1971, Toney 1977, Toney and Coble 1979, Bernard and Fox 1997), most likely due to the well-established overwinter metabolic deficit fish commonly experience in northern latitudes (Garvey et al. 2004). Thus in years when summer growth was reduced for age-0 crappie in Brownlee Reservoir, winter survival was also reduced, and this may have been exacerbated by the severity of winters (McCollum et al. 2003). Indeed, McCollum et al. (2003) demonstrated reduced age-0 white crappie survival when water temperatures dropped below 4 °C, which in Brownlee Reservoir occurred 41% of the time during winter. Our modeling results suggest that one of the primary conditions creating slower age-0 crappie growth in the summer was lower mean water temperature, which concurs with numerous previous studies linking centrarchid larval fish growth to warmer water temperature (e.g., Sabo and Orht 1995, Claramunt and Wahl 2000, Pine and Allen 2001). However, a density-dependent response was also observed for age-0 crappie summer growth. Our results therefore highlight a tradeoff in crappie

year-class strength, where years with higher summer larval abundance led to more age-0 crappie in the autumn, but that diminished their summer growth, which negatively influenced the abundance of age-1 crappie the following spring, apparently by reducing overwinter survival.

Although the relationships we observed between crappie indices of abundance and reservoir environmental conditions are biologically reasonable, they are correlative in nature and may be influenced by other abiotic factors that we did not directly monitor. For example, warmer summer water temperature may not have led directly to better growth for larval crappie, but instead may have indirectly benefitted crappie growth by increasing zooplankton abundance in warmer years. Likewise, the positive relationship we observed in spring electrofishing CPUE between age-1 crappie and smallmouth bass large enough to prey on them was undoubtedly not causative. Rather, their correlative relationship likely indicates a parallel response to mutually advantageous environmental conditions in the reservoir. Considering how much larger, deeper, steep-sided, and fluctuating some western waters, such as Brownlee Reservoir, are from those in central and eastern North America, we urge additional investigations of the factors influencing crappie year-class strength in study waters comparable to ours to further highlight similarities and differences in crappie population dynamics in such disparate environments.

While larval summer, autumn age-0, and spring age-1 CPUE all appeared to accurately depict crappie year-class strength, autumn age-0 electrofishing data had several advantages for monitoring the strength of crappie year classes at Brownlee Reservoir. First, electrofishing provided an index of abundance not only for age-0 crappie but also for larger size classes of crappie and for other species. Second, electrofishing provided immediate data, whereas larval sampling required a great deal of sample processing in the lab to identify larvae to species and enumerate them. Third, the advantage of electrofishing in the autumn rather than the spring was that autumn data provided information on the size of age-0 crappie entering their first winter, which was apparently important for age-0

overwinter survival. Finally, the sampling effort needed to collect adequate crappie information with boat electrofishing was much shorter (usually one week) than the window needed to monitor larval crappie abundance over the summer (several weeks). Although peak and mean larval CPUE were highly correlated, sampling for peak rather than mean larval abundance would still take several weeks because peak abundance varied annually by almost six weeks during our study. The factors contributing to strong or weak year classes of larval crappie in the summer appear to be elusive at Brownlee Reservoir, but strong age-0 year classes in the autumn consistently persisted to older year classes, thus age-0 autumn electrofishing CPUE appears to be a better indicator of subsequent crappie year-class strength than summer larval trawl CPUE. Comparison of crappie catch from summer larval trawls and autumn electrofishing of multiple age classes at other steep-sided canyon reservoirs, where shorelines are often too steep to sample fish with trap nets, would be useful to support or refute this conclusion. While we observed very little size overlap in younger age classes, combining autumn electrofishing with age determinations would strengthen the inferences that could be drawn regarding year-class strength.

A better understanding of crappie fisheries in general in the waters of western North America is critical for managing them in this region, especially considering that crappie fisheries are often supported by only one or two age classes due to extreme annual recruitment variability (e.g., Allen 1997, Boxrucker and Irwin 2002, Maceina 2003, Martin and Maceina 2004). While previous studies have highlighted several factors that may influence crappie recruitment variability in other regions of North America, our results suggest that applying those generalizations to large, fluctuating, steep-sided reservoirs in the arid western US may be inappropriate. Our results suggest that autumn near-shore electrofishing can be used to annually characterize age-0 crappie recruitment as well as or better than summer surface larval trawls, while also providing additional information on size and abundance of other crappie age or size classes as well as other sympatric species that may affect crappie year-class strength in a density-dependent

manner. Long-term monitoring of crappie populations in other waters of western North America would not only facilitate a better understanding of crappie fisheries in this region, but also help establish standard monitoring methods for crappie populations in steep-sided canyon reservoirs where more traditional sampling methods may be inappropriate, and allow better communication with angling groups regarding annual expectations of the quality of crappie fisheries in such waters.

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