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ABSTRACT Freshwater drum (*Aplodinotus grunniens*) represent one of the most widely distributed fish species in North America. Identifying biotic and abiotic factors that influence larval freshwater drum densities can improve understanding of early life history. Our objective was to investigate correlations between annual peak density of larval freshwater drum and combinations of five variables (chlorophyll *a*, growing degree days [GDD], reservoir discharge, turbidity, and cladoceran density) from a long-term (2003–2017) monitoring program in a Nebraska irrigation reservoir. Twenty-eight a priori candidate models were assessed to determine the relative support of explanatory variables associated with annual peak density of larval freshwater drum using Akaike's information criterion. During the course of the study, larval freshwater drum annual peak densities ranged from <0.1 (±0.1 SE) to 4.5 (±0.8 SE) /m^3 and variations were best explained by chlorophyll *a* (highest relative importance, 0.77). Chlorophyll *a* was positively associated with higher densities of larval freshwater drum. This study highlights the importance of chlorophyll *a* to larval freshwater drum annual peak densities and provides a greater understanding of freshwater drum early life history.

KEY WORDS chlorophyll *a*, early life history, freshwater drum, irrigation reservoir

Freshwater drum (*Aplodinotus grunniens*) are a member of the Sciaenidae family and inhabit the largest latitudinal range of any North American fish species (Barney 1926, Boschung and Mayden 2004). This species spawns when water temperatures are between 18º C and 25º C, are highly fecund, and can live for more than 10 years (Swedburg and Walburg 1970, Bur 1984, Pereira et al. 1995). Eggs are semi-buoyant, and after hatching the larvae drift at the surface for approximately two weeks while they absorb their yolk sac and develop orientated movement (Priegel 1967). Ichthyoplankton samples commonly report freshwater drum are the most abundant species in ichthyoplankton samples, and Wallus and Simon (2006) have summarized several studies that reflect the inter- and intra-annual variability in relative abundance demonstrated by this species. Freshwater drum dominate abundance in most egg and ichthyoplankton surveys; they can also exhibit high rates of mortality (Cada and Hergenrader 1980, Wallus 2006) and entrainment loss (Walburg et al. 1971).

While the role of freshwater drum in most aquatic systems is not well defined, they can represent a large proportion of the fish community biomass (Rypel 2007). Larval freshwater drum rely heavily on zooplankton as their primary food source, as other potential diet items are restricted by gape limitations (Swedburg and Walburg 1970, Schael et al. 1991, Sullivan et al. 2012). Previous studies have found adult freshwater drum to consume zebra mussels (*Dreissena polymorph*) in the Great Lakes (French and Love 1995, French and Bur 1996, Morrison et al. 1997) and Arkansas (Magoulick and Lewis 2002); however, the presence of these aquatic invasive species may also alter conditions for larval freshwater drum survival.

A variety of environmental factors have been associated with relative abundance, growth, survival, recruitment, year-class strength, and diet of freshwater drum in riverine systems (Braaten and Guy 2002, Wallus 2006, Jacquemin et al. 2014, Jacquemin et al. 2015); however, the factors that drive larval freshwater drum annual peak density in irrigation reservoirs are less understood. Because larval freshwater drum are normally absent as prey items of predatory fish in Nebraska reservoirs (Olson et al. 2007, Miller et al. 2019, Uphoff et al. 2019), we hypothesize that year-class strength may be driven by lower trophic or abiotic factors. For these reasons we explored how cladoceran density, turbidity, chlorophyll *a*, discharge, and growing degree days explain the variable recruitment of larval freshwater drum in Harlan County Reservoir, Nebraska. Cladoceran density was selected because larval freshwater drum in Harlan County

Reservoir positively selected for this prey taxa (Sullivan et al. 2012) and therefore the availability could be associated with larval survival. Water turbidity has been found to alter distribution (Matthews 1984) and negatively impact feeding ability in other species (Johnston and Wildish 1982, Zamor and Grossman 2007). Chlorophyll *a* concentrations have been associated with reservoir primary productivity and have been linked to relative abundance of higher trophic levels in irrigation reservoirs and Harlan County Reservoir specifically (Olds et al. 2014). The weak swimming ability of larval freshwater drum make them susceptible to entrainment loss in Midwest rivers (Walburg 1971) and reservoirs (Smith and Brown 2002, Fryda 2005) and may also impact relative abundance in Harlan County Reservoir. Growing degree days were also included because available temperature can influence fish growth rates and potentially subsequent survival (Neuheimer and Taggart 2007, Chezik et al. 2013, Uphoff et al. 2013). Understanding which factors impact larval freshwater drum densities in irrigation reservoirs is not well documented. Therefore, the objective of this study was to evaluate which factors influence annual peak density of larval freshwater drum within a Nebraska irrigation reservoir.

STUDY AREA

Harlan County Reservoir is an irrigation reservoir built in 1952 and is located on the Republican River drainage in south-central Nebraska. Harlan County Reservoir encompasses more than 5,362 ha, has 121 km of shoreline, and has mean and maximum depths of 4 m and 18 m (Uphoff et al. 2013). Daily inflows averaged 2.8 m^3/sec (SE = 1.0) from 2003–2017 (USBR 2018). During the study timeframe drought years were recorded that resulted in a net loss of inflow and nearly 50% loss of the conservation pool (Olds et al. 2011, Olds et al. 2014). Long-term monitoring and research at Harlan County Reservoir since 2003 has provided insight on changes in water quality (Olds et al. 2011), zooplankton (Olds et al. 2014), game fish species such as walleye (*Sander vitreus*; Uphoff et al. 2013– Miller et al. 2018*a*), white bass (*Morone chrysops*; Olson et al. 2007, Miller et al. 2018*a*), and larval fish including gizzard shad (*Dorosoma cepedianum*; Sullivan et al. 2011, Miller et al. 2018*b*) and freshwater drum (Sullivan et al. 2012).

METHODS

Since 2003, larval freshwater drum have been collected at dusk using bow-mounted ichthyoplankton push nets of two different diameters (1.0-m diameter with 1.80-mm mesh and 0.5-m diameter with 0.75-mm mesh) deployed simultaneously as one unit of sampling effort. A sample consisted of pushing the pair of nets for 5 min in a single direction at a speed of 4 km/hr (Sullivan et al. 2012). Each net was outfitted with a flowmeter (General Oceanics Inc., Miami, FL, USA) to estimate the volume of water sampled. Push-net sampling began in early June (2003–2004) or the last week of May (2005–2017) and was conducted once a week for eight consecutive weeks at standardized-GPS reservoir sites (Sullivan et al. 2012). Additional sites were added as the study progressed and ranged from eight sites in 2003 and 2004, to 24–48 sites during the remaining years (2005–2017). Collected larval fish were preserved in 70% ethyl alcohol and transported to the University of Nebraska at Kearney for identification, measurement (total length [TL]; mm), and enumeration.

Larval freshwater drum density at each site was determined by summing the number of freshwater drum <8-mm TL from the smaller-diameter net and the freshwater drum ≥8-mm TL from larger-diameter net and dividing by the respective volumes sampled. Freshwater drum <8-mm TL were counted from the smaller-diameter net and those ≥8 mm TL from the larger-diameter net to avoid double counting similar sized fish (Sullivan et al. 2012). Site-specific larval freshwater drum densities were averaged to determine a weekly mean. Annual peak larval density was therefore determined to be the week with the greatest density. Annual peak densities were used to be consistent with methodology in similar studies (Sullivan et al. 2011, Sullivan et al. 2012, Miller et al. 2018*b*) because an additive approach could introduce gear bias caused by catchability that may vary with freshwater drum length.

Zooplankton samples were collected concurrently with larval push-net samples at 15 standardized sites distributed across the reservoir using a Wisconsin plankton net (0.5-m diameter with 80-µm mesh) towed vertically from the bottom substrate to the surface (Peterson et al. 2005). Water depth (m) was recorded to calculate the water volume sampled. Samples were preserved in a sucrose-buffered 4% formalin solution to prevent osmotic distortion (Haney and Hall 1973) prior to being identified and quantified within the laboratory (Peterson et al. 2005). Cladoceran densities (number/L) were determined for each site and averaged for the sampling date across the reservoir (Sullivan et al. 2012).

Weekly water quality sampling was conducted to coincide with zooplankton and larval freshwater drum sampling at 15 standardized sites distributed across the reservoir, all of which were also sampling locations for larval freshwater drum. At each site, a Van Dorn bottle sampler collected water samples at 1 m and every subsequent 3 m at the sampling site (i.e., 1, 4, 7, and 10 m). All collected water samples from each site were pooled in a bucket and stirred to assumed homogeneity, at which time a subsample was processed. Turbidity (Formazin Attenuation Units, FAU) was measured using a Hach(TM) colorimeter and chlorophyll *a* (µg/L) was measured using a Turner Designs Aquafluor(TM) Handheld Fluorometer. Mean spring (April and May) values were used for the analysis of turbidity and chlorophyll *a* to coincide with initial larval freshwater drum development. Turbidity and chlorophyll *a* were restricted to 2004–2017 because data were not collected in 2003. Discharge that coincided with annual peak density dates were obtained from 2003 through 2017 from the United States Bureau of Reclamation website (USBR 2015). Air temperature data were obtained for Republican City, Nebraska, for 2003–2017 from the National Oceanic and Atmospheric Administration's National Center for Environmental Information (NCEI 2018). Daily air temperature data were used to calculate growing degree-days (GDD) using the following:

$$\mathrm{GDD} = \left[\frac{T_{\max} + T_{\min}}{2}\right] - T_{\mathrm{base}}$$

where T_{max} is the maximum daily temperature, T_{min} is the minimum daily temperature, and T_{base} is the base temperature at which larval development and growth is thought to occur. In this case, T_{base} was set at 9° C, which is a species-specific value for freshwater drum (McInerny and Held 1995). Growing degree days were summed from 1 April through 31 May for each year between 2003 and 2017 in which the average air temperature was ≥9° C. Growing degree days were used instead of water temperatures because daily air temperatures were available, and air temperatures have been found to be strongly correlated to water temperatures (Shuter et al. 1983, Livingstone and Padisak 2007).

A set of 28 a priori candidate models were established to assess the relative support of explanatory variables using Akaike's information criterion (AIC; Akaike 1987). Due to small sample size relative to model parameters, second order Akaike's information criterion (AIC_c) was used to more conservatively rank competing models (Burnham and Anderson 2002). Models with the lowest difference between AIC_c values (Δ_i) and highest model weight (W_i) were chosen for model inference. Model averaging was used across all candidate models with associated parameter estimate and standard error by calculating,

$$\tilde{\bar{\beta}} = \sum_{i=1}^{R} w_i \hat{\beta}_i$$

$$\widehat{var}\left(\tilde{\bar{\beta}}\right) = \sum w_i \left[\widehat{var}\left(\tilde{\bar{\beta}}\right) + \left(\beta_i - \tilde{\bar{\beta}}\right)^2\right]$$

where $\tilde{\bar{\beta}}$ is the parameter estimate, w_i is the perspective model weight, and β_i is the regression estimate for i (Burnham and Anderson 2002). Using the K-L method, AIC_c weights are summed for all models containing a predictor variable and models with zero weights are omitted to determine relative importance (Burnham and Anderson 2002). Variables with the largest total weight are considered to have the greatest relative importance for explaining the dependent variable (Burnham and Anderson 2004). Simple linear regression was performed between the predictor variable with the most support and larval freshwater drum annual peak densities ($\alpha = 0.05$; Fig. 1).

RESULTS

Five variables were assessed to determine which factors were associated with annual peak density of larval freshwater drum. Between 2003 and 2017, annual peak densities of larval freshwater drum averaged 1.3 larvae/m^3 (SE = 0.3, $n = 15$) and ranged from <0.1 to 4.5 larvae/m^3, most often peaking around mid- to late June. Cladoceran density (during peak weeks) ranged from 2.7 to 30.5 organisms/L with a mean of 15.6 organisms/L (SE = 4.0) from 2003 through 2017. Turbidity (during peak weeks) ranged from 10.7 to 39.7 FAU with a mean of 23.1 FAU (SE = 6.0) from 2004 to 2017. Spring (April–May) chlorophyll *a* averaged 56.1 µg/L (SE = 8.3) between 2004 and 2017 and ranged from 6.7 to 70.4 µg/L. Discharge (during peak weeks) averaged 6.6 m^3/sec (SE = 1.7) between 2003 and 2017 and ranged from 0.0 to 18.5 m^3/sec. Growing degree days from April to May averaged 253 days (SE = 17.4) between 2003 and 2017 and ranged from 162 to 387 days.

The best supported model ($W_i = 0.41$) included chlorophyll *a* (Table 1; Fig. 1) and explained 36% of the annual variability in annual peak density of larval freshwater drum. Additionally, chlorophyll *a* was present in four of the top five models offering support for this variable. Other models evaluated were not supported by the data (i.e., high Δ_i and low W_i; Table 1). Relative variable importance weights suggested that chlorophyll *a* had the greatest relative importance on larval freshwater drum annual peak density ($W_i = 0.77$; Table 2) and chlorophyll *a* was significantly related to larval freshwater drum annual peak density ($P = 0.02$).

DISCUSSION

We found that chlorophyll *a* was the most supported variable of those we examined, associated with annual peak density of larval freshwater drum within Harlan County Reservoir. Chlorophyll *a* has also been linked to increased density of crappie (*Pomoxis* spp.) (McInerny and Cross 1999, Bunnell et al. 2006), largemouth bass (*Micropterus salmoides*), threadfin shad (*Dorosoma petenense*), and gizzard shad (Siler et al. 1986, Allen et al. 1999). While commonly used to index trophic state of lakes and reservoirs (Carlson 1977), chlorophyll *a* is primarily responsible for energy absorption during photosynthesis (Brönmark and Hansson 2005). During primary production, chlorophyll *a* has been found to be linked to zooplankton production (Pace 1986), which ultimately supports and enhances fish production (Oglesby et al. 1987, Downing et al. 1990). The availability of chlorophyll *a* may also be linked to other potential variables we included as predictors because it can be related to phytoplankton blooms (Boyer et al. 2009), which decrease

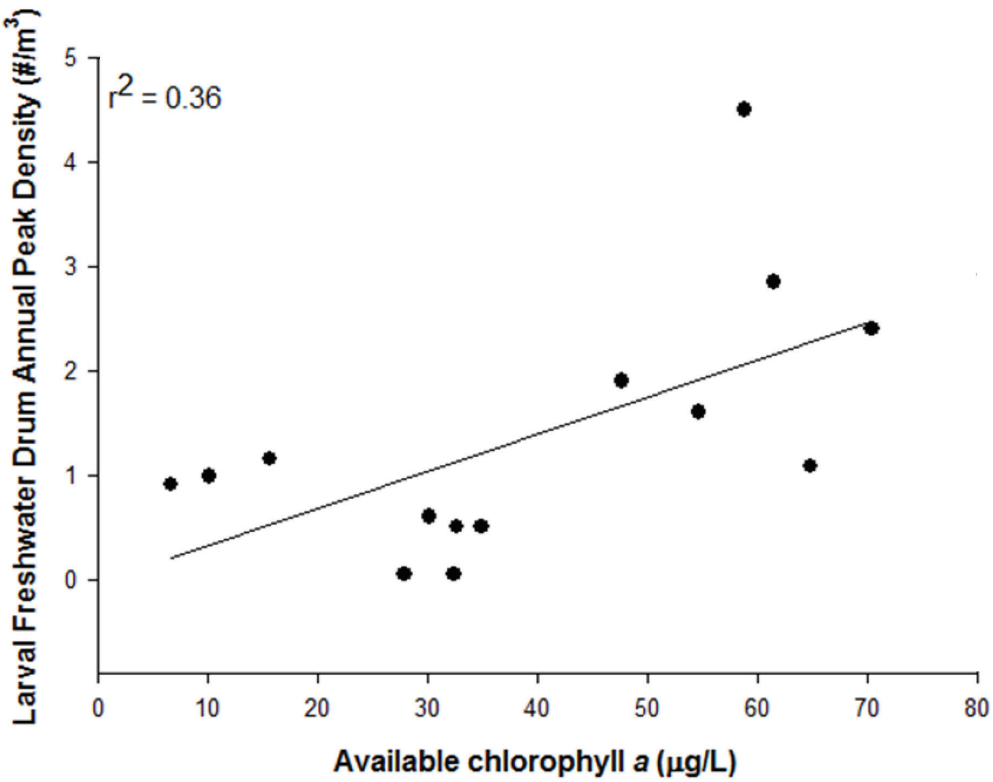

Figure 1. Larval freshwater drum annual peak densities (n/m^3) from Harlan County Reservoir, Nebraska, from 2004–2017 to compared chlorophyll *a* (µg/L) during the spring (April and May). Solid line indicates line of best fit from simple linear regression. The regression was significant ($P = 0.02$).

water clarity and manifest in higher productivity with warmer water temperatures (Elliot et al. 2006). Considering that discharge, turbidity, growing degree days, and cladoceran density all were included with chlorophyll *a* as weighted descriptors, it is likely that conditions conducive to nutrient rich waters offer a suite of survival advantages for hatching success and immediate larval survival.

Freshwater drum are not typically managed by biologists but understanding their ecological role in irrigation reservoirs is valuable. Historically, larval freshwater drum have been collected alongside larval gizzard shad in this reservoir (Sullivan et al. 2011, Sullivan et al. 2012, Miller et al. 2018*b*). Nutrient rich reservoirs can create size-selective feeding of particular taxa (Stenson 1976). A similar study found larval gizzard shad abundance was correlated to zooplankton density and reservoir elevation rather than chlorophyll *a* (Miller et al. 2018*b*). Larval densities of both species peak at similar times; however, they may have developed niche separation as larval gizzard shad primarily consumed copepod nauplii and cyclopoida taxa (Sullivan et al. 2011) and larval freshwater drum ate *Bosmina spp.* in this reservoir (Sullivan et al. 2012).

There is a need to investigate more factors associated with higher nutrient conditions to specifically identify the mechanisms driving year-class development of freshwater drum in irrigation reservoirs. As with all applications of AIC modelling, it needs to be recognized that this approach identifies which of the selected variables best describes the variability in relative abundance of larval freshwater drum. The use of AIC is common in the environmental field because it assists managers in identifying the relative importance of specific predictors for biological trends (Guthery 2008); however, it is limited by the biological interpretation of which variables can and should be included. Future studies could investigate spatial distributions of larval freshwater drum to determine if densities differ within reservoirs, especially considering that the availability of chlorophyll *a* has spatial patterns in this reservoir (Olds et al. 2011). Also, understanding what factors drive yearly densities for other species can allow for a wholistic management approach in assessing fish assemblages.

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Table 1. Coefficient of determination (r^2), number of parameters (K), AIC_c values, difference between successive AIC_c values (Δ_i), and model weights (W_i) describing support of 28 models to evaluate abiotic and biotic factors influencing annual peak density of larval freshwater drum in Harlan County Reservoir, Nebraska, during 2003–2017. Factors included chlorophyll *a* (CL), growing degree days (GDD), discharge (DI), turbidity (TB), and cladoceran density (CD).

Model	r^2	K	AIC_c	Δ_i	W_i
CL	0.36	3	5.43	0.00	0.41
CL + DI	0.41	4	8.10	2.66	0.11
DI	0.25	3	8.83	3.40	0.07
CL + TB	0.37	4	9.00	3.56	0.07
CL + GDD	0.44	4	9.10	3.66	0.07
CL + CD	0.36	4	9.25	3.81	0.06
TB	0.16	3	9.51	4.08	0.05
TB + DI	0.32	4	10.33	4.90	0.04
GDD + CL +DI	0.50	5	12.59	7.16	0.01
CD + DI	0.25	4	12.60	7.17	0.01
GDD + DI	0.39	4	12.65	7.21	0.01
CL + DI +TB	0.41	5	12.75	7.31	0.01
CL + DI + CD	0.41	5	12.75	7.32	0.01
CD	0.02	3	12.85	7.41	0.01
GDD	0.12	3	12.89	7.45	0.01
GDD + TB	0.33	4	13.02	7.58	0.01
CD + TB	0.18	4	13.10	7.67	0.01
GDD + CL + TB	0.47	5	13.57	8.13	0.01
GDD + CL + TB	0.37	5	13.66	8.23	0.01
CL + TB + CD	0.45	5	13.76	8.32	0.01
TB + DI +CD	0.32	5	14.98	9.55	0.00
GDD + TB + DI	0.45	5	14.99	9.56	0.00
GDD + CD	0.12	4	16.55	11.11	0.00
GDD + DI + CD	0.40	5	17.26	11.83	0.00
GDD + TB + CD	0.33	5	17.58	12.15	0.00
CL + TB + DI +CD	0.41	6	18.56	13.13	0.00
GDD + TB + DI + CD	0.46	6	20.81	15.38	0.00
GDD + TB + CL + DI + CD	0.53	7	25.88	20.44	0.00

Table 2. Final model averaged estimates, standard error, and relative variable importance for chlorophyll *a* (CL), growing degree days (GDD), discharge (DI), turbidity (TB), and cladoceran density (CD). AICc weights are summed for all models containing a predictor variable and models with zero weights are omitted to determine relative importance. The relative importance is the summation of the model weights for each variable.

i	Parameter estimate	SE	Relative importance
Chlorphyll *a* (CL)	0.03	0.05	0.77
Growing degree days (GDD)	0.00	0.01	0.14
Discharge (DI)	-0.02	0.01	0.28
Turbidity (TB)	0.01	0.02	0.21
Cladoceran density (CD)	0.00	0.01	0.11

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