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Degree-day accumulation influences annual variability in growth of age-0 walleye

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ABSTRACT

The growth of age-0 fishes influences survival, especially in temperate regions where size-dependent over-winter mortality can be substantial. Additional benefits of earlier maturation and greater fecundity may exist for faster growing individuals. This study correlated prey densities, growing-degree days, water-surface elevation, turbidity, and chlorophyll *a* with age-0 walleye *Sander vitreus* growth in a south-central Nebraska irrigation reservoir. Growth of age-0 walleye was variable between 2003 and 2011, with mean lengths ranging from 128 to 231 mm by fall (September 30th–October 15th). A set of a priori candidate models were used to assess the relative support of explanatory variables using Akaike's information criterion (AIC). A temperature model using the growing degree-days metric was the best supported model, describing 65% of the variability in annual mean lengths of age-0 walleye. The second and third best supported models included the variables chlorophyll *a* ($r^2 = 0.49$) and larval freshwater drum density ($r^2 = 0.45$), respectively. There have been mixed results concerning the importance of temperature effects on growth of age-0 walleye. This study supports the hypothesis that temperature is the most important predictor of age-0 walleye growth near the southwestern limits of its natural range.

1. Introduction

Growth of age-0 fishes can be an important indicator of survival (see review by Sogard, 1997), as size attained in the first year can affect over-winter survival and thus, recruitment to the fishery (Chevalier, 1973). Over-winter survival can be size-dependent as smaller age-0 fishes have higher mortality rates due to greater risks of starvation (Biro et al., 2004; Post and Evans, 1989; Post and Parkinson, 2001) and predation (Forney, 1966). Model simulations predicted that early differences in growth changed the probability of larval fish survival by as much as 30 times (Rice et al., 1993). Growth of age-0 fishes can also affect the age at which fish reach harvestable sizes and age at maturity, fecundity, and overall fitness (Beverton and Holt, 1959).

Abiotic factors, in particular, temperature can directly affect the growth of poikilotherms, such as fish (Atkinson, 1994; Kitchell et al., 1977; van der Have and de Jong, 1996) by influencing enzymatic activity, and therefore, metabolic rates (Higley et al., 1986). Fish experience higher growth rates when their metabolic activity rises with increasing temperature (Clarke and Johnston, 1999). For example, walleye have higher growth rates at higher water temperatures regardless of latitudinal differences among populations (Galarowicz and Wahl, 2003). Other factors include turbidity, which can negatively affect the feeding efficiency of visual predators (Chesney, 1989; Utne-Palm, 2004), as well as primary productivity (inferred from chlorophyll *a* concentrations), which can affect food availability at higher trophic levels (McQueen et al., 1986). Resource availability can affect lower trophic levels, as increased nutrients from resuspension of sediments (Schindler, 1978) can increase phytoplankton biomass that may lead to increases in zooplankton biomass.

Biotic factors including prey size and availability can also affect fish growth (Paloheimo and Dickie, 1966). Walleye typically undergo a series of ontogenetic diet shifts in their first growing season, moving from zooplankton, to macroinvertebrates and finally to fish (Beck et al., 1998; Fox, 1989; Fox and Flowers, 1990; Fox et al., 1989; Johnston and Mathias, 1994a; Mathias and Li, 1982). The complexity of age-0 walleye food habits during the first growing season allows for many different scenarios in which food could be limiting (Colby and Nepszy, 1981).

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The observed growth of age-0 walleye at Harlan County Reservoir in south-central Nebraska has been variable over the last 8 years. As an irrigation reservoir, this system is dynamic and characterized by large fluctuations in water levels and water quality, in particular during a 4-year drought (2003–2006) (Olds et al., 2011). During the drought years, reservoir volume decreased from almost 400 million m^3 to less than 150 million m^3; during this time turbidity and chlorophyll *a* were significantly higher (Olds et al., 2011). In Harlan County Reservoir, the main prey sources of age-0 walleye have been larger calanoid copepods, age-0 gizzard shad *Dorosoma cepedianum* and some age-0 freshwater drum *Aplodinotus grunniens* (Uphoff, 2012). Densities of age-0 gizzard shad and freshwater drum are highly variable in Harlan County Reservoir (Sullivan et al., 2011a,b). At Harlan County reservoir, age-0 walleye have variable growth and abiotic and biotic factors that have influenced the growth rate of age-0 walleye cohorts in other studies also vary (Forney, 1966; Madenjian, 1991; Quist et al., 2003; Smith and Pycha, 1960; Staggs and Otis, 1996). Therefore, the objective of this study was to elucidate those factors that most strongly influenced growth of age-0 walleye among years.

2. Methods

2.1. Study site

Harlan County Reservoir is an irrigation/flood-control reservoir located in south-central Nebraska. At conservation pool the reservoir is approximately 5362 surface hectares with a mean depth of 4 m and a maximum depth of 18 m (USACE, 2010). In this polymictic system, long fetch and prevailing high winds allow only weak (i.e., temporary) thermal stratification during summer (Olds et al., 2011). The fishery is primarily managed for walleye and white bass *Morone chrysops* with gizzard shad constituting the dominant prey fish.

2.2. Data collection

Annual mean length (TL, mm) and catch-per-unit-effort (CPUE, *n*/min) were determined from age-0 walleye captured during boat electrofishing surveys conducted annually between September 30 and October 15 from 2003 through 2011. Age-0 walleye were collected from Nebraska Game and Parks Commission fixed shoreline stations. Electrofishing surveys were conducted at night and the typical run time at each station was 10 min.

Ten different variables were assessed for effects on annual variability in age-0 walleye growth (Table 1). Water quality and ichthyoplankton sampling protocols were established in 2003, and have been conducted every year. Zooplankton collections and water quality assessments occurred semi-weekly during April–September at 15 fixed sampling locations located throughout the reservoir (Peterson et al., 2005). Assessment occurred semi-weekly during April–September. Zooplankton were collected with an 80-μm Wisconsin plankton net (0.5 m^2 opening) towed vertically from the substrate to the surface. Contents from these tows were preserved in sucrose and 4% formalin to prevent osmotic distortion (Haney and Hall, 1973). Zooplankton were identified to lowest possible taxon under a compound microscope and enumerated by taxon group. When possible at least 25 calanoid copepods (both adults and copepodites) were measured to the nearest 0.1 mm for each tow. Chlorophyll *a* concentrations and turbidity readings were taken at each station by collecting water samples every 3 m starting at 1 m with a Van Dorn bottle sampler. All water samples from each site were pooled in a bucket and stirred to assumed homogeneity. A subsample was drawn from the integrated water sample and analyzed with an Aquafluor(tm) Handheld Fluorometer and Hach DR/890 Colorimeter.

Nightime collections of larval gizzard shad and freshwater drum were conducted weekly during June and July at 24 fixed sampling stations (Sullivan et al., 2011a). Sampling was accomplished by pushing two ichthyoplankton nets for 5 min at a speed of 0.5 m/s. Each ichthyoplankton net was circular with the larger net having a diameter of 1.0 m (1.8 mm mesh) and the smaller net having a diameter of 0.5 m (0.75 mm mesh). These nets were mounted to the front of a boat at a depth of 0.5-m on a metal frame. Flow meters were placed at the mouth of each net to determine total volume of water sampled.

Air temperature data were obtained for Republican City, Nebraska, which is located approximately 1 mile from Harlan County Reservoir, for 2003–2011 from the National Oceanic and Atmospheric Administration's National Climatic Data Center (NCDC, 2012). Daily air temperature data were then used to calculate growing degree-days (GDD) using the following formula:

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

where $T_{\max}$ is the maximum daily temperature, $T_{\min}$ is the minimum daily temperature, and T_{base} is the base temperature at which development is thought to occur. In this case, T_{base} was set at 5 °C as this temperature has previously been used to describe the walleye growing season (Kitchell et al., 1977; Neuheimer and Taggart, 2007; Shuter et al., 1983; Venturelli et al., 2010). The GDD were summed from April 1st through September 30th for all days in which the average air temperature was ≥5 °C. The GDD were used instead of water temperatures because air temperatures are more widely available and water and air temperatures are closely correlated (Livingstone and Padisak, 2007; Quist et al., 2003; Shuter et al., 1983). Daily reservoir elevation data were obtained from the U.S. Bureau of Reclamation (USBR, 2011). Mean reservoir water elevation was calculated based on daily elevations from April through September.

2.3. Data analysis

A set of a priori candidate models were developed to assess the relative support of explanatory variables using Akaike's information criterion (AIC). Given that all explanatory variables were available from 2003 to 2007 and 2009 to 2011, the analysis was restricted to those years. Due to small sample size relative to model parameters, second order Akaike's information criterion ($\mathrm{AIC_c}$) was used to more conservatively rank competing models (Burnham and Anderson, 2002). The most parsimonious models [i.e., lowest difference between model $\mathrm{AIC_c}$ values (Δ_i) and highest model weight (W_i)] were chosen for model inference.

3. Results

The sample size for determining annual mean length ranged from 6 to 54 age-0 walleye, with all but one year having a sample size of 15 or more. No age-0 walleye were collected during 2008, therefore data from 2003 to 2007 and 2009 to 2011 were used in this analysis. Annual mean lengths of age-0 walleye varied throughout the 8 years of this study, with a mean annual length of 199 (±SE 11.8) mm and a range of 128–231 mm. The GDD model was the best supported by the data (i.e., lowest Δ_i and highest W_i) describing 65% of the variability in mean age-0 walleye length (Table 2). The GDD accumulation from April through September varied from 4391 to 5034 with a mean of 4792 (±SE 75) GDD from 2003 through 2011. Because mean length of age-0 walleye and GDD data were available prior to 2003 (from 1995 through 2011), we

Table 1
Minimum, mean, and maximum values for each variable used to explain annual variations in mean age-0 walleye length from Harlan County Reservoir, Nebraska, during 2003–2011.

Variable	Description	Minimum	Mean	Maximum
Cal_Den	Mean calanoid copepod density (#/L) during May and June	15.7	24.3	41.8
Cal_Length	95th percentile length of calanoid copepods (mm) during May and June	46	54	70
Chlor_a	Mean Chlorophyll *a* (μg/L) values during April–September	17.9	84.2	116.6
Clad_Den	Mean cladoceran density (#/L) during May and June	6.9	17.4	29.7
Drum_Den	Peak larval freshwater drum density (#/L)	0.0	0.8	2.2
GDD	Accumulation of growing degree-days (Base 5 °C), from April–September	4391	4792	5034
Res_Elev	Mean reservoir elevation (ft) during April–September	1926.4	1936.6	1947.1
Shad_Den	Peak larval gizzard shad density (#/L)	0.6	2.7	5.6
Turb	Mean turbidity (FAU) values during April–September	17	29	42
WAE_CPUE	Mean CPUE (#/h) of age-0 walleye	5	24	43

Table 2
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 rankings of a priori models based on level of support (i.e., AIC_c) to evaluate interannual variability in mean age-0 walleye length from Harlan County Reservoir, Nebraska, during 2003–2011.

Model	r^2	K	AIC_c	Δ_i	W_i
GDD	0.65	3	75.14	0.00	0.623
Chlor_a	0.49	3	78.22	3.07	0.134
Drum_Den	0.45	3	78.82	3.68	0.099
Turb	0.28	3	81.00	5.85	0.033
Res_Elev	0.19	3	82.30	7.16	0.017
GDD, Shad_Den	0.73	4	82.38	7.23	0.017
Clad_Den	0.11	3	82.75	7.61	0.014
Shad_Den	0.11	3	82.75	7.61	0.014
Cal_Den	0.11	3	82.77	7.62	0.014
GDD, Chlor_a	0.70	4	83.43	8.28	0.010
WAE_CPUE	0.00	3	83.67	8.52	0.009
GDD, Cal_Den	0.66	4	84.23	9.09	0.007
Res_Elev, GDD	0.66	4	84.45	9.30	0.006
Res_Elev, Chloro_a	0.50	4	87.41	12.27	0.001
Turb, Chlor_a	0.49	4	87.52	12.38	0.001
Shad_Den, Drum_Den	0.46	4	88.12	12.97	0.001
Cal_Den, Cal_Length	0.18	4	91.43	16.29	0.000
Shad_Den, Cal_Den	0.15	4	91.65	16.50	0.000
Clad_Den, Cal_Dem	0.36	4	91.76	16.62	0.000
GDD, Shad_Den, Chloro_a	0.75	5	100.66	25.51	0.000
GDD, Shad_Den, Cal_Den	0.73	5	101.02	25.88	0.000
Clad_Den, Cal_Den, Cal_Length	0.25	5	109.30	34.16	0.000

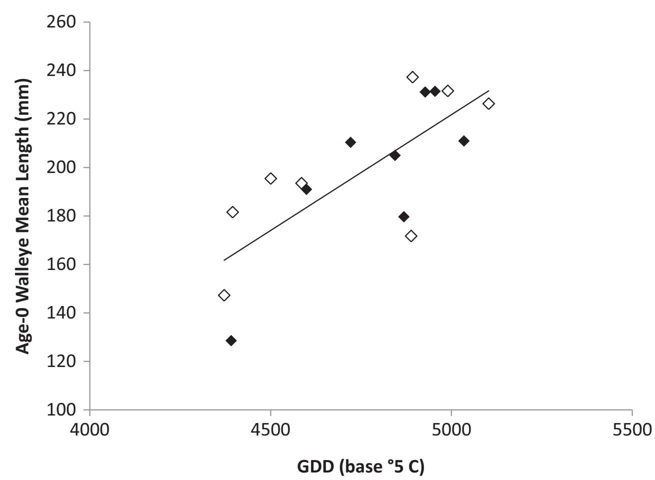

Fig. 1. Mean length of age-0 walleye collected from Harlan County Reservoir, Nebraska, from 1995 through 2002 (open symbols) and 2003 through 2011 (closed symbols) during fall (September 30th–October 15th) electrofishing surveys compared to the accumulation of growing degree-days [GDD (base 5 °C)] from April through September of that year for the region. Solid line indicates line of best fit from simple linear regression.

have included these additional years to show the robustness of the correlation between age-0 walleye growth and GDD over time in Harlan County Reservoir (Fig. 1). The chlorophyll *a* model and the larval freshwater drum density model were the second and third best supported models explaining 49 and 45% of the variability in mean age-0 walleye length, respectively. Other models evaluated were not supported by the data (i.e., high Δ_i and low W_i; Table 2).

4. Discussion

Growth of age-0 walleye in Harlan County Reservoir was comparable to *Sander* spp. growth in other Great Plains reservoirs (Quist et al., 2003; Sprenkle, 2010). Past studies examining the effects of temperature on walleye growth have had mixed results. Similar to this study, summer temperatures largely explained variability in the growth of age-0 walleye in Lake Winnebago, Wisconsin (Staggs and Otis, 1996) and growth of larval walleye in culture ponds was also positively related to water temperature (Johnston, 1999). Conversely, age-0 walleye growth in a Kansas reservoir and several northern lakes appeared unrelated to temperature (Quist et al., 2003; Smith and Pycha, 1960). Forney (1966) and Madenjian (1991) both reported that temperature had a small effect on growth of age-0 walleye in Oneida Lake and in both cases prey size and availability had a larger effect on growth.

Temperature can directly influence fish growth, and results from this study indicate that the GDD metric was the best indicator of age-0 walleye growth in Harlan County Reservoir. The use of the GDD metric in fisheries science is widely applicable because temperature influences many physiological processes, such as growth due to changes in metabolic rate and consumption (Atkinson, 1994; van der Have and de Jong, 1996). Enzymatic reaction rates that govern metabolic rates, and therefore fish growth, increase with higher temperatures (Clarke and Johnston, 1999; Higley et al., 1986). For example, age-0 tiger muskellunge *Esox masquinongy* × *Esox lucius* grew faster under higher temperatures independent of feeding levels (Chipps et al., 2000). Food consumption rates can also increase with increasing temperatures, as was observed in laboratory experiments with zooplanktivorous age-0 walleye (Johnston and Mathias, 1994b).

Temperature could also be an important regulator of age-0 walleye growth through indirect effects on lake productivity. Similar to the GDD model, there was a positive relationship between chlorophyll *a* values and mean length of age-0 walleye. Both the GDD metric and chlorophyll *a* could be an index of lake productivity and phytoplankton biomass, as increased phytoplankton biomass has been associated with warming temperatures under eutrophic conditions (Tadonleke, 2010). Increased growth rates of age-0 walleye associated with increased chlorophyll *a* concentrations could also be a result of bottom-up trophic interactions as increases in productivity at the bottom of the food chain could resonate up through the food chain and generate greater prey availability to age-0 walleye (McQueen et al., 1986). However, abundance of larval gizzard shad was not supported as a factor affecting age-0 walleye growth. The strength of the bottom-up effect usually weakens up the food chain (McQueen et al., 1986), although occasions in which bottom-up interactions have affected fish production have been reported (Ware and Thomson, 2005).

The GDD model does not differentiate between a growing season in which daily temperatures are static above the growth threshold of 5 °C and a growing season in which temperatures are variable and high for only a short period. The optimum temperature for walleye growth falls in the range of 20–23 °C (Christie and Regier, 1988; Coutant, 1977), and a growing season in which temperatures are static, within the optimum growth threshold would likely result in greater growth than would a growing season with variable high temperatures. Although the relationship of GDD and annual mean length of age-0 walleye is seemingly linear under the range of conditions during this study, the relationship likely has an upper limit or an asymptote. High daytime temperatures in southern systems may produce water temperatures that limit thermal refugia and possibly stress walleye resulting in reduced activity and slower growth (Kocovsky and Carline, 2001). Indeed, growth of mature walleye was greatest during late summer and autumn in a Kansas reservoir when water temperatures were lower than during mid summer peak when prey availability was greater (Quist et al., 2002). Summer water temperatures of 30 °C or greater that could cause stress in walleye have been observed in Kansas reservoirs and other Great Plains systems (Quist et al., 2002), however water temperatures this high do not typically occur in Harlan County Reservoir (Olds et al., 2011).

Prey abundance can influence walleye growth (Hartman and Margraf, 1992). The only model using a prey variable that was supported in this study was the larval freshwater drum density model. Occasionally age-0 freshwater drum are abundant in Harlan County Reservoir (Sullivan et al., 2011a), and at times age-0 walleye utilize freshwater drum as a prey source as in other systems (Hartman and Margraf, 1992; Uphoff, 2012). A positive relationship between water temperature and larval drum survival was reported in impoundments of the Mississippi River (Butler, 1965). Therefore, in years that age-0 walleye experienced faster growth because of greater GDD accumulation, larval freshwater drum may also experience higher survival, depicting a positive correlation between age-0 walleye mean lengths and larval drum densities.

We used a variety of models to assess the annual variability in age-0 walleye growth; however, most of these models were not supported by the data. Some of the other prey variables, such as larval gizzard shad peak densities and calanoid copepod densities, were not predictors of age-0 walleye growth likely because these prey sources are not limiting in Harlan County Reservoir (Sullivan et al., 2011b). Also, cladoceran densities may not have had an effect on growth because age-0 walleye in Harlan County Reservoir selected for calanoid copepods (Uphoff, 2012), unlike previous studies that reported cladocerans to be an important prey of age-0 walleye (Beck et al., 1998). Relationships between prey variables and age-0 walleye growth would likely become increasingly more important if prey become limiting. Non-limiting prey sources would also explain why age-0 walleye growth was not density-dependent. The *a priori* assessments may not have included the best possible descriptor of age-0 walleye growth in Harlan County Reservoir. Other variables that could influence age-0 walleye growth are mean length of age-0 gizzard shad in October and densities of macroinvertebrates. Overall, this study adds to previous research supporting the importance of temperature on the growth of age-0 walleye, due to direct and indirect influences of temperature on metabolic rates, consumption, and lake productivity.

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