ARTICLE IN PRESS

Fisheries Research xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Research paper

Understanding the effects of density and environmental variability on the process of fish growth

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ARTICLE INFO

Handled by A.E. Punt

Keywords:
Fish growth
Density dependence
Environmental variation
von Bertalanffy model
Length-weight relationship
Bayesian statistics

ABSTRACT

For many fish species, variation in somatic growth can drive changes in population productivity through the dependence of survival, fecundity, and reproductive schedules on size. Changes in growth arise from many density-dependent and -independent sources. Many assessments of temporal variation in somatic growth rely on methods that lack biological underpinning in the model structure to describe observed relationships between size and environmental conditions. However, biologically-based growth models are needed to examine how density-dependent and − independent factors influence the underlying process of growth (i.e., growth = anabolic factors − catabolic factors). Our objective was to extend biologically-based growth models to estimate temporal variation in somatic growth patterns. A set of hierarchical non-linear mixed effects models based off the von Bertalanffy model and length-weight relationship were developed. We applied the models to a Black Crappie (BC; *Pomoxis nigromaculatus*) population to assess the impacts of density, chlorophyll A concentration (Chl-a), water level, and temperature on somatic growth. Growth in length was influenced by temperature, with fastest growth at optimal temperatures and slower growth when temperatures were coldest (48% slower) or hottest (82% slower), and was negatively related to density, with 25% slower growth at high density. Weight of age-0 BC was negatively related to chlorophyll A, individuals were 18% lighter at high Chl-a, and positively to temperature, individuals were 10% lighter when water was cooler. Finally, growth in weight of age-1 + BC was negatively related to all factors, with 5–11% lighter fish at high densities, Chl-a, water levels, and temperatures. The model structure developed in this manuscript has broad applicability to populations that have time series data of size-at-age observations, growth increments, or back-calculated sizes and adequate environmental data.

1. Introduction

Climate and ecosystem change impact aquatic population, community, and ecosystem dynamics through effects on hydrological and oceanic regimes, primary and secondary production, nutrient availability, trophic structure, and predator-prey relationships (see Rijnsdorp et al., 2009; Crozier and Hutchings, 2014). This will result in some populations having higher population growth rates than in current conditions due to longer or more productive growing seasons, decreased competition, predator reductions, etc. (Enberg et al., 2009; Crozier and Hutchings, 2014). Other populations will lose productivity due to prolonged periods of thermal stress, higher total mortality, increased competition, etc. (Enberg et al., 2009; Heino et al., 2013; Crozier and Hutchings, 2014). As environmental conditions and trophic structure change, life history traits within a population such as somatic growth, survival, fecundity and reproductive patterns may change. Detecting these changes in life history traits can be challenging. However, survival, fecundity, and reproductive schedules for many fish species depend on size and thus somatic growth patterns.

Somatic growth is an important process that influences population growth through survival, fecundity, and reproductive schedules (Stearns, 1992; Charnov, 1993; Roff, 1993). The relationships between size and survival, fecundity, and reproductive schedules have received much attention and are well-established for most teleost fishes. For instance, smaller individuals generally have high natural mortality, which decreases as individuals attain larger body sizes (Pauly, 1980; Lorenzen, 1996a, 2000). Fecundity is often assumed to be proportional to size (i.e., weight or length cubed; Beverton and Holt, 1957; Ricker, 1975; Walters and Martell, 2004). Finally, reproductive schedules (i.e., timing of maturation) are often directly dependent on size or implicitly

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http://dx.doi.org/10.1016/j.fishres.2017.08.018
Received 1 May 2017; Received in revised form 24 August 2017; Accepted 26 August 2017

Please cite this article as: Matthias, B.G., Fisheries Research (2017), http://dx.doi.org/10.1016/j.fishres.2017.08.018

dependent through the relationship between size and age (Dieckmann and Heino, 2007). Through these size-dependent relationships we can make predictions of how survival, fecundity, and reproductive schedules change if we can determine how density-dependent and −independent processes influence somatic growth.

Understanding and identifying the sources of variation in somatic growth patterns has been a major focus of fisheries ecology and population dynamics (e.g., Beverton and Holt, 1957; Lorenzen, 2016). For many fish populations density-dependent somatic growth in adults is a key regulatory process (Lorenzen and Enberg, 2002) and the effects of which are one of the best-established forms of density dependence (Beverton and Holt, 1957). Because somatic growth depends on food availability, reductions in per capita food availability lead to an inverse relationship between density and growth rates (e.g., Beverton and Holt, 1957; Post et al., 1999; Lorenzen and Enberg, 2002). Density-independent factors such as temperature, water clarity, water level, etc. also play major roles in the somatic growth of fish (e.g., Haugen et al., 2007; Vøllestad and Olsen, 2008; Davidson et al., 2010). Density-independent factors are expected to impact metabolic rates (Beverton and Holt, 1957; Lorenzen, 2016) and feeding rates/foraging efficiency (Gardner, 1981; Craig and Babaluk, 1989). Methods commonly used to assess the impacts of density-dependent and −independent processes are designed to identify the sources of variation in somatic growth patterns (e.g., ANOVA or multiple regression; Hale, 1999; Vøllestad and Olsen, 2008; Michaletz et al., 2012; Morrongiello et al., 2014). To further our understanding of how somatic growth patterns change through time, biologically-based models that incorporate density-dependent and −independent factors are needed.

By using biologically-based growth models, we can explore how density-dependent and − independent factors influence the process of somatic growth instead of just describing observed trends. When using ANOVA or multiple regression models to estimate somatic growth patterns we ignore the underlying biological process of growth (i.e., $\frac{dw}{dt} = HW_t^d - kW_t^n$; growth = anabolic factors − catabolic factors; from Beverton and Holt, 1957; Lorenzen, 2016) and instead describe the observed changes in length or weight over time (i.e., $\frac{dw}{dt} = W_{t+\Delta t} - W_t$; growth = weight at time $t + \Delta t$ − weight at time t). Several studies have modified biologically-based somatic growth models (i.e., the von Bertalanffy model) to estimate the effects of environmental variation on somatic growth (e.g., Dorn, 1992; Lorenzen, 1996b; Porch et al., 2002; Shelton et al., 2013). However, these studies have generally assessed a single factor (but see Dorn, 1992). In this manuscript, we extended the von Bertalanffy growth curve and standard allometric length-weight relationship to estimate the impacts of density and environmental variation on somatic growth patterns. This model was then applied to a Black Crappie *Pomoxis nigromaculatus* (hereafter referred to as BC) population in a north central Florida lake as a case study.

2. Methods

2.1. Case study

Lochloosa Lake is a 2310 ha hypereutrophic lake located in north central Florida. The lake is shallow (average depth of 1.7 m) and does not stratify (Tuten et al., 2008). The Lochloosa Lake BC population is characterized as having high total mortality, relatively few large fish, and high recruitment variation (Tuten et al., 2008; Allen et al., 2013). As a result, Lochloosa Lake BC provide a unique case study due to their relatively short life span (< 10 years in Lochloosa Lake) and highly variable recruitment allowing large fluctuations in population size over short time periods. North central Florida has experienced several droughts and hurricanes over the study period, resulting in a high level of environmental variation that allowed us to assess the impacts of fluctuating water levels on BC growth. There are no length limits on BC in Lochloosa Lake, but there is a daily bag limit of 25 fish. Annual angler effort on Lochloosa Lake has been found to be highly variable ranging from about to 5–23 h/ha between 2006 and 2010 (Allen et al., 2013).

2.2. Data

Black Crappie length (in mm), weight (in g), and age data were obtained from Florida Fish and Wildlife Conservation Commission (FWC) annual bottom trawl surveys (October or November 1998–2013; see Tuten et al., 2008, 2010 for description of trawl and trawling methods) and length and age data were obtained from FWC recreational catch sampling (January through April from 2006 to 2013) from Lochloosa Lake. For recreational catch sampling, 250–300 BC were annually sampled from discarded carcasses collected at fish camps and boat ramps on Lochloosa Lake (for detailed sampling methods see Wilson et al., 2015). Only trawl data from 2002 to 2013 were used to assess variation in the length-weight relationship because fish weights were not sampled prior to 2002 or from recreational catch samples.

Ages of 0 and 1-year-old fish from the trawl surveys were estimated by visually assessing the length-frequency distributions and verified using a subsample of aged fish (up to 10 were aged fish per cm group). Clear breaks in the length-frequency distributions were evident between age-0, age-1, and age-1+ fish and the aging subsample was used to confirm those breaks in the length-frequency distributions. It is important to note that no fish captured in the 1998–2000 and 2004 trawl surveys were aged, and ages of young-of-year fish were assigned only from the length-frequency distribution during these years. Small sample sizes of fish age-1+ fish prevented the use of length-frequency distributions to obtain ages of age-1 BC for the 1998–2000 samples. Adequate sample sizes and clear breaks in the length-frequency distribution in 2004 allowed us to assign ages for the 1-year-old fish using the length-frequency distribution. Fish sampled from both trawls and recreational catches, including the age-0 and 1 subsample, were aged using either whole or sectioned otoliths following Florida FWC protocols outlined in (Tuten et al., 2008, 2010). Briefly, two independent readers examined whole otoliths and if three or more annuli were found, one of the otoliths was sectioned. Ages, in months between hatching and capture date, were used in the analysis and all fish were assumed to have a birthdate of March 1st.

Water quality data (i.e., Chlorophyll A concentrations, turbidity, water level, and water temperature) were obtained from the St. John's Water Management District (2014). Collection methods followed the Florida Department of Environmental Protection field collection techniques (http://www.dep.state.fl.us/water/sas/sop/sops.htm). Water quality surveys were usually completed monthly or every other month from 1997 through present at the same location on the lake (Fig. 1). For the analysis, months that were not sampled were averaged over the two closest sample dates to obtain monthly estimates. Estimates of relative density were assumed to be proportional to the trawl catch per unit effort (CPUE) of all fish less than age-1 (hereafter referred to as age-0 trawl CPUE) and greater than or equal to age-1 during the specified year (hereafter referred to as age-1+ trawl CPUE; Fig. 1). All CPUE and environmental variables used in the model were standardized to have a mean of zero and a standard deviation of one to improve model convergence and stability. Preliminary analyses indicated that chlorophyll A concentrations (hereafter referred to as Chl-*a*) and turbidity were highly correlated ($R^2 = 0.77$) and turbidity was excluded from the analysis to aid model convergence. Therefore, Chl-*a* was used as indices of both productivity and water clarity.

2.3. Growth in length

An incremental formulation of the von Bertalanffy model was fitted to the combined length-at-age data from both gears using a Bayesian hierarchical mixed effects model to estimate impacts of density and environmental variation on length (i.e., skeletal growth). The predicted

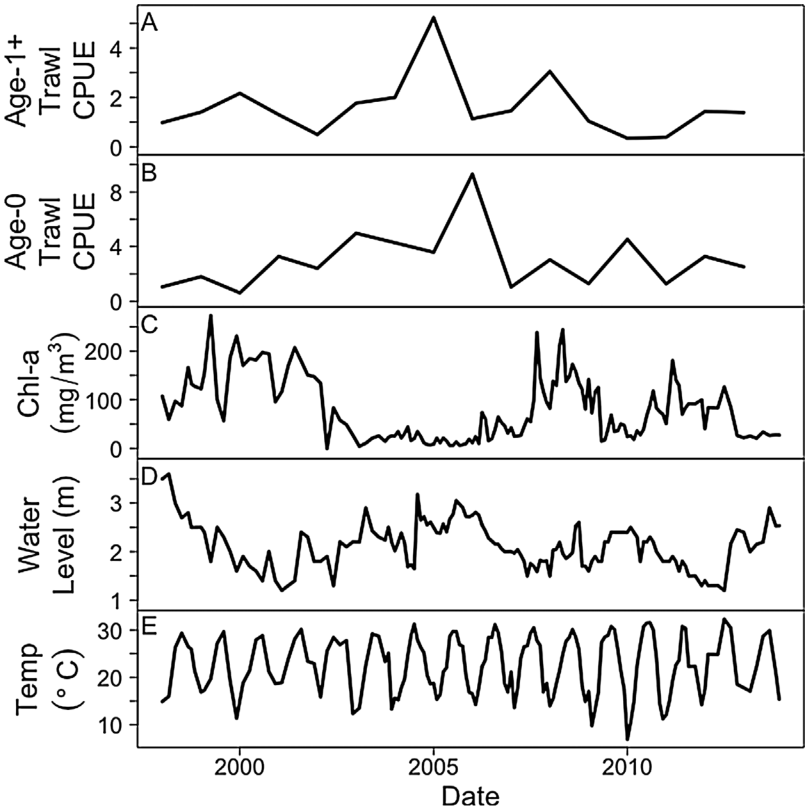

Fig. 1. Trawl catch per unit effort (CPUE) for ages greater than 1 and for young of year (Age-0) from annual FWC trawl surveys representing yearly and cohort-specific estimates of relative density (A and B), Chlorophyll A concentration (C), maximum depth (D), and water temperature (E), from 1998 through 2013 obtained from the St. John's Water Management District (2014).

length at age $a + 1$ (in months) for an individual in cohort c at time t ($L_{a+1,c}$) was calculated using

$$L_{a+1,c} = L_{a,c} + [(L_{\infty,c} - L_{a,c})^* \exp(\varphi_t)]^* \left[1 - \exp\left(-\frac{K_t}{12}\right)\right] \tag{1}$$

where $L_{a,c}$ is the predicted length at age a, $L_{\infty,c}$ is the cohort-specific asymptotic length representing the ratio between anabolism and catabolism, K_t (in years) is the Brody growth coefficient representing catabolism and a temperature effect between time t and $t + 1$, and φ_t is the time effect on the growth increment between time t and $t + 1$. Predicted length at age-0 was assumed to be 0 mm (i.e., $t_o = 0$) for simplicity and to aid in convergence. Following the arguments of Walters and Post (1993) and Lorenzen (2016), processes related to food acquisition and consumption (e.g., per capita prey availability, foraging efficiency, foraging rate, etc.) should have the greatest impact on anabolism, thus the ratio between anabolism and catabolism. Therefore, φ_t should impact $L_{\infty,c}$ or the increment ($L_{\infty,c} - L_{a,c}$), not catabolism K_t.

The incremental form of the von Bertalanffy model was used because it can be easily modified to account for changes in growth between time t and $t + 1$ (i.e., Δt). This can be accomplished by multiplying the predicted growth increment (i.e., the expected increase in length over Δt) by a lognormal regression $\exp(\varphi_t)$ representing conditions between time t and $t + 1$

$$\varphi_t = \begin{cases} \sum_{j=1}^{3} \beta_j x_{j,t}, & if \quad x_{4,t} < T^* \\ \sum_{j=1}^{3} \beta_j x_{j,t} + \beta_4 (x_{4,t} - T^*), & else \end{cases} \tag{2}$$

where the β_j s are regression coefficients for j = (1–4), $x_{j,t}$ is the condition (j) at time t (i.e., age 1+ trawl CPUE, Chl-a, water level, and temperature respectively), and T^* is the critical temperature at which temperatures above T^* impact the growth increment. Priors for β_j were uninformative [$\beta_j \sim N(0, 10^4)$]. The informative normal prior for T^* [$T^* \sim N(0.49, 300^{-1})$] was truncated to prevent negative values with a mean around 25 °C, which was 0.49 when standardized, and high precision to aid convergence because there were no observations from May through September when temperatures were the hottest. This temperature was chosen because it is close to optimal temperatures for juvenile growth (22–25 °C; Brungs and Jones, 1977) and preferred temperatures for both juvenile and adult BC (27–29 °C; Neill and Magnuson, 1974; Moyle, 2002). Additionally, maximum consumption in White Crappie *P. annularis* (hereafter referred to as WC) was found to be around 24 °C (Hayward and Arnold, 1996; Bajer, 2005) and temperatures above 26–28 °C have been found to decrease growth rates in Crappies *Pomoxis* spp. (Ellison, 1984; Hale, 1999; Michaletz et al., 2012).

In addition to the temperature effect on the growth increment, we chose to incorporate a temperature effect on K_t because it is proportional to catabolism (Beverton and Holt, 1957; Lorenzen, 2016). It is less likely that density, Chl-a, or water level would influence catabolism and thus were not included as effects on K_t (e.g., Beverton and Holt, 1957; Walters and Post, 1993; Lorenzen, 2016). The Brody growth coefficient was modified by temperature using the linear relationship

$$K_t = k + \beta_5 x_{5,t} \tag{3}$$

where k is the estimated Brody growth coefficient at the mean observed annual temperature, β_5 is the regression coefficient, and $x_{5,t}$ is the water temperature at time t scaled relative to the mean annual temperature. Uninformative gamma and normal priors were assumed for k and β_5 respectively [$k \sim Gamma(1,1)$ and $\beta_5 \sim N(0, 10^4)$]. Using a linear relationship between the Brody growth coefficient and temperature could result in negative values for K_t, which would result in negative growth. Preliminary analyses indicated that using a linear relationship did not result in negative values of K_t, therefore it was not necessary to constrain K_t to be positive for this analysis.

Temperature effects were incorporated on both the growth increment (Eq. (2)) and on the Brody growth coefficient (Eq. (3)) to approximate a dome-shaped temperature effect on growth (Parker, 1974).

We expected a positive relationship between temperature and K_t due to the increase in metabolic rates with temperature (i.e., positive β_5; Beverton and Holt, 1957). A two-part relationship between temperature and the growth increment was used to represent a decrease in growth at high temperatures (Eq. (2)). When temperatures were below T^*, there was no temperature effect on the growth increment. At temperatures above T^*, a temperature effect was implemented and we expect a negative impact on the growth increment (i.e., negative β_4).

To account for differences in the growth potential and variation around mean length-at-age, we estimated cohort-specific asymptotic length ($L_{\infty,c}$) and associated coefficient of variation ($l_{cv,c}$).

$$L_{\infty,c} \sim N(\overline{L}_{\infty}, \tau_{L_\infty}^{-1}) \tag{4}$$

$$\log(l_{cv,c}) \sim N(\overline{l_{cv}}, \tau_{cv}^{-1}) \tag{5}$$

Cohort-specific values are assumed random effects drawn from normal distributions with a mean of $\overline{L}_{\infty}$and a precision (inverse of variance) of τ_{L_∞} for asymptotic size and a mean of the logarithm of coefficient of variation of $\overline{l_{cv}}$ and a precision of τ_{cv}. The cohort-specific age-independent coefficient of variation was used to model a multiplicative error structure around the mean length-at-age relationships. Random effect priors were informed via uninformative hyper-parameters representing the population mean [$\overline{L}_{\infty} \sim N(0, 10^4)$and $\overline{l_{cv}} \sim N(0, 10^4)$] and precision [$\tau_{L_\infty} \sim Gamma(1,1)$ and $\tau_{cv} \sim Gamma(1,1)$] for each set of random effects. Using cohort-specific $L_{\infty,c}$ assumed a different growth potential for each cohort, but the average rate at which they approached $L_{\infty,c}$ remained constant over each cohort by using a global mean value for k. Attempts at estimating cohort-specific values for k did not converge.

A gear effect was incorporated into the likelihood component due to the selectivity of recreational anglers. Recreational anglers tend to harvest BC larger than 20 cm and select for older ages (ages 3–6; Miranda and Dorr, 2000; Wilson et al., 2015). The size selectivity of harvest-oriented fisheries tends to result in the removal of the largest individuals in the younger age classes (i.e., ages 2–3; Conover and Munch, 2002; Hamilton et al., 2007; Conover et al., 2009) and can lead to biased estimates of mean length at age for the age classes that are not fully vulnerable to harvest (Miranda et al., 1987). Separate likelihood functions were applied to describe the trawl-caught fish ($g_i = 0$) and angler-caught fish ($g_i = 1$) using a normal and truncated normal distribution respectively,

$$L_{a,c,i} \sim \begin{cases} N(L_{a,c}, L_{a,c}{*}l_{cv,c}) & if \quad g_i = 0 \\ N(L_{a,c}, L_{a,c}{*}l_{cv,c})\,T(L_{cap}, \infty) & if \quad g_i = 1 \end{cases} \tag{6}$$

where $L_{a,c,i}$ is the length-at-age observation of individual i, g_i represented the gear individual i was sampled with, L_{cap} is the lower bound used to truncate the normal likelihood for angler-caught fish and the function $T(L_{cap}, \infty)$ was used to truncate the normal distribution between L_{cap} and ∞. This method was similar to those developed by McGarvey and Fowler (2002) used for estimating the von Bertalanffy parameters in many commercially harvested species. An uninformative normal prior was used for L_{cap} [$L_{cap} \sim N(0, 10^4)$].

Attempts to estimate separate effects of density and environmental effects between age 0 and age 1+ BC did not converge, similar to methods used to estimate growth in weight (see below for description and justification). Therefore, we made the simplifying assumption that the impacts of density and environmental variation were not influenced by age or size.

2.4. Growth in weight

Variation in mean weight $W_{c,t}$ (i.e., fatness or condition) for cohort c at time t was assessed using a modified length-weight relationship

$$W_{c,t} = aL_{c,t,i}^{b_{c,t}} \tag{7}$$

where the log of scaling parameter a was given an uninformative normal prior [$\ln(a) \sim N(0, 10^4)$], $b_{c,t}$ is a shape parameter, and $L_{c,t,i}$ is the length-at-weight observation. Following the arguments used in the derivation of the von Bertalanffy model (i.e., $W = aL^3$) the a parameter is a product of specific gravity, a conversion factor, and a space factor that represents the fraction of a cube an individual of length L would occupy if we assume isometric growth (i.e., $b = 3$; Beverton and Holt 1957). When assuming allometric growth (i.e., $b \neq 3$), either specific gravity or the space factor needs to change as a function of length because a cubic relationship is needed to convert length to weight (i.e., $mm^3 \Rightarrow g$). This results in

$$W = (aL^x)L^3 = aL^{3+x} = aL^b \tag{8}$$

where W represents weight, a, x, and b are scaling factors describing specific gravity, a conversion factor, and body shape [from the Beverton and Holt (1957) derivation of the von Bertalanffy model]. Assuming specific gravity is independent of length, then $3 + x$, or b, describes both allometric growth (i.e., the average body shape of the population or species) and the volume occupied by an individual because a skinny fish occupies less space than a fat fish. Thus, a was assumed to remain constant over time as it is a function of specific gravity and converts cubic length to the appropriate unit of weight (e.g., millimeters to grams, centimeters to kilograms, etc.).

The model incorporated changes in the shape parameter describing fish body shape (e.g., b) using a fixed effects regression

$$b_{c,t} = \begin{cases} \bar{b} + \sum_{j=1}^{4} \alpha_j^* x_{j,t}, & if \quad age_i < 1 \\ \bar{b} + \sum_{j=1}^{4} \alpha_j x_{j,t}, & else \end{cases} \tag{9}$$

where $\bar{b}$ is the mean body shape parameter, α_j^*s and α_js are the regression coefficients, and $x_{j,t}$ is the condition (j) at time t (i.e., trawl CPUE, Chl-a, water level, and temperature respectively). Trawl CPUE were divided into age-0 and age-1+ to differentiate between density effects for young-of-year fish and fish older than age-1. Regression coefficients for the environmental effects were also divided into young-of-year and age-1+ to determine if the impacts of environmental factors change after age-1. This cutoff was chosen because zooplankton and macroinvertebrates are the major diet components of BC less than 14 cm (Keast, 1968; Tuten et al., 2008) and age-0 BCE from the trawl samples were between 6 and 14 cm. Black Crappie begin to prey on fish between 14 and 20 cm (Keast, 1968; Tuten et al., 2008) and about 76% of BC trawl samples and 92% of all samples for age-1+ BC were larger than 14 cm, indicating a dietary shift between age-0 and age-1. This same cutoff was used for the environmental effects as dietary shifts are often associated with changes in habitat (for review see Werner and Gilliam, 1984). Chlorophyll A, water level, and temperature were averaged over the year prior to the trawl sample because weight data were not obtained from recreational catches. The averaged effects were standardized to have a mean of zero and a standard deviation of one to aid in convergence. All regression coefficient priors were used in the model were uninformative [$\bar{b} \sim N(0, 10^4)$, $\alpha_j^* \sim N(0, 10^4)$, and $\alpha_j \sim N(0, 10^4)$].

A normal likelihood was used to describe the error structure around the mean weight-at-length

$$W_{c,t,i} \sim N(W_{c,t}, W_{c,t}{*}w_{cv}) \tag{10}$$

where $W_{c,t,i}$ is the observed weight of individual i and w_{cv} is the coefficient of variation to incorporate a multiplicative error structure around the length-weight relationship. An uninformative gamma prior was used for the precision of the coefficient of variation [$w_{cv}^{-1} \sim Gamma(1,1)$]. A single coefficient of variation with an uninformative prior was used to describe the uncertainty around the weight-at-length relationship.

We did not conduct a model-selection framework in this analysis, instead we tested the effects of the hypothesized growth determinants using a biologically-based growth model. This model was fit in program R version 3.1.3 using runjags version 3.3.0 (R Development Core Team, 2013; Denwood, 2016). It was fit using four MCMC chains, a burn-in period of 1000 iterations, posterior distributions were sampled for one million iterations with a thinning rate of one hundred, and random starting values were used for the different chains. Convergence of the posterior distribution was verified using Gelman and Rubin diagnostics (Gelman and Rubin, 1992; Brooks and Gelman, 1998) and trace plots for each parameter were visually inspection to ensure adequate mixing and no trends.

3. Results

A total of 6195 Black Crappie were sampled with 4156 (67%) from FWC trawl surveys from 1998 to 2013 and 2039 (33%) from recreational catch samples from 2006 to 2012. The trawl survey selected primarily for young (less than age-3), but did catch larger and older fish as well. Recreational anglers selected for larger, older fish (greater than age-3). Trawl CPUE for age-1+ BC were highest in 2005 and 2008, indicating years of high relative densities, and appeared to be low in 2002, 2010, and 2011, indicating years of low relative densities (Fig. 1A). Age-0 trawl CPUE varied through time with an exceptionally large recruiting class in 2006 and relatively large cohorts in 2003, 2004, and 2010 (Fig. 1B). It is important to note that the 2007 age-1+ trawl CPUE was not high given the size of the 2006 cohort. However, the 2006 cohort accounted for about 78% of the age-1+ trawl CPUE in 2007. Chl-*a* concentrations were quite variable between 1998 and 2013 (Fig. 1C) ranging from 0 to 273 $\mathrm{mg/m^3}$ and were, on average, higher from 1998 to 2002 with another peak between 2008 and 2009 (Fig. 1C). Water level at the sample station ranged from 1.2-3.6 m and fluctuated throughout this period (Fig. 1D). Water temperature seasonally fluctuated, with maximum summer water temperatures remaining relatively consistent each year between 28 and 32 °C and minimum winter water temperatures reaching between 7 and 18 °C (Fig. 1E).

Mean observed length of age-0 BCE, sampled when they were approximately 8 months old, ranged from 7.7 to 11.3 cm (Fig. 2A). The 2001 and 2012 cohorts had the highest average length and the 2004, 2010, and 2011 cohorts had the smallest average length (Fig. 2A). Mean weight of age-0 BCE ranged from 7.5 to 22.0 g (Fig. 2B). The 2002 and 2010 cohorts had the highest and lowest mean age-0 weights, respectively (Fig. 2B). Mean weight of age-1 BCE, which were approximately 20 months old, ranged from 30.6 to 154.6 g (Fig. 2C). The 2009 and 2004 cohorts had the highest and lowest mean age-1 weights, respectively (Fig. 2C).

3.1. Growth in length

Population-level von Bertalanffy parameter estimates were 32 cm for $\overline{L}_\infty$, 0.64 yr^{-1} for *k*, and 0.13 for $\overline{l_{cv}}$ (Table 1). Anglers caught larger fish than the trawl at younger ages, and the model accounted for this bias by estimating a lower capture limit of 15.3 cm for recreational anglers (i.e., lower bounds used to truncate the likelihood for angler-caught fish; Table 1). Density (i.e., age 1+ trawl CPUE) and temperature influenced BC growth in length, but Chl-*a* and water level did not influence growth in length (i.e., the 95% credible intervals for the regression coefficients contained zero; Table 1; Fig. 3A–D). Growth in length decreased with age 1+ trawl CPUE with predicted length at age-1 ranging from about 18 cm at low CPUE to 13 cm at high CPUE (growth in length was arbitrarily represented as length at age-1 in Fig. 3A). Growth in length increased with temperatures up to a T^* of 0.57 (from 9 cm at 7.0 °C to 17 cm at 25.5 °C) and subsequently decreased at temperatures above T^* (from 17 cm at 25.5 °C to 3 cm at 32.3 °C; Fig. 3D). The increased growth at lower temperatures corresponded with the increase in K_t with temperature (i.e., positive β_5) and the subsequent decrease at higher temperatures corresponded with negative impacts of temperature on the growth increment (i.e., negative β_4; Fig. 3D). Convergence was achieved (i.e., Gelman Rubin diagnostics were between 1.000 and 1.001 and trace plots were well-mixed without any trends) for all von Bertalanffy parameters and regression coefficients for growth in length.

3.2. Growth in weight

Population-level weight-length parameter estimates were −12.6 for ln(*a*), 3.24 for $\overline{b}$, and 0.13 for w_{cv} (Table 1). Growth in weight for age-0 fish was influenced by Chl-*a* and water temperature, but not age-0 trawl CPUE or water level (Table 1; Fig. 3E–H). Predicted weight at age-1 (arbitrarily selected to represent growth in weight of age-0 fish) showed fatter fish as a result of low Chl-*a* concentrations (47 vs. 38 g) and high water temperatures (45 vs. 40 g; Fig. 3F and H). Density (age-1+ trawl CPUE) and all environmental variables negatively influenced the growth in weight of for BC greater than age-1 (Table 1; Fig. 3I–L). Predicted weights for an average age-2 BCE (arbitrarily chosen to represent age-1+ growth in weight), showed fatter fish at lowest age-1+ trawl CPUE (177 vs. 158 g), Chl-a (174 vs. 160 g), water levels (176 vs. 158 g), and temperatures (172 vs. 162 g; Fig. 3I–L). Convergence was achieved for all weight-length parameters and regression coefficients for growth in weight.

3.3. Model fit and residuals

The model captured cohort-specific growth trajectories for all cohorts, regardless of sample size or age distribution (Fig. 4). The mean length-at-age of older (age 2 or 3+) individuals in the 2003, 2004, and 2010 cohorts were underestimated (Figs. 4 and 5). For the 2003 and 2004 cohorts there were high numbers of fish aged 2.6–2.8 years and 1.6 years of age that were below the predicted mean length-at-age, which is difficult to see in the length-at-age plot (Fig. 4), but is easier to see when comparing observed against predicted values (Fig. 5). Comparing the observed against the predicted values for the length-weight relationship showed that the model underestimated weight of the largest fish for the 2001, 2005, 2006, 2007, and 2010 cohorts (i.e., the smoothed fitted line was above the ideal 1:1 line; Fig. 6). Some of these cohorts had small sample sizes of large fish, specifically the 2005 and 2007 cohorts

4. Discussion

The von Bertalanffy model is the most widely used growth model in fisheries (Lorenzen, 2016), but we have only found one other study that has used a modified von Bertalanffy model to detect the impacts of multiple density-dependent and −independent processes on fish growth (i.e., Dorn, 1992). Our results show that biologically-based growth models can be used to detect changes in somatic growth patterns from multiple density-dependent and −independent sources. Applying these models to a BC population, we estimated the impacts of density, Chl-*a*, water level and temperature on growth in both length and weight. For BC, temperature had the largest impact on growth in length, with the fastest growth near optimal temperatures and slowest growth when temperatures were hottest. Chl-*a* had the greatest impact on growth in weight of age-0 fish, with a negative relationship between Chl-*a* and weight. All factors had relatively similar effect sizes on growth in weight of age-1+ fish and all had negative relationships between the effect and weight of age 1+ fish. Methods similar to those developed here need to become more common to further our understanding of how density-dependent and -independent factors influence the process driving fish growth.

Relatively few studies have assessed temporal trends in density-dependent growth in BC. Black Crappie experience highly variable

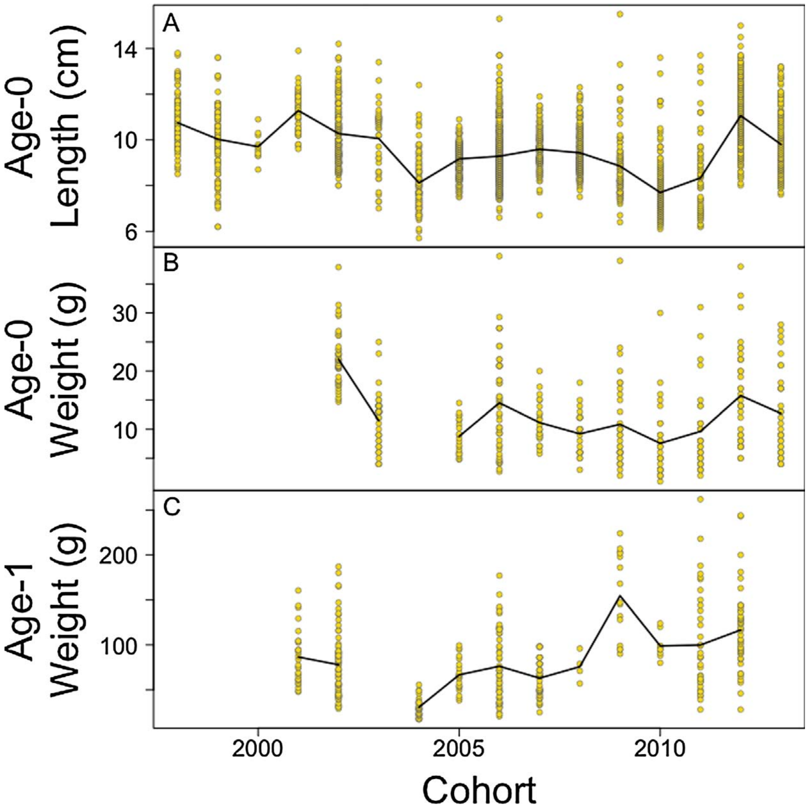

Fig. 2. Observed (circles) and mean (black lines) age-0 length (measured at approximately 8 months old; A), age-0 wt (B), and age-1 wt (measured at approximately 20 months old; C) of Black Crappie for the 1998–2013 cohorts.

Table 1
Parameter estimates and 95% credible intervals (CI; in parentheses) from the von Bertalanffy model and the length-weight relationship along with their associated fixed effects regression coefficients representing density and environmental effects. Regression coefficients in bold are different from zero.

Component	Est.	(95% CI)
von Bertalanffy Parameters		
$\overline{L}_\infty$ (cm)	32.3	(30.6, 33.8)
k (yr^{-1})	0.643	(0.604, 0.684)
$\overline{l_{cv}}$	0.129	(0.104, 0.161)
L_{cap} (cm)	15.2	(15.1, 15.3)
$\tau_{L\infty}$	0.001	(0.001, 0.002)
τ_{cv}	5.748	(2.624, 10.592)
Length-Weight Parameters		
ln(a)	−12.6	(−12.7, −12.5)
$\overline{b}$	3.244	(3.242, 3.264)
w_{cv}	0.128	(0.123, 0.134)
Regression Coefficients (Length)		
β_1–Age-1 + Trawl CPUE	**−0.073**	**(−0.083, −0.065)**
β_2 − Chl-a	0.001	(−0.019, 0.016)
β_3 − Water Level	0.009	(−0.011, 0.030)
β_4 − Temperature (inc.)	**−1.327**	**(−1.651, −1.011)**
β_5 − Temperature (K_t)	**0.164**	**(0.129, 0.200)**
T^* − Critical Temperature	**0.573**	**(0.552, 0.601)**
Regression Coefficients (Age 0 Weight)		
α_1^* − Age-0 Trawl CPUE	0.001	(−0.002, 0.004)
α_2^* − Chl-a	**−0.010**	**(−0.016, −0.004)**
α_3^* − Water Level	−0.003	(−0.009, 0.003)
α_4^* − Temperature	**0.005**	**(0.003, 0.007)**
Regression Coefficients (Age 1 + Weight)		
α_1 − Age-1 + Trawl CPUE	**−0.005**	**(−0.007, −0.003)**
α_1 − Chl-a	**−0.004**	**(−0.007, −0.001)**
α_1 − Water Level	**−0.005**	**(−0.009, −0.001)**
α_1 − Temperature	**−0.003**	**(−0.004, −0.001)**

growth patterns, and several studies have assessed the density-growth relationship across water bodies (Guy and Willis, 1995; Allen et al., 1998; Pope et al., 2004), but none of these evaluated temporal trends. Similar to studies of other species (e.g., Beverton and Holt, 1957; Walters and Post, 1993; Post et al., 1999; Lorenzen and Enberg, 2002; Sass et al., 2004; Casini et al., 2014), higher relative densities of BC within a year were associated with decreased growth in length and weight of age-1+ fish. Growth in weight of age-0 BCE was not influenced by age-0 trawl CPUE, suggesting that prey resources were not limiting until fish entered into diets between 14 and 20 cm (Keast, 1968; Tuten et al., 2008) or after the first year for Lochloosa Lake BC. We were unable to test for a growth shift after age-1 for the length analysis and it would be beneficial for future studies to explore this.

One of the most important and well-studied environmental factors influencing growth is temperature because it influences consumption, metabolism, and behavior of fish (Fry, 1947; De Staso and Rahel, 1994; Kazyak et al., 2014). The relationship between growth rate and temperature is generally observed to be dome-shaped, with the highest growth rates at an optimal temperature and decreasing growth rates as temperatures deviate from optimal (Parker, 1974), which was modeled using a 2-part function with temperature effects on both the Brody growth coefficient and the growth increment. We used an informative prior on T^* and length-at-age observations between May to September will be needed to estimate this parameter without the informative prior. A positive relationship between temperature and growth in weight for age-0 BCE was identified, but found a negative relationship for age-1+ BC. This would suggest age- or stage-based temperature selection and it would be interesting if future studies could detect similar trends with growth in length.

Increased temperatures from climate change could lead to increased growth rates for some species (e.g., Haugen et al., 2007; Vøllestad and Olsen, 2008; Davidson et al., 2010; Morrongiello et al., 2011, 2014) or decreased growth rates for species in which water temperatures exceed optimal growth for part of the year (e.g., Hayward and Arnold, 1996; Hale, 1999; Michaletz et al., 2012; Kazyak et al., 2014). Lochloosa Lake

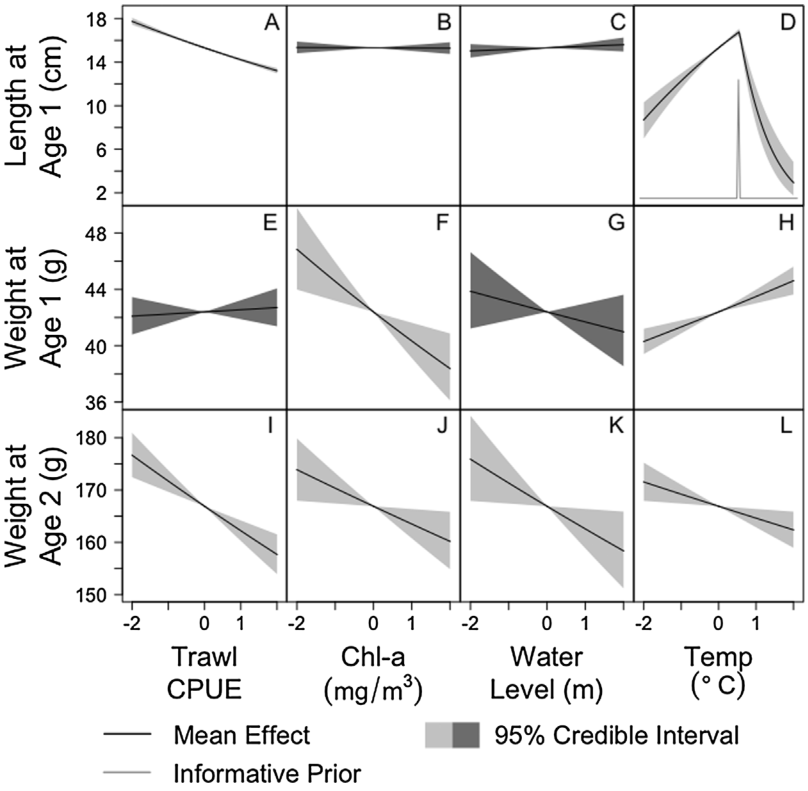

Fig. 3. Fixed effects on mean length at age-1 (panels A–D), mean weight at age-1 (representing age-0 effects; panels E–H), and mean weight at age-2 (representing age-1+ effects; panels I–K) of Lochloosa Lake Black Crappie. Predicted values are over the ranges of effects (standardize between −2 and 2) while holding all other effects at the mean value (i.e. zero). Black lines represent the mean effects, light grey shading indicates credible intervals that do not contain zero, and dark grey shading indicates credible intervals that contain zero. The grey line (panel D) represents the distribution of the informative prior on critical temperature (T^*).

BC experienced temperatures above optimal for about four months per year (e.g., temperatures exceeding 25.5 °C) and temperatures above 30 °C almost yearly between 2004 and 2012. Higher maximum water temperatures and/or prolonged periods of temperatures above optimal and would be expected to decrease growth in length of BC. However, reductions in growth during the hottest months could be offset by increased water temperatures during the other seasons when temperatures would be below optimal. This highlights the need to account for increased growth during months below optimal temperatures and decreased growth during months when temperatures are above optimal

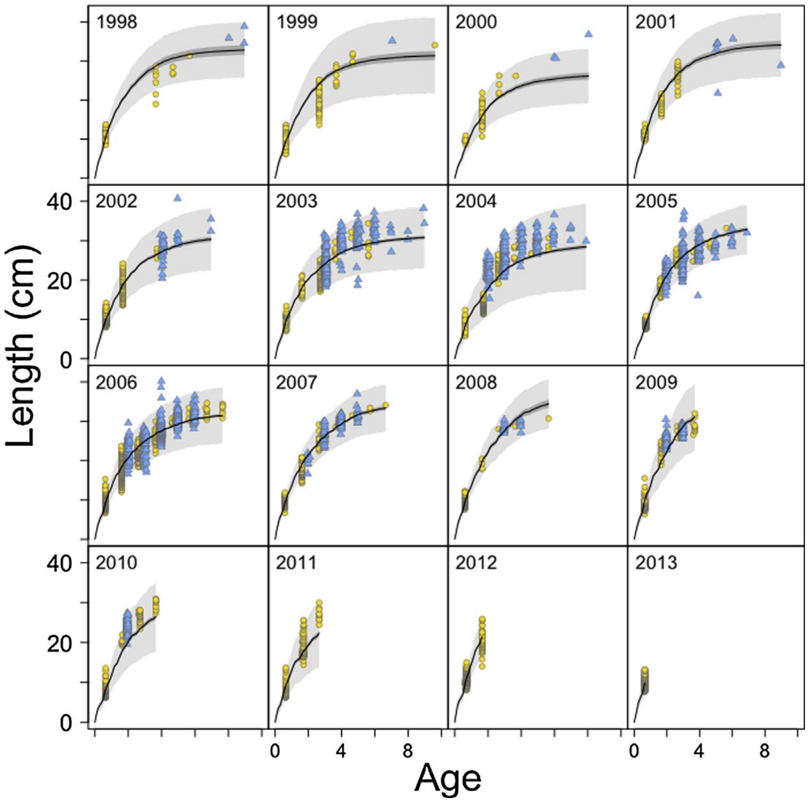

Fig. 4. Predicted cohort-specific von Bertalanffy growth curves (solid black lines) with 95% credible intervals for the mean length-at-age (dark grey area) and for observations (light grey area) for Black Crappie caught by trawling (yellow circles) and recreational anglers (blue triangles) for 1998–2013 cohorts. Dashed lines represent the mean growth curves without fixed or random effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

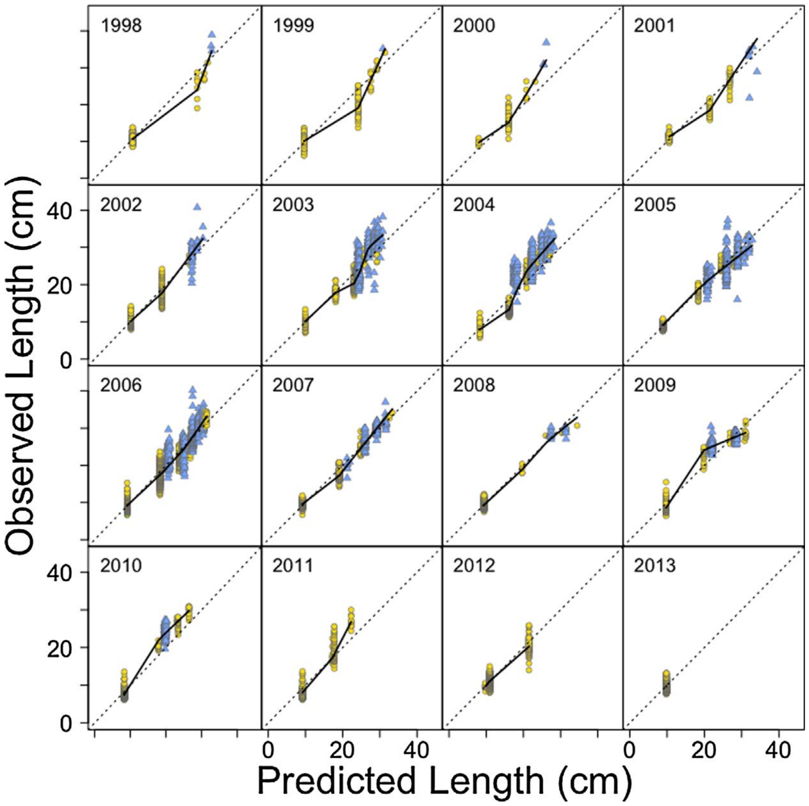

Fig. 5. Observed versus predicted length-at-age for Black crappie sampled by trawling (yellow circles) and recreational anglers (blue triangles) for 1998–2013 cohorts. Solid lines represent Lowess smoothers and the dotted lines are 1-to-1 lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

when making predictions about the effects of climate change.

Chlorophyll A has been used as an index of system productivity and is often positively correlated with growth in fish (Tomcko and Pierce, 2005; Wagner et al., 2007; Schultz et al., 2008; Hoxmeier et al., 2009). The link between Chl-*a* and BC is thought to be through increased zooplankton biomass as a result of increased prey resources for zooplankton (Pace, 1986; Bunnell et al., 2006) and should lead to increased growth when BC prey on zooplankton (i.e., at young ages; Keast, 1968; Tuten et al., 2008). In this study, Chl-*a* had a negative impact on BC growth in weight for all ages, but no impact on growth in length. This

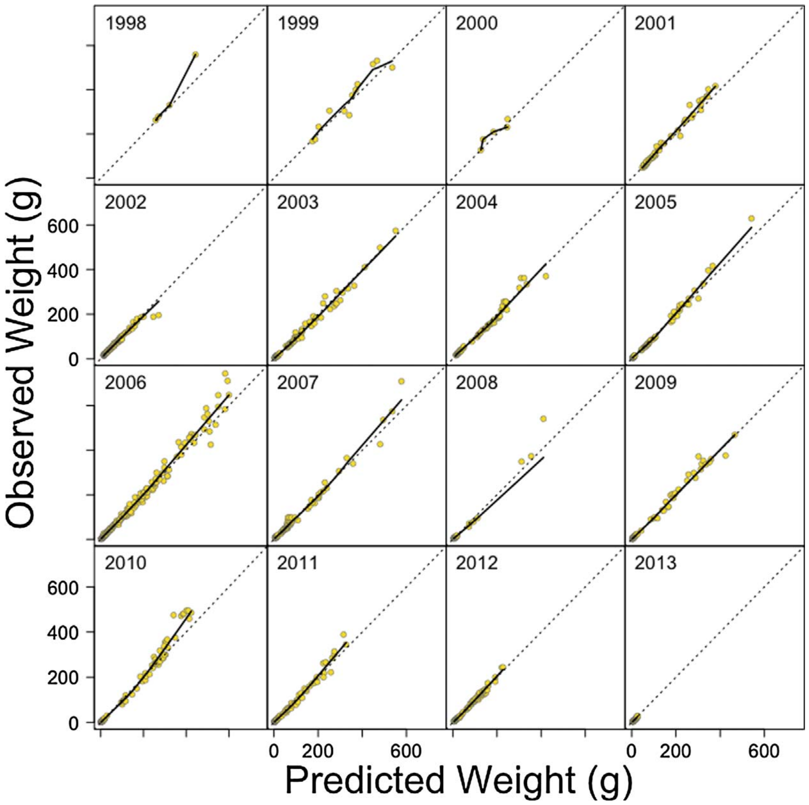

Fig. 6. Observed versus predicted weight-at-length for Black crappie sampled by trawling (yellow circles) for 1998–2013 cohorts. Solid lines represent Lowess smoothers and the dotted lines are 1-to-1 lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

could have resulted from the relationship between Chl-*a* and turbidity/water clarity ($R^2 = 0.77$ from preliminary analyses). Numerous studies have assessed the impacts of water clarity on fish growth and foraging efficiency. For many species including BC, decreased water clarity has been found to decrease the activity of visual predators, foraging efficiency, reactive distances, and feeding rates (Moore and Moore, 1976; Vinyard and O'Brien, 1976; Ellison, 1984; Miner and Stein, 1993). Additionally, Hydrilla *Hydrilla verticillata*, an invasive submersed aquatic plan present in Lochloosa Lake, also negatively interacts with Chl-*a*, turbidity and water clarity (Canfield et al., 1983, 1984) and studies have shown increased BC growth after Hydrilla removal (Maceina and Shireman, 1982; Maceina et al., 1991). Therefore, relationships between Chl-*a* and growth in both length and weight observed in this study were likely impacted by turbidity and the presence of Hydrilla in Lochloosa Lake.

Effects of fluctuating water level in lakes on growth have received much less attention than other environmental factors, but is of increasing importance due to predicted increase of droughts due to climate change (Lake, 2011; Romm, 2011). Reductions in lake levels often decrease the amount of littoral habitat available (Ficke et al., 2007; Lake, 2011) due to the loss of important structures such as fallen trees (Gaeta et al., 2014). Consistent with a study on Largemouth Bass *Micropterus salmoides* (Gaeta et al., 2014), reductions of growth in weight of age-1 + BC were associated with decreased water levels. However, no significant effects for growth in length or weight for age-0 BCE were identified from changes in water levels observed in this study. Morrongiello et al. (2011) found similar results for Golden Perch *Macquaria ambigua,* where water level (indexed by cumulative changes in lake level) did not significantly impact growth in length. They assessed otolith growth increments and suspected that the yearly scale was too coarse to detect impacts of within-season water level changes. Given the annual sampling schedule from 1998 to 2005 and sampling between October and April starting in 2006, it is also possible that this temporal scale was too coarse to detect changes in growth in length for BC. With the prospects of increased environmental variability along with increased duration of droughts and wet periods (IPCC, 2015), future studies may need to consider finer temporal resolution to detect the effects of water level on growth.

Several major assumptions were made using this model. Some of the assumptions were addressed in the methods. However, we think it is appropriate to further address some concerning the length-weight relationship and interactions between explanatory variables. Many studies use the Fulton condition factor (i.e., $\kappa = 100WL^{-3}$) to represent changes in condition through time, which assumes isometry ($b = 3$; see Froese, 2006 for review or Thorson and Minte-Vera, 2016). By assuming growth is allometric ($b \neq 3$), we are essentially assuming the Fulton condition factor changes as a function of length. For fish species that do not follow isometric growth, using the Fulton condition factor will introduce systematic bias when comparing individuals across a wide range of sizes (Clark, 1928). The assumption of constant *a*, representing specific gravity and a conversion factor, might not be appropriate when comparing individuals across seasons due to differences in seasonal gonad development (e.g., pre-spawn vs. post-spawn), differences between the specific gravity of male and female gonads, changes in individual fat content, or muscle mass. However, Le Cren (1951) points out that changes in the length-weight relationship are likely due to changes in the volume occupied, not specific gravity. Impacts of seasonal variation in *a* for this study were likely minimal because weights were only sampled in the fall. Finally, we chose to ignore interactions between environmental/density effects to aid in model convergence. Future studies should focus on identifying temporal changes in specific gravity and testing for interactions between variables using models similar to those developed in this manuscript.

Studies assessing the impacts of environmental variation or density often use methods such as comparing growth over large spatial areas (e.g., Donald et al., 1980; Guy and Willis, 1995; Allen et al., 1998; McInerny and Cross, 1999; Hoxmeier et al., 2009; Gertseva et al., 2010; Casini et al., 2014) or growth increment analyses to assess temporal changes in growth. Growth increments can be obtained via mark recapture methods (e.g., Haugen et al., 2007; Vøllestad and Olsen, 2008; Davidson et al., 2010; Kazyak et al., 2014) or by using back-calculation methods (e.g., Maceina and Shireman, 1982; Maceina et al., 1991; Morrongiello et al., 2011; 2014; Urbach et al., 2012; Glover et al., 2013). Often, growth increment analyses use ANOVA or multiple regression to determine the impacts of environmental conditions on growth. The methods developed in this manuscript can be applied to mark-recapture or back-calculation data, but might require additional parameters to account for variation between individual fish (i.e., Kimura, 2008). We used a time series of individual length-at-age and length-weight observations to test for changes in growth using the von Bertalanffy model and length-weight equation. Many populations already have this type of data, therefore constructing models similar to those developed in this manuscript will be relatively easy if there are adequate environmental data.

Acknowledgements

We thank John Walter from the National Marine Fisheries Service and the reviewers of this manuscript for revisions that helped improve this manuscript. This study was funded through the National Marine Fisheries Service Recruitment Training and Research Program, grant number NA11NMF4550121, in collaboration with the University of Florida.

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