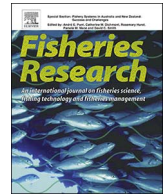




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Research paper

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

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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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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

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