ECOLOGY OF
FRESHWATER FISH

Climate–growth relationships for largemouth bass (*Micropterus salmoides*) across three southeastern USA states

Abstract – The role of climate variability in the ecology of freshwater fishes is of increasing interest. However, there are relatively few tools available for examining how freshwater fish populations respond to climate variations. Here, I apply tree-ring techniques to incremental growth patterns in largemouth bass (*Micropterus salmoides* Lacepède) otoliths to explore relationships between annual bass growth and various climate metrics in the southeastern USA. Among six rivers and seven reservoirs in Georgia, Alabama, and Mississippi, strong correlations between annual bass growth indices and climate were detected (73 of 96 possible correlations were significant at $\alpha < 0.05$). All but two ecosystems exhibited the following pattern: annual bass growth was significantly negatively correlated with annual precipitation metrics, and significantly positively correlated with annual temperature metrics. Based on multiple regressions, climate, on average, accounted for ~50% of variability (R^2) in bass growth, although these values ranged from 28% to 65% depending on the ecosystem. Furthermore, every population showed significant correlations with at least one of the following global climate factors: El Niño-Southern Oscillation (ENSO), North Atlantic Oscillation (NAO), and the Arctic Oscillation (AO). Largemouth bass growth in the southeast is apparently influenced by climate in major ways. Fish ecologists and managers in the region should be aware of the strong links between annual climate conditions and annual fish growth.

Andrew L. Rypel

Biology Department, The University of Mississippi, USDA Forest Service Stream Hydrology Lab

Introduction

Climate variations are increasingly viewed as central drivers of the structure, function, and long-term stability of aquatic ecosystems (Stenseth et al. 2002; Ficke et al. 2007; Black et al. 2008). Aquatic food webs are constantly being modified by combinations of bottom-up, top-down and middle-out trophic processes that are mediated through climate (Kitchell & Carpenter 1993; Vanni & Layne 1997; Francis et al. 1998). For example, patterns of upwelling, nutrient availability, net primary production, and fishery production throughout the Pacific Ocean are driven by ocean currents (Glynn 1988; Mantua et al. 1997).

Climate also influences the birth and death rates of many primary and secondary consumer species (Stenseth et al. 2002; Leaper et al. 2006), and thus the trophic interactions that occur between these organisms in food webs. Climate change threatens to alter many of these relationships and may consequently destabilise numerous aquatic ecosystems (Power et al. 1996; Wilcove et al. 1998; Rahel & Olden 2008). A comprehensive knowledge of climatic impacts is essential for the future conservation and management of aquatic biodiversity and ecosystems. A key step in this process is the development of more tools that can be used to assess how climate variations affect freshwater ecosystems and fishes.

Recently, a novel science has emerged that applies tree-ring techniques to the growth rings of aquatic taxa, e.g., in mussel shells (Schöne 2003; Rypel et al. 2008, 2009), fish otoliths and fins (LeBreton & Beamish 2000b; Black et al. 2008), and coral skeletons (Schuhmacher et al. 1995; Lazier et al. 1999). Tree rings have long been used in terrestrial ecology to reconstruct climate variation, place contemporaneous climate observations within a historical context, and gain an appreciation for the role of climate in the development and dynamics of forest ecosystems (Douglas 1921; Fritts 1971; Cook et al. 2007). In addition to climate reconstructions, these same techniques hold promise for establishing the effects of climate on growth in more ecologically-oriented investigations. Black et al. (2008), used tree-ring techniques to show how marine fish populations in California and Alaska responded differently, in terms of annual growth, to different ocean current regimes. Studies of the Holarctic pearl mussel (*Margaritifera margaritifera*) and ocean quahog (*Arctica islandica*) in Europe, and on the freshwater mussels in North America have also linked growth variations to diverse climate conditions (Witbaard 1996; Schöne et al. 2003, 2004; Dunca et al. 2005; Rypel et al. 2008). Other studies have used tree-ring approaches to illustrate the complex relationships between growth and climate that characterise neighbouring/connected riparian and riverine ecosystems (Guyette & Rabeni 1995; LeBreton & Beamish 2000a; Drake & Naiman 2007; Rypel et al. 2009).

Although some of the original sclerochronology research examined growth variations in long-lived freshwater fishes (Pereira et al. 1995), many recent studies have favoured long-lived bivalve mussels and marine fishes (but see Smith et al. 2008). This is perhaps because longer growth chronologies for these taxa (e.g., in the 100s of years for bivalves) facilitates more statistically robust correlations between annual growth and climate variables. However, longevity is not a necessity for the development of growth chronologies. Schöne et al. (2003) developed useful growth chronologies, as short as 6 years, for an estuarine mussel population, and Rypel et al. (2008) assembled growth chronologies as short as 8 years for freshwater mussel species. Most of the world's freshwater fish diversity is composed of species with lifespans that rarely exceed 20 years (Das 1994).

The goal of this study was to establish growth-climate relationships for a ubiquitous sportfish, the largemouth bass (*Micropterus salmoides* Lacepède) in southeastern USA waterbodies using tree-ring techniques. Growth chronologies were developed for individuals from six rivers and seven reservoirs across three southeastern USA states, and correlated to local observations of temperature, precipitation, flow (for rivers), and global climate factors. Multiple linear regression models for each population were also constructed to evaluate how strongly climate variations predicted bass growth.

Materials and methods

Adult largemouth bass populations were sampled from six rivers and seven reservoirs throughout southeastern USA during the summer and autumn of 2005–2008. Individuals were collected using Smith Root® boat-mounted electrofishers and DC pulsed current. Each fish was measured (total length, TL, mm), weighed (g) and stored on ice for transport back to a laboratory. In the laboratory, otolith sagittae were extracted, sterilised in isopropyl alcohol, and stored in coin envelopes prior to incremental growth analysis. The annual periodicity of growth-increment formation has been validated for largemouth bass by a number of independent studies (Taubert & Tranquilli 1982; Hoyer et al. 1985; Buckmeier & Howells 2003).

Each otolith was cross-sectioned using standard methodology (Maceina 1988). Annual growth increments were identified and measured using a binocular microscope and digital camera interfaced with video imaging software. Growth increments were measured on a standardised transect so that samples could be compared without variation in measurement because of transect location. For each fish, measurements began the margin (i.e., the outermost growth increment) and proceeded towards the core (i.e., the inner most annulus), so as to associate calendar years with each annual growth increment. Each sample was interpreted by two independent readers.

All otoliths were then crossdated both visually and statistically to ensure that each increment was assigned the proper calendar year. Each sample was first visually crossdated using the list-year method (Yamaguchi 1991). This is a simple method used in tree-ring science, whereby calendar years with relatively narrow (and/or wide) ring widths are cross-matched among samples to ensure all growth increments have been correctly identified. Otolith samples were then crossdated again statistically using the dendrochronology program COFECHA (Holmes 1983; Grissino-Mayer 2001). The COFECHA routine is a standard tree-ring crossdating procedure in which each measurement series is detrended using a cubic spline and the detrended measurement time-series correlated to a master growth chronology (the average of all detrended measurement time-series in a fish population minus the individual being examined) to see how synchronous each sample is with the master chronology of the population (Holmes 1983; Grissino-Mayer 2001). A lack of synchrony (i.e., a low correlation, R) suggests a potential error, and that sample should be re-examined.

An error is strongly suggested when the R-value improves significantly when an individual detrended time-series is lagged by ±1 or 2 years which suggests rings may have been missed or added. In this study, a 50% cutoff value of 15 years was chosen over the default value of 32 years in COFEECHA to compensate for more rapid growth declines in largemouth bass during early ontogeny. Any samples identified as potentially problematic by COFECHA were re-examined for accuracy by both readers. 30 samples were re-examined for errors following COFECHA crossdating, and 8 samples contained an error. The other 22 samples that contained no errors were retained even though they did not crossdate well. No samples were discarded.

After crossdating, individual growth chronologies were assembled. Each individual measurement time-series was detrended to remove annual growth variations due to age and transformed into unitless growth indices. In fisheries science, ontogenetic growth trends are often removed by using age as a covariate in a multiple linear regression analysis (i.e., Maceina 1992). However, this approach assumes linearity in the relationship between age (or log age) and growth increment, does not allow flexibility in detrending functions across samples, and results can be nonintuitive (e.g., it is difficult to plot chronologies of nonage-related growth variation). Tree-ring scientists solved this problem by developing a statistical routine and software program (ARSTAN) to remove variation in annual growth due to age prior to modelling efforts (Cook & Holmes 1984). ARSTAN removes age-related variation in growth due to ontogeny using one of several detrending functions. To retain as much of the climate signal as possible in this study, each measurement series was detrended using a simple negative exponential curve (Fritts 1976). The observed increment value was divided by the value predicted from the curve to generate a unitless index of growth centred around a value of 1 (values > 1 imply above average annual growth, values <1 imply below-average annual growth). ARSTAN also allows users to graphically inspect curve fits for each measurement time-series. Thus, in this study, if the standard exponential did not provide a quality fit (e.g., produced excessively large, or nonvariable growth indices), a modified exponential curve or a simple linear regression was used to detrend the series. Annual growth indices for each individual fish were used in subsequent climate correlation and modelling analyses. In dendrochronology, master chronologies are often >100 years in length, allowing sufficient overlap with climate variables to establish robust climate–growth relationships. However, largemouth bass chronologies are much shorter, increasing the potential for spurious correlations. To overcome this problem, many individual largemouth bass growth chronologies were developed in this study. Though they may be short in length, chronologies and climate–growth relationships are well replicated and corroborate one another. To avoid confusion, it is worth noting that the ARSTAN process differs significantly in purpose and scope from the COFECHA process previously described. COFECHA is used strictly for crossdating purposes (i.e., to ensure that growth years are assigned the proper calendar year) whilst ARSTAN is used for generating growth indices to be used in all climate correlations and models. More detailed descriptions of the fish growth chronology development process can be found in previous studies (Pereira et al. 1995; Black et al. 2008).

For each site, historical climate data were obtained from the closest available weather station from the Southeast Regional Climate Center (http://www.sercc.com). Data collected included mean annual and growing season values for air temperature, maximum air temperature, minimum air temperature, and precipitation total. For riverine sites, climate data were supplemented with mean annual and growing season discharge data from each river from the U.S. Geological Survey (USGS, http://waterdata.usgs.gov/usa/nwis/rt). For each river, the closest available streamflow gage to the collection site was used.

Annual indices of three global climate variables known to influence southeastern USA climate [El Niño-Southern Oscillation (ENSO) multivariate index, North Atlantic Oscillation (NAO), and the Arctic Oscillation (AO)] were obtained from the National Climatic Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html). The multivariate ENSO index is measured as an integrative index of six climatic variables taken over the tropical Pacific Ocean. Sustained positive phases of ENSO (i.e., La Niña), tend to bring hot and dry conditions to the southeast, whereas sustained negative phases (i.e., El Niño) tend to bring cool, wet conditions (Stenseth et al. 2003). The NAO is measured as the difference of atmospheric pressure at sea-level between the Icelandic Low and the Azores high (Stenseth et al. 2002, 2003). Whilst the NAO pattern drives much of the precipitation variability in northern Europe, it can also have an impact in North America. During highly positive NAO phases, the Icelandic low circulates in a strong, south-west orientation over the eastern half of North American, preventing Arctic air from penetrating southward (Stenseth et al. 2002, 2003). In combination with the ENSO, this effect can produce significantly warmer winters in southeastern USA (Stenseth et al. 2003). The AO is measured as sea-level pressure (SLP) variations north of 20°N, and it is characterised by SLP anomalies of one sign in the Arctic and anomalies of an opposite sign centered at ~37–45°N (Stenseth et al. 2003). The AO is strongly

influenced by the dynamics of the melting ice sheets and thus by trends in global warming (Stenseth et al. 2003).

Pearson product moment correlations (calculated for all annual growth indices across all individuals, $\alpha < 0.05$) were used to initially explore relationships between annual largemouth bass growth and annual climate variables. This established the relationships present between climate and largemouth bass growth. To assess the predictability of climate–growth relationships, stepwise multiple regressions were conducted (Fritts 1976). Given that many of the climate variables used are collinear, a principle components analysis (PCA) was performed on all annual climate data for each site to reduce the number of climate variables to only 2–4 variables that were uncorrelated with one another (Fritts 1976). Only PC axes with eigenvalues ≥1 were used in subsequent multiple regressions ($\alpha < 0.05$ for model inclusion).

Results

A total of 397 largemouth bass were collected and analysed from six rivers and seven reservoirs for interannual growth. Following detrending, synchronous annual growth patterns were revealed for largemouth bass within and among study systems. This was denoted by shared years of enhanced or reduced growth across both individuals and ecosystems – i.e., pointer years (Fig. 1). Within populations, interseries correlations ranged from 0.27 to 0.88, with an average value of 0.62 (Table 1), thus growth chronologies of individuals correlated well with growth chronologies of other individuals from the same populations. In general, the years 2000 and 2007 were pointer years of exceptionally above average largemouth bass growth across the southeast, whilst 1994, 1997 and 2003 were years of below-average growth (Fig. 1). Any population for which 2007 growth data were available (i.e., populations sampled in 2008), showed their highest growth value for the 2007 growing season. Other chronologies (i.e., those for which 2007 data were unavailable) showed their highest growth value for the 2000 growing season. Average growth years were observed in the majority of chronologies during 2001, 2004, and 2005.

Annual largemouth bass growth indices were correlated with annual and growing season climate indices (Table 2). Of 96 possible correlations, 73 were considered significant (Table 2). In most ecosystems, there were numerous significant correlations with climate variables, whilst in one or two ecosystems, fewer significant correlations were observed (Table 2). Lake Acworth, Sloppy Floyd Lake and the Satilla River showed significant correlations between bass
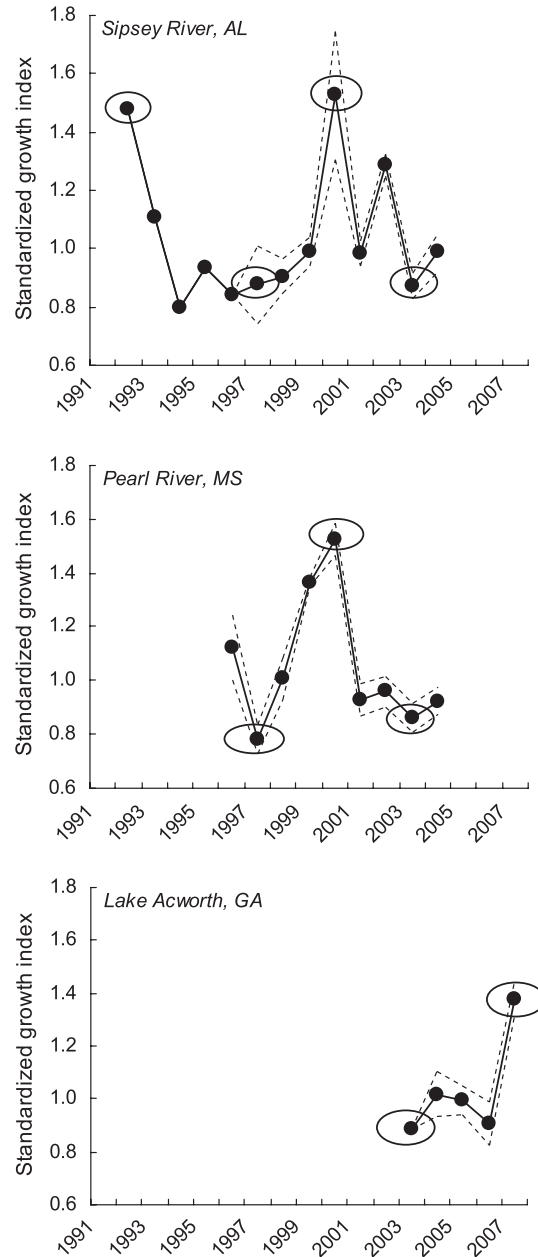

Fig. 1. Three examples of nonage-related variation in annual growth of largemouth bass from southeastern USA ecosystems. Data are 'master growth chronologies' (i.e., average annual growth index values for all individuals sampled in a population). Dashed lines represent the mean ± 1 SE. Ellipses indicate pointer years of exceptionally above- or below-average growth.

growth and every climate variable examined. Within and across ecosystems, relationships between growth and climate followed a relatively consistent pattern. Annual largemouth bass growth was negatively correlated to annual and growing season precipitation totals and positively correlated to mean air temperatures. One lake ecosystem (Fort Mountain Lake) failed to show any correlations to temperature or precipitation metrics, and another lake ecosystem (Antioch

Table 1. Largemouth bass chronology characteristics.

	Latitude	Longitude	Otolith sample size	Chronology length	TL range (mm)	Sample size (years)	Mean interseries R
Reservoirs/Lakes							
Antioch Lake	33.193687	84.252366	77	2001–2006	188–400	248	0.52
Banks Lake	31.013685	83.060259	27	2003–2006	125–385	94	0.57
Fort Mountain Lake	34.452579	84.422719	25	2000–2007	115–460	102	0.47
Lake Acworth	34.032322	84.405016	25	2003–2007	262–374	109	0.86
Lowhead Lake	32.372633	89.442359	11	1999–2004	241–438	69	0.27
Randy Poynter Lake	33.44461	83.563601	25	2002–2006	280–380	91	0.65
Sloppy Floyd Lake	34.262382	85.202415	85	2002–2007	138–332	257	0.53
Rivers							
Sipsey River	33.135425	87.464014	10	1996–2004	140–503	76	0.71
Ogeechee River	32.161922	81.262613	20	2002–2006	300–475	86	0.62
Pearl River	32.501057	89.060373	13	1996–2004	214–523	84	0.76
Satilla River	31.142293	82.192953	32	2003–2006	253–418	113	0.88
Upper Savannah River	32.561938	81.301015	14	2002–2006	285–420	59	0.59
Lower Savannah River	32.141046	81.090975	20	2002–2006	298–461	62	0.68

Otolith sample size refers to the actual number of fish examined at each site. Sample size (years) reflects the number of unitless, annual growth indices, generated for each site that were then correlated to climate variables. Mean interseries R is a metric of annual 'growth synchrony' for a population and is assayed as the average Pearson correlation coefficient between an individual detrended measurement time-series and the master growth chronology for that same site without the individual included.

Table 2. Pearson correlations (R) between annual largemouth bass growth and annual climate variables.

Climate variable	Antioch Lake	Banks Lake	Ft. Mtn. Lake	Lake Acworth	Lowhead Lake	Randy Poynter Lake	Sloppy Floyd Lake
Mean annual temperature	*−0.62	*0.63	−0.03	*0.48	0.01	*0.46	*0.36
Mean annual minimum temperature	*−0.62	*−0.42	0.17	*0.36	*−0.27	*0.35	*0.32
Mean annual maximum temperature	*−0.39	*0.32	0.00	*0.48	0.07	*0.46	*0.36
Total annual precipitation	*0.59	*−0.61	−0.12	*−0.48	*−0.36	−0.22	*−0.38
ENSO Index	−0.17	0.23	−0.23	*−0.58	*−0.25	−0.02	*−0.70
AO Index	*−0.40	*0.67	0.27	*0.46	0.00	−0.02	*0.38
NAO Index	*−0.21	0.09	*0.64	*0.36	*0.42	0.05	*0.31
Mean growing season temperature	*−0.40	0.09	0.09	*0.49	0.04	*0.48	*0.38
Mean growing season minimum temperature	*−0.30	*−0.32	0.14	*0.36	−0.21	*0.42	*0.33
Mean growing season maximum temperature	*−0.39	*0.42	−0.04	*0.49	0.13	*0.46	*0.38
Total growing season precipitation	*0.59	*−0.63	−0.10	*−0.58	*−0.36	*−0.38	*−0.38
Growing season ENSO index	*−0.67	*0.61	*−0.46	*−0.61	−0.21	*0.38	*−0.74
Growing season AO Index	*−0.37	*0.63	0.10	*0.46	0.00	0.04	*0.37
Growing season NAO index	0.14	*−0.45	*0.64	*0.45	*0.42	−0.08	*0.63

Climate variable	Sipsey R.	Ogeechee R.	Pearl R.	Satilla R.	Upper Savannah R.	Lower Savannah R.
Mean annual temperature	*0.44	*0.56	*0.40	*0.87	*0.79	*0.60
Mean annual minimum temperature	*0.27	*−0.39	*−0.23	*0.82	−0.24	−0.13
Mean annual maximum temperature	*0.43	*0.65	*0.42	*0.87	*0.75	*0.60
Total annual precipitation	*−0.60	*−0.39	*−0.53	*−0.82	*−0.51	*−0.69
Mean annual discharge	*−0.52	*−0.30	*−0.52	*−0.75	*−0.52	*−0.69
ENSO Index	0.15	0.02	*−0.37	*−0.41	0.33	0.41
AO Index	0.05	*0.50	−0.11	*−0.36	*0.59	0.38
NAO Index	0.05	−0.06	0.03	*−0.82	0.24	*0.64
Mean growing season temperature	*0.43	0.02	*0.23	*0.87	0.33	0.41
Mean growing season minimum temperature	*0.31	*−0.39	*−0.28	*0.32	−0.24	−0.13
Mean growing season maximum temperature	*0.44	*0.65	*0.46	*0.87	*0.75	*0.60
Total growing season precipitation	*−0.66	*−0.39	*−0.44	*−0.82	*−0.64	*−0.69
Mean growing season discharge	*−0.26	*−0.30	*−0.32	*−0.75	*−0.52	*−0.69
Growing season ENSO index	*0.31	*0.45	*−0.37	*−0.75	*0.81	*0.83
Growing season AO Index	0.02	*0.64	0.16	*0.32	*0.48	0.03
Growing season NAO index	*0.37	*−0.50	*0.37	*−0.87	−0.30	0.11

Significant correlations are indicated in bold with an asterisk.

Lake) showed opposite correlations from those observed in other systems. Largemouth bass growth in all ecosystems was frequently correlated with global climate variables. Every population showed at least one significant correlation between annual bass growth and annual indices of ENSO, AO, or the NAO.

For every ecosystem, significant multiple linear regressions were generated that predicted largemouth bass growth indices using available climatological data (Table 3). However, coefficients of determination varied across ecosystems. In general, model R^2-values were higher for rivers (mean $R^2 = 0.55$) than for reservoirs (mean $R^2 = 0.46$), but ranged from 0.28 to 0.65 across all systems. For every population, PC1 (which was driven by temperature and precipitation) explained the majority of model variation whereas PC2 (driven by minimum temperatures and ENSO), and PC3 (driven mainly by AO) usually added 1–6% additional variation. The mean R^2 for all models was 0.50. Additionally, a plot of observed versus predicted

Table 3. Results of stepwise multiple linear regressions to predict annual largemouth bass growth indices in six river and seven reservoir ecosystems based on annual climate variations.

	PC axes included in final model	Model P	Model R^2
Reservoirs/Lakes			
Antioch Lake	1, 3	<0.0001	0.56
Banks Lake	1, 2, 3	<0.0001	0.61
Fort Mountain Lake	2, 3	0.002	0.46
Lake Acworth	1, 3	<0.0001	0.50
Lowhead Lake	1, 3	0.001	0.35
Randy Poynter Lake	1	0.01	0.28
Sloppy Floyd Lake	2	0.001	0.46
Rivers			
Sipsey River	2	<0.0001	0.40
Ogeechee River	1, 2, 3, 4	<0.0001	0.49
Pearl River	1, 2	<0.0001	0.47
Satilla River	1	<0.0001	0.65
Upper Savannah River	1	<0.0001	0.61
Lower Savannah River	1, 2	0.01	0.65
Mean			0.50

Eigenvalues and loadings on the components for each site can be found in Supporting Information.
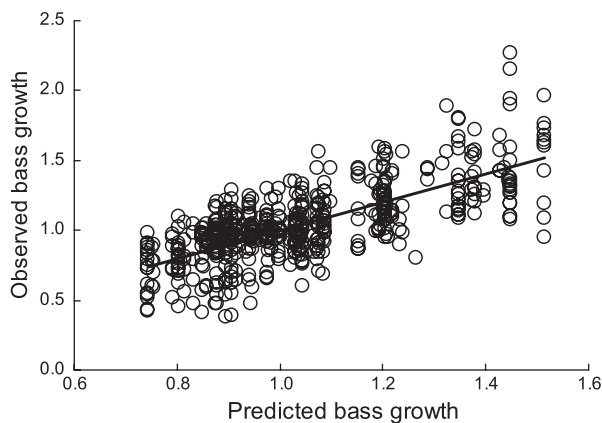

Fig. 2. Regression of observed annual growth indices for largemouth bass from six rivers and seven reservoirs throughout the southeastern USA against annual growth indices predicted from site-specific multiple regressions based on climate data ($y = 1.0x + 1e^{-13}$, $R^2 = 0.51$, $P < 0.0001$).

growth values for all fish examined produced a significant linear relationship with a slope of 1, an intercept of 0 and $R^2 = 0.51$ (Fig. 2).

Discussion

Significant relationships were found between annual indices of largemouth bass growth and climate variations. Annual growth indices were typically above average during the warmest, driest years (i.e., drought years), and below-average during the coldest, wettest years. Several factors could help explain such a pattern.

1. Increased basal carbon resources during drought (i.e., bottom-up effects). Droughts and water-level reductions are known to stimulate the nitrogen and phosphorus cycles in aquatic ecosystems and cause spikes in primary production (Freeman et al. 1994; Dahm et al. 2003; Kampbell et al. 2003; Lake 2003). If these resources are transmitted upwards through the food chain, tertiary predators such as largemouth bass should exhibit enhanced growth.

2. Increased temperature during droughts. Temperature stimulates metabolism, and enhances growth rates of fishes (Beitinger & Fitzpatrick 1979; Brander 1995). A simple increase in temperature in these ecosystems during drought years could positively enhance growth rates of largemouth bass.

3. Prey concentration during dry years and prey dilution during wet years. As water-levels retreat during drought, shoreline snag and shallow-water habitat refugia for prey are lost (Pelicice & Agostinho 2006; Rypel et al. 2007). Without refugia, the probability of predators encountering prey increases (Gause 1934; Sih 1984). Vigorous bass growth during drought may therefore be linked to increased prey availabilities. Conversely, during wet years, prey refugia may become abundant causing predators to expend more energy seeking prey, resulting in below-average somatic growth.

In this study, the two exceptions to this general pattern were Antioch Lake, GA, USA (which showed an opposite pattern) and Fort Mountain Lake, GA, USA (which showed weaker correlations to climate). These systems differ from the other study reservoirs in that they are small impoundments of creeks located in suburban Atlanta, GA, USA. Urbanization could potentially alter climate–growth relationships. For example, a change in the direction of correlation to precipitation (i.e., Antioch Lake) could be explained by an over-abundance of nutrients from surrounding suburban developments, to the point where growth is enhanced by runoff from nutrients during wetter years. Furthermore, biotic factors may play much larger roles in determining bass growth in small impoundments, and may even buffer bass growth from climate

variability. For example, annual variations in prey supply and bass population size could be of much greater consequence for bass growth in small impoundments than in other ecosystem types (Swingle & Smith 1942; Reynolds & Babb 1978; Schindler et al. 1997). Further research on sclerochronology of fishes in small impoundments is needed to better address these possibilities.

Results from multiple regressions suggested that on average roughly 50% of the annual variability in largemouth bass growth was attributable to climatic variations. This percentage varied across systems as some sites had high proportions of variation explained by climate (Satilla River, Savannah River) whereas others had low proportions explained (e.g., Fort Mountain Lake, Lowhead Lake). In general, rivers had higher coefficients of determination than reservoirs, perhaps because streamflow in the studied rivers is unregulated and might therefore be affected by climate vagaries more than reservoirs where streamflow and water-levels are regulated. The percentages of annual growth variation unexplained by climate are likely influenced largely by biotic interactions, e.g., density, competition (Swingle & Smith 1942; Reynolds & Babb 1978; Schindler et al. 1997). Again, this may be particularly true in small impoundments (especially those <40 ha), where increased densities of largemouth bass typically lead to reduced growth, size structure and condition (Paukert & Willis 2004). Even in large impoundments and rivers, variations in biotic factors can explain large fractions of growth variation (Maceina 1996; Grenouillet et al. 2001). Future investigations might examine the influence of both climatic and biotic factors to explain a maximum amount of variation in annual bass growth rates. Additionally, an analysis of climate–growth coupling across differing waterbody types and sizes could be enlightening.

Few studies have examined freshwater fish growth in relation to global climate factors in southeastern USA. It is not surprising that large-scale climate drivers might impact fisheries in the region. A previous study revealed that ENSO strongly affected agricultural yields of peanut, tomato, cotton, tobacco, corn and soybean across all the same southeastern states from which largemouth bass were sampled for this study (Hansen et al. 1998). Childers et al. (1990) documented that shrimp catches off the coast of Louisiana were significantly influenced by ENSO phase. However, bass growth is not directly impacted by ENSO, NAO or AO. A correlation of bass growth with these variables most likely reflects secondary connections between global climate variables and the local climate variables that affect bass growth (i.e., temperature, precipitation, and discharge). Further research is required to more firmly establish the links between global climate and largemouth bass growth across a range of ecosystem types and sizes.

Climate–growth relationships for largemouth bass in the southeast have practical implications for fisheries management. Achieving fisheries management goals (e.g., trophy fish production, high relative conditions, time-to-maturity) is highly desirable and can result in large community revenues. Chen et al. (2003) estimated that a single trophy largemouth bass fishery in Texas generated ~27.5 million US dollars annually and created 163 new jobs. However, management goals might not be achievable during periods of unfavourable climatic conditions, especially if such conditions persist for several years. Knowledgeable managers might eventually learn to manipulate climate–growth systems to their advantage, e.g., by modifying stocking practices, size limits, tournament schedules, fertilizer and liming schedules, or reservoir drawdowns, to coincide with favourable climate or to mitigate its negative effects.

Acknowledgements

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