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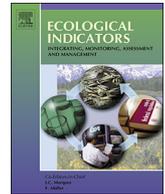Jonathan Spurgeon

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Ecosystem-specific growth responses to climate pattern by a temperate freshwater fish

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ABSTRACT

Somatic growth patterns among animal populations are maintained through complex processes that vary among ecosystems. Changes in growth patterns may be concomitant with changes in climate; however, understanding how growth will manifest among ecosystems is limited. Information embedded within fish hard-parts (i.e., otoliths, spines, vertebrae) can account for variation in growth patterns resulting from changing climate conditions. Channel catfish *Ictalurus punctatus* is a freshwater fish species widely distributed across North America with limited information regarding climate influences on growth and differences in climate-growth relations among ecological systems. We assessed growth (total length) response to changing climate conditions for channel catfish among three waterbody types—pit lakes, irrigation and power-generation reservoirs, and flood-control reservoirs in Nebraska, USA. We used linear mixed-effect models and an information theoretic approach to assess the relative strengths among competing hypotheses. The most supported linear mixed-effect model of channel catfish growth was a function of fish age and an interaction between waterbody type and growing-degree-day (GDD). A positive trend existed in GDD from 1990 through 2008 whereby the predicted increase in GDD among waterbody types ranged from 182 GDD to 189 GDD. The predicted change in channel catfish growth resulting from increased GDD ranged from 1% to 39% among waterbody types. Channel catfish population rate functions, thus, may not respond similarly to climate conditions across ecosystem types. Changes in climate variables may contribute to system-specific responses in population dynamics for channel catfish as well as other similar freshwater species. The establishment of relations between climate and growth variables for a freshwater generalist with a plastic diet and broad temperature tolerance serves as an indication of the breadth of responses possible for freshwater fishes under global changes in climate conditions.

1. Introduction

Fish somatic growth (hereafter growth) patterns are created through a combination of intrinsic and extrinsic processes (Morrongiello and Thresher, 2015; Rypel and David, 2017). Individual growth rate decreases as a fish ages and energy is used for reproduction following attainment of sexual maturity (Nater et al., 2018; Weisberg et al., 2010). Changes in food availability and fish density across seasons and years alter growth (e.g., within a waterbody; Matthias et al., 2018). Climate mediates growth through—among other variables—changes in temperature and growing season length (Neuheimer and Taggart, 2007; Richard and Rypel, 2013). Growth patterns, thus, may emerge among spatially separated populations as a result of within system processes (e.g., variation in age-at-maturity) and broad-scale gradients in climate

(Massie et al., 2018; Richard and Rypel, 2013). Assessments of fish growth patterns that consider processes influencing intrinsic and extrinsic variation are, therefore, central to understanding fish responses to climate patterns and to inform fisheries management. For instance, fish growth may dictate application of system-specific or regional management strategies dependent on the similarity of growth responses among freshwater systems (Forbes et al., 2015; Shoup and Michaletz, 2017).

Assessment of growth response to climate requires analyses and growth data that account for physiological change throughout an individual fish's lifespan as well as span gradients in climate conditions. Individual-level growth variation is reflected in fish hard-part structures (i.e., otoliths, spines, vertebrae) through changes in width among incremental growth bands (Quist et al., 2012). For instance, the widths

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of individual growth bands inherently become smaller from the center to the edge of fish hard-part structures reflecting reduced growth as individuals age (Quist et al., 2012). Furthermore, increment widths among individuals of similar ages may vary due to individual physiological responses to favorable or harsh environmental conditions (Whitney et al., 2016). Decadal growth chronologies for a fish population can be established when multiple age groups within a population are present in samples of hard-part structures over several years (Richard and Rypel, 2013). Growth chronologies derived from fish hard-part structures have been used to assess growth patterns among system types (Richard and Rypel, 2013) as well as along changing climate gradients (e.g., precipitation and temperature; Guyette and Rabeni, 1995; Morrongiello et al., 2011). Growth information from fish hard-part structures, thus, enables the assessment of growth patterns among spatially separated populations that incorporate individual-level growth information as well as gradients in climate conditions (Rypel, 2009; Morrongiello et al., 2011).

Channel catfish *Ictalurus punctatus* is a freshwater fish species widely distributed across North America (Hubert, 1999) that has exhibited varied growth patterns across its range (Hubert, 1999; Rypel, 2011). Hydrologic characteristics (e.g., flow regime), landscape features (e.g., soil fertility), and length of growing season have influenced channel catfish growth (Durham et al., 2005; Shephard and Jackson, 2006; Spurgeon and Pegg, 2017). The existence of environmental gradients, therefore, may influence channel catfish growth patterns among populations embedded within different ecological systems. Understanding population demographic changes due to environmental—including climate—gradients may enable predictions regarding future responses as changes in climate occur (Frauendorf et al., 2019). The extent to which relations between climate and growth variables for channel catfish as well as other similar freshwater species persist among ecological systems under changing climate conditions is, however, limited. Therefore, the goal of this study was to enhance understanding regarding fish growth patterns among ecosystem types under changing climate conditions. The objective of this study was to assess the direction and magnitude of channel catfish growth response among ecosystem types due to biotic (i.e., fish age) and abiotic (e.g., waterbody size, location, and climate variables) conditions. Assessments directed at understanding the links between climate conditions and population rate functions may enhance understanding regarding ecosystem productivity under different climate-change scenarios.

2. Methods

We used fish and climate data from 35 lentic waterbodies across Nebraska, USA (Fig. 1) between 1990 and 2008. We used the
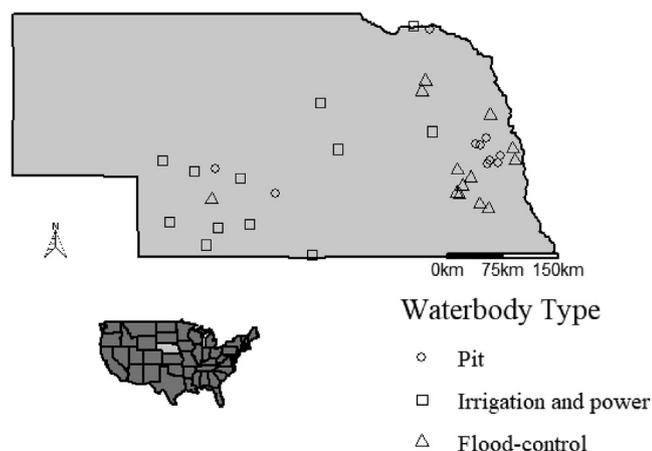

Fig. 1. Locations of individual waterbodies in Nebraska, USA where channel catfish growth was assessed.

classification convention—based on construction method, intended use, and ecosystem attributes—from the Nebraska Game and Parks Commission to assign each waterbody to a waterbody type (Hurley, 2001; Porath and Hurley, 2005). Waterbody types included pit lakes (N = 10), irrigation and power-generation reservoirs (N = 12), and flood-control reservoirs (N = 13; Table 1). Pit lakes were excavations created following sand and gravel mining operations or from highway overpass construction (i.e., Borrow pits). Pit lakes were primarily located along the rivers across the central section of the State. Pit lakes in this study ranged in size from 1 to 100 ha (Table 1). Irrigation and power-generation reservoirs were created by impoundment of irrigation canals and rivers. Irrigation and power-generation reservoirs were used in row-crop agriculture irrigation and to meet electricity use demands. Irrigation and power-generation reservoirs were predominantly located in the south-central and western portions of the State. Irrigation and power-generation reservoirs ranged in size from 80 to 12,000 ha (Table 1). Flood-control reservoirs were created by impoundment of rivers. Flood-control reservoirs were used to minimize flood damage to erodible agriculture lands. Flood-control reservoirs were predominantly located in the eastern portion of the State and ranged in size from 20 to 720 ha (Table 1).

We acquired daily mean precipitation (mm), daily minimum and maximum air temperature (°C), and daily mean air temperature (°C) for each waterbody between 1990 and 2008. All climate data were acquired from the PRISM Climate Group database (Oregon State University, http://prism.oregonstate.edu, assessed September 1, 2018). We estimated growing degree days (GDD) above 10 °C for each growth year and waterbody (Chezik et al., 2014; Neuheimer and Taggart, 2007) using:

$$GDD = \sum_{day_1}^{day_n} \left(\frac{T_{max} + T_{min}}{2} \right) - T_o$$

where n is the number of days in a year, T_{max} is the maximum daily temperature, T_{min} is the minimum daily temperature, and T_o is the temperature below which growth is assumed negligible (i.e., 10 °C). The daily average temperature was set to T_o when below T_o and those days did not contribute to the estimated cumulative GDD for the year for a given waterbody (McMaster and Wilhelm, 1997). The GDD provided a physiologically relevant indicator of annual thermal regime to document changes in fish growth under changing climate conditions (Neuheimer and Taggart, 2007; Richard and Rypel, 2013).

2.1. Channel catfish age and growth data

We acquired age-at-capture (years), length-at-capture (mm total length [TL]), and annuli measurement data for channel catfish from monitoring and research efforts—spanning 1990 to 2008—by the Nebraska Game and Parks Commission and the University of Nebraska-Lincoln. Age data were collected from each of the 35 waterbodies where climate data were collected. Age data were based on pectoral spine annuli, which provide similar age and back-calculated length estimates as otoliths for channel catfish (Barada et al., 2011; Michaletz et al., 2009). The distances between the spine center and each annulus were estimated using digital photographs and image analysis software. We combined channel catfish age data from multiple gear types including boat electrofishing, tandem hoop-nets, and gill nets. We constrained the dataset to only include waterbodies with > 100 channel catfish regardless of gear-type (Table 1). We estimated back-calculated length-at-age using the direct proportion (i.e., Dahl-Lea) method as:

$$L_i = (R_i/R_c)L_c$$

where L_i = length at annulus i, L_c = length at capture, R_c = spine radius at capture, and R_i = spine radius at annulus i (Shoup and Michaletz, 2017). We estimated growth as the difference in length between two successive ages using the back-calculated length-at-age data

Table 1

Characteristics for each of the 35 waterbodies used to assess channel catfish growth response among waterbody type and climate variables. The number of channel catfish (N) used from each waterbody, the minimum (Age$_{Min}$) and maximum (Age$_{Max}$) ages, the number of collections, and the period in which collections occurred (# Collections) are given.

Waterbody Name	Type	Size (ha)	N	Age$_{Min}$	Age$_{Max}$	# Collections
Calamus	Irr./Power	2,050	331	1	17	8 (1994–2010)
Fremont 2	Pit	6	122	1	8	6 (1994–2003)
Fremont 15	Pit	19	116	2	11	1 (2009)
Johnson Park	Pit	6	154	2	8	1 (2008)
Summit Lake	Flood	76	312	1	7	6 (1994–2009)
Willow Creek	Flood	280	790	1	14	10 (1994–2014)
Lake North	Irr./Power	80	134	2	13	2 (2009–2010)
Skyview	Flood	20	150	1	6	2 (2001–2010)
Cottonwood	Pit	100	146	1	10	6 (1997–2007)
Lewis and Clark	Irr./Power	12,000	158	1	12	3 (2005–2009)
Wellfeet	Flood	20	136	2	13	2 (2004–2008)
Lake McConaughy	Irr./Power	12,000	587	1	17	11 (1994–2016)
Jeffery	Irr./Power	440	107	1	20	3 (2003–2009)
Sutherland	Irr./Power	1,200	451	1	18	6 (1995–2010)
North Platte I80	Pit	11	146	1	15	5 (2001–2009)
Enders	Irr./Power	683	150	1	13	7 (1995–2010)
Medicine Creek	Irr./Power	740	164	1	15	6 (1994–2009)
Red Willow	Irr./Power	651	182	1	17	5 (1995–2009)
Swanson	Irr./Power	1,990	219	1	13	9 (1994–2010)
Two Rivers 1	Pit	2	118	1	9	7 (2001–2015)
Two Rivers 2	Pit	1	257	1	10	5 (2002–2015)
Two Rivers 3	Pit	2	209	1	13	7 (2001–2015)
Two Rivers 4	Pit	2	109	1	9	6 (2002–2015)
Branched Oak	Flood	720	667	1	12	10 (1991–2008)
Conestoga	Flood	92	193	2	11	5 (1994–2009)
Pawnee	Flood	296	410	2	14	7 (1992–2009)
Stagecoach	Flood	78	504	1	8	7 (1995–2009)
Wagon Train	Flood	126	236	1	10	3 (1994–2009)
East Twin	Flood	84	320	1	10	5 (1994–2009)
Wildwood	Flood	41	171	1	10	6 (1993–2012)
Glenn Cunningham	Flood	156	120	1	8	2 (1994–1997)
Zorinski	Flood	102	206	1	11	5 (1995–2009)
Lexington City	Pit	3	129	2	7	1 (2009)
Harlan County	Irr./Power	5,400	312	1	12	7 (1994–2009)
Sherman	Irr./Power	1,138	327	1	21	7 (1994–2008)

(Shoup and Michaletz, 2017).

2.2. Channel catfish growth modelling

We used linear mixed-effect models to assess channel catfish growth patterns (Morrongiello and Thresher, 2015; Weisberg et al., 2010). We constructed a candidate set of 20 models defined *a priori* that included additive and interactive influences of both intrinsic (fish age) and extrinsic (waterbody size, waterbody type, and climate) variables. The models assessed channel catfish growth as a function of (1) fish age (i.e., fish growth decreases as fish age) only, (2) fish age and waterbody size (i.e., fish growth increases with waterbody size), (3) fish age and waterbody location (i.e., fish growth decreases with latitude, and fish growth increases with longitude), (4) fish age and waterbody type (i.e., fish growth differs among the three waterbody types), (5) fish age and climate variables (i.e., fish growth responds to changes in temperature and precipitation), (6) fish age, waterbody type, and climate variables (i.e., fish growth responds to changes in temperature and precipitation that differ among the three waterbody types), and (7) a null model with no explanatory variable. Models with interaction terms also included the main effects. Fish age was assigned to each back-calculated length measurement (i.e., based on annuli count). We determined the growth year by aligning the calendar year of growth to correspond with appropriate age of life for fish alive during that year. The growth year was used to link fish growth and climate data. We limited growth years to where each waterbody type was represented (i.e., growth data between 1990 and 2008). Fish age, waterbody size, waterbody type, and climate variables were included in models as fixed effects, and the individual fish were treated as the random effect (Morrongiello et al., 2011;

Morrongiello and Thresher, 2015). An autocorrelation structure (AR1) was applied to individual fish because growth measurements from growth years closer together (e.g., 1990 and 1992) were assumed to be more correlated than growth measurements from growth years farther apart (e.g., 1990 and 2000; Zuur et al., 2007). Linear mixed-effect models were fit and assessed using the nlme package (Pinheiro et al., 2017) in Program R (R version 3.4.2; R Core and Team, 2017). We used an information theoretic approach to rank competing models with the second order variant of Akaike's Information Criteria (AICc; Burnham and Anderson, 2002).

3. Results

3.1. Channel catfish growth

A total of 35,034 growth measurements from 8,619 individuals were used to assess channel catfish growth. The number of growth measurements varied by waterbody type and year with 4,946 (min = 38 growth measurements, 1990; max = 768 growth measurements, 2007) growth measurements from pit lakes, 14,357 (min = 593 growth measurements, 1990; max = 943 growth measurements, 2007) growth measurements from irrigation and power-generation reservoirs, and 15,731 (min = 328 growth measurements, 1997; max = 1,584 growth measurements, 2007) growth measurements from flood-control reservoirs. The most supported linear mixed-effect model of channel catfish growth was a function of the additive influence of fish age and an interaction between waterbody type and GDD (Table 2). Channel catfish growth declined with fish age. Channel catfish growth increased with GDD (Fig. 2). Channel catfish growth was

Table 2
Model rankings for mixed-effects models comparing channel catfish growth among intrinsic (fish age, Age) and extrinsic (waterbody type; waterbody size, Area; latitude, Lat.; longitude, Long.; precipitation, Prec.; minimum temperature, Tmin; maximum temperature, Tmax; growing degree day, GDD) variables in Nebraska, USA between 1990 and 2008. The random effect for each model was an individual fish. An autoregressive correlation structure (AR1) was used for repeated measurements of growth taken from back-calculated ages from individual fish. The second order variant of Akaike's Information Criteria (AICc), difference in AICc from top model (ΔAICc), the number of parameters (K), and the model weight (wt.) are provided.

Mixed-effects Model	AICc	K	ΔAICc	wt.
~Age + Waterbody Type + GDD + Waterbody Type*GDD	326196.70	18	0.00	0.923
~Age + Waterbody Type + Tmin + Waterbody Type*Tmin	326201.70	18	4.95	0.077
~Age + Waterbody Type + GDD	326310.40	16	113.67	0.000
~Age + Waterbody Type + Tmax + Waterbody Type*Tmax	326344.00	18	147.29	0.000
~Age + Waterbody Type + Prec. + Waterbody Type*Prec.	326370.00	18	174.16	0.000
~Age + Waterbody Type + Prec.	326379.30	16	182.60	0.000
~Age + Waterbody Type + Long.	326397.00	16	200.27	0.000
~Age + Waterbody Type + Tmax	326401.80	16	205.08	0.000
~Age + Waterbody Type + Tmin	326402.70	16	205.97	0.000
~Age + Waterbody Type	326409.20	15	212.45	0.000
~Age + Waterbody Type + Lat.	326410.70	16	213.99	0.000
~Age + GDD	326777.20	14	580.44	0.000
~Age + Prec.	326833.30	14	636.56	0.000
~Age + Long.	326898.40	14	701.69	0.000
~Age + Long.	326926.70	14	729.92	0.000
~Age + Area	326931.80	14	735.01	0.000
~Age + Tmin	326942.70	14	746.00	0.000
~Age + Tmin	326956.60	14	759.86	0.000
~Age	326957.00	13	760.25	0.000
~1	360085.70	2	33889.00	0.000

Fig. 2. Predicted channel catfish growth (mm total length TL) in response to changes in fish age and growing degree days (GDD). The minimum (e.g., 1306, Irrigation and power) and maximum (2093, Irrigation and power) GDD for each waterbody type between 1990 and 2008 are presented. The most supported linear mixed-effect model indicated the influence of GDD on channel catfish growth was dependent on waterbody type with the most pronounced change in growth occurring in irrigation and power-generation reservoirs (middle plot). The dotted horizontal line at y = 30 mm TL yr^{-1} is provided for reference.

generally greater in pit lakes compared to irrigation and power-generation and flood-control reservoirs (Fig. 2). The predicted mean difference in GDD between 1990 and 2008 was 189 GDD (pit lakes = 186 GDD; irrigation and power-generation reservoirs = 199 GDD; flood-control reservoirs = 182 GDD; Fig. 3). The least GDD was 1,280 and the greatest was 2,225 (74% increase) for pit lakes. The 74% increase in GDD resulted in a mean 1% (standard deviation [sd] = 0.24) increase in channel catfish growth across all ages for pit lakes (Fig. 4). The least GDD was 1,306 and the greatest was 2,093 (60% increase) for irrigation and power-generation reservoirs. The 60% increase in GDD resulted in a mean 39% (sd = 14.16) increase in channel catfish growth across all ages for irrigation and power-generation reservoirs (Fig. 4). The least number of GDD was 1,344 and the greatest was 2,200 (64% increase) for flood-control reservoirs. The 64% increase in GDD resulted in a mean 3% (sd = 0.88) increase in channel catfish growth across all ages for flood-control reservoirs (Fig. 4).

4. Discussion

The relation between channel catfish growth and GDD was positive suggesting channel catfish growth responded to changes in climate conditions. Previous work has suggested environmental characteristics including hydrologic regimes influenced differences in channel catfish growth (Hubert, 1999; Rypel, 2011; Spurgeon and Pegg, 2017) and, in particular, differences have been reported among lentic and lotic systems (Rypel, 2011; Rypel and Bayne, 2009). Within lentic system, temperature patterns likely influence growth patterns of channel catfish. For instance, Durham et al. (2005) provided evidence that the length of growing season (defined as the number of frost-free days) influenced length-at-age for channel catfish. The relation between
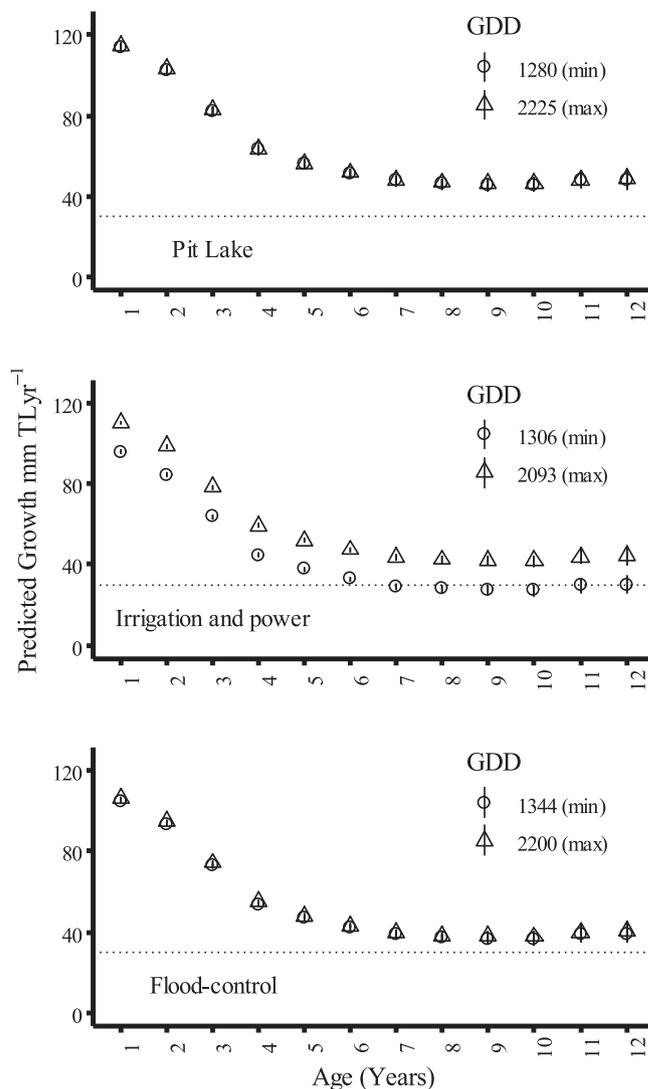
channel catfish growth and GDD in the current study furthers the evidence that climate variables related to the period that temperature is above a certain point may serve as an important indicator in detecting channel catfish growth response to changing climate conditions. Furthermore, the rate of change in growth depended on waterbody type. Relations between climate variables and channel catfish growth among lentic systems may, thus, be context dependent as our results show and may vary depending on ecosystem characteristics similar to differences in channel catfish growth responses between lentic and lotic systems. The pit lakes in this study were characterized as possessing established littoral zones with less turbidity compared to flood-control reservoirs (Porath and Hurley, 2005) which may stimulate energy production and increase growth rates for channel catfish (Shoup et al., 2007). The greatest growth response to increases in GDD for channel catfish occurred in irrigation and power-generation reservoirs. The irrigation and power-generation reservoirs were the largest systems in this study with greater habitat heterogeneity (e.g., water depth) and connections to
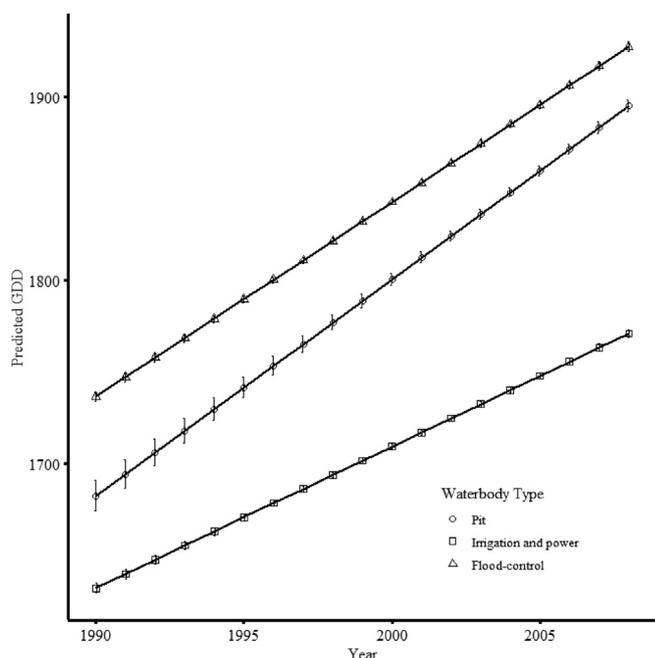
Fig. 3. The predicted increase in growing degree days (GDD) for pit lakes, irrigation and power-generation reservoirs, and flood-control reservoirs in Nebraska, USA between 1990 and 2008. Vertical bars are the standard error estimates.

other aquatic environments (e.g., tributaries). Furthermore, irrigation and power-generation reservoirs initially experienced the least number of GDD in the study. The potential influences of reservoir size, habitat heterogeneity, movement among habitats, and increasing GDD may have incited growth within irrigation and power-generation reservoirs. Further investigation into the mechanisms for the system-specific responses including—among other variables—food web complexity and stability may provide a valuable line of inquiry to better predict system responses to climate patterns. In the meantime, inferring channel catfish growth patterns using growth information from different waterbody types may mask important changes in population rate functions due to changing climate variables.

Changes in channel catfish demographic parameters may occur among waterbody types as increased temperatures occur. Studies assessing demographic responses of freshwater fishes to changes in temperature have focused on cold-water species (i.e., namely salmonids), whereas much less is understood regarding how warm-water and trophic-generalist species such as channel catfish will respond to changes in climate (Lynch et al., 2016). The upper Great Plains including Nebraska has experienced an overall warming trend that will likely continue under both low and high emission scenarios (Bathke et al., 2014). As such, GDD will likely further increase across the region. Increased GDD may, thus, lead to increased growth of channel catfish as well as other warm-water species based on the assumption of a linear response between GDD and growth. For instance, Richard and Rypel (2013) suggested an increase in the number of GDD resulted in greater freshwater drum *Aplodinotus grunniens* growth in the southeastern USA. Additionally, Morrongiello et al. (2011) suggested growing season length (defined using GDD) resulted in increased growth of golden perch *Macquaria ambigua* in Australian lakes. The timing of reproduction and fecundity in some warm-water fish species, including channel catfish, is strongly linked to fish size (Hubert, 1999). Channel catfish in irrigation and power-generation reservoirs exhibited the greatest growth response to changes in GDD and thus may obtain larger sizes with increased fecundity at younger ages as changes in GDD continue. Increased growth may thus create changes in reproductive output among pit lakes, irrigation and power-generation reservoirs, and flood-
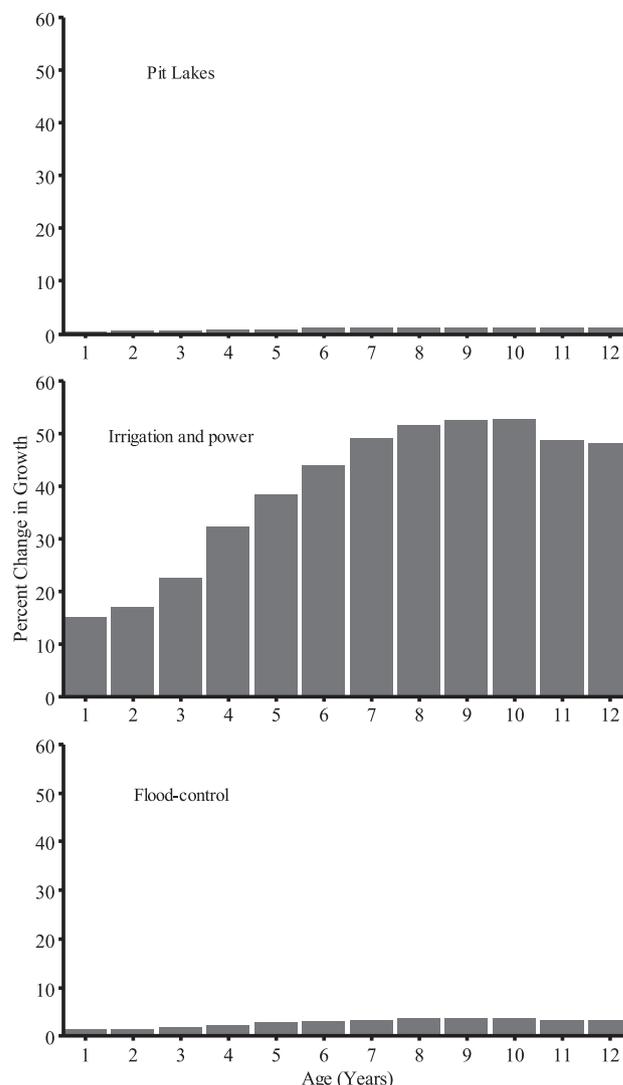

Fig. 4. The predicted difference in growth (% change) in response to increased growing degree days across ages for channel catfish in pit lakes, irrigation and power-generation reservoirs, and flood-control reservoirs in Nebraska USA between 1990 and 2008.

control reservoirs. However, physiological constraints to growth and potential system changes in ecological health due to increased temperatures or increased hydrological fluctuations to meet irrigation or power demands may no longer sustain increased growth with increased GDD.

5. Conclusion

Understanding growth patterns among waterbodies is a fundamental component needed to inform conservation and management of fishes. Additionally, understanding climate-growth responses may aid in prediction of population demographics under changing climatic patterns (Morrongiello et al., 2011). Few studies have explicitly identified climate change as a primary driver of changes in population rate functions (i.e., a change in climate has influenced population demography over time; Lynch et al., 2016). The use of GDD as an indicator of phenologic timing and production has been applied in agriculture settings (McMaster and Wilhelm, 1997; Anandhi, 2016). We provided evidence that further supports the use of GDD as an ecological indicator in establishing climate-demographic responses for freshwater fishes (Chezik et al., 2014). Development of GDD as an ecological indicator of

fish growth may benefit from study of species' responses to GDD among diverse habitat conditions. The use of mixed-effects models in conjunction with biochronologies from fish hard-part structures can provide a statistically robust framework to examine long-term changes in population demographics in relation to GDD. The establishment of a growth response to changing climate patterns for a freshwater species with a plastic diet and broad temperature tolerance also further serves as an indication of the breadth of responses possible for freshwater fishes under global changes in climate conditions.

CRediT authorship contribution statement

Jonathan J. Spurgeon: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Mark A. Pegg:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **Kevin L. Pope:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **Lin Xie:** Formal analysis, Writing - review & editing.

Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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