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Metabolic theory explains latitudinal variation in common carp populations and predicts responses to climate change

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Abstract. Climate change is expected to alter temperature regimes experienced by fishes, which may also alter life history traits. However, predicting population-level responses to climate change has been difficult. Metabolic theory of ecology has been developed to explain how metabolism controls a variety of ecological processes, including life history attributes. Thus, this theory may be a useful tool for predicting fish population responses to climate change. To understand how climate change may alter freshwater fish life history, we measured population characteristics (e.g., recruitment, growth, body size, and mortality) of 21 North American common carp *Cyprinus carpio* populations spanning a latitudinal gradient of >2,700 km. We then evaluated (1) how metabolic rates vary with body size and temperature (i.e., metabolic theory of ecology) to interpret latitudinal patterns in life history traits and (2) how predicted increases in annual temperature as a result of climate change may alter metabolism and population characteristics. Common carp growth and mortality decreased whereas fish size and age increased with increasing latitude. Common carp growth rate was 22% faster but mortality was 31% higher for the most southern population compared to the most northern population. Incorporating latitudinal population patterns into metabolic theory of ecology models explained substantial variation in mortality and longevity among populations and suggested that metabolism will increase with temperature according to three global warming scenarios. The greatest metabolic increase occurred at the largest predicted increase in temperature and metabolism increased more for southern populations compared to northern populations. Combined, our findings suggest common carp and other fishes may experience increased growth and metabolic demands but populations may attain smaller body size due to higher mortality in response to climate change.

Key words: Bergmann's rule; biogeography; climate change; *Cyprinus carpio*; global warming; intraspecific variation; invasive species; latitudinal relationships; life history traits; metabolism; North America.

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INTRODUCTION

Global climate change and subsequent long-term alterations in water temperatures are anticipated to have substantial effects on aquatic organisms (Magnuson et al. 1990, Sharma et al. 2007, Carmona-Catot et al. 2011). However, the effects of global climate change on aquatic

populations are often difficult to predict because long-term data sets needed to establish correlations between climate and population characteristics are lacking in most instances. Latitudinal patterns in animal population characteristics may be reflective of future population responses to a changing climate (Benejam et al. 2009, Walther et al. 2009) and therefore could be a useful tool to evaluate possible effects of climate change on populations where long-term datasets are lacking.

Many fishes have broad geographic distributions and are exposed to a gradient of ecological conditions that can alter life history characteristics. Temperature is a dominant factor that produces latitudinal trends in animal populations (Magnuson et al. 1990, Brown et al. 2004, Heibo et al. 2005). Bergmann's rule predicts that endotherms living at colder temperatures and higher latitudes will achieve larger body size compared to those living at warmer temperatures and lower latitudes because of the thermal advantage of reduced surface-to-volume ratio inherent in large individuals (Bergmann 1847, Watt et al. 2010). Although originally developed for interspecific relationships, the concept was later extended to intraspecific relationships (James 1970, Belk and Houston 2002). In the Northern Hemisphere, body size of most endotherms tends to increase from south to north due to decreasing temperature regimes in conjunction with the properties of thermoregulation and endothermic metabolism (Angilletta and Dunham 2003). Although Bergmann's original rule was only intended to be applied to interspecific relationships among endotherms, attempts have been made to identify similar latitudinal patterns in ectotherms but with mixed success (Ray 1960). For instance, while body size of some fishes increase with increasing latitude, others have larger body sizes at southern latitudes (Belk and Houston 2002, Rypel 2014). Variation in body size among fishes may be because some species have unique mechanisms to cope with suboptimal environmental conditions. For example, counter-gradient growth variation (i.e., faster growth at higher latitudes) can result in similar individual body size in northern versus southern latitudes despite lower temperatures and shorter growing seasons (Conover and Present 1990). Regardless of the mechanism, documented latitudinal patterns in life history traits are inconsistent among species (e.g., Rypel 2014). Despite our poor understanding of latitudinal patterns of most freshwater fishes, understanding relationships between life history traits and latitude has become increasingly important as ecologists attempt to predict future population responses to climate change (Teplitsky et al. 2008, Walther et al. 2009, Merilä 2012).

Organisms have two options to cope with climate change: migration to new habitats or physiological or behavioral adaptions to changing conditions. Fishes inhabiting lentic environments may migrate vertically in stratified lakes to locate preferred temperatures to cope with changing thermal regimes (Busch et al. 2012), but long distance latitudinal migration to more suitable habitats, which is possible in lotic systems, is rarely an option. Thus, many fishes must adapt to climate change through alterations in physiological tolerances and energy demands (Gillooly et al. 2001). Metabolism is an important aspect of autecology because it regulates organism physiology and may therefore alter individual responses to ecosystem changes. Recently, metabolic theory of ecology has been developed to predict how metabolic rate controls ecological processes, including life history attributes (Brown et al. 2004) and could offer a powerful approach to evaluate the ecological effects of climate change and link the performance of individuals to population, community and ecosystem levels (Brown et al. 2004, Munch and Salinas 2009, Dillon et al. 2010). Mass-specific metabolic rate typically increases with temperature and decreases with body size (Gillooly et al. 2001). Because higher ambient temperatures result in greater metabolic demands, individuals living at higher latitudes and cooler temperatures are expected to live longer compared to individuals living at lower latitudes that experience warmer temperatures and longer growing seasons (Brown et al. 2004).

Climate change predictions suggest temperate regions of North America will experience increased mean annual air temperatures up to 3.5°C over the next 100 years (Solomon et al. 2007). Potential impacts of climate change on thermally stratified lakes include increased warming of surface waters, reduced ice coverage (Busch et al. 2012), increased duration of strati-

fication, and prolonged hypoxic periods in the hypolimnion (Stefan et al. 2001). Changes to lake heat budgets and metabolism may in turn alter primary producer and consumer assemblages and biomass (Schindler et al. 2005, Carter and Schindler 2012). Although climate change impacts on physical characteristics and lower trophic levels are relatively well understood, substantially less in know regarding how these future changes could impact fishes. Due to predicted increases in surface water temperatures, ectotherm metabolism should increase (Dillon et al. 2010), influencing population characteristics of these organisms, community interactions, and their commensurate ecosystems effects (Brown et al. 2004). Linking and understanding latitudinal patterns of population characteristics together with metabolic demands would help ecologists predict the effects of climate change on these populations.

Climate change presents a significant threat to fish populations. However, identifying and disentangling the effects of climate change on fishes is difficult. Most current research has focused on predicting changes in species distributions that may result from climate change, but little research has evaluated population-level consequences. Predicting the effects of climate change at the population level is an important first step towards understanding broader ecological effects. Although many hypotheses have been put forth suggesting potential effects of climate change on organisms (Hellmann et al. 2008, Rahel and Olden 2008), predicting population-level effects of climate change on freshwater fishes is difficult (Carmona-Catot et al. 2011) and few have tested their hypotheses or identified potential specific responses of species to climate change.

Because temperature is the dominant factor influencing latitudinal trends in life history variables, latitude can provide a powerful surrogate to test ecological and evolutionary responses to temperature gradients (Power et al. 2005). Yet, due to difficulties in collecting simultaneous samples across a wide geographic region, most studies evaluating intraspecific latitudinal variation of populations have relied on summarizing data from a myriad of technical and scientific publications instead of standardized sampling of target organisms consistently across study areas. Differences in data collection and processing methods across systems can induce sampling biases and potentially mask latitudinal patterns in population characteristics. Thus, identifying latitudinal population patterns in the context of climate change remains an important but elusive goal of ecology. Understanding changes in life history parameters and population dynamics of a species across a wide range of latitudes coupled with knowledge about how metabolism may change in responses to increases in temperature may provide a 'window' to forecast the consequences of global climate change on the population dynamics of fishes (Houghton et al. 2001, Brown et al. 2004, Power et al. 2005).

One of the major challenges to evaluating latitudinal patterns in body size of freshwater fishes is that population structure of many species can be altered through exploitation or other management manipulations, making it difficult to detect latitudinal thermal responses (Beard and Kampa 1999). Unfortunately, most research evaluating relationships between latitude and fish population characteristics have used recreationally important species subject to differences in harvest regulations and exploitation rates across populations, complicating detection of latitudinal patterns in population characteristics. Common carp *Cyprinus carpio* provide a useful model to evaluate latitudinal population patterns and test for potential effects of climate change because they have been established in North America for >100 years, experience limited exploitation that would otherwise bias latitudinal patterns, and are large-bodied fishes that are widely distributed across the region that may display latitudinal variation in population characteristics.

In this study, we used two approaches to predict how common carp populations may respond to climate change. First, we used a standardized dataset to evaluate latitudinal variation in common carp abundance, recruitment, growth, and mortality to predict potential effects of climate change on life history characteristics of common carp across North America. Second, we used a metabolic theory of ecology (Brown et al. 2004) to evaluate the effect of temperature on common carp longevity patterns across North America and predict how metabolism and lifespan may change in response to

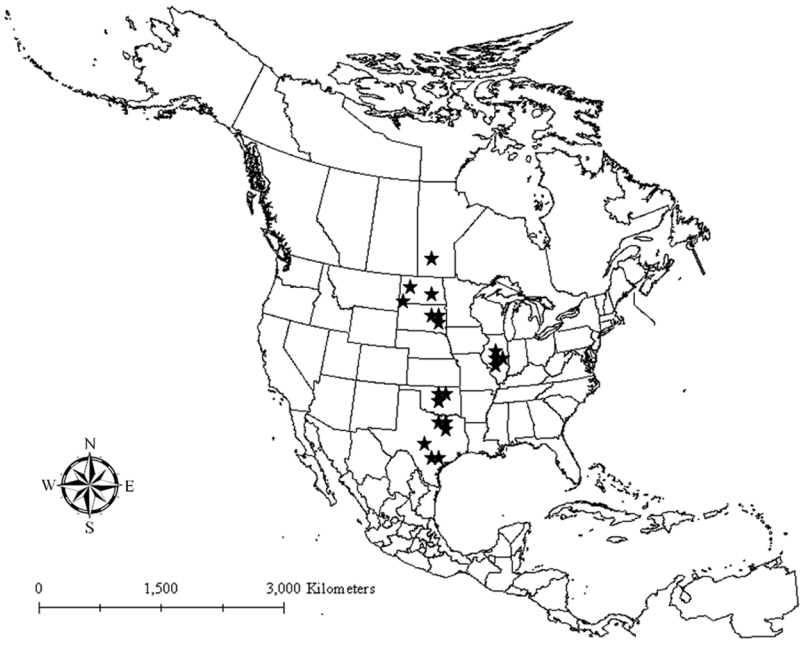

Fig. 1. Map of North America depicting the locations of the 21 populations of common carp sampled (stars) in Manitoba, Canada ($n = 1$), North Dakota ($n = 3$), South Dakota ($n = 3$), Illinois ($n = 4$), Oklahoma ($n = 4$), and Texas ($n = 6$), United States.

predicted increases in annual temperatures as a result of climate change. The use of these two techniques applied to a ubiquitous species such as common carp provides a useful approach to predict fish population responses to climate change.

Materials and Methods

Common carp were collected from natural lakes and reservoirs in Manitoba, Canada, and in North Dakota, South Dakota, Illinois, Oklahoma, and Texas, United States to cover the majority of their latitudinal range throughout North America (Fig. 1). The linear distance between the most southern and northern locations was >2,700 km. Common carp were collected during spring 2009 from 18 populations in North Dakota, South Dakota, Illinois, Oklahoma, and Texas using daytime pulsed-DC electrofishing at each location. The amount of effort at each location varied but sampling continued until approximately 100 individuals were captured (Table 1). Common carp in one lake in Canada were collected with large mesh experimental gill nets (137 m long; six panels [23 m each] consisting of 3.8-, 5-, 7.6-, 8.9-, 10.8-, and 12.7-cm bar mesh). Two sites in North Dakota (lakes Edward Arthur Paterson and Bowman Haley) were sampled following a rotenone application. Although different methods were used to capture common carp in three lakes, all techniques represent standard gears for sampling warmwater fish in large lentic waters (Miranda and Boxrucker 2009) and these techniques either target all individuals in the population (i.e., rotenone) or have been previously verified to produce an unbiased population sample (i.e., large mesh experimental gill nets; Clark et al. 1991). Thus, all gears were assumed to provide a similar representative sample of the population. Captured individuals were measured for total length (1 mm) and the anterior dorsal fin spine was removed at the base and used for age analysis (Weber and Brown 2011*a*). Dorsal spines were air dried for two weeks and transverse sections (0.8 mm width) were removed from the proximal portion of the spine using a low-speed Isomet diamond saw. Annuli were counted under a dissecting microscope on separate occasions by two independent readers who were experienced with aging common carp spines. If age estimates differed between the two

Table 1. Lake geographic location and common carp sample size (N), relative abundance (CPUE), and recruitment variability (RVI) of the 21 populations surveyed. All lakes are located in the United States except for Lake Manitoba which is located in Manitoba, Canada.

Lake	Location	Latitude	Longitude	Surface area (ha)	Max. depth (m)	N	CPUE (no./hr)	RVI
Manitoba	Manitoba	50.199	−98.205	462,400	7.0	250	35.2	0.00
Jamestown	North Dakota	46.931	−98.709	848	11.6	106	70.7	0.13
Dickinson	North Dakota	46.858	−102.851	387	8.2	108	NA	0.29
Bowman Haley	North Dakota	45.976	−103.266	733	9.1	104	NA	0.15
Herman	South Dakota	43.991	−97.175	521	4.0	198	78.2	0.23
Madison	South Dakota	43.958	−97.019	1,069	4.6	200	65.3	0.49
Brant	South Dakota	43.921	−96.947	420	4.3	196	110.5	0.39
Clinton	Illinois	40.160	−88.817	1,981	18.3	118	18.9	0.19
Paradice	Illinois	39.410	−88.437	71	4.9	107	22.7	0.23
Shelbyville	Illinois	39.408	−88.778	4,492	20.4	115	67.6	0.52
Carlyle	Illinois	38.614	−89.363	9,947	10.7	104	9.1	0.48
Sooner	Oklahoma	36.458	−96.995	2,185	27.1	111	48	0.25
McMurtry	Oklahoma	36.164	−97.177	467	22.3	89	61.8	0.40
Carl Blackwell	Oklahoma	36.135	−97.192	1,364	14.0	103	37	0.30
Guthrie	Oklahoma	35.819	−97.440	111	7.6	110	50.4	0.19
Ray Roberts	Texas	33.405	−97.059	10,360	32.3	101	114.6	0.47
Arlington	Texas	32.709	−97.220	785	18.6	102	59.5	0.11
Benbrook	Texas	32.606	−97.494	1,471	21.3	100	96.5	0.14
LBJ	Texas	30.556	−98.338	2,610	27.4	80	11.8	0.30
Woodlawn	Texas	29.452	−98.534	15	6.1	101	77.6	0.53
Hi Lions	Texas	29.385	−98.427	4	3.4	101	30.2	0.38

readers (5% of spines aged), the spine was re-evaluated by both readers until a unanimous agreement was made. In total, nearly 1,900 common carp were aged from 21 populations.

Indices of relative abundance, recruitment, growth, size structure, and mortality were calculated for each population. Catch per unit effort (CPUE) was used as an index of relative abundance and was calculated as the number of fish collected per hour of electrofishing. Electrofishing CPUE data were not available for two North Dakota populations where rotenone was applied to collect fish or from the Manitoba population where gill nets were used, so these populations were not included in correlations requiring CPUE. Common carp recruitment variation was calculated using the recruitment variability index (RVI) as

$$\text{RVI} = [S_{\text{N}}/(N_{\text{m}} + N_{\text{p}})] - N_{\text{m}}/N_{\text{p}}$$

where S_{N} is the sum of the cumulative relative frequencies across year classes, N_{m} is the number of year classes missing from the sample, and N_{p} is the number of total year classes present (Guy and Willis 1995). The recruitment variability index can range from −1 to 1 with values close to 1 indicating stable recruitment and values near −1 indicating erratic recruitment. To index growth and maximum length, we used the K and L_∞ parameters from the von Bertalanffy growth function

$$L_t = L_\infty \times 1 - e^{-K(t-t_0)}$$

where L_t = length at time t, L_∞ = the theoretical maximum length of common carp in the population, K = the growth coefficient, and t_0 = time when length would theoretically equal 0 mm. Initial fitting of von Bertalanffy models to the data resulted in illogical intercept (t_0) estimates, likely due to the low numbers of fish captured <3 years of age in some populations. Consequently, t_0 was constrained to zero when deriving K and L_∞ from the von Bertalanffy models for all populations (Weber et al. 2011*b*). In addition to K and L_∞, we calculated length at age 3 (generally defined as the age at maturation for common carp; Panek 1987). Total length of the largest individual captured in each population was also compared as a metric for growth and body size. Population size structure was quantified using proportional size distribution indices (PSD, PSD-P; Neumann et al. 2012). Because catch-curve slopes from some populations were positive due to erratic recruitment at northern latitudes, total annual mortality (A) was estimated using Heincke's method (Ricker 1975, Miranda and Bettoli 2007)

$$A = 1 - [(n - n_0) \times n^{-1}]$$

where n is the total of all age frequencies in the sample, including the first fully recruited age (age 3 for most populations), and n_0 is the frequency of the first fully recruited age. Mean ages of each population were also used as metrics of mortality. Variability in common carp life history characteristics (CPUE, recruitment variability, growth, size structure, and mortality) were examined across latitude using Pearson's correlation analysis. Level of significance was set at $\alpha = 0.05$.

Recently, a metabolic theory of ecology (Brown et al. 2004) has been used to explain variation in lifespan across a species' latitudinal range (Munch and Salinas 2009). Because metabolism is a known predictor of lifespan (Van Voorhies 2001), geographic variation in lifespan may be explained by temperature regimes using the metabolic theory of ecology. Lifespan (l) is hypothesized to scale as

$$l \propto m^{\frac{1}{4}} \cdot \exp\left(\frac{E}{kT}\right)$$

where m is body bass, E is activation energy of metabolism, k is Boltzmann's constant (8.62×10^{-5} eV/K), and T is temperature in degrees Kelvin (°K). Metabolic activation energy is the primary parameter that is estimated but is thought to range between 0.2 and 1.2 eV (Gillooly et al. 2001, Munch and Salinas 2009). We also regressed log-mean age and mortality rate (e.g., indices of carp lifespan) with the inverse of mean annual temperature as

$$\ln(a) = b + \frac{1}{kT}$$

where a is mean age or mortality rate (A) of the population, b is the slope of the regression line, k is Boltzmann's constant, and T is mean annual temperature (Munch and Salinas 2009). Twenty-year average annual air temperatures were derived for each population location from an online database (www.usgs.gov; accessed March 6, 2012). Due to the difficulty in obtaining accurate, local water temperature data, many studies use air temperature as a surrogate for water temperature (e.g., Britton et al. 2010, Rypel 2014). Further, climate change models predict widespread future changes in air temperature whereas similar data on lake-specific changes in water temperature are not generally available. Fortunately, air temperatures are a good predictor of surface water temperature, even in deep lakes that can thermally stratify (Zhang et al. 2014), and can be successfully applied to models evaluating the effects of climate change on fishes (Sharma et al. 2007). Bioenergetic models for most fishes are not sensitive to growing season temperature differences that occur across geographical ranges spanning even 6° of latitude (Evans et al. 2014). Thus, any error introduced by the use of air temperature as a surrogate of water temperature should be negligible. Therefore, we assumed that local ambient air temperature was an approximate indicator of water temperature and a relative indicator of latitudinal effect among populations.

Latitudinal temperature data was used to predict patterns of physiological responses to climate change (Dillon et al. 2010). Metabolic rates of ectotherms can be predicted by

$$\ln(\mathrm{IM}^{-0.75}) = -E\left(\frac{1}{kT}\right) + C$$

where IM is the mass-corrected metabolic rate, E is activation energy (0.69), k is Boltzmann's constant (8.62×10^{-5}), T is mean annual temperature in degrees Kelvin (°K), and C is a normalization constant (fish = 20.83; Brown et al. 2004). Because fish mass is a dominant factor influencing metabolic rate (Gillooly et al. 2001), we calculated metabolic rate for each fish collected from each population before calculating a mean metabolic rate for each population. Individual fish weight information was not available for most of common carp populations we collected. Thus, we used a standard weight (W_s) equation to estimate individual weights. This approach provided standardized weights across populations and eliminated potential biases associated with individual fish condition. Standard weight for common carp is $\log_{10}(W_s) = -4.639 + 2.920 \cdot \log_{10}\mathrm{TL}$ (Bister et al. 2000). Climate change scenarios predict temperature increases of 0.5, 1.7, and 3.5°C across much of North America by 2100 under current, low growth, and high growth emissions scenarios, respectively (Solomon et al. 2007). Thus, we also modeled common carp metabolism under these three climate change scenarios to evaluate chang-

Table 2. Common carp growth, size structure, and mortality characteristics of the 21 populations surveyed. K = instantaneous growth parameter; L_∞ = maximum attainable size; PSD = proportional size distribution; PSD-P, M, and T = proportional size distribution of preferred (P), memorable (M), and trophy (T) length fish; A = annual mortality rate. Lengths are in mm total length and age is in years.

	Growth				Size structure				Mortality		
Lake	K	L_∞	Length at age 3	Max. length	PSD	PSD-P	PSD-M	PSD-T	A	Mean age	Max. age
Manitoba	0.22	791	384	857	99	97	62	3	0.03	9.5	21
Jamestown	0.26	769	409	655	100	35	23	1	0.03	6.0	16
Dickinson	0.34	582	374	850	95	38	0	0	0.08	7.4	16
Bowman Haley	0.53	640	508	740	100	63	13	0	0.07	6.7	27
Herman	0.39	778	533	933	99	83	76	9	0.07	9.2	21
Madison	0.50	727	562	824	100	100	84	0	0.01	8.4	15
Brant	0.39	730	502	831	98	98	82	0	0.01	12.1	20
Clinton	0.61	435	365	580	78	8	1	0	0.01	9.3	20
Paradice	0.50	470	365	605	48	8	0	0	0.10	5.1	16
Shelbyville	0.44	524	385	615	99	25	0	0	0.01	7.8	14
Carlyle	0.55	534	430	642	96	34	0	0	0.06	8.6	22
Sooner	0.83	559	513	701	98	59	4	0	0.12	6.1	14
McMurtry	0.48	552	420	658	90	27	0	0	0.06	5.4	11
Carl Blackwell	0.53	560	445	647	90	50	1	0	0.10	7.1	16
Guthrie	0.56	636	517	767	94	51	11	0	0.16	4.6	14
Ray Roberts	0.75	502	449	600	91	8	0	0	0.11	4.6	8
Arlington	0.63	591	501	695	99	66	4	0	0.07	5.5	13
Benbrook	1.00	484	460	636	89	5	0	0	0.23	3.8	9
LBJ	0.98	591	560	750	99	85	6	0	0.15	8.3	19
Woodlawn	0.69	580	506	735	100	88	2	0	0.03	6.2	19
Hi Lions	0.89	567	528	715	98	34	4	0	0.32	3.3	7

es in metabolic rate. Potential changes in metabolic rate estimated under the three increased temperature scenarios were calculated as the difference between projected metabolic rate under each of the three increased temperature scenarios and metabolic rate estimated under current temperatures. Ordinary least-squares regression was then used to relate latitude with current metabolic rates and multiple linear regression was used to test for the combined and partial effects of latitude, temperature increase, and their interaction on change in common carp metabolism. Significance was determined at $\alpha = 0.05$.

Results

Lakes ranged in size from 4 to 462,400 ha surface area and 3.4 to 32.3 m maximum depth (Table 1). However, lake morphology characteristics were not related to latitude ($r^2 < 0.20$ for surface area and maximum depth). Common carp displayed a wide range of life history traits and population characteristics across populations (Tables 1 and 2). Relative abundance of common carp ranged between 9.1 and 114.6 fish per hour of electrofishing but was not related to latitude ($r = 0.04$, $P = 0.85$). Similarly, common carp recruitment variability was not related to latitude (Fig. 2A). In contrast, some important common carp life history characteristics were highly correlated with latitude. Instantaneous growth rate (K) was negatively correlated with latitude (Fig. 2B) whereas maximum theoretical size (L_∞) was positively correlated with latitude (Fig. 2C) and negatively related to instantaneous growth rates (K; $L_\infty = -270.57 \times K + 755.3$; $r^2 = 0.32$, $P = 0.007$). Mean length at age 3 (average age at maturation) tended to decrease with latitude but was only marginally significant because fish were much larger than predicted for the three lakes in South Dakota and one lake in North Dakota (Fig. 2D). The average size of common carp at age 3 was 144 mm larger (38%) for the most southern population compared to the most northern population.

Large common carp (>840 mm) were only found in three of the five most northern populations. Larger (Fig. 2F) and older (Fig. 2G) individuals were captured at more northern latitudes but population size structure (PSD-P) was not related to latitude (Fig. 2E). Common carp mortality rates declined with increasing latitude (Fig. 2H) and were positively related to

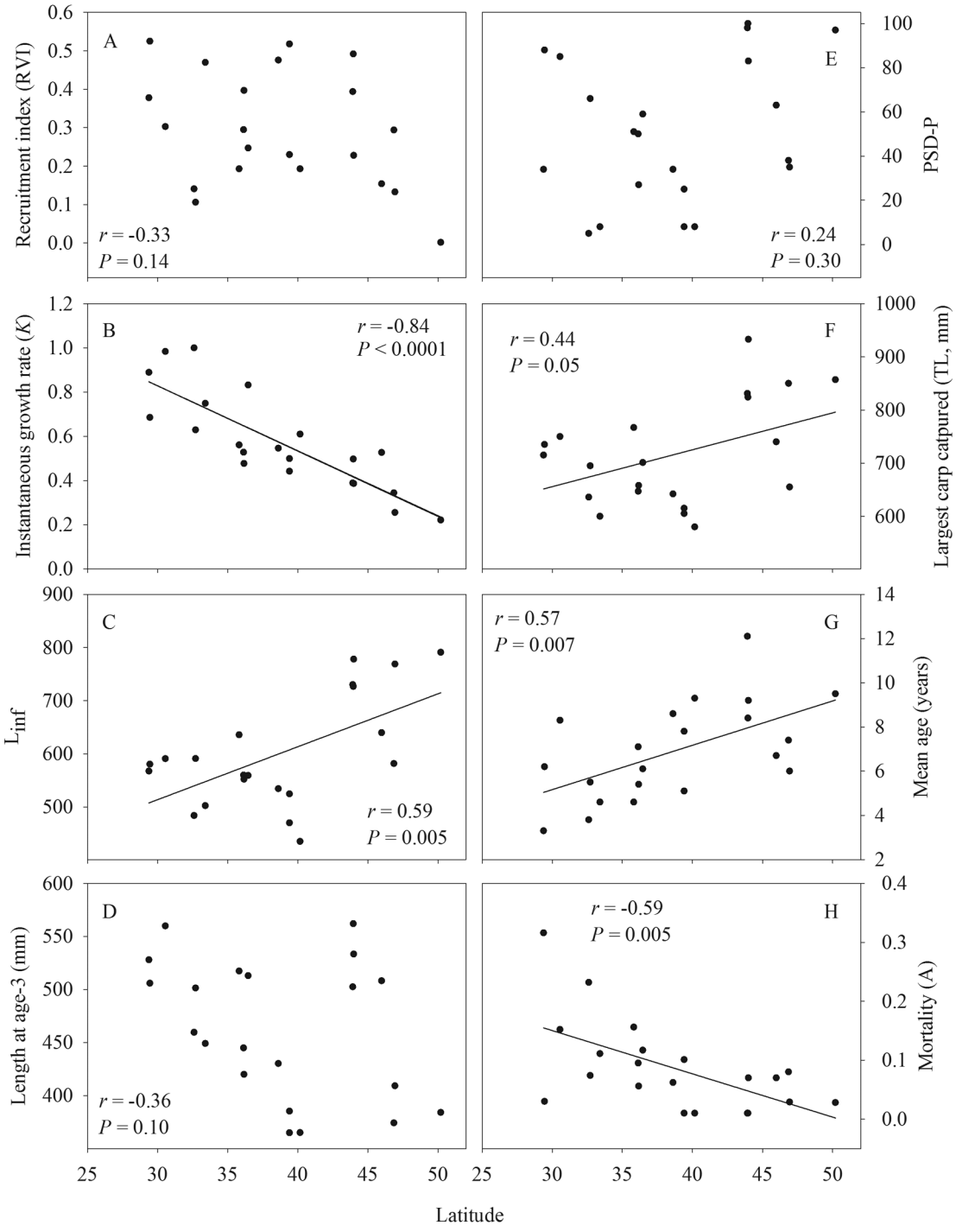

Fig. 2. Relationships between latitude and common carp recruitment index (A), instantaneous growth rate (von Bertalanffy *K*; B), theoretical maximum attainable size (L_∞; C), length at age 3 (D), proportional size distribution of preferred length fish (PSD-P; E), largest observed size (F), mean population age (G), and mortality (*A*; H) for 21 common carp populations across North America.

instantaneous growth rates (K; $A = 0.25 \times K - 0.06$; $r^2 = 0.50$, $P < 0.001$). Mortality was >31% higher and maximum fish age was 14 years younger (7 versus 21 years) for the most southern population compared to the most northern population.

Comparing predictions of common carp longevity across latitudes revealed several patterns. Mean age of common carp populations was related to the thermal environment (Fig. 3A). Metabolic theory of ecology calculates temperature as an inverse function ($1/kT$). Thus, common carp populations located at lower latitudes with warmer annual temperatures (lower $1/kT$) had younger mean ages compared to populations further north where temperatures were cooler and fish were older. Metabolism activation energy (i.e., slope of the relationship between temperature and mean age) was 0.22 eV. Conversely, mortality of common carp was negatively related to temperature ($1/kT$): lower mortality rates occurred at higher latitudes (with higher $1/kT$) and colder temperatures compared to lower latitudes (and warmer temperatures) with a metabolism activation energy of 0.64 eV (Fig. 4B).

Common carp metabolic rate, estimated as a function of variation in body size, was negatively related to temperature ($1/kT$) with fish at lower latitudes and warmer temperatures having higher metabolism (Fig. 3C). All three global warming scenarios evaluated predicted increases in common carp metabolism associated with predicted increases in mean annual temperature. Increases in common carp metabolism following three global warming scenarios across a latitudinal gradient were explained by the equation: $I = 0.004 + 0.062 \times T - 0.00008 \times \text{Lat} - 0.001 \times T \times \text{Lat}$ ($r^2 = 0.70$, $P < 0.0001$; I = metabolic rate, T = global warming temperature increase, Lat = latitude; Fig. 4). Common carp metabolism increased only modestly with a 0.5°C increase in temperature but increased dramatically with temperature increases of 1.7° and 3.5°C. For example, at a latitude of 30° N, carp metabolism increased 0.0002 $\text{mW}\cdot\text{g}^{-0.75}$ at a temperature increase of 0.5°C but increased 0.075 $\text{mW}\cdot\text{g}^{-0.75}$ when temperatures increased 1.7°C and 0.095 $\text{mW}\cdot\text{g}^{-0.75}$ when temperature increased 3.5°C. However, metabolism of populations at lower latitudes increased more with increasing temperatures compared to populations at higher latitudes. A 3.5°C temperature increase produced a 0.03 $\text{mW}\cdot\text{g}^{-0.75}$ metabolism increase at 50° N latitude (32% decrease in metabolism between 30° N and 50° N locations).

Discussion

Our results indicate that life history characteristics of common carp vary with latitudinal temperature gradients and suggest that population-level changes may occur for this species as climate change progresses in accordance with a metabolic theory of ecology. Common carp populations at higher latitudes had lower growth rates but achieved larger maximum size and had lower mortality rates compared to populations at lower latitudes, suggesting that global warming may promote shorter life spans and smaller body size. Each degree of warming has been suggested to decrease organism body size by 6–22% (Desai and Singh 2009). Reproductive output and offspring quality of many fishes, including common carp, are strongly tied to maternal body size (Weber and Brown 2012). Thus, reductions in body size as a result of climate warming may reduce reproductive potential of these populations. Temperature and growing season duration are important factors influencing latitudinal variation in population characteristics of fishes (Philipp 1992, Braaten and Guy 2002, Carmona-Catot et al. 2011). Average annual temperatures were approximately 19.5°C different between the most southern and northern population locations, which likely had a substantial influence on latitudinal differences observed in population characteristics.

Latitudinal clines in fish growth rates are relatively common (e.g., Belk and Houston 2002, Heibo et al. 2005). Being ectotherms, fishes at high latitudes have reduced growth due to cooler temperatures and truncated growing seasons. Although some fishes at higher latitudes can experience faster growth rates that offset shorter growing seasons (counter-gradient variation; Conover and Present 1990, Kokita 2004), our results indicate that common carp annual growth rates declined with increasing latitude. Common carp length at age 3 was 77% larger at the most southern compared to most northern population. Despite reductions in growth rates, maximum size within common carp populations

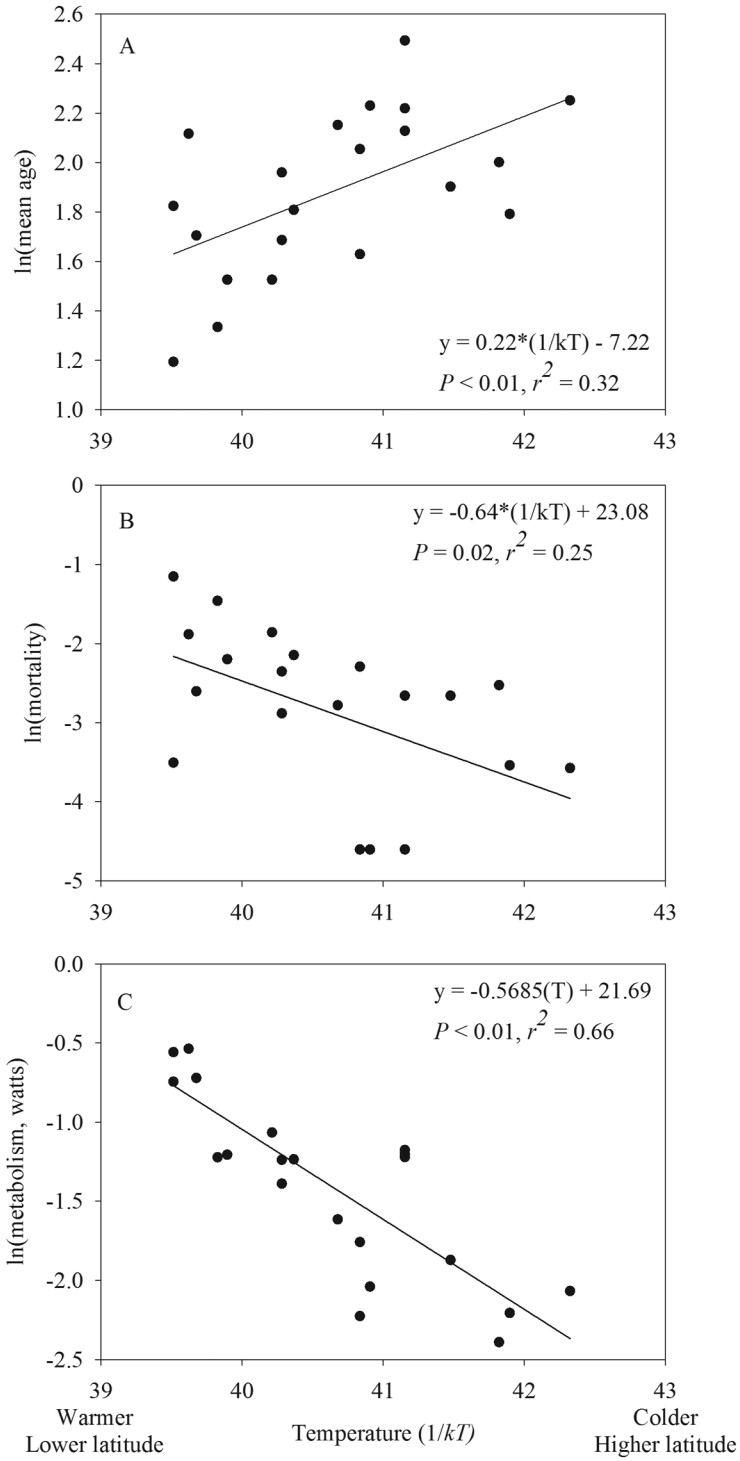

Fig. 3. Relationship between mean age (years; A), mortality (*A*; B), and metabolic rate (C) and annual mean temperature for 21 common carp populations across North America. *k* is Boltzmann's constant (8.62×10^{-5} eV/K) and *T* is mean annual temperature in degrees Kelvin.

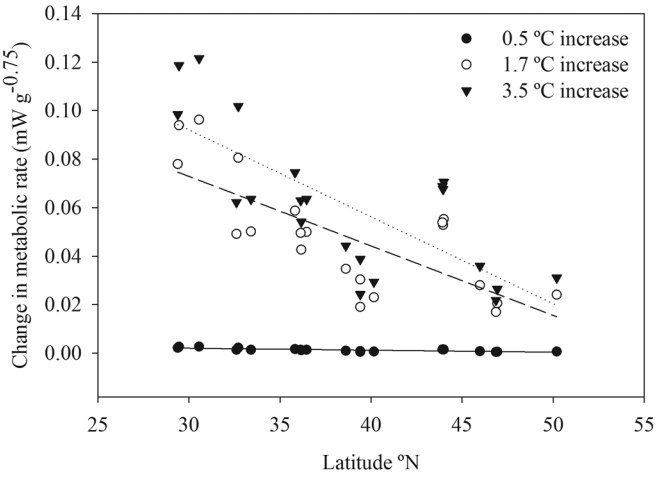

Fig. 4. Change in metabolic rate of common carp across latitudes under warming scenarios of 0.5 (black circle), 1.7 (white circle), and 3.5°C (black triangle) by 2100.

at the highest latitudes were up to 80% larger compared to those at lower latitudes, suggesting that other mechanisms besides growth rates may be responsible for producing latitudinal clines in ectotherm body size. Similar intraspecific trends of larger body size at higher latitudes (often incorrectly referred to as Bergmann's rule) have been identified in a wide range of other animals including birds (Yom-Tov et al. 2002), mammals (Ashton et al. 2000), and amphibians (Ashton 2002) but limited and conflicting supporting evidence exists for freshwater fishes (e.g., Heibo et al. 2005, Benejam et al. 2009, Carmona-Catot et al. 2011, Rypel 2014).

Bergmann (1847) originally proposed that observed interspecific relationships between endotherm body size and temperature was a result of energy conservation in cold environments: large-bodied endotherms lose less heat relative to mass compared to smaller individuals. Since the original development of Bergmann's rule, this theory has been broadly applied outside this context to include intraspecific relationships and ectotherms, producing substantial confusion regarding Bergmann's original hypothesis (Watt et al. 2010). However, if the mechanism for Bergmann's rule is thermal adaptation of heat conservation, then Bergmann's rule cannot be applicable for ectotherms and other mechanisms need to be developed to explain latitudinal clines in these populations (Watt et al. 2010). Yet, ectotherms, such as fishes, may provide better insight into latitudinal patterns because they have indeterminate growth that may permit a wider range of adult body sizes compared to endotherms that generally have determinant growth. We suggest that in the case of common carp, body size increased with latitude as a result of lower mortality and prolonged lifespan. Although it may seem obvious that organism age needs to be accounted for when testing for latitudinal clines in population characteristics such as body size, surprisingly few studies have accounted for this important source of variation. This oversight may be due in part to the difficulty associated with accurately estimating organism age for other wild taxa beyond fishes. Nonetheless, latitudinal patterns indicate that common carp lifespan of will likely decrease by >60% in response to increased metabolic demands initiated by climate change. Longer lifespans of fishes inhabiting higher latitudes have been documented for other species (e.g., Heibo et al. 2005, Blanck and Lamouroux 2007) and may explain latitudinal gradients in fish body size in lieu of Bergmann's rule of endotherm energy conservation, but this hypothesis should be evaluated more rigorously for other taxa to test the scale of inference for this relationship.

Since Bergmann (1847) first proposed his hypothesis regarding geographical variation in endotherm body size, there have been numerous studies that have evaluated these relationships for a variety of taxa. More recently, spatial trends

associated with Bergmann's rule have been applied to temporal changes in animal body size in an effort to predict population responses to climate change. Several observations indicate that animal body size is decreasing in response to climate warming (e.g., Gardner et al. 2011, Sheridan and Bickford 2011). However, limited information is available evaluating the mechanisms underlying this shift in body size. Although documenting spatial and temporal changes in life history characteristics is important, understanding mechanisms driving these changes is critical to allow predictions of future climate change impacts (Watt et al. 2010). Our results, along with others (e.g., Sheridan and Bickford 2011), indicate that increased longevity of common carp at higher latitudes is strongly related to metabolic theory of ecology. Mortality rates of fishes are positively related to temperature (Pauly 1980, Munch and Salinas 2009) and growth rates (Charnov and Berrigan 1990), the two major determinants of metabolic rate in ectotherms (Gillooly et al. 2001). Thus, decreased metabolic rate, caused by lower annual temperature at high latitudes, ultimately leads to longer lifespan at northern latitudes, consistent with the metabolic theory of ecology (Brown et al. 2004, Munch and Salinas 2009) and the rate of living theory (Sohal and Allen 1986). Similarly, Munch and Salinas (2009) found lifespan was positively correlated with latitude as a result of temperature clines in 85% of 1,082 populations of ectotherms representing a wide range of taxa, consistent with the metabolic theory of ecology. Higher ambient temperatures result in higher metabolic demands with larger effects at lower latitudes. This pattern likely occurs because populations at lower latitudes are already near their optimal temperature (25°C for common carp) and are sensitive to even slight temperature increases whereas populations at higher latitudes experience temperatures much lower than their thermal optimum and are therefore more tolerant of temperature increases (Deutsch et al. 2008).

Our results indicate that while small (0.5°C) increases in temperature may have minimal effects on metabolism, larger temperature increases (1.7°C) will have more pronounced effects. However, metabolic increases were not constant across latitudes. Effects of climate change on populations are predicted to be more dramatic at higher latitudes because these latitudes will experience greater increases in temperatures (Parmesan 2007, Rosenzweig et al. 2008). Our results also indicate climate change effects will interact with latitudinal gradient. However, in contrast to the current paradigm, increases in metabolism will be greatest at lower latitudes and decline at higher latitudes. Body size and temperature are the primary factors responsible for intraspecific variation in metabolic rate and longevity (Gillooly et al. 2001, Munch and Salinas 2009). Body size is important because metabolic rate decreases with increasing body size; because individuals at more northern latitudes are typically larger than individuals at more southern latitudes, northern individuals would be expected to have lower metabolic rates than southern individuals under similar ambient temperatures. Temperature is important because metabolic rates are generally exponentially higher in warmer climates (Deutsch et al. 2008), resulting in greater energy demand on individuals at lower latitudes (Dillon et al. 2010). For instance, climate warming at lower latitudes had a greater effect on insects because they are already living closer to their thermal maxima compared to populations at more northern latitudes (Deutsch et al. 2008). Predicted increases in metabolism will have physiological effects through increased food requirements and vulnerability to starvation that can subsequently affect ecosystem structure including food web dynamics (Estes et al. 2011).

Although metabolism was a useful predictor of lifespan for common carp in our study, considerable variation in the model remained, indicating that other localized variables likely also influence latitudinal clines in populations. Metabolism activation energy estimates derived with common carp in this study (longevity = 0.22 eV; mortality = 0.64 eV) are similar to rates estimated in other studies for longevity (0.2–1.2 eV; Gillooly et al. 2001, Munch and Salinas 2009) and mortality rate (0.60–0.70 eV; Gillooly et al. 2001, Brown et al. 2004) across a broad range of taxa, suggesting biased parameter estimates were not an important influential factor. Alternatively, increased population density and ensuing density-dependent effects can influence common carp population characteristics (Weber et al. 2010) and metabolic theory (Brown et al. 2004). However,

common carp relative abundance was not related to latitude, indicating that density-dependent effects were likely not influencing the observed latitudinal patterns. Instead, variation in other environmental conditions (e.g., food availability, competition, predation, etc.) across this latitudinal range likely influenced variation in life history traits.

Although common carp are an introduced species to North America and much of the world, predictable latitudinal trends in population characteristics indicate that they have adapted to localized conditions. Species introductions can result in rapid evolution (10–36 years) and a diversification of phenotypes (Whitney and Gabler 2008). Similar to common carp in this study, many other introduced species have been shown to rapidly adapt to localized conditions. For example, modified thermal habitats resulted in amphibian evolution after only 36 years (Skelly and Freidenburg 2000) and icefish *Neosalanx taihuensis* population characteristics rapidly adapted to thermal regimes less than 25 years following introduction (Zhu et al. 2014). Clearly, strong selective pressures can result in rapid adaptation of introduced species and similar processes have likely produced the latitudinal variation in population characteristics of common carp documented in this study. Yet, the extent to which genetic differences or phenotypic plasticity contributed to patterns in population characteristics remains unknown but may have contributed to unexplained variation among populations. Our current understanding of latitudinal clines in animal populations and potential responses to climate change would benefit from future field, laboratory, and modeling research aimed at disentangling these potential confounding effects (Gienapp et al. 2008).

Body size of many fishes appears to be declining in response to climate change (Gardner et al. 2011) but the mechanisms responsible for this shift have remained elusive. Metabolic theory of ecology has been proposed as a framework for evaluating local adaptation (Munch and Salinas 2009). However, limited information is available regarding intraspecific variation in mortality rates (Bevacqua et al. 2011). We found a strong latitudinal gradient in common carp population characteristics including longevity and mortality rates that closely follow latitudinal variation in metabolic rates. Thus, metabolic theory of ecology, driven by latitudinal clines in ambient temperature, may serve as a powerful predictor of population-level responses to climate change. Similar models incorporating latitude or temperature, body size, and mortality rates could be easily adapted to other ectotherms in both terrestrial and aquatic habitats to evaluate potential population shifts as a result of climate change.

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