



Growth rate responses of Missouri and Lower Yellowstone River fishes to a latitudinal gradient

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Growth rate coefficients estimated for channel catfish *Ictalurus punctatus*, emerald shiners *Notropis atherinoides*, freshwater drums *Aplodinotus grunniens*, river carpsuckers *Carpionodes carpio* and saugers *Stizostedion canadense* collected in 1996–1998 from nine river sections of the Missouri and lower Yellowstone rivers at two life-stages (young-of-the-year and age 1+ years) were significantly different among sections. However, they showed no river-wide latitudinal trend except for age 1+ years emerald shiners that did show a weak negative relation between growth and both latitude and length of growing season. The results suggest growth rates of fishes along the Missouri River system are complex and could be of significance in the management and conservation of fish communities in this altered system.

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Key words: growth rate; counter gradient variation.

INTRODUCTION

Fish growth is a fundamental and often critical element of fish population assessment that can be influenced by many biotic and abiotic factors (Jearld, 1983; Summerfelt & Hall, 1987; Chambers & Miller, 1995). Among these factors, water temperature is an influential component of growth in fish populations (Picard *et al.*, 1993; Dutta, 1994; Oxenford *et al.*, 1994; Radtke & Fey, 1996). Because there can be a large thermal gradient from higher to lower latitudes within the geographic range of any species, there is a potential for differences in growth rates among populations. Several studies have made comparisons of physiological responses, including growth rates, to latitudinal variation on fishes and other aquatic organisms (Conover & Present, 1990; Mina, 1992; Conover & Schultz, 1995; Gudkov, 1996; Schultz *et al.*, 1996; Conover *et al.*, 1997; Parsons, 1997; Brown *et al.*, 1998). Some of these studies suggest that fishes obtain larger sizes in lower latitudes (Carlander, 1969, 1977; Modde & Scalet, 1985), with the idea that these areas provide more opportunity for growth due to longer growing seasons. Conversely, others have reported lengths of same age fish to be comparatively equal to or greater in populations from higher latitudes than their lower latitude counterparts implying faster growth rates to compensate for the shorter growing season (Isley *et al.*, 1987; Conover & Present, 1990).

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A flexible capacity for growth may allow a species to compensate for negative environmental influences such as lower water temperatures and shorter growing season as latitude increases. This type of compensation is a response to the negative covariance of genetic and environmental effects upon growth and was termed 'counter gradient variation' (CnGV) by Levins (1969). Counter gradient variation has been observed in estuarine zooplankton and invertebrates (Dehnel, 1955; Levinton, 1983; Levinton & Monahan, 1983; Lonsdale & Levinton, 1985), amphibians (Berven *et al.*, 1979), marine fishes (Leggett & Carscadden, 1978; Conover & Present, 1990; Present & Conover, 1992), and to a limited extent freshwater fishes (Isley *et al.*, 1987; Power & McKinley, 1997). Here, CnGV meant these organisms put energy towards body growth over the same temperature range regardless of geographic location, but growth rates were higher to compensate for the shorter growing season at higher latitudes. Some studies even reported that fishes in higher latitudes attain larger sizes than their lower latitude equivalents in the first year of life (Conover & Present, 1990; Mina, 1992).

Most research focusing on latitudinal patterns in fish growth comes from experiments on marine and estuarine fishes (Leggett & Carscadden, 1978; Conover, 1990; Conover & Present, 1990; Present & Conover, 1992), whereas freshwater fishes have generally not been specifically studied. Phenomena such as CnGV are best tested by looking at the genetic basis for growth via common-environment or reciprocal transplant experiments. However, testing for latitudinal differences in growth from wild populations may provide some indication of whether fish populations vary in a counter gradient manner. Present data from a study on the Missouri and lower Yellowstone rivers, provide an opportunity to examine latitudinal patterns of growth for several wild, freshwater fish species from different phylogenetic groups and varying life histories. Studying species from varying backgrounds is beneficial because they can provide insight into the broad evolutionary trends that exist in an ecosystem (Conover, 1990). The objectives were to: (1) determine growth rates for five fish species from the Missouri and lower Yellowstone rivers [channel catfish *Ictalurus punctatus* (Rafinesque), emerald shiners *Notropis atherinoides* Rafinesque, freshwater drums *Aplodinotus grunniens* Rafinesque, river carpsuckers *Carpionodes carpio* (Rafinesque), and saugers *Stizostedion canadense* (Smith)] and (2) determine if there is evidence to support CnGV theory for these five species.

MATERIALS AND METHODS

LIFE HISTORY SUMMARIES

Channel catfish are native to the rivers and streams of central North America and have since been widely introduced into lentic systems (Hubert, 1999). This species is considered to be mainly a habitat generalist, consumes an omnivorous diet, and can reach lengths >800 mm. Lifespan of channel catfish can exceed 20 years, but a maximum of 8–10 years are more commonly reported (Hubert, 1999). Spawning typically occurs once annually, in nests guarded by the males with fecundities ranging from 1000 to 60 000 eggs per female (Jearld, 1970). Channel catfish are a fairly mobile species with movements >100 km in several rivers (Hubert, 1999).

Emerald shiners are one of the most abundant pelagic cyprinids in central North America (Pflieger, 1997) and provide an important forage base for large river piscivores

(Etnier & Starnes, 1993). Diet consists mainly of macro- and micro-invertebrates. Spawning is believed to occur in shallow water over firm substrata where the non-adhesive eggs eventually settle on the bottom. Fecundities typically range from 2000 to 3000 eggs per female (Pflieger, 1997). Emerald shiners are fairly short-lived with few individuals surviving to their third summer and rarely exceed 100 mm in length (Pflieger, 1997).

Freshwater drums are common to slack-water areas of rivers and reservoirs in central North America (Etnier & Starnes, 1993). Diet is somewhat varied, but centred around benthic associated organisms such as aquatic insects, fishes, and molluscs. Reproductive behaviour is not well documented, but is believed to occur in midwater areas where their eggs float until hatch. This reproductive strategy has resulted in fairly high fecundity rates of *c.* 40 000 and 60 000 eggs per female (Etnier & Starnes, 1993). Little information is known about movement patterns of freshwater drums, but the pelagic eggs assist in dispersion. This species is quite long-lived and can attain ages >10 years and can reach lengths of 500 mm (Pflieger, 1997).

River carpsuckers are benthic detritivores, typically found in larger rivers throughout much of central North America (Etnier & Starnes, 1993). This species is often found in large schools and spawning occurs over soft substrata with the eggs broadcast over a relatively large area. Females produce from 100 000 to 300 000 eggs year⁻¹ (Etnier & Starnes, 1993). This species has a maximum age of *c.* 10 years and maximum size of *c.* 640 mm.

Saugers are predominantly found in large rivers and reservoirs throughout the central portion of North America. Diet of adult saugers is almost exclusively fishes (Pflieger, 1997). Fecundity ranges from 20 000 to 60 000 eggs per female and spawning usually occurs over fairly firm substrata allowing the eggs to be dispersed along the substratum by the current. Additionally, this species is highly mobile and can move large distances (>100 km) in a relatively short time (Pegg *et al.*, 1997a). Maximum life span is *c.* 10 years and maximum length is *c.* 610 mm (Etnier & Starnes, 1993).

FISH AND BODY STRUCTURE COLLECTION

The goal of the sampling design was to quantitatively characterize fish growth throughout the Missouri and lower Yellowstone river systems. The sampling protocol divided the rivers into several spatial scales implementing a hierarchical framework (Frissell *et al.*, 1986; Hawkins *et al.*, 1993). From this framework, growth rate comparisons were made from fishes collected among nine sections of the Missouri and lower Yellowstone rivers during the late summer and early autumn in 1996–1998 (Fig. 1). An attempt was made to sample five replicates of each dominant habitat type (inside and outside bend, thalweg at crossover point, non-connected and connected secondary channels, tributary mouth) per section using a boat electrofisher, beam trawl, bag seine, stationary gillnet and drifting trammel net. At least two gears were typically used in each habitat type to reduce size-selective biases present in each gear. Complete details and rationale for sampling design, sampling procedures, data processing, and quality assurance are reported in Sappington *et al.* (1998).

A variety of calcified structures were collected to determine growth rates from these five species following established methods (Busacker *et al.*, 1990; Devries & Frie, 1996). Scales were collected for emerald shiners and river carpsuckers, otoliths were collected for freshwater drums and saugers, and pectoral spines were collected for channel catfish. Standardized procedures were followed to prepare each body structure (Jearld, 1983; Pegg *et al.*, 1998) and inter-annual measurements made using an image analysis system. Growth rate estimates required some information on back-calculated lengths at prior ages so the Fraser-Lee method was used to back-calculate lengths at age for river carpsuckers and emerald shiners (Busacker *et al.*, 1990) using mean inter-annual distance measurements on five scales from each individual. The intercept was calculated by regressing scale radius on length at capture. For channel catfish, freshwater drums and saugers, the direct proportion method was used because the structures used for these species were present at hatch (Devries & Frie, 1996).

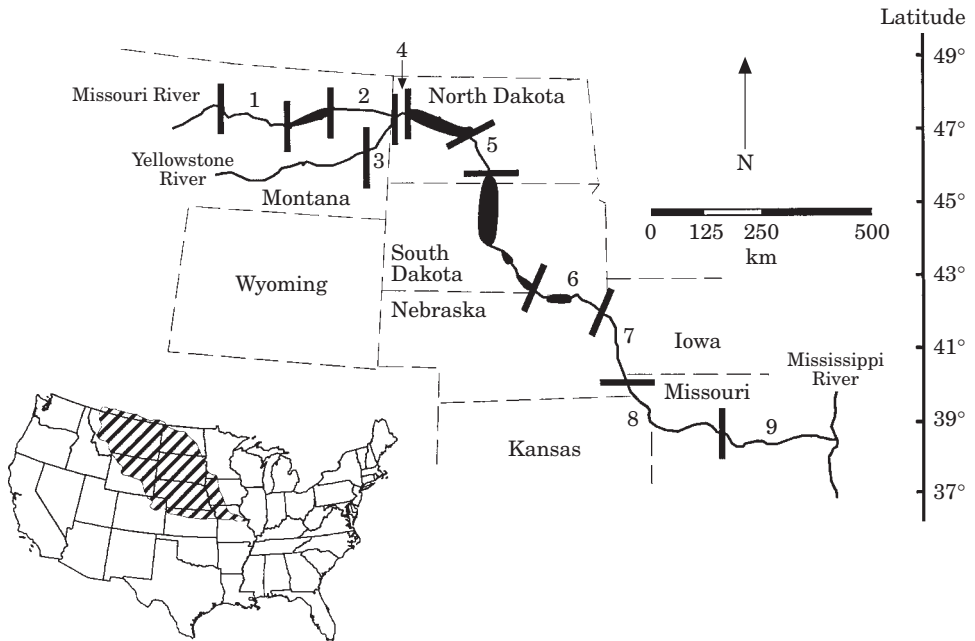


FIG. 1. Location of the nine sections used to compare fish growth rates. The numbers between the solid bars indicate a specific section of river where fish data were collected. The inset shows the location of the Missouri River Basin within the United States.

GROWTH RATE ESTIMATION AND COMPARISON

Energy is more readily put towards growth in the first year of life compared to later years when other energy demands, such as gamete production, come into play (Busacker *et al.*, 1990). Therefore, each individual was placed into one of two life-stage groups that reflected more homogeneous growth: (1) young-of-the-year (YOY) and (2) age 1+ years individuals for each species.

The sampling techniques provided an opportunity to catch fishes during the growing season throughout the rivers, so it was felt appropriate to estimate growth rates from body length increases that occurred during the sampling period rather than from estimates based on back-calculation. Calculating growth rates over the standardized sampling period was also advantageous because the beginning and endpoints were clearly defined. This aspect of the rate assessment was beneficial because identifying the precise date of hatch or annulus formation as a growth boundary criterion has been difficult to accurately assess (Machias *et al.*, 1998).

Growth rate coefficients were first estimated for each species for each life-stage and river section. Growth for each individual was calculated as the difference between total length (L_T) at capture and the back-calculated estimate of length at the start of the growing season (Liao *et al.*, 1995). Conceptually, the growth rate for each section was then estimated by regressing the growth increment data on date of capture during the standardized sampling period (Fig. 2). In this example, the slope of the regression is 1.17 mm day^{-1} which could then be used for comparisons among the other sections. The analyses followed this approach, but the actual growth rates were calculated in a slightly different manner. Growth estimates (mm) were used from hatch to date of capture as the response variable for YOY analyses. Individuals in the age 1+ years life-stage represent many size groups that could result in widely varying size-dependent growth rates. Therefore, to account for this bias residual values were used from the growth to size (length at capture) regression as a surrogate estimate of growth. The initial data used to describe the relation between growth and size for age 1+ year individuals were

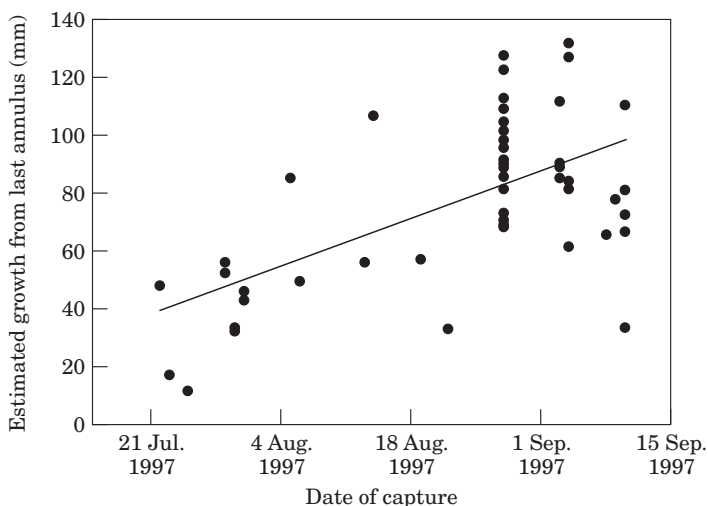


FIG. 2. Example plot of channel catfish growth (mm) by date of capture from the Iowa/Nebraska section of the Missouri River. The regression (specifically slope) conceptually illustrates how growth rates were determined for each species, section and life-stage. Regression line: slope=1.17, $r^2=0.35$, $P=0.0001$.

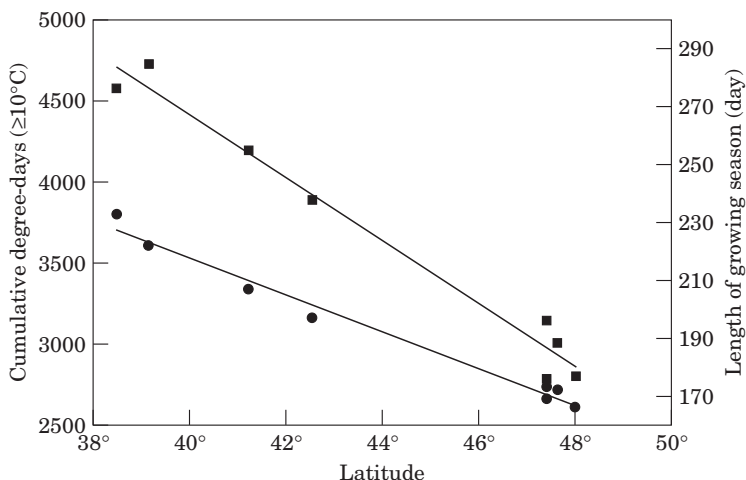


FIG. 3. Relation between cumulative degree-days (■) and length of growing season (●) for water temperatures $\geq 10^\circ\text{C}$ and latitude on the Missouri and Lower Yellowstone rivers. Regression line: for degree-days, slope= -194.84 , $r^2=0.97$, $P<0.001$ and for length of growing season, slope= -6.37 , $r^2=0.98$, $P<0.001$.

log-transformed because they did not meet assumptions of linearity and homogeneity of variance. After calculating growth estimates for each species and section, analysis of covariance (ANCOVA) was then used to simultaneously estimate slopes of growth for each species on date for all sections (classification variable) using the GLM procedure in SAS (Littel *et al.*, 1991). These slopes, while still reflecting the relative growth rate in each section, do not directly translate to a daily growth rate in mm and are further referred to as growth rate coefficients. Next, differences in growth rate coefficients were tested for

TABLE I. Growth coefficient estimates for five fish species collected throughout the Missouri River and lower Yellowstone rivers. Each estimate represents relative growth rates within each sample section. Species specific coefficients are given for young-of-the-year (YOY) and age 1+ years life-stages. Sauger YOY growth coefficients were not included due to low sample size. Estimates highlighted in bold are significantly different from zero ($P < 0.05$). Sections are arranged from upstream (left) to downstream (right). Sample size in parentheses

Section	1	2	3	4	5	6	7	8	9
Channel catfish (YOY)	1996	—	0.338 (15)	—	—	—	0.180 (51)	0.448 (163)	0.511 (69)
	1997*	0.368 (5)	0.350 (14)	—	—	0.702 (36)	0.918 (57)	0.459 (114)	0.340 (97)
	1998*	—	0.547 (25)	—	—	0.482 (22)	0.947 (68)	0.806 (112)	0.581 (89)
Channel catfish (1+ years)	1996*	0.029 (23)	0.025 (44)	0.111 (12)	—	0.014 (8)	0.024 (37)	0.003 (55)	0.019 (10)
	1997*	0.001 (71)	0.005 (72)	0.017 (55)	—	0.020 (214)	0.017 (70)	—	0.22 (56)
	1998*	0.013 (60)	0.003 (58)	0.022 (85)	0.013 (31)	—	0.004 (38)	—	—
Emerald shiner (YOY)	1996*	—	—	—	—	0.222 (11)	0.635 (81)	0.208 (548)	0.142 (61)
	1997	0.214 (22)	—	0.190 (14)	—	—	0.522 (76)	0.316 (428)	0.365 (192)
	1998*	—	0.209 (9)	—	—	0.144 (162)	0.251 (54)	0.452 (192)	0.146 (145)
Emerald shiner (1+ years)	1996*	0.007 (130)	—	—	—	0.005 (46)	—	—	—
	1997*	0.013 (195)	—	0.012 (42)	0.007 (25)	0.004 (441)	0.012 (58)	0.004 (76)	—
	1998*	0.010 (231)	0.015 (40)	0.013 (107)	0.056 (33)	—	0.004 (69)	0.007 (22)	—
Freshwater drum (YOY)	1996*	—	2.521 (14)	—	—	1.808 (23)	3.655 (6)	0.374 (97)	0.779 (107)
	1997*	—	—	—	—	1.142 (43)	3.081 (6)	0.756 (343)	0.194 (132)

TABLE I. *Continued*

Section	1	2	3	4	5	6	7	8	9
Freshwater drum (YOY) <i>Continued</i>	1998*	—	—	—	—	0-906 (77)	0-632 (109)	1-127 (177)	1-211 (117)
Freshwater drum (1+ years)	1996	0-011 (57)	—	—	—	0-015 (5)	0-011 (6)	0-008 (18)	0-013 (16)
	1997*	0-015 (113)	—	—	—	0-022 (21)	0-018 (16)	0-004 (38)	0-002 (56)
	1998	0-005 (82)	0-014 (11)	0-011 (9)	—	0-005 (13)	0-003 (8)	0-006 (16)	0-005 (52)
River carpsucker (YOY)	1996	—	0-232 (22)	—	—	0-498 (48)	1-094 (10)	0-160 (62)	— 0-205 (4)
	1997	0-164 (20)	0-431 (13)	—	—	—	1-214 (35)	0-512 (117)	0-586 (122)
	1998*	2-699 (45)	0-916 (27)	—	—	0-703 (46)	0-323 (54)	0-302 (45)	0-055 (27)
River carpsucker (1+ years)	1996	— 0-015 (9)	0-030 (13)	—	— 0-007 (10)	0-003 (80)	0-001 (36)	— 0-005 (24)	0-008 (18)
	1997*	0-009 (13)	0-013 (25)	— 0-003 (12)	— 0-002 (12)	0-001 (148)	0-008 (51)	0-006 (61)	0-008 (41)
	1998*	0-002 (20)	0-003 (111)	—	— 0-053 (11)	0-005 (89)	0-002 (41)	— 0-008 (38)	— 0-380 (44)
Sauger (1+ years)	1996*	—	—	—	—	—	0-031 (9)	0-010 (18)	—
	1997*	0-001 (30)	— 0-008 (7)	0-009 (18)	—	0-037 (16)	0-009 (34)	— 0-003 (8)	—
	1998	0-009 (31)	0-012 (26)	— 0-041 (12)	—	0-008 (20)	0-021 (43)	0-016 (6)	—

*Growth coefficients for each section were different ($P < 0.05$) within a given year; —, no fish caught.

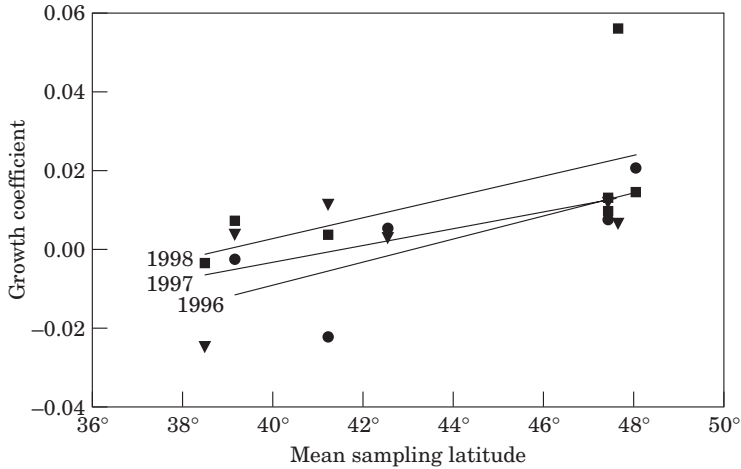


FIG. 4. Growth coefficient plots for age 1+ years emerald shiners for each section of the Missouri and Lower Yellowstone rivers with the resulting regression on latitude for each year. The slopes for each line suggest a counter gradient response in growth rate. ●, 1996: slope=0.0013, $r^2=0.52$, $P=0.17$; ▼, 1997: slope=0.0009, $r^2=0.42$, $P=0.12$; ■, 1998: slope=0.0011, $r^2=0.36$, $P=0.11$.

among sections using a test for heterogeneity of slopes (Littel *et al.*, 1991). Growth coefficient estimates were not reported for sections that did not exhibit a correlation ($P>0.10$) with date of capture.

An attempt was then made to identify statistically significant trends in growth rate coefficients with several independent variables that reflected a longitudinal gradient on the Missouri and lower Yellowstone rivers. These variables included mean sampling latitude, cumulative degree-days and length of growing season. Mean sampling latitude for each section was determined by calculating the mean latitude from all sampling locations within a section. Unpublished water temperature data were obtained from several water treatment facilities, state agencies and the U.S. Army Corps of Engineers to calculate cumulative degree-days and length of growing season for each section. Methods by Allan (1995) were followed to calculate cumulative degree-days above a threshold temperature of 10° C which encompassed the majority of the growing season for the five species studied. Similarly, length of growing season was calculated as the number of days in which water temperatures were >10° C.

RESULTS

Length of growing season increased by 27% and cumulative degree-day increased by 39% from the uppermost to the lowermost sections. Likewise, both degree-day and length of growing season for each section had a strong negative correlation to latitude ($P<0.001$; Fig. 3) indicating that the overall thermal potential decreases with an increase in latitude. The findings made from analyses using any of the three variables were similar when making system-wide comparisons due to this high correlation. Therefore, latitudinal comparisons are mainly presented to reduce confusion.

GROWTH RATE COEFFICIENT ESTIMATES

Tests were made for year effects on growth rate coefficients and significant ($P<0.01$) among year effects were found within all species and life-stage categories and thus data from all three years could not be combined. The

resulting growth coefficients are summarized for each species in Table I. The negative values shown for some species and sections are largely an artifact of transformation and using the covariates in the analyses rather than indicating a negative growth response. Therefore, these estimates should be viewed as relative to growth rate coefficients identified in other sections of the river rather than absolute. Generally, growth rate coefficients were lower in areas influenced most heavily by reservoirs (sections 2, 4, 5 and 6; Fig. 1; Table I) across both life-stages and all species.

Channel catfish growth rate coefficients were estimable for nearly every section, life-stage and year (Table I). The growth coefficients within sections for each year and life-stage were significantly different ($P < 0.05$) except for YOY estimates in 1996 (Table I). The coefficients were quite variable in both life-stages with YOY and age 1+ year estimates showing no visually identifiable trend establishing higher or lower coefficients in one area of the river over another.

Growth rate coefficients were estimable for emerald shiners at most life-stages and they were significantly different ($P < 0.05$) among sections for most years (Table I). Estimable coefficients in the upper sections of the river were somewhat limited especially for YOY over the three years of study. However, age 1+ year growth rate coefficient estimates were generally higher in the higher latitudes.

Growth rate coefficients for freshwater drums were sporadic in the upper Missouri and lower Yellowstone rivers among the three sample years (Table I). The lack of data from the upper river generally precluded making any river-wide comparisons for the YOY and age 1+ year life-stages. However, there were no discernable patterns among the YOY life-stage for a given year. Growth rate coefficients were quite variable for age 1+ year groups among the nine sections with only the 1997 estimates exhibiting significant differences ($P < 0.05$).

River carpsucker growth rate coefficients were significantly different ($P < 0.05$) and quite variable among the nine study sections for most years and life-stages (Table I). When estimates were possible, sections 5 and 6 tended to consistently have the lowest growth coefficients for the age-1+ year life-stage. Age-1+ year carpsuckers from the lower Yellowstone River (section 3) were among the fastest growing throughout the river.

Sauger growth rate coefficients could not be estimated for almost all sections over the YOY life-stage due to low sample sizes and are not presented here. Similar to the other species studied, growth rate coefficients for the age-1+ year group were variable across sample sites and tests for differences among sections were not significant ($P > 0.05$). The lack of estimates in many sections was predominantly due to low sample sizes, especially for the 1996 sampling year. Adult sauger growth rates in the inter-reservoir sections tended to contradict the trend of lower growth observed in the other species analyzed.

LATITUDINAL ESTIMATES

It was possible to compare growth coefficients among sections over a 9.5 degree gradient covering nearly the entire warm water portion of the Missouri and lower Yellowstone rivers (Fig. 1). The tests for latitudinal trends were highly variable and somewhat inconclusive for four of the five species. While visual inspection of the data may suggest a slight increase in growth coefficients

with an increase in latitude (Table I), it was generally found that there were no significant latitudinal patterns in the coefficients of any life-stage for most species studied. However, growth rate coefficients for adult emerald shiners did show a marginally significant relation to latitude (Table I; Fig. 4). This trend indicated higher growth rates with an increase in latitude supporting CnGV theory and this relation was similar among the other variables that were highly correlated with latitude (e.g. length of growing season and degree-day).

DISCUSSION

Latitudinal trends were observed only in adult emerald shiners that exhibited increased growth coefficients with higher latitudes along the Missouri and lower Yellowstone rivers. This suggests some supporting evidence for a CnGV response in emerald shiners. However, no significant latitudinal correlations were found in the other species. There are several explanations that could hinder identification of latitudinal trends. First, growth rate coefficient estimates could be consistently made for emerald shiners in most sections; whereas, consistent estimates for other species were largely restricted to localized regions. This is due to lower sample sizes in some of the upper and middle study sections and is especially prevalent in the YOY analyses for freshwater drums (Table I). Therefore, higher variability, a result of low sample sizes from some sections, could hinder ability to detect a latitudinal gradient in growth rate coefficients from wild populations.

Emerald shiners were also the only relatively short-lived species studied. This may indicate that differences in growth rates along a latitudinal gradient are more pronounced and easier to detect from field data in short-lived species using the present approach. However, further research is needed to assess this hypothesis. Growth and growth rates are dependent upon several factors including an individual's growth history meaning that future growth potential is dependent upon prior growth (Busacker *et al.*, 1990). Emerald shiners have a relatively short lifespan and few emerald shiners were collected beyond age 1 years over the course of this study. It is then reasonable to assume that a majority of the growth potential an individual emerald shiner possesses is expressed in the first 1 to 2 years of life. Conversely, the longer-lived species may have a decreased growth potential as they increase in both size and age (Busacker *et al.*, 1990) thereby hindering the ability to detect growth rate differences through natural variation among individuals of different sizes and ages. A potential bias in growth estimation could result by not taking these ontogenetic shifts into consideration. An attempt was made to account for this size bias in age 1+ year fish, but it is possible that the correction did not remove all size biases.

Water management practices such as impoundment and channelization may have also influenced growth rate variability of these fish species along the Missouri River system. No sampling was undertaken in the reservoirs (Sappington *et al.*, 1998), but some fish were collected in tailwater areas immediately downstream of dams. Sections 2, 4, 5 and 6 are all affected by impoundments in some manner (Pegg, 2000; Fig. 1). Most of these dams have hypolimnetic water release structures that force a localized reduction in the

length and quality of the growing season in parts of these sections. Overall, a consistent latitudinal gradient does exist for both length of growing season and cumulative degree days (Fig. 3). However, individuals that have been subjected to these localized coldwater releases may have lower growth rates than expected compared to other individuals within the same section increasing within section variability.

Channelization may have also forced a shift in growth and other life history characteristics in a non-latitudinal manner. Hesse & Mestl (1993), Pegg (2000) and Galat & Lipkin (2000) reported that the hydrologic regime along the upper channelized portion of the Missouri River has been drastically altered from the pre-impoundment condition. Some of these changes include higher flow rates, reduced flow variability and loss of slack water habitats for refugia suggesting a more extreme environment than was historically present. Living under these higher flow conditions probably requires more energy to maintain position in the river and to find food resources. This increased bioenergetic demand can have an effect on many life history characteristics such as reduced age at maturity (Cardinale & Modin, 1999), younger age structure, and increased growth to attain maturity at an earlier age (Wedemeyer *et al.*, 1990). No site-specific information is available on age at maturity for the Missouri River populations in this study but the age structure was much younger and back-calculated lengths at age did tend to be higher in the channelized portion of the river for channel catfish, river carpsuckers and saugers than from those sections further upstream (Pegg *et al.*, 1997b) possibly in response to these extreme conditions.

The present results could also be confounded by the longitudinal gradient of the biological communities found along the Missouri River. Most studies focussing on latitudinal growth responses used distinct populations or strains generally separated by large geographic distances (Conover & Present, 1990; Power & McKinley, 1997; Brown *et al.*, 1998). The present study focussed on sites where the geographic separation and latitudinal differences between adjacent sections was relatively small (Fig. 1). Therefore, some interdependency among the fish populations along the Missouri River system is possible and could inhibit clearly identifying large-scale trends in growth coefficients. This emphasizes a strong need for evaluation of growth rates from populations outside the Missouri River Basin and from other latitudes to validate the existence of a latitudinal response.

The species studied are capable of moving large distances or their reproductive strategies allow for wide ranging egg dispersal (Pegg *et al.*, 1997a; Hubert, 1999), which can inhibit identification of distinct populations. However, the construction of six mainstem impoundments in the early to mid 1900s (Fig. 1) has prohibited fish movements and possibly gene flow, at the very least, in an upstream direction. Unfortunately, little genetic work has been performed on Missouri River populations of the species studied. However, Young (2001) did report some genetic differences between Missouri River and Yellowstone River emerald shiners. Additionally, from an evolutionary perspective, the relatively recent construction of the mainstem impoundments may encourage genetic divergence among Missouri River populations. The potential micro-evolution that may result from this isolation could strengthen the ability to detect

latitudinal trends in growth rates and other physiological responses of Missouri River fishes.

Natural variability among individual growth rates may also prevent consistent latitudinal trends. Latitude, degree days and length of growing season are not the only variables that influence growth rates. Factors such as food availability, water velocities, oxygen levels and biotic interactions in the form of intra- and interspecific competition are also influential (Wootton, 1990). Therefore, growth rates are probably the result of a compromise between the adaptation to maximize growth in one environment and the possible poor physiological performance in other environments that may not adhere to a strict latitudinal trend in regulated river systems.

Generally, few clearly defined river-wide latitudinal trends were found, but there do appear to be some regional patterns that may support CnGV theory. This is most prevalent in the channelized portion of the river in sections 7, 8 and 9 (Fig. 1) for channel catfish, emerald shiners, freshwater drums and river carpsuckers (Table I). The latitudinal, growing season, and degree day gradients are not large among these three sections compared to the entire basin, yet growth rate estimates were consistently higher in section 7. Earlier, it was alluded to that management practices may obscure the overall results when trying to detect system-wide trends. It is recognized that many factors beyond a latitudinal gradient can influence fish growth. However, evaluating growth rates from populations that have been subjected to relatively similar environmental conditions over a latitudinal gradient in intensely managed systems may provide the best *in situ* perspective to detect evidence of a gradient response. The lower, channelized portion of the Missouri River provides such an opportunity and the present results suggest higher growth rates in the higher latitudinal reaches, prompting the need for further investigation.

Assessing growth rates and other physiological responses to latitudinal gradients is emerging as an important aspect in the understanding of fisheries ecology (Conover, 1990). Many factors can influence fish growth rates, confounding detection of the CnGV phenomenon. Despite these problems, some evidence of a correlation between growth rate and latitude was found, albeit at a more regional scale in four of the five species studied. The evolutionary background of these species are quite diverse suggesting that this response can go beyond a single phylogenetic line. Likewise, the impact of CnGV is quite complex and could have far reaching effects on how fishes and other aquatic organisms are perceived and managed. As more insight is gained into how organisms respond to latitude and length of growing season, knowledge will also be advanced on the evolutionary and ecological significance of this phenomenon. Accordingly, future controlled experiments are needed to further elucidate latitudinal differences in fish growth rates.

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