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Growth and mortality of prairie stream fishes: relations with fish community and instream habitat characteristics

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Abstract – Few studies have been conducted to describe the age structure, growth rates and mortality of fishes in small stream ecosystems. The purpose of this study was therefore to determine age structure, growth rates and mortality (i.e., total annual mortality and, age-specific mortality) of central stonerollers *Campostoma anomalum*, creek chubs *Semotilus atromaculatus*, red shiners *Cyprinella lutrensis* and green sunfish *Lepomis cyanellus* from 13 streams on Fort Riley Military Reservation, Kansas, using incremental growth analysis. Further, we were interested in determining the influence of fish community and instream habitat characteristics on growth rates. The age structure of central stonerollers, creek chubs, and red shiners was dominated by young individuals (i.e., less than age 2); however, over 60% of the green sunfish were age 2 to age 4. Mean total annual mortality was >60% for cyprinids and averaged approximately 44% for green sunfish. The age-specific mortality of central stonerollers and red shiners was generally less than 45% between age 0 and 1 and increased to over 85% for fishes greater than age 1. Fish community characteristics (e.g., catch per unit effort of trophic guilds) and chemical habitat (e.g., total phosphorous) were not related to growth rates ($P>0.05$). Growth of central stonerollers was not significantly correlated with physical habitat ($P>0.05$). However, the growth increments of creek chubs, red shiners, and green sunfish were related to the amount of woody debris (e.g., total woody debris, log complex habitat; $r>0.60$; $P\leq0.05$). The results of this study provide important information on the population dynamic rate functions of cyprinid and green sunfish populations in small prairie streams. Furthermore, these data suggest that woody debris is important habitat influencing growth of stream fishes.

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Key words: growth; mortality; prairie; community; habitat

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Unlike research conducted on lakes and reservoirs, most studies in small stream systems have focused on community-level attributes. For example, many researchers have used measures of community structure (e.g., index of biotic integrity [IBI]; Karr 1981; Karr et al. 1986) to summarize fish assemblage characteristics into a single metric. The IBI scores are then correlated with habitat features to determine the influence of instream conditions on fish community structure (Steedman 1988; Bramblett and Fausch 1991). Other researchers have compiled species into trophic guilds or tolerance categories to determine the influence of habitat on fish communities (Schlosser 1982a; Gorman 1988; Hughes and Gammon 1987). At the population-level, numerous models have been developed to predict standing crop of fishes from habitat characteristics (Fausch et al. 1988). However, most of these studies have been conducted in large streams and rivers and have focused on sportfish production. Although these approaches may be appropriate for many research hypotheses, they rarely provide information on the factors that influence population dynamic rate functions (i.e. growth, mortality, and recruitment) – especially with respect to nongame species in small streams.

Growth and mortality are important population-level dynamics influencing the ecology and management of fish populations; however, most studies on growth and mortality have been conducted on sportfish in lakes, reservoirs or large-river systems (e.g., Colvin 1991; Guy and Willis 1995). Conversely, studies investigating these processes are rare in stream ecosystems. This is unfortunate because growth and mortality rates directly influence the ecological role of individuals within the community and interactions among species, especially in size-structured populations (Werner and Gilliam 1984).

Incremental growth data (i.e., from hard structures) are labor intensive and expensive to collect (DeVries and Frie 1996). Consequently, most studies on growth of stream fishes have used length-frequency distributions to determine age structure and growth rates (e.g., Schlosser 1982a, 1985; Bayley 1988). However, these analyses are usually limited to determining age and growth of younger age classes (i.e., less than age 2; DeVries and Frie 1996). Moreover, length-frequency analysis is suitable when an individual cohort is followed through time or when the population is comprised entirely of young individuals. If the population contains older fish (e.g., older than age 2), it may be difficult to delineate age groups; thereby complicating or preventing growth analysis (DeVries and Frie 1996). Furthermore, analysis of length-frequency distributions only provides a measure of cumulative growth to the most recent age (unless cohorts are followed through time). Conversely, incremental growth analysis provides a detailed history of growth for each individual and may provide important information when habitat characteristics influence age-groups differently. For example, Putnam et al. (1995) studied the influence of habitat on size-specific growth rates of several species in Illinois streams. The authors found that habitat variables explained up to 90% of the variation in growth of several sportfish (e.g., channel catfish *Ictalurus punctatus*, largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, bluegill *Lepomis macrochirus*). Furthermore, the authors found that the influence of habitat depended on the size of individuals.

The purpose of this study was to describe growth and mortality of fishes inhabiting small prairie streams and to determine the influence of fish community structure and physical and chemical habitat on growth rates. We selected four species for this study based on their differing habitat requirements and trophic characteristics. Central stonerollers *Campostoma anomalum* are usually found in small streams and rivers dominated by cobble, gravel and sand substrates (Pflieger 1997). We selected central stonerollers, which primarily feed on benthic algae (Kraatz 1923; Pflieger 1997), to represent a herbivorous species. Creek chubs *Semotilus atromaculatus* and red shiners *Cyprinella lutrensis* were selected to represent insectivorous species. Creek chubs are ubiquitously distributed throughout the central United States and are most abundant in habitats consisting of cobble and gravel substrates, well-defined pool-riffle sequences and abundant cover (McMahon 1982; Pflieger 1997). Red shiners are also highly abundant in prairie streams, especially in highly degraded habitats, due to their ability to tolerate a wide variety of environmental conditions (Matthews and Hill 1979; Pflieger 1997). Throughout life, red shiners live in schools near the surface or in mid-water column habitats, while creek chubs form loose schools as juveniles and are solitary as adults. Thus, even though these species are both insectivores, their life-history characteristics are quite different, and the factors that influence growth likely differ between species. The insectivore-piscivore guild was represented by green sunfish *Lepomis cyanellus*. Green sunfish are able to tolerate extremes in turbidity, dissolved oxygen, temperature and flow; consequently, green sunfish are one of the most widely distributed species in the central United States (Horkel and Pearson 1976; Carlander 1977; Pflieger 1997). Because these four species are common throughout much of the midwest, the results from this study provide important life-history information (i.e., growth rates, longevity, mortality rates) and insight into the factors that influence population dynamics of stream fishes. We hypothesized that the abundance of conspecifics and closely related species (i.e., trophically similar species) would result in slow growth rates. We also hypothesized that growth rates would be related to habitat characteristics conducive to abundant prey production (i.e., periphyton, aquatic macroinvertebrates). Specifically, we hypothesized that growth rates of central stonerollers would be highest at sites with rocky substrate, open canopies, and high phosphorous concentrations and that growth of creek chubs, red shiners, and green sunfish would be highest in areas with rocky substrate and abundant woody debris.

Study area

Streams were sampled on Fort Riley Military Reservation, located in the Flint Hills region of north-eastern Kansas (Riley and Geary counties). A detailed review of the history, terrestrial plant community, stream characteristics, and fish communities on Fort Riley are provided by Quist (1999). The Flint Hills region is characterized by extensive limestone breaks and shallow soil (Zimmerman 1985). Due to the steep topography and rocky soils, row-crop agriculture is minimal; consequently, the Flint Hills contain the largest remnant of tallgrass prairie in North America (Bragg and Hulbert 1976; Zimmerman 1985). Streams in the Flint Hills region have relatively high gradients, with substrates dominated by limestone gravel and cobble, and support the most diverse fish fauna in the Kansas River basin (Metcalf 1966). Abundant fishes in the study streams include central stonerollers, creek chubs, red shiners, green sunfish, common shiners *Luxilus cornutus*, fathead minnows *Pimephales promelas*, bluntnose minnows *Pimephales notatus*, and orangethroat darters *Etheostoma spectabile* (Quist 1999).

Methods

Nineteen stream reaches were sampled from 13 different streams during June and July, 1997 and 1998 (see Quist 1999 for detailed descriptions). Two sites were randomly selected from each reach to represent the habitat characteristics of the reach. Sites were generally 35 times the mean stream width (MSW; Lyons 1992; Simonson et al. 1994), but never exceeded 300 m due to logistical constraints. Water chemistry samples were collected from three equally spaced locations at each site. Temperature (°C) and conductivity ($\mu S\ cm \cdot cm^{-1}$) were measured with a Hach CO150 conductivity meter. Dissolved oxygen ($mg \cdot l^{-1}$ as O_2; Hach HRDO Method 8166), turbidity (Formazin turbidity units [FTU]; Hach absorptometric method 8237), and total phosphorous ($mg \cdot l^{-1}$ as PO_4^{3-}; Hach PhosVer 3 method 8048) were measured using a Hach DR-EL/2000 portable laboratory kit. Boyd (1977, 1980) found that field kits are adequate for measuring water quality. In addition, one Hobo Temp® temperature logger was placed at each site during the last week of May and was removed in August, 1997 and 1998. Temperature loggers measured temperature (°C) at 3.25-h intervals. Maximum daily temperature, mean daily temperature, and maximum daily range in temperature between June 1 and August 17, 1997 and 1998, were determined from each reach.

Physical habitat and fish populations were sampled from each pool and riffle macrohabitat independently. Total length of each macrohabitat was measured. Stream width (m), depth (m), current velocity ($m \cdot s^{-1}$) and substrate particle size were measured along transects following methods described by Platts et al. (1983). Substrate particle size was classified according to a modified Wentworth scale (Cummins 1962), except for the inclusion of a bedrock category and pooling of sand categories. The percentage canopy closure was measured with a spherical densiometer at four points along each transect (Murphy et al. 1981). Instream cover (i.e., aquatic vegetation, undercut bank, branch complex, bank root, log, log complex and rootwad; see Quist 1999 for detailed descriptions) was defined as any object $\geq$0.3 m long and in water $\geq$0.3 m deep. Length (m), width (m) and depth (m) were measured from all cover types. Additionally, total woody debris was defined as the compilation of branch complex, bank root, log, log complex and root wad habitats. The amount of cover was quantified as m^2 of a cover type per ha.

Central stonerollers, creek chubs, red shiners and green sunfish were sampled by conducting one upstream electrofishing pass per macrohabitat using a Smith-Root Model 15-C backpack electrofisher. Electrofishing efforts were supplemented by conducting two seine hauls (bag seine; 7.6 m×2.0 m with a 1.0 m×1.0 m bag and 6.0 mm bar-measure mesh) in each macrohabitat. Fifty fish of each species were measured to the nearest millimeter (total length) and additional fish were counted. Each fish species was categorized as a benthic-insectivore (BI), generalized-insectivore (GI), herbivore-detritivore (HD), insectivore-piscivore (IP) or omnivore (OM), following Schlosser (1982b), Gorman (1988), and Tripe and Guy (1999). Catch per unit effort (C/*f*) was used to index species and trophic guild abundance and was expressed as the number of fish per minute of electrofishing (fish/min). Although seining was also used to collect fish, over 90% of the individuals used in this study were collected using electrofishing techniques.

Scales from ten fish per centimeter length group were collected from central stonerollers, creek chubs, red shiners, and green sunfish sampled from pool and riffle macrohabitats (DeVries and Frie 1996). Although riffle macrohabitats may be important habitats for many stream fishes, we found that catch rates were highest in pools, and over 85% of the individuals were sampled from pool macrohabitats (Quist 1999). Therefore, only data from pool macrohabitats were used in the analysis.

Scales were either pressed on acetate slides or mounted between glass slides and examined with a microfiche reader. The Fraser-Lee method was used to determine mean back-calculated length at age for green sunfish using a standard intercept value of 10 mm (Carlander 1982). Standard intercept values have not been proposed for central stonerollers, creek chubs, or red shiners and the body-scale relationships were weak (i.e., $r^2<0.80$); therefore, the direct proportion method was used to calculate mean back-calculated length at age. Age structure of each species was estimated using age-length keys and assessed by determining the proportion of age classes within a sample (DeVries and Frie 1996).

Total annual mortality was determined using catch curves (Ricker 1975). Total annual mortality likely represents only natural mortality because central stonerollers, creek chubs and red shiners are nongame species and harvest of green sunfish from Fort Riley streams is minimal (Kyle Hedges, Fort Riley Military Reservation, personal communication). We also estimated age-specific mortality rates (e.g., mortality between age 0 and age 1, mortality between age 1 and age 2) by determining changes in the relative frequency of individuals within successive age groups (Ricker 1975).

Emigration and immigration of fishes are important considerations when conducting stream research, especially with regard to studies investigating the factors that influence growth rates. Similarly, age-specific habitat use (e.g., pools, riffles) may also affect the interpretation of growth and mortality estimates. Although movement of short-lived stream fishes is difficult to quantify, it is unlikely that emigration and immigration substantially influenced our results because our experimental unit was a large stream reach (up to 10 km long). Within each reach we sampled two sites and each site contained up to 20 individual pools. Therefore, our estimates of growth and mortality represent a large spatial area within each reach. In addition, we did not find any evidence of age-specific habitat use for any of the species examined.

Linear regression analysis was used to determine the influence of fish community characteristics (e.g., C/*f* of cental stonerollers) and physicochemical habitat on growth increments. Because older fishes may not have lived in a stream reach for its entire life, we limited our analysis to the most current year of growth. For example, if age-3 green sunfish were collected, the growth increment (i.e., growth increment 3) used in the analysis was defined as the difference between mean back-calculated lengths at age 2 and age 3. For this example, growth increment 1 (i.e., mean back-calculated length at age 1) and growth increment 2 (i.e., difference between mean back-calculated lengths at age 1 and age 2) were not included in the analysis. Relationships with Pearson's product-moment correlation coefficients $(r)\geq|0.60|$ and P-values ≤ 0.05 were retained for further analysis. Stepwise-multiple regression was used to determine which of the remaining variables explained most of the variation in growth. The contribution of individual variables was tested using F-tests, and regression equations were limited to variables which contributed significantly ($P\leq 0.05$) to the model. Models containing more than one independent variable were compared to reduced models by examining Mallows' C_p statistic and reductions in the coefficient of determination (r^2, R^2; Mallows 1973; Ott 1993). Multicollinearity was analyzed by examining tolerance values and variance inflation factors as recommended by Sokal & Rohlf (1981). All statistical analyses were conducted using SAS (1996).

Results

Central stonerollers and creek chubs were sampled from 95% of the reaches, while green sunfish and red shiners were sampled from 84% and 37% of the reaches, respectively. Central stonerollers were the most abundant of the four species examined in this study, followed by creek chubs, red shiners and green sunfish (Table 1). The herbivore-detritivore guild was the most abundant trophic guild; however, central stonerollers were the only species representing this guild. Benthic-insectivores were rarely collected; whereas, generalized-insectivores and omnivores were common in our samples. The high variability in C/*f* of omnivores was due to localized, but highly abundant, populations of bluntnose minnows *Pimephales notatus*, common carp *Cyprinus carpio* and bullheads *Ameiurus* spp.

Physical and chemical habitat was highly variable among study reaches (Table 2). Mean dissolved oxygen was never below $6.5\ mg \cdot l^{-1}$, despite temperatures in excess of 25°C (Table 2). Mean total phosphorous concentration was generally below $0.50\ mg \cdot l^{-1}$; however, total phosphorous con-

Table 1. Mean, coefficient of variation (CV=[standard error/mean]×100), minimum, and maximum catch per unit effort (fish/min) of species and trophic guild (central stoneroller [CSTR]; creek chub [CRCB], red shiner [REDS]; green sunfish [GRSF]; benthic-insectivore [BI]; generalized-insectivore [GI]; herbivore-detritivore [HD]; insectivore-piscivore [IP]; omnivore [OM]) sampled from streams on Fort Riley Military Reservation, Kansas, during June and July, 1997 and 1998.

Species or trophic guild	Mean	CV	Minimum	Maximum
CSTR	1.8	28.3	0.0	7.8
CRCB	0.7	25.2	0.0	2.9
REDS	0.6	43.8	0.0	3.6
GRSF	0.4	27.3	0.0	2.1
BI	0.5	24.9	0.0	1.7
GI	1.7	22.6	0.0	5.4
HD	1.8	28.3	0.0	7.8
IP	0.7	27.4	0.0	3.3
OM	1.4	36.6	0.0	10.3

Table 2. Mean, coefficient of variation (CV=[standard error/mean]×100), minimum, and maximum for chemical and physical habitat variables sampled from streams on Fort Riley Military Reservation, Kansas, during June and July, 1997 and 1998.

Variable	Mean	CV	Minimum	Maximum
Dissolved oxygen ($mg \cdot l^{-1}$)	7.5	2.7	6.6	9.7
Total phosphorous ($mg \cdot l^{-1}$)	0.9	44.4	0.2	5.5
Conductivity ($\mu S \cdot cm^{-1}$)	599.0	2.7	488.0	731.0
Turbidity (FTU)	30.7	18.2	0.0	88.9
Temperature (°C)	21.0	3.3	14.5	26.8
Mean daily temperature (°C)	21.7	2.3	15.2	24.1
Maximum daily temperature (°C)	26.8	2.2	21.0	30.0
Maximum daily range in temperature (°C)	8.7	10.3	5.0	16.7
Width (m)	4.7	6.4	2.7	8.8
Depth (m)	0.3	6.7	0.2	1.8
Velocity ($m \cdot s^{-1}$)	0.02	25.0	0.001	0.08
Bedrock (%)	2.4	54.2	0.0	22.7
Boulder (%)	4.1	29.3	0.0	18.6
Clay (%)	10.4	22.1	0.0	40.0
Cobble (%)	8.5	8.8	0.0	26.7
Gravel (%)	15.8	15.8	0.0	40.0
Pebble (%)	10.0	20.0	0.0	30.5
Silt (%)	49.2	11.8	4.4	87.3
Canopy cover (%)	78.4	4.8	37.4	99.8
Aquatic vegetation ($m^2 \cdot ha^{-1}$)	1,313.3	41.4	0.0	7,447.2
Undercut bank ($m^2 \cdot ha^{-1}$)	46.2	42.8	0.0	253.7
Branch complex ($m^2 \cdot ha^{-1}$)	49.3	27.5	0.0	205.6
Bank root ($m^2 \cdot ha^{-1}$)	39.7	32.9	0.0	234.9
Log ($m^2 \cdot ha^{-1}$)	17.5	24.5	0.0	65.8
Log complex ($m^2 \cdot ha^{-1}$)	285.7	18.7	0.0	864.7
Root wad ($m^2 \cdot ha^{-1}$)	43.0	27.7	0.0	185.9
Total woody debris ($m^2 \cdot ha^{-1}$)	435.2	1.3	0.0	950.3

Table 3. Mean back-calculated length at age (mm), number of fish used to determine mean back-calculated lengths (N), mean proportion of fish within each age group (%), and total annual mortality (%) of central stonerollers (CSTR), creek chubs (CRCB), red shiners (REDS), and green sunfish (GRSF) sampled from streams on Fort Riley Military Reservation, Kansas, during June and July, 1997 and 1998. The number in parentheses represents one standard error.

	Mean back-calculated length at age								Proportion at each age						
Species	1	2	3	4	5	6	7	*n*	0	1	2	3	4	5	Mortality
CSTR	55 (1.4)	81 (2.1)	121 (24.3)					1,071	50	47	3	[a]			61 (9.1)
CRCB	63 (2.2)	102 (2.6)	144 (5.6)	181 (10.1)				883	33	46	20	1	[a]		72 (3.7)
REDS	37 (1.7)	59 (2.2)						728	34	62	4				71 (0)
GRSF[b]	44 (1.4)	71 (2.8)	92 (2.7)	112 (2.2)	141 (2.9)	167 (0.2)	205 ([c])	625	2	28	33	23	11	3	44 (4.7)

[a] Comprises <0.01% of the sampled fish. [b] Less than 0.01% of the green sunfish were older than age 5. [c] Unable to calculate standard error.

centrations >5.0 $mg \cdot l^{-1}$ were recorded from Forsythe Creek. It is likely that an upstream sewage treatment facility influenced phosphorous concentrations at this site. Substrate in pool macrohabitats was dominated by silt, followed by gravel, clay and pebble. Overall, aquatic vegetation was the most abundant form of instream cover. However, aquatic vegetation (Lemnaceae and *Potamogeton* spp.) was present at <60% of the study reaches and, when present, covered >90% of the reach. Woody debris was abundant in nearly all of the reaches and was dominated by log complex habitats. Riparian vegetation, primarily oak *Quercus* spp. and hackberry *Celtis occidentalis,* was highly abundant at many sites and was positively correlated with the amount of bank roots (r=0.57, P=0.01), root wads (r=0.48, P=0.04) and total woody debris (r=0.52, P=0.02).

Age and growth analysis was conducted on approximately 3300 individuals (Table 3). Mean back-calculated length at age varied among reaches, especially for the older ages (e.g., age-3 central stonerollers). The age structure of cyprinids was dominated by young individuals (Table 3). However, the age structure of green sunfish was more evenly distributed among age groups. The maximum age of green sunfish was age 7.

The mean total annual mortality was >60% for the cyprinids and 44% for green sunfish (Table 3). Age-specific mortality rates provided a clearer interpretation of the mortality data (Fig. 1). Mortality was generally low for the younger age classes of central stonerollers, creek chubs, red shiners, and green sunfish. However, mortality rates were greater than 85% once individuals approached their maximum age. For example, the mortality rate of red shiners between age 0 and age 1 was less than 20%, but mortality between age 1 and age 2 was 94%.

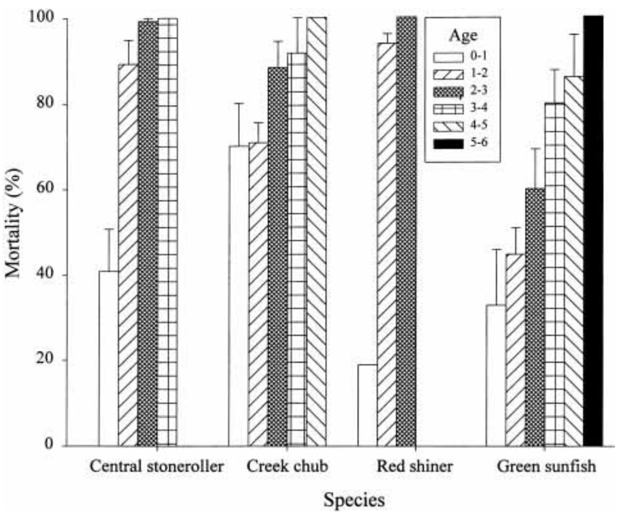

Fig. 1. Mortality between age-0 to age-1 (0–1), age-1 to age-2 (1–2), age-2 to age-3 (2–3), age-3 to age-4 (3–4), age-4 to age-5 (4–5), and age-5 to age-6 (5–6) for central stonerollers, creek chubs, red shiners, and green sunfish sampled from streams on Fort Riley Military Reservation, Kansas, during June and July, 1997 and 1998. The error bars represent one standard error

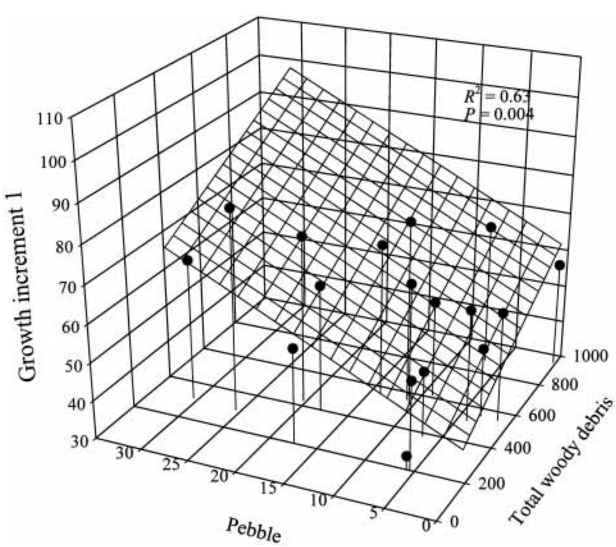

Fig. 2. The relationship between growth of age-1 (i.e., growth increment 1 [mm]) creek chubs, pebble substrate (%), and total woody debris ($m^2 \cdot ha^{-1}$) in streams sampled on Fort Riley Military Reservation, Kansas, during June and July, 1997 and 1998. The linear plane represents the multiple-regression model (growth increment 1=31.99+1.18 [pebble]+0.03 [total woody debris]), and the solid circles represent raw data

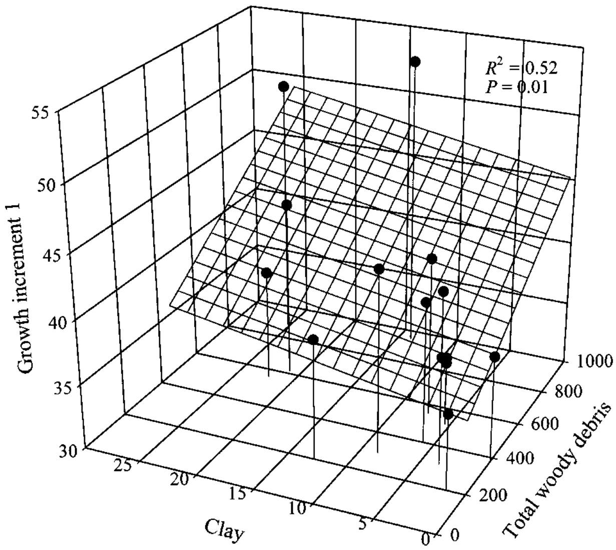

Fig. 3. The relationship between growth of age-1 (i.e., growth increment 1 [mm]) green sunfish, clay substrate (%), and total woody debris ($m^2 \cdot ha^{-1}$) in streams sampled on Fort Riley Military Reservation, Kansas, during June and July, 1997 and 1998. The linear plane represents the multiple-regression model (growth increment 1=33.15+0.15 [clay] +0.01 [total woody debris]), and the solid circles represent raw data

No significant relationships were found between fish community characteristics (i.e., C/*f*) and growth increments (P=0.06–0.97). Similarly, chemical habitat did not appear to influence growth of the species examined in this study (P= 0.07–0.90). No significant relationships (P>0.05) were found between growth increments of central stonerollers and physical habitat variables. Total woody debris and pebble substrate explained 63% of the variation in the first growth increment for creek chubs (Fig. 2). Total woody debris explained most of the variation (r^2=0.52) in the model. No significant relationships were determined between habitat characteristics and growth increments 2 and 3 for creek chubs; however, growth increment 1 and 2 of red shiners was positively correlated with total woody debris (r>0.61, P=0.04). Variation in growth of green sunfish during the first year was best explained by clay substrate and abundance of total woody debris (Fig. 3). However, total woody debris explained most of the variation (r^2=0.46) in the model. Growth increment 3 was weakly related to the amount of log complex ($r=0.55$, $P=0.02$), and growth increment 5 was positively correlated with the amount of rootwad habitat ($r=0.75$, $P=0.03$) for green sunfish.

Discussion

Few studies have used incremental growth analysis to determine the age structure and growth rates of stream fishes. Furthermore, most studies have used length-frequency distributions, limiting their analyses to age-0 and age-1 fishes (e.g., Lotrich 1973; Schlosser 1982a, 1982b, 1985; Bayley 1988). Lennon and Parker (1960) used scales to age central stonerollers in several Tennessee and North Carolina streams. Although the authors used scales to determine age, they did not estimate mean back-calculated length at age. Similar to our study, Gunning & Lewis (1956) used incremental growth analysis and reported that central stonerollers were 51 mm, 79 mm, and 99 mm at age 1, 2, and 3 in an Illinois stream, respectively. We hypothesized that a high abundance of rocky substrate (possible attachment sites for algae), low canopy cover (exposure to sunlight) and high phosphorous concentrations (an index to productivity) would enhance growth rates; however, habitat characteristics were not correlated with growth of central stonerollers. The inability to develop a significant model for central stonerollers does not imply that their growth was beyond the influence of biotic or environmental factors. Rather, it is possible that growth was related to factors not measured in this study or that the variability in fish community and habitat characteristics inhibited model development.

Mean back-calculated length of creek chubs from Fort Riley were within 20 mm of lengths reported for Illinois (Gunning & Lewis 1956) and Iowa streams (Dinsmore 1962). Gunning & Lewis (1956) and Dinsmore (1962) did not estimate mortality rates but reported that the age structure was dominated by young individuals (i.e., less than age 2). Similar to Fort Riley streams, Schlosser (1998) found that mortality averaged over 80% between age 0 and age 1 for creek chubs in a Minnesota stream.

Growth of creek chubs during the first year was related to the amount of total woody debris. Numerous studies have demonstrated the importance of woody debris for invertebrate production (e.g., Benke et al. 1984). Instream woody debris is an important component of nutrient processing in stream ecosystems because it enhances retention of organic matter and inorganic sediments by forming debris dams (Speaker et al. 1984). Debris dams become important nutrient sources and provide substrate for aquatic invertebrates, forming an important component of lotic food webs (Triska et al. 1983; Benke et al. 1984) and are especially important in habitats with unstable or unproductive substrate (e.g., silt, sand; Nilsen and Larimore 1973; Angermeier and Karr 1984; Benke et al. 1984). Creek chubs are particularly dependent on aquatic macroinvertebrates during their early life history (Dinsmore 1962; McMahon 1982; Schlosser and Angermeier 1990). Although creek chubs were defined as insectivores for this study, older creek chubs are largely opportunistic foragers and exhibit diverse diets consisting of plant material, aquatic and terrestrial invertebrates, and fishes (Dinsmore 1962). The mechanism underlying the observed trends is unknown. However, the relationship of growth increment 1 with woody debris and pebble substrate, and lack of significant relationships for older ages, likely reflects an ontogenetic shift in diet from aquatic insects to a diversified diet not dependent on instream production (e.g., terrestrial insects).

Mortality of red shiners between age 0 and age 1 was lower (<20%) than the other species, indicating that most red shiners survive their first year of life but then disappear from the community thereafter. Thus, high variability in recruitment can substantially influence the community structure and associated indices (e.g., species diversity, evenness) from year to year. The amount of woody debris influenced growth increments at all ages for red shiners. Red shiners are highly dependent on aquatic macroinvertebrates throughout life (Pflieger 1997). Thus, woody debris may enhance growth through increased aquatic invertebrate production.

Information on the growth of green sunfish is abundant for midwestern lakes, reservoirs, and streams (Carlander 1977). However, this is the first study to report age structure, growth, and mortality of green sunfish in northeast Kansas streams. On Fort Riley, green sunfish were the longest-lived species and experienced the lowest total annual mortality rate. In general, green sunfish growth is faster in lentic environments compared to lotic environments (Carlander 1977). Green sunfish from Fort Riley grew at rates similar to studies reported in Carlander (1977) and were most similar to Missouri streams. Cross et al. (1959) reported mean back-calculated lengths at age for green sunfish from Farlington Lake, Kansas, where mean back-calculated lengths were 20 mm to 40 mm greater at each age than green sunfish from Fort Riley. Moreover, Cross et al. (1959) used the direct proportion method, which tends to underestimate lengths when compared to methods used in this study.

Similar to creek chubs and red shiners, growth of green sunfish was related to the abundance of woody debris. Green sunfish are insectivores during their early life history and then switch to a piscine diet (Pflieger 1997). Thus, woody debris may provide benefits to green sunfish in different ways during ontogeny. For example, woody debris may function as a source of invertebrate prey during early ontogeny and as structure (e.g., ambush areas) for adults. Tillma et al. (1998) found that the area of root wad and undercut bank habitat explained over 60% of the variation in the relative abundance and biomass of spotted bass *M. punctulatus* in Kansas streams. The authors suggested that woody debris was important because it often formed the only source of structural diversity in their study streams. Therefore, it is possible that woody debris concentrates prey fish and serves as cover (e.g., ambush areas) for stream piscivores. It is apparent from this study that woody debris is an important habitat component influencing growth of small stream fishes in prairie ecosystems.

Although the specific mechanisms underlying these relationships are unknown (e.g., invertebrate production, ambush areas), these data provide a framework for further observational and experimental research on the mechanistic processes influencing population dynamics of stream fishes. The results of this study suggest that approaches traditionally used in lake and reservoir systems can provide important information regarding the population dynamic rate functions (e.g., growth, mortality) of stream fishes. Furthermore, the results of this study provide information that is fundamentally important for conserving prairie stream fishes and their habitats. Although these methods are more labor intensive than many other techniques (e.g., analysis of length-frequency distributions), they provide detailed information on the factors that influence fish populations and ultimately fish community structure and function.

Resumen

1. El fin de este estudio fue determinar la estructura de edades, y las tasas de crecimiento y mortalidad (mortalidad anual total y mortalidad específica de la edad) en *Campostoma anomalum*, *Semotilus atromaculatus*, *Cyprinella lutrensis* y *Lepomis cyanellus* en 13 ríos de la Reserva militar de Fort Riley (Kansas, USA). Pusimos especial interés en determinar la influencia de la comunidad de peces y de las características del habitat sobre las tasas de crecimiento.

2. La estructura de edad en *C. anomalum*, *S. atromaculatus* y *Cy. lutrensis* estuvieron dominadas por individuos jóvenes (<2 años); sin embargo, mas del 60% *L. cyanellus* tuvieron entre 2 y 4 años. La mortalidad total anual media fue $>60\%$ para los ciprínidos y 44% de promedio para *L. cyanellus*. En general, la mortalidad específica de la edad en *C. anomalum* y *Cy. lutrensis* fue menor del 45% entre la edad 0 y 1, e incrementó al 85% en los individuos mayores de 1 año.

3. Las características de la comunidad de peces (e.g. Capturas por unidad de esfuerzo de grupos tróficos) y el habitat químico (e.g. fósforo total) no parecieron estar relacionados las tasas de crecimiento ($P>0.05$). El crecimiento de *C. anomalum* tampoco pareció estar relacionado con el habitat físico. Sin embargo, incrementos en el crecimiento de *S. atromaculatus*, *Cy. lutrensis* y *L. cyanellus* estuvieron relacionados con la cantidad de “debris” (e.g. log complejidad de habitat; $r>0.60$, $P\leq 0.05$).

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