RELATIONSHIPS OF DROUGHT AND BIOTIC INTERACTIONS TO CRAYFISH

ASSEMBLAGE STRUCTURE IN GULF COASTAL HEADWATER STREAMS

A Thesis

by

BRIAN DANIEL HEALY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2002

Major Subject: Wildlife and Fisheries Sciences

RELATIONSHIPS OF DROUGHT AND BIOTIC INTERACTIONS TO CRAYFISH

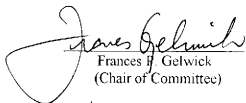## ASSEMBLAGE STRUCTURE IN GULF COASTAL HEADWATER STREAMS

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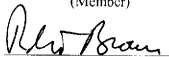MASTER OF SCIENCE

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August 2002

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ABSTRACT

Relationships of Drought and Biotic Interactions to Crayfish Assemblage Structure in Gulf

Coastal Headwater Streams. (August 2002)

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Chair of Advisory Committee: Dr. Frances P. Gelwick

Relationships between environmental variability and natural communities have been extensively studied. However the relative strengths of abiotic and biotic factors in structuring stream communities continues to be debated. Although North American crayfish are taxonomically diverse, occur across a variety of habitats, and are important components of stream ecosystems, when compared to other invertebrates or fish, factors influencing their distribution are poorly studied. Crayfishes may respond differently to disturbance and predators or competitors. In intermittent streams of East Texas, fishes that may influence the distribution of crayfish are rare or absent, so crayfish assemblages may differ between hydrologically variable and stable streams. In order to understand abiotic and biotic factors structuring native crayfish assemblages, environmental variables and densities of fishes and crayfishes were quantified simultaneously in 16 East Texas streams during June and October 1999, and February and April 2000. Three crayfish species, <u>Procambarus clarkii</u>, <u>Orconectes palmeri</u>, and <u>Procambarus kensleyi</u>, and several fishes were collected. Although fish and crayfish assemblages were similar in all streams during June before drought occurred, relative densities varied across intermittent and perennial streams following drought. After flow resumed in intermittent streams, densities of juvenile <u>P. kensleyi</u> were higher, but predatory fishes and adult <u>O. palmeri</u> were reduced, whereas in perennial streams, the opposite pattern occurred. These results suggest that <u>P. kensleyi</u> could tolerate abiotic stress, exploit resources, and maintain

higher densities in intermittent streams where predators were reduced, but its smaller size may have facilitated higher predation by fish in perennial streams. Assemblages in perennial streams suggested interactions among crayfishes and fishes favored <u>O. palmeri</u> and <u>P. clarkii</u>, which appeared to be superior competitors and resistant to predators. <u>Procambarus clarkii</u> was not strongly correlated with either abiotic or biotic factors measured in this study, including stressful conditions associated with drought. These results are consistent with life history trade-offs among stress tolerance, resistance to disturbance and predation, and competitive ability. The occurrence of both perennial and intermittent streams within a drainage provides a range of habitats that maintains more crayfish species from among those in the regional species pool than would either habitat alone.

DEDICATION

This thesis is dedicated to Dr. Terry Balding, whose teaching and mentoring inspired me to pursue my interest in ecology.

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I would like to sincerely thank my advisor, Fran Gelwick, for the many hours she spent discussing ideas, as well as her guidance throughout my graduate studies. In addition, my graduate committee members Dan Roelke and Kevin Heinz helped me to focus my research, and provided valuable comments on drafts of this thesis. David Lonzarich also provided helpful comments on early versions of the thesis proposal. I would like to thank David Peterson, USDA Forest Service, for logistical support and funding for this study through the National Fish and Wildlife Foundation. I am also indebted to Sarah Healy, Nikki Dictson, Bill Ellison, Stuart Willis, Senol Akin, Todd Lantz, John Goff, Angie Skeeles, and Mike Morgan, for help and companionship in the field, and Christopher A. Taylor of the Illinois Natural History Survey for verifying the identification of crayfish voucher specimens. The Office of Graduate Studies at Texas A&M University also provided financial assistance for this study, and the Chippewa National Forest provided funding for travel, as well as computer resources. I would like to thank my parents for their encouragement and support, and last, but certainly not least, I am extremely grateful to my wife Sarah, for her editorial comments, understanding, and patience during the completion of this thesis.

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INTRODUCTION

Relationships between environmental variability and assemblage structure have been extensively studied for stream fishes (e.g. Matthews 1983, Meador and Mathews 1992, Poff and Allen 1995) and macroinvertebrates (e.g. Berkman et al. 1986, Lenat 1993, Kerans and Karr 1994). Abiotic and biotic effects on community structure in streams vary greatly within and among systems, but relative strengths of these effects are still debated (Page and Schemske 1978, Ross 1986, Power et al. 1988, Capone and Kushlan 1991, Fausch and Bramblett 1991, Harvey and Stewart 1991). Power et al. (1988) suggested the need for more research addressing interactions of abiotic and biotic (i.e. competition and predation) processes in order to better explain species' distributions.

In the last several decades, studies have demonstrated an intimate link between the importance of biotic factors and abiotic variability in assembling stream communities (Power et al. 1988). As predicted by Peckarsky (1983) and later demonstrated (Schlosser 1982, Schlosser 1987b, Schlosser and Ebel 1989), abiotic disturbances, such as flooding and drought, generally are more important than competition or predation in structuring stream communities. Nonetheless, studies also indicate biotic factors can affect assemblage dynamics within stable streams (Page and Schemske 1978, Baker and Ross 1981, see review in Ross 1986), such as when predators cause prey to use sub-optimal habitats (Schlosser 1987a, Gelwick et al. 1997, Englund and Krupa 2000) or reduce prey abundance (Kushlan 1976, Meffe 1984).

Biotic processes and abiotic factors may also interact, as when environmental conditions and habitat structure control the outcome of species interactions (Fraser and Cerri 1982,

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This thesis follows the style and format of the Journal of the North American Benthological Society.

Schlosser 1987b, Gelwick 2000). Long-term discharge records for streams throughout the United States indicate frequency and predictability of floods, and periodicity and predictability of discharge are related to the importance of biotic factors structuring stream communities (Poff and Ward 1989). For example, falling water levels (as in intermittent streams) may cause crowding which increases competition and predation rates (Zaret and Rand 1971, Kushlan 1976, McCormick 1990, Capone and Kushlan 1991). Highly variable discharge can reduce species richness and fish abundance (Schlosser 1985). Alternatively, it may have little effect on assemblage structure when whole assemblages are physiologically adapted to tolerate such conditions (Matthews 1987, Meador and Mathews 1992). This adaptation to the natural disturbance regime helps to maintain assemblages of native species by reducing populations of non-native species not similarly adapted (Meffe 1984).

North American crayfish are taxonomically diverse and occur across a wide range of habitats and selection gradients resulting in a variety of adaptations (Hobbs 1991, Taylor et al. 1996). Forty-eight percent of all known crayfish species in North America are imperiled (Taylor et al. 1996) and conservation measures for crayfish are needed because of their importance to stream ecosystem functions (Lorman and Magnuson 1978, Momot 1995). Crayfish can comprise a large proportion of the invertebrate biomass in stream communities (Whitledge and Rabeni 1997), but in comparison to other invertebrates and fish, less attention has been given to environmental factors and processes influencing their distribution. Crayfish are opportunistic omnivores that can burrow to reach lowered water tables, from which they readily re-colonize previously de-watered reaches when flow returns (Hobbs 1991). In headwater streams where allochthonous input is the primary source of energy, crayfish process detritus (Huryn and Wallace 1987) and convert larger particulate organic matter into forms more usable at other trophic levels (Momot 1995, Whitledge and Rabeni 1997). By consuming algae (Creed 1994,

Gelwick 2000) and macrophytes (Chambers et al. 1990, Lodge et al. 1994, Hill and Lodge 1995) crayfish modify foraging space and cover for fish, resulting in behavioral and trophic cascades (Gelwick et al. 1997, Gelwick 2000). Whereas crayfish are important prey for some fish species (Rabeni 1992, Roell and Orth 1993), they also prey on, or compete with others (Rahel and Stein 1988, Rahel 1989, Guan and Wiles 1997).

Although initially considered omnivores (Lorman and Magnuson 1978, Momot et al. 1978), further evidence for carnivory suggests that crayfishes could be considered benthic invertivores (Momot 1995, Whitledge and Rabeni 1997). As such, crayfish may directly compete with invertivorous benthic fishes for food (Stelzer and Lamberti 1999, Keller and Moore 2000) or shelter (Rahel and Stein 1988, McNeely et al. 1990). Moreover, different sized crayfish may function or use resources differently (Polis 1984, Keller and Moore 2000), within as well as among species (Rabeni 1985), but effects of each on the other's distribution are not well studied.

For many crayfish species, little is known of their distribution or basic biology (Taylor et al. 1996). In addition, factors influencing population dynamics, as well as life histories of many species have not been studied (Hobbs 1991). One such crayfish, <u>Procambarus kensleyi,</u> has been classified as a species of special concern by the American Fisheries Society Endangered Species Committee (Taylor et al. 1996). <u>Procambarus kensleyi</u> occurs in East Texas and is sympatric with the burrowing crayfish <u>Procambarus clarkii</u> (Hobbs 1990), which is indigenous to the southern United States (Hobbs 1989a), but has been introduced worldwide and implicated in the displacement of native crayfishes (Hobbs 1989b). Success of <u>P. clarkii</u> is attributed to its tolerance of a wide range of habitat conditions, resilience to disturbance, and aggressive nature (Hobbs 1989b). Burrowing crayfish may be more resistant to drought than predatory fishes because the latter are generally less abundant in intermittent streams and are among the last to re-

colonize when flow resumes (Larimore et al. 1959). Ability to burrow varies among crayfishes (Hobbs 1991) and survival of burrowing species is enhanced in drought-prone areas (Taylor 1983). Therefore, competitive exclusion among crayfish species might be rare if drought prevents interactions from reaching equilibrium (Connell 1978, Reice 1994). In order to conserve native crayfishes, environmental factors, which limit crayfish distribution and abundance, and control population dynamics, must be determined. As in many stream systems, complex interactions likely occur among species and environmental factors, but those structuring natural assemblages of crayfish are ambiguous or rarely studied (Mitchell and Smock1991).

In headwater streams of an East Texas drainage, periodic drought and flooding were strongly correlated with the distribution of stream fishes (Herbert 1999). If these abiotic factors reduce populations of fishes that consume crayfish, then biotic factors might be less important in structuring crayfish assemblages. Conversely, in perennial streams with more stable flow, the presence of additional fish species and large-bodied predators might influence abundance and size distribution of crayfishes (Stein 1977) by either reducing competition among crayfish, or increasing competition for predator-free space (Gelwick 2000). However, if fish and crayfish species present in these streams are adapted to variable hydrologic regimes, little difference in crayfish assemblages might be expected across perennial and intermittent streams. The objectives of this study were to survey fish and crayfish in four consecutive seasons across a range of stream habitats in order to (1) evaluate relationships between environmental factors and distribution of crayfishes and (2) to compare crayfish assemblage structure across streams with intermittent and perennial flow, relative densities of potential competitors (both fish and crayfish), and predatory fishes.

METHODS

Study area

This study was completed within the boundaries of the Sam Houston National Forest, which lies within the coastal plain of eastern Texas, U. S. A. Sampling sites were chosen from among first to third order streams of the East and West Forks of the San Jacinto River (14 sites) and the Trinity River (2 sites; Fig. 1) and were distributed throughout the National Forest (Appendix A). Many of the streams were chosen (14 of 17 streams) because they were also included in a 1997 study that evaluated effects of hydrologic variability on stream fish assemblages (Herbert 1999). Additionally, sampling sites were restricted to those streams accessible through National Forest lands. Streams had mainly sandy substrates, pool-run morphology, relatively low to moderate gradient, and either intermittent or perennial flow.

Field protocol and data collection

Surveys were made during daytime, under baseflow conditions and repeated in June-July and September-October in 1999, and January-February and March-April in 2000 (herafter referred to as June, October, February, and April). Crayfish and fish were collected simultaneously using a Smith-Root® model 12-B backpack electrofisher. Electrofishing has been found to be more effective for sampling all size classes of crayfish when compared with quadrat sampling, direct observation, and hand-netting at night (Rabeni et al. 1997). Crayfish and fish were removed to depletion from block-netted reaches that were 35 times the mean stream width in length (Simonson et al. 1994). Species abundance of both crayfish and fish were standardized by area sampled (number/m^2) before statistical analyses.
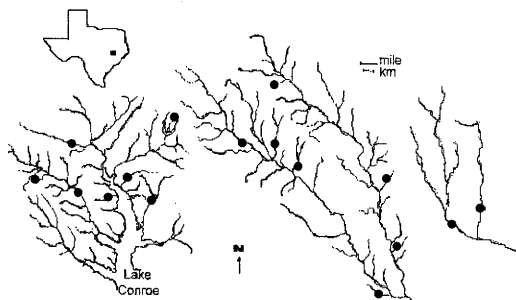
Fig. 1. The distribution of the sampling sites across the drainages included in this study including (from left to right) the West and East Forks of the San Jacinto River, and the Trinity River drainage.

Individuals were identified to species using published keys for fishes (Robison and Buchanan 1988, Hubbs et al. 1991) and crayfishes (Hobbs 1989a, Hobbs 1990), with crayfish identification confirmed by C. A. Taylor (Curator for Crustaceans, Illinois Natural History Survey). Individuals that could be identified to species in the field were measured and released. Voucher specimens were anesthetized by immersion in MS-222, initially preserved in 10% formalin, then transferred to 70% ethanol and archived. Fishes were deposited in the Texas Cooperative Wildlife Collections at Texas A&M University. Crayfish were deposited in the Crustacean Collection of the Illinois Natural History Survey. Following Garvey et al. (1994), crayfish were assigned to either large (adult) or small (juvenile) size classes based on carapace length (either $<$ or $\geq$ 25 mm from anterior tip of rostrum to posteriomedian tip of carapace edge).

To correlate habitat conditions with fish and crayfish densities, habitat variables were measured at each reach for each monthly collection. Variables were measured on across-stream transects distributed at 3-m intervals along each sampled reach (Angermeier and Karr 1984). Environmental variables used in analyses are listed in Table 1. Wetted channel width was measured across each transect, and velocity, stream depth, and substrate, were measured either at 1-m intervals (starting 10 cm from the bank) or at three evenly spaced points (when stream width was $\leq$ 3.1 m) across each transect. Velocity was measured at mid-depth using a Marsh-McBirney Model 2000 Flo-mate® electromagnetic flow meter. At each transect point, the dominant substrate was visually categorized as clay, silt, sand, or small gravel (Gorman and Karr 1978). Cover was defined as in-stream structure that could provide refuge for crayfish from terrestrial or aquatic predators. Percentage of area containing each cover type (% depth >35cm, % woody debris, % root, % undercut bank, % detritus, % no cover) was visually estimated by the same observer (BDH) along each transect within one meter of either side. The average across all transect measurements from each reach was calculated to describe mean habitat values

Table 1. Environmental variables included in analyses and a description of how data were quantified for each variable. In addition, groupings for partial canonical ordination analysis are indicated. For variables abbreviated in figures, codes are listed in parentheses. For competitor and predator density, species codes are made up of the first letter of the genus, followed by the first letters of the species name, except for <u>Lepomis</u> and <u>Etheostoma</u> variables (see Appendix B).

Variable (code)	Description of methods/ data collection
Abiotic Variables	
Velocity (MnVel)	Transects- Marsh-McBirney Flo-mate Flow Meter Measured at mid-depth, calculate mean
Depth (MnDepth)	Transects-measure, calculate mean

Substrate-
    % Clay
    % Silt
    % Sand
    % Small Gravel
     (SmGrav)
	Transects- estimate at each point, sum for entire reach.

Cover- % No Cover (NoCover) % Depth (>35 cm) % Woody debris (Wood) % Root % Undercut bank (Undcut) % Detritus	Transects- estimate Estimated within 0.5 m of each transect (percent of area within 0.5 m of transect covered by each habitat variable)
CV of depth (CVdepth)	Calculated for each stream reach at each sampling period
CV of velocity (CVvel)	Calculated for each stream reach at each sampling period
CV of substrate (CVsub)	Calculated for each stream reach at each sampling period
Wetted Stream Width (Width)	Transects-measure, calculate mean
CV of width (CVwidth)	Calculate for each stream reach at each sampling period
Maximum Depth (MxDepth)	Transects- maximum depth along each transect, Calculate mean for reach
CV of maximum stream depth (CVMaxD)	Calculate for each stream reach at each sampling period, using max depth measurements from transects
Conductivity (Cond)	Yellow Springs Instruments (YSI model 85)

Table 1. Continued.

Variable (code)	Description of methods/ data collection
	Hydrologic Variables
Drought	Nominal variable for the occurrence of drought in a stream among the four collecting periods
Discharge (Disch)	Calculated ($Q = width \times depth \times velocity$)
Minimum Discharge (MinQ)	Minimum discharge among the 4 sampling periods
	Drainage
West, East, Trinity	Nominal variable indicating the drainage where each study stream was located (West or East Fork San Jacinto River, or Trinity drainage)
	Temporal Variables
June, October, February, April	Nominal variable for each collecting period
	Biotic Variables
Predator density	Density (individuals/m^2) of predatory fishes (A. natalis, L. cyanellus, E. americanus, L. gulosus, L. punctatus, L. macrochirus, Lepomis spp., or M. salmoides)
Competitor density	Density (individuals/m^2) of potential competing crayfish or fish (P. kensleyi, P. clarkii, O. palmeri, A. sayanus, Etheostoma spp., P. sciera, E. oblongus, N. noturus., or Lepomis young-of-year)

for each variable during each collection. Coefficient of variation (CV) was calculated for each

of the following variables measured on transects: depth, maximum depth, velocity, channel

width, and substrate size. Discharge was calculated for each stream during each collecting

period from measurements of wetted channel width, water velocity, and depth (Gordon et al.

1992). To determine the effects of different hydrologic regimes on crayfish and fish

distributions, temporal hydrologic variation was characterized for each stream as CV of

discharge across monthly collections. Minimum discharge for each reach across monthly

collections also was included as a variable in analyses. A nominal variable for drought indicated

reaches with either perennial (0) or intermittent flow (1). Three nominal variables (West Fork

San Jacinto, East Fork San Jacinto, or Trinity) indicated the drainage for each stream and four

variables (June, October, February, or April) indicated the month in which each collection

occurred.

Statistical analyses

Complex relationships among abiotic and biotic factors often structure species

assemblages (reviewed in Matthews 1998) and species may vary in their response to single or

multiple factors. Therefore, the relative influence of such factors on assemblage structure is

difficult to determine using only univariate statistical analyses. Multivariate methods are more

effective for analyzing trends in community data, particularly those with many species and

samples. In this study, both univariate and multivariate methods were used to evaluate

relationships among species densities across complex environmental gradients and to determine

the relative importance of several factors hypothesized to structure crayfish assemblages. Some

of these methods emphasized relationships among species, while others emphasized those between species and environmental (explanatory) variables.

Detrended correspondence analysis (DCA), a multivariate ordination method, was used to infer environmental gradients structuring assemblages as derived from collections of fish and crayfish, and to compare species composition between pre- and post-drought collections. Ordination techniques, which include principal components analysis (PCA), correspondence analysis (CA) and DCA, arrange species and collections simultaneously along theoretical axes representing major environmental gradients based solely on the similarity in species composition among collections (Gauch 1982). Those collections with similar species composition and relative abundance lie closer together along an ordination axis. One assumption of these methods is that most of the variation in relative species' abundance among sites is related to one or a few underlying environmental variables, the most important of which are generally represented along the first few axes. The importance of each axis in accounting for variation ("maximized dispersion" or widest spread among species and collection scores) among species' abundance is indicated by its eigenvalue (ter Braak 1995, ter Braak and Smilauer 1998).

PCA assumes a linear relationship between species and environment gradients (i.e. a species either decreases or increases along the underlying environmental gradient), while CA (and DCA) relates to a unimodal response (bell-shaped response curve), where a species occurs in a limited range across an environmental gradient (ter Braak 1995). Species response curves, relative to continuos environmental gradients, are generally unimodal (bell-shaped) in nature (reviewed by Pianka 1994), and the degree of unimodality in species' responses can be tested using DCA (ter Braak and Smilauer 1998). Gradient lengths approaching four standard deviations indicate a strong unimodal response among at least some of the species collected (see below for more explanation, ter Braak 1995). An initial DCA of species data collected during

this study indicated a gradient length of 3.85 standard deviations indicating linear methods (e.g. PCA) were not appropriate for this analysis.

A fault of CA is that the second axis may have a quadratic relationship to the first; therefore, the ends of the first axis may be compressed relative to the middle and the distance between collection scores (i.e. position along an axis) on an axis may not represent the similarity among them accurately (Gauch 1982). In DCA, axes are detrended, where axis 1 is divided into a number of segments within which the axis 2 collection scores are standardized to a mean of 0 and a variance of 1, thereby eliminating the relationship between the first and second axis and the corresponding "arch-effect" (Gauch 1982, ter Braak 1995). Since a Gaussian response curve (approximated by a unimodal species curve) with a variance of 1 rises and falls over an interval of 4 standard deviations, detrending allows for a more uniform, quantifiable change in species composition (or faunal turnover) as standard deviation units along the first axis (Gauch 1982, ter Braak 1995). Axis lengths greater than four standard deviation units indicate a complete (100%) faunal turnover between collections (where no species are in common) and the distance between scores along an axis can be used as a measure of similarity among them (Gauch 1982, ter Braak 1995, ter Braak and Smilauer 1998). In addition, because DCA more clearly displays true community gradients than ordination methods with axes only constrained to be orthogonal (e.g. CA), ecological interpretation of the gradient based on the spatial position of species and collections is often easier to perform (Gauch 1982). However, hypotheses subjectively derived by interpretation of the ordination diagram must be tested by other methods.

Canonical correspondence analysis (CCA), a multivariate method of direct gradient analysis, was used to simultaneously evaluate abiotic, temporal, and biotic (i.e. competitors and predators) explanatory variables hypothesized to influence crayfish assemblage structure. Direct gradient analyses display the ecological niche of all the species in a community along

synthetic environmental gradients made up of measured variables (Gauch 1982), and can be used to statistically test hypothesized ecological gradients presented by DCA ordinations (ter Braak 1995). Unlike DCA, CCA simultaneously orders species and collections along axes that are constrained to be linear combinations of explanatory variables (i.e., canonical axes; ter Braak 1995). Further, the best combination of explanatory variables is selected by CCA to maximize the dispersion (i.e. explain variation), or separate the niches, of the species across the first few canonical axes (ter Braak 1986, ter Braak 1995). Each additional axis explains an additional, and successively, smaller amount of variation in species distribution (as indicated by its eigenvalue), therefore, as many axes can be derived as there are explanatory variables (ter Braak 1995). As with DCA, a unimodal response of species to environmental gradients is a requirement of CCA. By using Monte Carlo randomization tests of significance, explanatory factors correlated with gradients identified by CCA (or interpreted from DCA) can be tested and their combined and individual contribution to the explained (canonical) variation in species' distributions can be quantified (ter Braak and Smilauer 1998). In addition, when DCA and CCA produce similar gradients among species scores, the measured explanatory variables are assumed to account for most of the observed variation in the species data (ter Braak 1986).

Explanatory variables in CCA (Table 1) included habitat variables that were measured or calculated for each collection, and densities of fishes that were either potential competitors (benthic invertivores) or predators, as determined from published information (Benke et al. 1985, Robison and Buchanan 1988). Similar to multiple regression, nominal variables (i.e. dummy variables, Ott 1994), in this case, fork, drought occurrence, and month of collection, can be included in the analysis. Dependent variables were densities of each crayfish species-size class. The densities of several darter species (Etheostoma parvipinne, E. chlorosomum, and E. gracile) were combined as a single variable (Etheostoma) in all analyses (except DCA) based on their

functional similarity (Robison and Buchanan 1998), as were densities of <u>Lepomis megalotis</u> and <u>L</u>. <u>marginatus</u> (as <u>Lepomis</u>). Because CCA standardizes values of explanatory variables to a mean of 0 and a variance of 1, variables with different raw values could be used simultaneously (ter Braak and Smilauer 1998).

Since species' abundance (versus presence/absence) data may be skewed (few large values, and many small values), a few high values may unduly influence the results of the ordination (ter Braak 1995, ter Braak and Smilauer 1998). However, to preserve the measured relationships in the species density data, and to evaluate the importance of species that may be rare, yet important in structuring a community (e.g. predators) no transformations were applied for either CCA or DCA. In addition, the variation in relatively rare species is usually fitted to axes with smaller eigenvalues, therefore the contribution of rare species to the first few axes is usually small (Legendre and Gallagher 2001). CCA was run separately with all untransformed variables, and then with all (except nominal) variables transformed. These results were compared with the goal of producing a model that explained the most variation in the species data. However, results were not expected to differ considerably because CCA is not influenced by linear transformations of environmental variables (ter Braak 1995). Continuous variables were log (X+1) transformed, whereas proportions were arcsine-square root transformed.

Initial runs of CCA using all biotic, abiotic, spatial, and temporal variables identified in Table 1 indicated those explanatory variables which were multicollinear (correlated with each other; e.g. mean maximum depth and mean depth). Multicollinear variables in CCA potentially inflate the amount of unexplained variance as in multiple regression (Sokal and Rohlf 1995). Therefore, explanatory variables with high variance inflation factor (VIF) scores (> 20; ter Braak and Smilauer 1998) were removed during several subsequent CCA runs (ter Braak 1986). Variance inflation factors are a measure of the degree to which an independent variable is

correlated with the other explanatory variables in the analysis (ter Braak and Smilauer 1998), and therefore would not explain additional variation in species data. Before removing any variables with high VIF from the analysis, the marginal effects of each variable, or the amount of variance explained by each variable alone (without other variables in the analysis), was considered (i.e. marginal effects report; ter Braak and Smilauer 1998). After each run, the variable with the highest VIF, and lowest marginal effect was removed for the next run. For example, if two variables had a VIF score greater than 20, that having lower marginal effect was removed and the analysis rerun. The procedure was repeated until all variables had VIF scores of < 20. The remaining variables in the analysis had VIF scores of 10 or less (variables with VIF of 1 are uncorrelated with other variables; ter Braak and Smilauer 1998). Except during designed experiments, some degree of multicollinearity is expected (ter Braak and Smilauer 1998), and may have been due to relationships of the biotic variables (predators or competitors) to other explanatory variables included in the analysis. For example, Herbert (1999) found $\underline{P}$. $\underline{sciera}$ to be correlated with streams having higher discharge, and both of these were used as explanatory variables in this analysis. This method of variable selection was preferred to the forward selection option, because important variables might be omitted from analysis simply due to the order in which they are selected by the analysis software.

The percentage of the variance in the species data (sum of all eigenvalues or "total inertia"; ter Braak and Smilauer 1998) that was represented by gradients of explanatory variables was calculated by dividing eigenvalues for each of the first four CCA axes, and for all canonical axes together, by the total inertia. Inter-set correlations were used to determine the importance of each variable in explaining the species' variation along each axis (ter Braak and Smilauer 1998). When using linear direct gradient analysis methods (e.g. Redundancy Analysis), t-values of partial regression coefficients, which are analogous to canonical coefficients, can be used for

statistical tests of the relationships of coefficients with each axis. In unimodal methods, t-values

of canonical coefficients can be used for exploratory purposes only (ter Braak and Smilauer

1998), where those greater than 2.1 would indicate the variable of interest contributed a high

proportion of explained species variation in addition to variation explained by the other variables

on an axis (ter Braak and Smilauer 1998). However, when some multicollinearity exists among

the explanatory variables, canonical coefficients can be unstable, and should not be used to rank

the relative importance of an explanatory variable on the axes (ter Braak 1995, ter Braak and

Smilauer 1998). Inter-set correlations are the correlation coefficients between the environmental

variables and the canonical axes, and are not effected by multicollinearity (ter Braak 1995). In

this case, each variable was considered highly correlated with an axis if its inter-set correlation

was the greatest across the first four canonical axes, and those with coefficients higher than 0.30

were also considered to be mutually correlated with the axis. In this way, variables representing

strong gradients along each CCA axis would be represented.

The relative influence of each CCA axis in explaining the variation in individual

crayfish densities was determined by the cumulative percent variance explained (or "cumulative

fit" for species, ter Braak and Smilauer 1998) by each of the first four CCA axes. A species'

relative abundance was considered highly correlated with the axis on which the highest

proportion of its variance was associated, and thereby with the combination of explanatory

variables most correlated with that axis (ter Braak and Smilauer 1998). Species scores on

ordination biplot diagrams (i.e. showing two CCA axes) can be represented as centroids, the

unimodal optimum (center of the species theoretical niche) of their distribution among

environmental gradients (ter Braak and Smilauer 1998). Explanatory variables were represented

by arrows (ter Braak 1986). The longer the arrow, and the closer it lies to a particular axis, the

greater the amount of its variance is represented on the axis. Nominal (class) variables were

shown as arrows, where the closeness of a species' centroid to the head of an arrow represents high values for that species in collections assigned that class (ter Braak 1995). Species centroids positioned close to the origin of the axes in the CCA ordinations have either little of their variation explained by explanatory variables associated with those axes, or are associated with intermediate values for those variables.

Several different groups of explanatory variables were included in CCA, including spatial, abiotic, biotic, temporal, and those relating to stream hydrology (see Table 1 for variable groupings). Partial canonical ordination was used to compare the relative importance of each group of variables in explaining variation in crayfish assemblage structure (Borcard et. al. 1992). Partial canonical ordination (partial CCA) is similar to decomposing variance in an analysis of variance (Borcard et al. 1992, ter Braak and Smilauer 1998). This is accomplished by separately analyzing each targeted group of variables (i.e. one analysis for each target group). In each analysis, variation explained by the non-target groups (including any explanatory variance shared between target and non-target variables) is accounted for (as in partial regression) by designating them as covariables. The remaining variance explained is unique to the target variables in the analysis. The proportion of total variation in species data explained by each of the 5 groups was determined by dividing the sum of all canonical eigenvalues (representing axes derived from the explanatory variables in the target group), by the total inertia (see Borcard et. al. 1992, ter Braak and Smilauer 1998). Monte Carlo permutation tests (1999 permutations) were used to evaluate significance ($p \leq 0.05$) of F-ratios in CCA and partial CCA. Because multiple comparisons may inflate the probability of Type I error (rejecting the null hypothesis when it is true), a sequential Bonferroni correction was applied to p-values determined for each group analyzed in partial CCA resulting in an overall ("table-wide") significance level of $p < 0.05$ across all ($k = 5$) comparisons. (Rice 1989).

Multiple regression was used to determine the best combination of variables for predicting the density of each individual species and size class combination of crayfish (i.e. species-size class), as measured by the coefficient of determination (R^2). A stepwise procedure was used to select the best-fit regression model from variables used in CCA, as well as species-size classes of other crayfish in order to evaluate associations between species. Because highly multicollinear variables were dropped during CCA, such effects on the multiple regression were reduced. Selection and retention criteria for variables was set at $p < 0.05$. Stepwise selection assembles variables that approximate the best-fitting linear model (highest R^2, but minimized unexplained variance; Sokal and Rohlf 1995). Separate datasets for transformed and untransformed explanatory variables were analyzed because data transformation might improve linearity between some of the dependant and independent variables, and the predictive power of the model (Ott 1993).

Multivariate Analysis of Variance (MANOVA) was used to assess variation in crayfish density attributed to species and month (within-subjects effects), and drought occurrence and crayfish size class (main treatment effects across subjects), with sites as replicates (subjects). With this analysis, the effects of drought could be specifically determined for each species, rather than for the entire community, as in CCA, while directly accounting for interaction effects among the dependent variables (species by month). A priori orthogonal contrasts were used to test specific hypotheses for within-subject effects (species, season, and species by month interactions) with significance set at $p \leq 0.05$. Three different sets of within-subjects contrasts were employed: one set (species effect) compared summed densities of each crayfish species across all sampling months; the second set (month effect) was used to identify trends in total crayfish density across sampling months (summed for all species); the third set (species by month effect) of contrasts compared combinations of crayfish species by month. Roy's greatest

root was the statistic used to determine significance, because it has the greatest statistical power of the four statistics supplied by the SAS statistical analysis program (Statistical Analysis System Institute, version 6.03 1988) used for this analysis, and is a measure of the first eigenvalue, where the greatest amount of among-group to within-group variation is measured (Scheiner 1993). As in a univariate ANOVA, a statistical difference among the groups is found if variation among them is greater than within-group variation, than would be expected by chance (Scheiner 1993). Contrasts were mutually orthogonal and the number of contrasts was equal to the number of degrees of freedom associated with the within-subjects source of variation. By using MANOVA and orthogonal contrasts, overall effects of drought, crayfish size, and their interactions, as well as simultaneous comparisons among mean densities of all three species could be tested with significance set at $p < 0.05$ for each contrast to identify the source of within-subjects variation, but without increasing probability of type I error (Scheiner 1993).

Univariate analyses and MANOVA were performed using SAS software (Statistical Analysis System Institute, version 6.03 1988). All other multivariate statistical analyses were performed using CANOCO software (Canoco for Windows: Software for Canonical Community Ordination, version 4, Microcomputer Power, Ithaca, NY).

RESULTS

Five of seventeen streams sampled were dry only during October, whereas East Fork
Caney Creek was dry during both October and April. In Caney Creek and Winters Bayou,
neither crayfish nor fish occurred in post-drought collections during February (i.e., after flow had
resumed). Five native crayfish species were collected, including (listed in order of decreasing
relative abundance; Appendix B) P. clarkii, P. kensleyi, Orconectes palmeri longimanus,
Cambarus ludovicianus, and Procambarus acutus acutus. The latter two were omitted from
analyses— C. ludovicianus, because it is considered a primary burrower (i.e. emerge from
burrows only to forage; Taylor et. al. 1996) and would not be effectively collected using
electrofishing, and P. a. acutus, because it occurred in only one collection and rare species tend
to skew results of ordination analyses (Gauch 1982). The overall relative abundance of each
crayfish species and size class varied across monthly collections (Fig. 2). Procambarus clarkii
and O. palmeri were captured in every month, however P. kensleyi was not collected during
October from either perennial or intermittent streams (Fig. 2). Density of juvenile P. kensleyi
increased following drought in intermittent streams, while adult O. palmeri was absent (Fig. 2).

Several fishes known to consume crayfish (Robison and Buchanan 1988, BDH
unpublished data this study) were collected from both perennial and intermittent streams,
including (in order of decreasing relative abundance; Appendix B) Ameiurus natalis, Lepomis
cyanellus, Esox americanus, Lepomis gulosus, and Micropterus salmoides. These potential
predators of crayfish occurred in each seasonal collection in perennial streams, but were absent
from intermittent streams during February (Fig. 3). Esox americanus and L. gulosus were the
only predators collected from post-drought streams (Fig. 3).

Detrended correspondence analysis indicated only a slight difference between log
transformed and untransformed species density data in the amount of variance accounted for
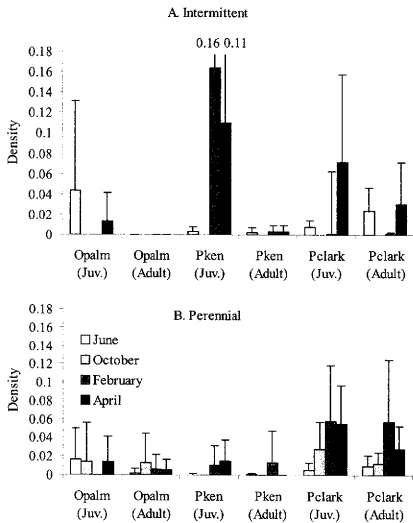
Fig. 2. Mean density (number /m^2) of juvenile and adult crayfishes collected from (A) intermittent and (B) perennial streams of the Sam Houston National Forest during four collecting periods (June, October, February, and April). Error bars indicate 1 standard deviation, and where the length of error bars exceed the length of the y-axis, the error is given on the graph.
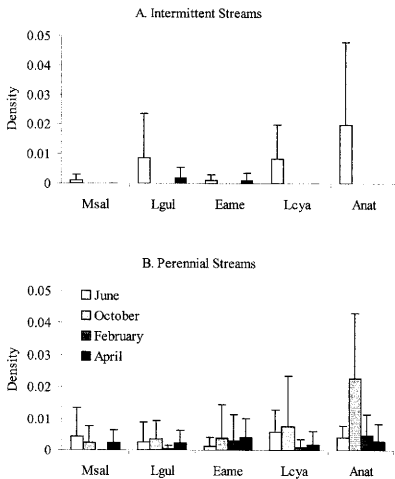
Fig. 3. Mean density (number /m^2) of predatory fishes collected from (A) intermittent and (B) perennial streams of the Sam Houston National Forest during four collecting periods (June, October, February, and April). Error bars indicate 1 standard deviation.

across the first axis (< 3%) and first axis gradient length (3.88 vs. 3.85 standard deviation units). In addition, the relative position of the species and site scores across the first and second axes was similar; therefore, the results of DCA using untransformed data are presented. Of the total variation in species density (all eigenvalues = 3.694, 36% across all 4 DCA axes), DCA 1 and DCA 2 accounted for 16.4% (eigenvalue = 0.604) and 10.6% (eigenvalue = 0.366). The first two DCA axes represented strong gradients in species densities among collections (eigenvalues > 0.30, ter Braak and Verdonschot 1995).

DCA axis 1 indicated a change (3.85 standard deviation units, 96.3% faunal turnover) in community composition across a gradient related to drought based on the relative order of DCA scores for collections at perennial sites, and pre- and post-drought collections at intermittent sites, and species (Fig. 4). For example, collections during June (pre-drought) were closer together on the DCA ordination, and were therefore similar in species composition across both perennial and intermittent streams (Fig. 4). However, centroids for post-drought collections from intermittent streams in February and April were distinctly separated on the ordination plot from those for perennial streams and pre-drought collections from intermittent streams during June (Fig. 4b). The variation accounted for on the first DCA axis (16.4%, eigenvalue = 0.604) was due to the separation between collections having many predators and competitors and those having high densities of juvenile $P.$ $kensleyi$ (Fig. 4a).

On DCA axis 2, ordering of species centroids indicated a gradient among sites with many predators ($Lepomis$ $macrochirus$, $L.$ $marginatus$, $L.$ $gulosus$, $Micropterus$ $salmoides$) and those having higher densities of $O.$ $palmeri$ (Fig. 4a). DCA axes 3 (eigenvalue = 0.226, 6.1%) and 4 (eigenvalue = 0.134, 3.6%) accounted for successively less of the variation in species composition among collections, and only weak gradients were represented (eigenvalues < 0.30). Although relatively low, most variation in species composition was explained along the first
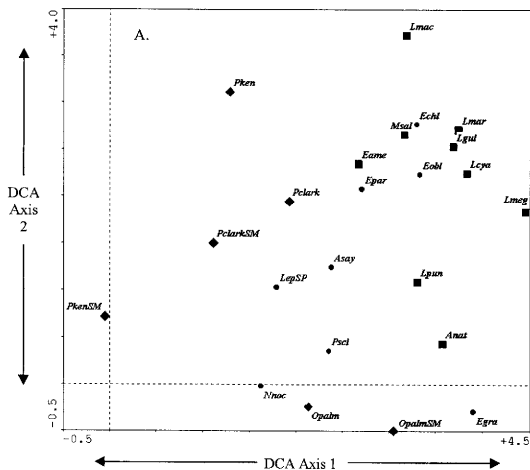
Fig. 4. Ordination of the detrended correspondence analysis showing species (A) and collection (B) centroids along DCA axes 1 and 2. Species centroids represent the center of the unimodal species distribution curve, while collection centroids derived from species scores are shown across axes of standard deviation units. The distance between collection centroids indicates the similarity of the collection's species composition, where a complete turnover in species composition occurs across 4 standard deviation units. In Fig. 4a, diamonds = crayfish, boxes = crayfish predators, and small circles = crayfish competitors. In Fig. 4b, open circles = collections from perennial streams, triangles = pre-drought collections, and solid circles = post-drought collections. See Table 1 for explanation of species abbreviations.
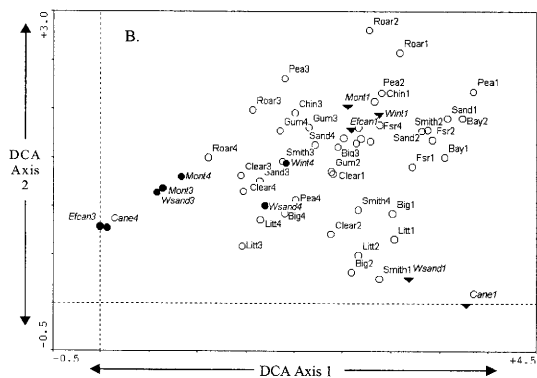
Fig. 4. (Continued)

axis, so the gradient it represented was presumed to be most ecologically meaningful to species'
distributions (Gauch 1982).

The two collections having highest densities of P. kensleyi were both in April following
drought. One was in East Fork Caney Creek (dry during October and February), and the other
was in Caney Creek (dry only in October). At this time, the darter E. parvipinne was the only
other species collected. Pre- and post-drought collections were ordered along DCA axis 1, thus,
faunal turnover could be compared between perennial and intermittent streams across seasonal
collections (Fig. 4b). Faunal turnover was measured for the greatest distance in standard
deviation units between June site scores and site scores for either February or April (Table 2).
Most (3 of 5) streams where drought occurred had greater faunal turnover than any perennial
stream, despite initially high similarity among all streams in June prior to drought. The average
faunal turnover rate for intermittent streams was 2.35 standard deviation units or 58.8% (range
23.9 – 92.6%), while in perennial streams the average faunal turnover was only 1.23 standard
deviation units or 30.8% (14.4 – 49.5%; Table 2). Along the second gradient (along DCA axis
2), sites ordered from higher to lower axis scores, indicated higher to lower predator density.
Species having higher relative densities at sites with low predator density included O. palmeri,
juvenile P. kensleyi, N. noturus, and P. sciera (Fig. 4b). Because DCA results strongly implied
relationships of drought and predator density to crayfish assemblage structure, these hypotheses
were tested using CCA.

The results of CCA confirmed the interpretation of results from the DCA; drought, and
predator and competitor density explained significant variation in crayfish assemblage structure
(Fig. 5). However, in addition to variation explained by biotic and hydrologic variables,
additional variation was explained by abiotic and temporal variables (Table 3). As in DCA,
there was little difference in the results of CCA using transformed or untransformed data. Thus,

Table 2. Faunal turnover in standard deviation units along the first DCA axis between collections made in June versus February or April (post-drought), for perennial and intermittent streams.

Stream	Standard deviation units	Faunal turnover (%)	Mean Turnover (%)
Perennial Streams			
Roark Creek	1.98	49.5	30.8
Pea Creek	1.95	48.8	
Sand Creek	1.94	48.6	
Little Creek	1.57	39.4	
Big Creek	1.11	27.9	
Smith Branch	1.01	25.2	
Clear Creek	0.97	24.1	
Gum Branch	0.84	21.0	
Big Chinquapin Creek	0.82	20.6	
Bay Branch	0.76	19.0	
Un-named Creek	0.58	14.4	
Intermittent Streams			
Caney Creek	3.70	92.6	58.8
W. Sandy Creek	2.60	65.0	
E. Fork Caney Creek	2.59	64.8	
Montague Creek	1.91	47.8	
Winters Bayou	0.96	23.9	

Table 3. Results of canonical correspondence analysis (CCA) and partial canonical ordination analysis showing the cumulative percent fit of the species to the first four CCA axes (% variance explained), eigenvalues for each CCA axis and the sum of all CCA axes, and the cumulative percent variance explained in the species data for the first four, as well as all CCA axes (top). Inter-set correlations of each variable with the first four CCA axes are given in the lower portion of the table (highest correlations across axes in bold). The results of partial canonical ordination, showing the amount of variation explained by each group and the significance level (after sequential Bonferroni correction, $p < 0.05$), are given with the variable groupings.

Species	Axis 1	Axis 2	Axis 3	Axis 4	Sum of all canonical axes
P. kensleyi (adult)	0.01	0.10	**0.51**	0.52	80.0
P. kensleyi (juvenile)	0.35	**0.92**	0.94	0.94	94.2
O. palmeri (adult)	0.22	0.23	0.28	**0.88**	88.0
O. palmeri (juvenile)	**0.71**	0.81	0.81	0.86	86.5
P. clarkii (adult)	0.01	**0.31**	0.63	0.63	71.8
P. clarkii (juvenile)	0.09	**0.34**	0.79	0.80	81.5
Eigenvalues	0.60	0.48	0.34	0.18	1.69
Cumulative % variance in species data	29.9	53.9	70.8	79.8	84.6

Explanatory variables	Inter-set correlations			
Abiotic F = 3.561, p < 0.05, 31.0%				
MnWidth	0.24	0.11	-0.02	**-0.31**
CVDepth	**-0.26**	-0.15	0.02	0.21
CVVeloc	**-0.31**	-0.07	-0.06	0.15
CVMaxD	-0.42	**-0.54**	0.12	0.05
CvSubs	**-0.22**	-0.08	0.04	0.08
Clay	-0.20	-0.21	**0.37**	0.14
Silt	0.15	0.11	**-0.26**	0.17
NoCover	-0.21	0.03	-0.12	**-0.25**
Wood	**0.32**	0.10	-0.06	**-0.27**
UndCut	-0.11	**0.34**	-0.18	-0.11
Root	-0.17	-0.03	**-0.35**	**-0.38**
Detritus	-0.07	-0.11	0.24	**0.45**
Cond	-0.22	0.08	-0.16	**0.24**
Hydrologic F = 4.395, p < 0.05, 5.9%				
Disch	**0.30**	0.03	-0.06	**-0.38**
Drought	**-0.32**	**-0.46**	0.07	0.29
Drainage F = 3.1, NS, 2.1%				
West	0.14	-0.05	0.03	**0.37**

Table 3. (Continued)

Explanatory variables	Inter-set correlations			
Biotic F = 2.453, p < 0.05, 18%				
Anat	**0.56**	-0.04	-0.10	0.19
Asay	0.07	-0.12	**0.22**	0.09
Eame	-0.10	**0.20**	-0.07	0.09
Eobl	0.06	**0.10**	-0.07	-0.09
Lcya	0.04	**0.20**	0.03	-0.10
Lgul	0.00	**0.18**	0.16	0.00
Lmac	-0.06	**0.41**	0.11	0.01
Etheost	0.27	0.06	0.13	**0.41**
Lpun	**0.37**	0.12	-0.17	**-0.45**
Nnoc	0.29	-0.05	-0.20	**-0.66**
Psci	**0.28**	0.02	0.08	**0.30**
Temporal F = 2.665, p < 0.05, 5.3%				
October	0.28	0.09	-0.23	**-0.40**
June	**0.53**	-0.08	0.14	0.36
February	**-0.41**	0.05	0.20	-0.11
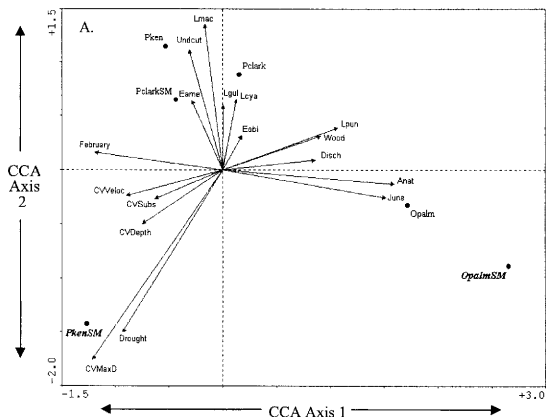
Fig. 5. Canonical correspondence analysis ordination of species scores in relation to explanatory variables along CCA axes 1 and 2 (A), axes 2 and 3 (B), and axes 3 and 4 (C). Arrow length and direction represent the relative amount of influence of environmental variables on species distribution along each axis. Species are represented by centroids, which indicate the position of each species' distribution in relation to the environmental variables. The closer a species centroid lies to the head of an arrow, the stronger the influence of that environmental variable on the species distribution. Species centroid labels in bold indicate those that have the greatest amount of their variance explained by variables correlated with the axes shown, and species labels with "SM" indicate centroids for juveniles.
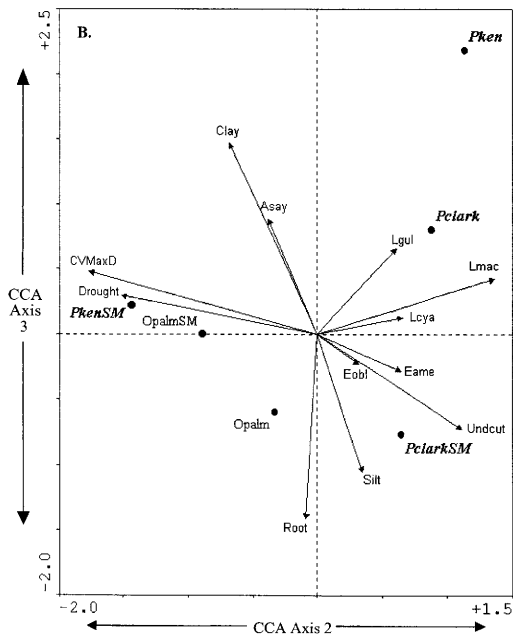
Fig. 5. (Continued)
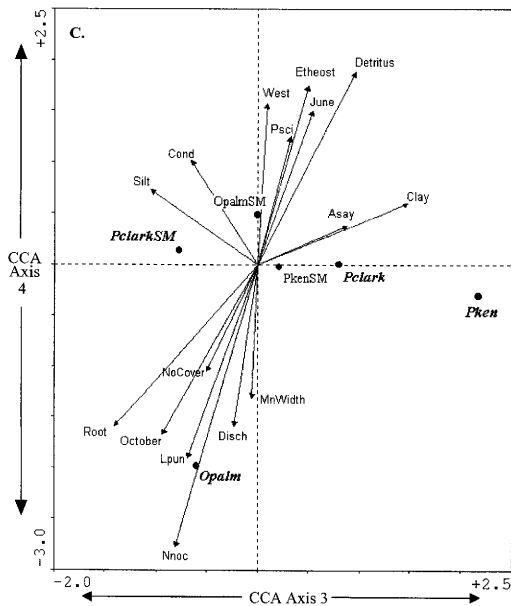
Fig. 5. (Continued)

results of CCA using untransformed data are presented. Monte Carlo randomization tests indicated that CCA axis 1 (eigenvalue = 0.597, F = 9.794), as well as all canonical axes together (eigenvalue = 1.693, F = 4.215), each explained a significant (p = 0.005) amount (29.9% and 84.6%) of the variation in crayfish density among collections (Table 3). Strong gradients in relative crayfish densities among sites were represented on CCA axes 1- 3 (eigenvalues > 0.30; Table 3).

Most variation among crayfish density was explained by eighteen variables correlated with CCA axis 1 (29.9% variation) and 2 (24.0%; Table 3). Along CCA axis 1, density of A. natalis, June, CV of maximum depth, February, density of L. punctatus, and, to a lesser extent, drought and wood explained the highest amount of variation in crayfish densities (Fig. 5a). Variables highly correlated with CCA axis 2 were CV of maximum depth, drought, L. macrochirus density, undercut bank (cover), and the densities of several competitors or predators (E. americanus, L. cyanellus, L. gulosus) (Table 3). Clay, root, silt, and A. sayanus density were correlated with CCA axis 3 (24.0% explained variation), while densities of N. nocturnus and L. punctatus, detritus, Etheostoma density, October, discharge, as well as several others explained 16.9% of variation in crayfish density along CCA axis 4 (Table 3).

Variation in density of juvenile O. palmeri and P. kensleyi was associated with variables correlated with CCA axes 1 and 2, respectively. The most variation among sites in adult and juvenile P. clarkii, and adult P. kensleyi density was explained along CCA axes 2 and 3 (Table 3). Variation in density of adult O. palmeri was generally explained by variables associated with CCA axis 4 (Table 3). Higher densities of juvenile O. palmeri occurred in June collections from perennial streams with higher densities of A. natalis and L. punctatus, more homogenous stream depths, and more woody cover (lower right of Fig. 5a). Although some (35%) of the explained variation in juvenile P. kensleyi density was accounted for by variables associated with CCA

axis 1, such as the nominal variable for February, they were more dense in intermittent streams with well-developed pool-riffle morphology (indicated by high variation in maximum depth), lower densities of centrarchids and $\underline{E}$. americanus, and few undercut banks (lower left of Fig. 5a). Higher densities of adult $\underline{P}$. clarkii and adult $\underline{P}$. kensleyi occurred in perennial streams having more clay substrate, and higher densities of $\underline{A}$. sayanus and centrarchids (upper left of Fig. 5b). In addition, high juvenile $\underline{P}$. clarkii densities were found in perennial streams with homogenous depths, more root and undercut bank cover, silt (less clay) substrates, and lower $\underline{A}$. sayanus densities (Fig. 5b). Densities of adult $\underline{O}$. palmeri were higher in October collections from perennial streams having greater discharge and stream width, more root cover, higher densities of $\underline{N}$. nocturnus and $\underline{L}$. punctatus, but lower darter density (Etheostoma species and $\underline{P}$. sciera) and less detritus (Fig. 5c). In addition, density of adult $\underline{O}$. palmeri was lower in collections from the West Fork San Jacinto River drainage (Fig. 5c).

The partial canonical ordination indicated abiotic (31%, $F = 3.564$), followed by biotic (18%, $F = 2.453$) variables independently explained the most ($p < 0.05$) amount of variance in crayfish assemblage structure (Table 3). Hydrologic (stream discharge, drought occurrence; 5.9%, $F = 4.395$) and temporal variables (October, June, February; 5.3%, $F = 2.665$) also explained a significant, but much lower amount as a group. The remaining variance in crayfish density (2.1%) among collections was accounted for by the drainage variable, West Fork, but was not significant after sequential Bonferroni correction (Table 3). Since the number of variables included in each group varied, the amount of variance explained among the groups wasn't comparable (i.e. more variation is expected to be explained, as more variables are included). However, abiotic (13 variables) and biotic (11 variables) groups had a similar number of variables, permitting comparison. Alternatively, after standardizing the variance explained by each significant group by the number of variables in the group (% variance explained / number

of variables), the hydrologic group ranked highest in variance explained (2.95%) per variable, followed by abiotic (2.38% per variable), temporal (1.77% per variable), and biotic (1.63% per variable).

Multiple regression models selected from explanatory variables used in CCA significantly ($p < 0.05$ after Bonferroni correction) predicted variation in densities of 3 of the 6 crayfish species-size classes, including juvenile $\underline{P}$. kensleyi, adult $\underline{O}$. palmeri, and adult $\underline{P}$. clarkii densities (Table 4). Variables common to several models included clay substrate (for adult and juvenile $\underline{P}$. kensleyi; arcsine-sqare root of clay, juvenile $\underline{P}$. clarkii), $\underline{A}$. sayanus density (for adult $\underline{P}$. kensleyi and $\underline{P}$. clarkii), and $\underline{L}$. macrochirus (for juvenile $\underline{P}$. kensleyi and juvenile $\underline{O}$. palmeri)(Table 4). For those crayfish species more associated with perennial streams (e.g. $\underline{O}$. palmeri), models included no abiotic variables, but did include either densitiy of competitors or predators (Table 4). In contrast, the model for juvenile $\underline{P}$. kensleyi (most dense in intermittent streams) contained more abiotic factors, such as CV of maximum depth and drought (as observed CCA). $\underline{Noturus\ nocturnus}$ density was a strong predictor ($R^2 = 0.60$) of adult $\underline{O}$. palmeri density, as was adult $\underline{P}$. clarkii density ($R^2 = 0.60$) for adult $\underline{P}$. kensleyi (and vice versa).

MANOVA detected a significant interaction between drought occurrence and body size (small/juvenile versus large/adult) ($F = 6.18$, $p = 0.007$) among contrasted pairs of crayfish species independent of collection month (Table 5). For juvenile $\underline{P}$. kensleyi more so than juvenile $\underline{O}$. palmeri, density was higher in intermittent than perennial streams ($F = 5.78$, $p = 0.024$; Fig. 6). In contrast, density of adult $\underline{P}$. kensleyi was similar across all streams, and adult $\underline{O}$. palmeri occurred only in perennial streams (Fig. 6). Body size differed between pairs of months, but effects depended on species ($F = 4.75$, $p = 0.003$; Table 5). This was detected as size differences between $\underline{P}$. clarkii and $\underline{O}$. palmeri in collections contrasted between June and October ($F = 7.00$, $p = 0.014$), and October and February ($F = 6.96$, $p = 0.014$; Table 5). For $\underline{P}$.

clarkii, adult density decreased from June to October, while juvenile density increased during the same time (Fig. 7). The opposite pattern in adult and juvenile density occurred across these months for O. palmeri (Fig. 7). From October to February, both adult and juvenile O. palmeri density decreased (no juvenile O. palmeri were collected in February), whereas density increased for both juvenile and adult P. clarkii (Fig. 7).

Table 4. Multiple regression models for each crayfish species-size class selected from both transformed (log x +1, or arcine-square root) and untransformed abiotic, biotic, temporal, hydrologic, and fork variables after removal of those with high multicollinearity. Stepwise selection was used with entry into the model set at $p = 0.05$. Explanatory variables retained in the model are untransformed unless indicated. Cumulative coefficients of determination and regression coefficients are listed for models. P-values for significant models after a sequential Bonferroni correction are shown in bold.

Dependent variable	Selected explanatory variables	Intercept	Regression coefficient	Coefficient of determination (R^2)	F	p
P. kensleyi (adult)	P. clarkii (adult)		0.290	0.51		
	Clay		0.020	0.56		
	A. sayanus	-0.00549	-0.064	0.60	4.71	0.035
P. kensleyi (juvenile)	CV Max. Depth		0.002	0.43		
	CV Depth		-0.002	0.74		
	Drought		0.019	0.76		
	L. macrochirus		0.071	0.78		
	Clay	0.0471	-0.606	0.81	7.51	**0.008**
O. palmeri (adult)	N. nocturnus		0.537	0.60		
	P. sciera	0.00012	-0.382	0.65	7.45	**0.009**
O. palmeri (juvenile)	A. natalis		1.250	0.11		
	E. americanus		-2.024	0.20		
	L. macrochirus	0.013	-0.439	0.26	4.58	0.037
P. clarkii (adult)	P. kensleyi (adult)		1.748	0.51		
	A. sayanus	0.0141	0.197	0.57	7.45	**0.009**
P. clarkii (juvenile)	June	0.952	-0.689	0.17		
	L. punctatus (Log x+1)		-2.468	0.23		
	Clay (Arcsine-sqrt)		-0.057	0.31		
	West Fork		-0.024	0.38	5.24	0.027

Table 5. Results of MANOVA on non-transformed crayfish density. Dependent variables were combinations of species and each month, while independent variables were occurrence of drought and crayfish size ($\geq$ or < 25 mm CL). Bold p-values are significant at $p < 0.05$. Under contrasts, species names are abbreviated in some cases (Pc = P. clarkii, Op = O. palmeri, Pk = P. kensleyi).

Effect		Contrast	df	F	p
Drought					
	Species		2,25	10.12	**<0.001**
		O.p.longimanus vs. P.clarki	1,26	1.26	0.273
		O.p.longimanus vs. P.kensleyi	1,26	9.91	**0.004**
	Month		3,24	3.68	**0.026**
		June-October	1,26	9.75	**0.004**
		October-February	1,26	2.06	0.160
		February-April	1,26	0.20	0.660
	Species X month		6,21	5.70	**0.001**
		Op vs. Pc June-October	1,26	0.09	0.760
		Op vs. Pc October-February	1,26	1.97	0.170
		Op vs. Pc February-April	1,26	1.33	0.260
		Op vs. Pk June-October	1,26	1.79	0.190
		Op vs. Pk October-February	1,26	1.42	0.240
		Op vs. Pk February-April	1,26	0.00	0.960
Size					
	Species		2,25	2.31	0.120
		O.p.longimanus vs. P.clarki	1,26	0.71	0.407
		O.p.longimanus vs. P.kensleyi	1,26	4.66	**0.040**
	Month		3,24	4.96	**0.008**
		June-October	1,26	0.29	0.580
		October-February	1,26	7.90	**0.009**
		February-April	1,26	0.16	0.690
	Species X month		6,21	4.75	**0.003**
		Op vs. Pc June-October	1,26	7.00	**0.014**
		Op vs. Pc October-February	1,26	6.96	**0.014**
		Op vs. Pc February-April	1,26	3.66	0.067
		Op vs. Pk June-October	1,26	2.69	0.110
		Op vs. Pk October-February	1,26	3.85	0.060
		Op vs. Pk February-April	1,26	0.17	0.680

Table 5. (Continued)

Effect		Contrast	df	F	p
Drought X Size					
	Species		2,25	6.18	**0.007**
		O.p.longimanus vs. P.clarki	1,26	0.90	0.351
		O.p.longimanus vs. P.kensleyi	1,26	5.78	**0.024**
	Month		3,24	1.76	0.180
		June-October	1,26	0.82	0.370
		October-February	1,26	3.59	0.069
		February-April	1,26	0.21	0.650
	Species X month		6,21	2.39	0.064
		Op vs. Pc June-October	1,26	0.32	0.580
		Op vs. Pc October-February	1,26	0.01	0.920
		Op vs. Pc February-April	1,26	0.11	0.740
		Op vs. Pk June-October	1,26	0.56	0.460
		Op vs. Pk October-February	1,26	3.34	0.079
		Op vs. Pk February-April	1,26	0.25	0.620
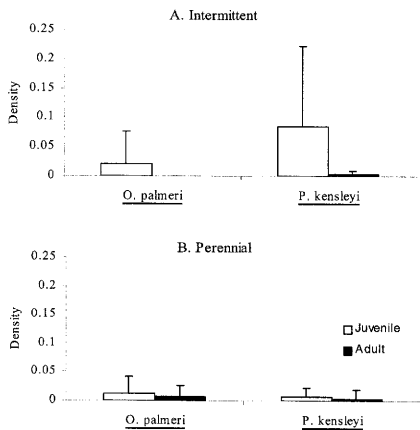
Fig. 6. Mean density of juvenile and adult O. palmeri and P. kensleyi in intermittent (A) and perennial (B) streams summed across all sampling months. Error bars indicate 1 standard deviation.
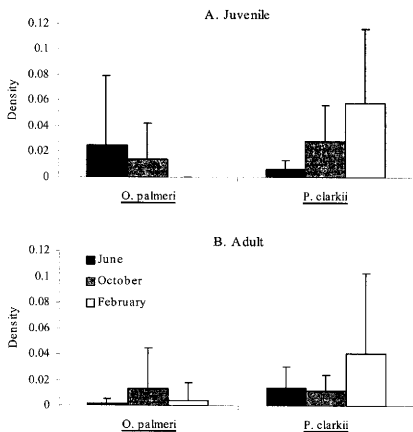
Fig. 7. Mean density of juvenile (A) and adult (B) O. palmeri and P. clarkii from June and October, 1999, and February, 2000 sampling months.

DISCUSSION

Several analyses indicated that clear ecological gradients distinguished assemblages of crayfish in streams of the Sam Houston National Forest. The strongest gradients were due to high variability in relative densities of O. palmeri and P. kensleyi among collections from intermittent versus perennial streams, however, gradients in abiotic and biotic (predators or competitors) factors were important as well. In addition, temporal variability in crayfish abundance was reflected in peak juvenile densities of P. kensleyi in February and O. palmeri in June. Patterns observed during this study are related to the results of a study of fishes in this region (Herbert 1999), in which hydrologically variable streams had fewer predatory fishes (centrarchids). Although explaining relatively less variation in crayfish densities across all streams than hydrologic or abiotic factors, the absence of drought appears to allow conditions when biotic factors more strongly determine crayfish assemblage structure. Similar conclusions have been reported for various assemblages of organisms across systems with contrasting hydrologic regimes (Poff and Ward 1989, Reice 1994).

The abundance of predatory and benthic fishes that may prey on or compete with crayfishes for food or space varied across study streams, as did flow intermittency. Crayfishes, such as O. palmeri and P. clarkii, which were more dense in perennial streams, were able to persist despite higher densities of competitors and predators in these streams (see also Herbert 1999). Procambarus kensleyi occurred in higher densities across all collections in intermittent streams, in contrast to O. palmeri, which was rare in post-drought collections in these streams. In intermittent streams, where larger-bodied predatory fishes were rare or absent, P. kensleyi dominated the crayfish assemblage and densities of juvenile P. kensleyi peaked after stream flow resumed. Drought appeared to affect O. palmeri more than it did Procambarus clarkii, a successful colonizing species (Hobbs 1989b). However juvenile P. clarkii were later than P.

kensleyi in recolonizing post-drought streams.

Crayfishes are not commonly distributed homogeneously throughout a drainage (Bovbjerg 1970, Capelli and Munjal 1982, Mitchell and Smock 1991). Therefore, large differences in relative densities among these species in this study are not surprising. Various mechanisms might account for their distribution patterns. However, the pattern for relative abundance of crayfish species across perennial and intermittent streams of the San Jacinto and adjacent Trinity River, suggests potentially complex interactions among crayfishes, predators, competitors, and abiotic conditions. In the absence of experimental data, these observed patterns are interpreted here as they relate to alternative hypotheses suggested by other published studies.

Crayfish assemblages in intermittent streams

Effects of drought on crayfish populations, which vary among species, include decreased body size and density (Bovbjerg 1970, Taylor 1988). The least affected species must possess behavioral or physiological adaptations to allow it to persist in intermittent streams under seasonally harsh habitat conditions. During drought, riffles dry and pools stagnate. Remaining fish and crayfish experience increased competition for declining resources, as well as the increased physicochemical stress of low dissolved oxygen and wide diel variation in temperature (Bovbjerg 1970, Caine 1978, Capone and Kushlan 1991). Following a drought event, two alternatives for reestablishing populations of crayfish in stream reaches might exist— recolonization or regeneration from survivors (Power et al. 1988). Adaptations observed for crayfishes that survive in dry reaches include burrowing (Caine 1978; Taylor 1983), strategically timed reproduction (Caine 1978, Taylor 1983), and tolerance of both low dissolved oxygen levels and high temperatures (Bovbjerg 1970). Others not similarly adapted might move toward persisting water (Momot 1966), or die.

Among crayfishes most commonly collected from streams of the Sam Houston National Forest, P. kensleyi and P. clarkii were best suited to persist during drought. In several post-drought collections, P. kensleyi and P. clarkii were the only species of either fish or crayfish collected. In contrast, O. palmeri occurred in only two intermittent streams, and only low densities of small individuals were collected following drought. Procambarus clarkii exhibits several life-history adaptations allowing it to survive harsh conditions in drought-prone stream systems (Hobbs 1989b). These include maturation in as few as three months, the capability to reproduce more than once each year, and high individual fecundity. Moreover, P. clarkii can survive in habitats with highly variable flows by constructing shallow burrows for refuge. Like P. clarkii, P. kensleyi remained abundant in intermittent streams following drought events. However, the ecology of P. kensleyi is not well described. Based on extensive collections made in another nearby Texas drainage, it appears P. kensleyi may have similar burrowing capability to that of P. clarkii (Hobbs 1990). Hobbs (1990) reported that all adults were collected from excavated burrows, but the broad, short, areola of P. kensleyi is typical of crayfish inhabiting well-aerated streams, and not characteristic of a primary burrowing species. In addition, the simple construction of its burrow (a single, straight shaft) indicated it is unlikely to be a primary burrower (Hobbs 1990).

During February, O. palmeri was collected only from perennial streams and, among crayfishes, was the last to re-appear in post-drought (April) collections following the return of flow to intermittent streams. In addition, although present in perennial streams, adult O. palmeri were not collected from intermittent streams during February and April sampling periods. These data suggest O. palmeri is intolerant of harsh abiotic conditions characteristic of drying streams. Therefore, rather than burrowing as streams dried, O. palmeri possibly migrated to a higher order reach or to pools retaining water (Momot 1966), or sustained high mortality and later

re-populated previously dry streams from other sources and refugia.

Juvenile P. kensleyi and P. clarkii were most abundant in February or April collections; suggesting reproductive timing is adapted to periodic stream intermittency. In contrast, densities of juvenile O. palmeri were low in collections from both perennial and intermittent streams during February, suggesting reproduction of O. palmeri was later than that of P. kensleyi and P. clarkii, and occurred after drought. Juveniles of P. kensleyi and P. clarkii probably emerged from burrows in early spring. Thus, it seems likely that females carrying either eggs or early instars had taken refuge in burrows during drought, a common behavior of brooding females (Hobbs 1991). Adult P. kensleyi was not collected from either intermittent or perennial streams during October, which suggests they burrowed during this time, regardless of flow conditions. A similar behavioral pattern was observed for several other crayfish species that survived in burrows in a dry streambed and then reoccurred in high numbers as soon as flow resumed (Larimore et al. 1959).

Under otherwise similar conditions, re-colonization by predatory fishes is more likely to follow, rather than precede, re-establishment of crayfish populations (Larimore et al. 1959). This would provide vulnerable species with advanced access to resources and habitats containing cover, and thus a temporal and spatial refuge from predators. If food resources were available after flow returned, early emergence would allow juvenile P. kensleyi foraging opportunities under low predation risk and low interspecific competition, which would allow for maximized individual and population growth. Procambarus kensleyi and P. clarkii might then be able to grow beyond the gape limit of many predatory fishes that would later re-colonize post-drought streams. In the months after flow returned in intermittent streams, densities of juvenile P. clarkii surged in perennial streams where P. kensleyi densities remained low. Seasonal collections were not spaced closely enough through time to determine if perhaps a similar (but earlier) surge in

density of juvenile P. kensleyi had occurred in perennial streams, but was not detected before being reduced by predators.

Change in fish and crayfish assemblage composition, as indicated by faunal turnover between collections made before (June) versus after (February or April) drought, was much greater in intermittent than perennial streams. However, faunal turnover also varied among intermittent streams. Several stream characteristics including channel geomorphology (Lonzarich et. al. 1998, Capone and Kushlan 1991), degree of intermittency (i.e. drought predictability; Poff and Ward 1989), and physiochemical habitat characteristics (Capone and Kushlan 1991) may have influenced the degree of change in species composition across intermittent streams. In a north Texas intermittent stream system, pool depth and persistence, channel size, canopy cover, substrate, and pH predicted fish assemblages in intermittent streams (Capone and Kushlan 1991). In Arkansas streams, recolonization rates of previously dry and defaunated reaches were predicted by distance to source pools, riffle depth, and riffle length (Lonzarich et. al. 1998). In this study of Sam Houston National Forest streams, high variation (CV) in maximum stream depth, indicating well-developed pool-riffle sequences, was positively correlated with P. kensleyi density. In streams where drought occurred and faunal turnover was greatest, the presence of shallow riffles likely slowed recolonization by deep-bodied predatory fishes. However, some study sites were only short distances from refuge pools or lacked strong pool-riffle development, which likely damped effects of drought on recolonization rate and assemblage structure. Although distance to refugia and their faunal composition were not measured at all sites during this study, these factors visually differed among study streams (B. Healy, personal observation). The smallest faunal turnover between seasonal collections occurred in Winters Bayou, where deep pools persisted within 100-m of the sampled reach during drought. The largest faunal turnover occurred in Caney Creek, where no refuge pools

remained in or near the study reach during drought (B. Healy, personal observation). In addition, West Sandy and East Fork Caney creeks ranked highest among intermittent streams in both variation in maximum depth, and magnitude of faunal turnover.

In Georgia, increased post-drought abundance of non-burrowing juvenile or small adult crayfish was observed, but drought had no effect on life stage or body size for a syntopic burrowing species (Taylor 1983, Taylor 1988). Change in life stage and size distribution was attribute to the reduction in deep-water habitats during low-flow (used more often by larger adults) and greater loss of adults to terrestrial predators in shallow areas (Taylor 1983). The size of all crayfish species was reduced in post-drought intermittent versus perennial streams in this study, but densities of large $\underline{P}$. $\underline{kensleyi}$ and $\underline{P}$. $\underline{clarkii}$ either persisted or increased in post-drought collections. Therefore, observed demographic changes for $\underline{P}$. $\underline{kensleyi}$ and $\underline{P}$. $\underline{clarkii}$ probably resulted from low juvenile mortality in the absence of predatory fishes (Herbert 1999 and this study). The absence of large $\underline{O}$. $\underline{palmeri}$ in post-drought intermittent streams suggests that growth was poor, and adults either died, or re-colonization from refugia was slowed.

Fish selectively feed on smaller crayfish due to reduced handling time, and consequently, increased foraging efficiency (Stein 1977). The observed size distribution of crayfish in these streams is concordant with differences in predation risk between perennial versus intermittent streams. Intermittent streams had fewer predatory fishes across all seasonal collections, which should favor survival of smaller-sized crayfish, especially in shallower pools, thus decreasing mean crayfish size.

The species composition of collections from intermittent and perennial streams was similar during June, but differed greatly in February and April. The observed pattern in intermittent streams corresponded to a model of community succession along an environmental gradient of disturbance and stress (Power et al. 1988). Crayfish assemblages ranged from those

dominated by colonizers, which are typically less successful competitors (P. kensleyi), to assemblages comprised of species characteristic of stable environments in which better competitors (O. palmeri) or predators are expected to dominate. Most predatory fishes in these streams, are not characteristically found in harsh environments such as those in drying stream pools, except for L. cyanellus (Capone and Kushlan 1990). Different adaptive behaviors in response to disturbance are expected if populations of morphologically similar species are to coexist (Meffe 1984). Burrowing ability of P. kensleyi and P. clarkii likely allowed them to thrive under drought conditions that could have reduced abundance of O. palmeri. Similar results for ecological isolation of two crayfish species were observed in the Midwestern United States (Bovbjerg 1970). Although Orconectes virilis was a better competitor in streams where it excluded Orconectes immunis from cover, its poor burrowing ability and intolerance to low dissolved oxygen restricted it from ponds that dried periodically, and subsequently contained a higher abundance of O. immunis (Bovbjerg 1970). Despite the return of flow to intermittent streams prior to February collections, the effects of drought on fish assemblages persisted until April, when predatory fishes and O. palmeri first reappeared in collections from intermittent streams. A similar effect of drought on predatory fishes was found in these streams during 1997 (Herbert 1999). Thus, drought was likely the disturbance mechanism that reset this successional process.

Crayfish assemblages in perennial streams

As lotic systems become more hydrologically stable, biotic factors become more important to community structure (Poff and Ward 1989). Biotic factors known to structure crayfish assemblages include predation by fish (DiDonato and Lodge 1993, Mather and Stein 1993), interspecific competition with other crayfishes (Bovbjerg 1970), and their interactive

effects (Garvey et al. 1994, Hill and Lodge 1994). The strength of predator effects in aquatic systems may vary according to relative sizes of predators and prey, number of predator and prey species, dynamic oscillations in predator and prey abundance, and variable effectiveness among predator species to control prey abundance or behavior (reviewed by Matthews 1998). In addition, predation effects may be ambiguous if the sampling scale and resolution (e.g., multiple habitats, whole reaches, or individual pools) are not appropriate to determine effects of some species. Nevertheless, differences in community composition between perennial and intermittent streams found in this study were consistent with effects of biotic interactions reported in others (Stein and Magnuson 1976, Stein 1977, Rabeni 1992, DiDonato and Lodge 1993, Garvey et al. 1994).

Densities of several fish species were correlated with crayfish assemblage structure, or were predictors of crayfish density, but results depended on the crayfish species and analysis methods. Of the three common species collected, P. clarkii and O. palmeri were least related to predatory fishes, whereas density of P. kensleyi was highest in streams where O. palmeri and predatory fishes were rare or absent. Crayfish species and size classes have different behavioral responses and susceptibility to predators (Stein and Magnuson 1976, Stein 1977). Specifically, crayfishes differ in their use of shelter, tactics for seeking cover, and types of defensive postures (Stein and Magnuson 1976). Such variation likely influences prey selection by predatory fishes (DiDonato and Lodge 1993, Garvey et al. 1994), and consequently, influences dominance and distribution of crayfishes (Rabeni 1992, Garvey et al. 1994).

Orconectes palmeri and P. clarkii densities remained high in streams where A. natalis and several centrarchids (predators of crayfish) were present. These crayfishes likely had morphological or behavioral traits that contributed to their coexistence with these predators (Stein and Magnuson 1976, Stein 1977, Garvey et al. 1994). For P. kensleyi, selective predation

appeared to be a likely reason for its lower density in perennial streams (DiDonato and Lodge 1993, Garvey et al. 1994). Crayfishes with larger chela or larger bodies are either more resistant to predation (Stein 1976a), or are more successful in defending their foraging territories and refuges than are smaller individuals. Orconectes palmeri had the largest maximum body size (50 mm CL) of the three common species captured, followed by P. clarkii (47 mm CL) and P. kensleyi (39 mm CL). The maximum size of P. kensleyi collected from the Neches River drainage in East Texas was similar to that found in San Jacinto and Trinity River drainages (maximum size, form I male 36.3 mm CL; Hobbs 1990). Therefore, the smaller size characteristic of P. kensleyi may explain its sparse distribution in perennial streams (Mather and Stein 1993).

The higher abundance of predators in perennial streams may have increased diurnal use of burrow habitats by some species (Stein and Magnuson 1976, Gelwick 2000). Procambarus clarkii and P. kensleyi were less abundant across all streams in June compared to other collection periods. Juveniles may have shifted to more nocturnal activity and remained under cover during daytime sampling (Hill and Lodge 1994, Gelwick 2000). If these crayfish used burrows to avoid predators (Gelwick 2000) they also might not have been affected by electrofishing gear, thus confounding direct and indirect effects of these factors on estimates of relative density. Several centrarchids (L. gulosus, L. cyanellus, L. punctatus, L. marginatus, L. megalotis, M. salmoides), as well as E. americanus and A. natalis, were abundant across all sampling periods in perennial streams and were present in several intermittent streams in June. These predators would be likely to forage diurnally on crayfish (Gelwick 2000) and have been found to effectively consume smaller-sized crayfishes in streams (Englund 1999), and to reduce abundance of crayfish such that alternative prey or size classes might be used (Probst et al. 1984). Centrarchids cause juvenile crayfish to decrease activity and increase time spent in burrows

(Stein and Magnuson 1976, Gelwick 2000); thus, juvenile crayfish, susceptible to predators (e.g.
P. kensleyi), may have become inactive during the daytime and foraged more nocturnally during
this study.

Biotic interactions among species can result in spatial or temporal niche partitioning
(reviewed by Schoener 1974). Ameiurus natalis, a nocturnally active omnivore (Robison and
Buchanan 1988), consumes crayfish in Sam Houston National Forest streams (B. Healy,
personal observation) and its density was negatively correlated with crayfish distribution. A
shift to nocturnal foraging activity by juvenile crayfish could facilitate predation by A. natalis.
Another nocturnal benthic invertivore, N. nocturnus (Robison and Buchanan 1988), is both a
potential predator and competitor of crayfish and was sympatric in collections with diurnally
active O. palmeri (B. Healy, personal observation). Therefore, temporal partitioning of
resources may have facilitated coexistence of O. palmeri with nocturnal predators.

Predation and competition for cover are important processes often linked during
establishment of crayfish assemblages (Garvey et al. 1994). For interspecific competition to
occur, a necessary resource (e.g. cover, food, space) must be limited in comparison to its demand
by two or more species occurring in sympatry. Although resource availability was not
quantified, streams in this study contained relatively simple habitat structure (B. Healy, personal
observation), and cover variables (e.g. % undercut bank, % wood, % root) were significantly
correlated with crayfish assemblage structure. Crayfish suffer higher predation rates when
excluded from limited cover by superior competitors (Garvey et al. 1994). In streams consisting
of mainly fine-grained sandy substrates, such as streams in this study, predation rates on young
crayfish are higher than in structurally more complex habitats (Stein 1977, Kershner and Lodge
1995) having coarse substrates and larger interstitial spaces for cover (Bovbjerg 1970, Stein and
Magnuson 1976, Garvey et al. 1994). Smaller substrate size and greater substrate embeddedness

can limit crayfish production (Mitchell and Smock 1991). Therefore, lack of suitable cover may have limited crayfish density in Sam Houston National Forest streams. Crayfish densities in San Jacinto and Trinity River tributaries (maximum of 0.49 crayfish m^{-2}) were considerably lower than in systems with more complex substrates. For example, crayfish densities reported from streams with cobble substrates ranged from 5-12 m^{-2} (Rabeni 1985, Huryn and Wallace 1987, Rahel and Stein 1988). If $\underline{O}$. $\underline{palmeri}$ is a more aggressive competitor, it may have excluded $\underline{P}$. $\underline{kensleyi}$ from cover and indirectly enhanced predation rates on $\underline{P}$. $\underline{kensleyi}$ by fishes.

Cause-and-effect relationships between crayfish and fish in these streams were not assessed with manipulative experiments, so it is difficult to assess the relative strength of intra- and inter-specific competition and predator-prey relationships. For example, negative correlations among potential competitors and crayfish could be attributed simply to differences in habitat use. However, abundance of $\underline{P}$. $\underline{sciera}$ (Herbert 1999) and adult $\underline{O}$. $\underline{palmeri}$ were positively correlated with streams having stable flows and higher discharge, and were negatively correlated with one another in this study, indicating potential interactions between these species. In addition, crayfish reduce abundance of invertebrates (Charlebois and Lamberti 1996, Stelzer and Lamberti 1999), thus increasing potential competition with benthic invertivorous fishes (Momot 1995, Stelzer and Lamberti 1999). Crayfish will consume darters confined to small areas (Rahel and Stein 1988) and attack darter nests to consume eggs (Rahel 1989). In two studies, predation rates on two benthic fishes increased when cover was limited and crayfish were present (Rahel and Stein 1988, McNeely et al. 1990). Such interactions between crayfish and darters also reduce foraging efficiency of small crayfishes (Stelzer and Lamberti 1999). Darters presented lateral displays toward small crayfish in wading pools regardless of cover, suggesting similar interactions are likely to occur in the field (Keller and Moore 2000).

CONCLUSIONS

The results of this study indicate biotic interactions and abiotic disturbance structured crayfish assemblages across streams of the Sam Houston National Forest. Moreover, the interaction of these two factors is important in maintaining regional species diversity. These results are contrary to those found by Meador and Matthews (1992), where highly variable hydrologic conditions had little effect on stream fishes, when compared to effects simply due to spatial variation. Although all three crayfish species occurred across intermittent and perennial streams, their relative densities were related to drought conditions, competitor and predator densities, and interactions among these factors. Where conditions were closer to equilibrium (perennial streams), the structure of crayfish assemblages was related more strongly to biotic than abiotic factors (Poff and Ward 1989). Periodic disturbances due to drought moved conditions away from equilibrium, and provided the abiotic "filter" (Closs and Lake 1994) for establishing different assemblages in intermittent streams.

Several studies have similarly documented large numbers of crayfish populating previously dry stream reaches as flows resume (Larimore et al. 1959, Bovbjerg 1970, Taylor 1983). Colonizing species are characteristically smaller, have high growth and developmental rates, may reproduce multiple times in a year, and produce extremely high numbers of young (Winemiller and Rose 1992). This life history strategy produces an advantage in harsh and unpredictable habitats, while compensating for mortality due to predation (i.e., an "opportunistic" strategy; Winemiller and Rose 1992). In addition, colonizing crayfish species are often replaced over time by those that are competitively dominant (Bovbjerg 1970). Seasonal abundance patterns for P. kensleyi and P. clarkii observed in this study reflected such differences. Thus, results in this study are consistent with hypothesized life history trade-offs among stress tolerance, resilience or resistance to disturbance and predation, and competitive

ability (Winemiller and Rose 1992).

Although the present study included only one seasonal cycle, a study in these same streams during 1997 documented similar patterns for hydrologic regimes and negative effects of drought on several predatory fishes and potential benthic competitors (Herbert 1999), thus drought is likely a regular occurrence. The effects of a variable hydrologic regime are expected to strongly influence fish and crayfish assemblage structure and regional diversity within these drainages.

Streams with variable flow regimes appear to be necessary for the persistence of $\underline{P}$. kensleyi, whereas streams with stable flow, or at least access to higher-order perennial streams for refuge from drought, are required for $\underline{O}$. palmeri to occur. Relative to $\underline{P}$. kensleyi and $\underline{O}$. palmeri, the distribution of $\underline{P}$. clarkii was relatively unrelated to density of other crayfish species, benthic fishes, or to any abiotic variables measured in this study. These results are not surprising, given this species' tolerance to a wide range of habitat conditions (Hobbs 1989b). It endures drought, predation, and competition, and may breed more than once per year, perhaps compensating for mortality during drought.

Little information is published about the behaviors or ecology of either $\underline{P}$. kensleyi or $\underline{O}$. palmeri, but the aggressive nature of $\underline{P}$. clarkii is known (Blank and Figler 1996, Antonelli et al. 1999). Additionally, the majority of published research regarding crayfish assemblage structure has addressed interactions between native and exotic crayfishes and fishes. To better understand factors structuring native crayfish assemblages, further experimental studies are needed to assess mechanisms producing the patterns of crayfish and fish distribution observed in this study. Evaluation of potential interactions, including those among crayfish and benthic or predatory fishes, should provide insight into abiotic and biotic processes maintaining biodiversity and function of stream systems.

LITERATURE CITED

Angermeier, P. L., and J. R. Karr. 1984. Relationships between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society 113:716-726.

Antonelli, J., C. Steele, and C. Skinner. 1999. Cover seeking behavior and shelter use by juvenile and adult crayfish, *Procambarus clarkii:* potential importance in species invasion. Journal of Crustacean Biology 19(2):293-300.

Baker, J. A., and S. T. Ross. 1981. Spatial and temporal resource utilization by southeastern cyprinids. Copeia 1981(1):178-189.

Benke, A. C., R. L. Henry, D. M. Gillespie, and R. J. Hunter. 1985. Importance of snag habitat for animal production in southeastern streams. Fisheries 10(5):8-13.

Berkman, H. E., C. F. Rabeni, and T. P. Boyle. 1986. Biomonitors of stream quality in agricultural areas: fish versus invertebrates. Environmental Management 10(3):413-419.

Blank, G. S., and M. H. Figler. 1996. Interspecific shelter competition between the sympatric crayfish species *Procambarus clarkii* (Girard) and *Procambarus zonangulus* (Hobbs and Hobbs). Journal of Crustacean Biology 16(2):300-309.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73(3):1045-1055.

Bovbjerg, R. V. 1970. Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). Ecology 51(2):225-236.

Caine, E. A. 1978. Comparitive ecology of epigean and hypogean crayfish (Crustacea: Cambaridae) from northwestern Florida. The American Midland Naturalist 99(2):315-329.

Capelli, G. M., and B. L. Munjal. 1982. Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*. Journal of Crustacean Biology 2(4):486-492.

Capone, T. A., and J. A. Kushlan. 1991. Fish community structure in dry-season stream pools. Ecology 72(3):983-992.

Chambers, P. A., J. M. Hanson, J. M. Burke, and E. E. Prepas. 1990. The impact of the crayfish *Orconectes virilis* on aquatic macrophytes. Freshwater Biology 24:81-91.

Charlebois, P. M., and G. A. Lamberti. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. Journal of the North American Benthological Society 15(4):551-563.

Closs, G. P., and P. S. Lake. 1994. Spatial and temporal variation in the structure of an intermittent-stream food web. Ecological Monographs 64(1):1-21.

Connell, J. H. 1978. Diversity of tropical rain forests and coral reefs. Science 199:1302-1309.

Creed, R. P. 1994. Direct and indirect effects of crayfish grazing in a stream community. Ecology 75(7):2091-2103.

DiDonato, G. T., and D. M. Lodge. 1993. Species replacement among *Orconectes* crayfishes in Wisconsin Lakes: the role of predation by fish. Canadian Journal of Fisheries and Aquatic Sciences 50:1484-1488.

Englund, G. 1999. Effects of fish on the local abundance of crayfish in stream pools. Oikos 87:48-56.

Englund, G. K., and J. J. Krupa. 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. Freshwater Biology 43(1): 75-83.

Fausch, K. D., and R. G. Bramblett. 1991. Disturbance and fish communities in intermittent tributaries of a western great plains river. Copeia 1991(3):659-674.

Fraser, D. F., and R. D. Cerri. 1982. Experimental evidence of predator-prey relationships in a patchy environment: consequences for habitat use patterns in minnows. Ecology 63(2):307-313.

Garvey, J. E., R. A. Stein, and H. M. Thomas. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. Ecology 75(2):532-547.

Gauch, H. G., Jr. 1982. Multivariate analysis in community ecology. Cambridge University Press, Melbourne, Australia.

Gelwick, F. P. 2000. Grazer identity changes the spatial distribution of cascading trophic effects in stream pools. Oecolgia 125:573-583.

Gelwick, F.P., M.S. Stock and W.J. Mathews. 1997. Effects of fish, water depth, and predation risk on patch dynamics in a north-temperate river ecosystem. Oikos 80: 382-398

Gordon, N. D., T. A. McMahon, and B. L. Finlayson. 1992. Stream hydrology: an introduction for ecologists. John Wiley & Sons, Chichester, England.

Gorman, O. T., and J. R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59(3):507-515.

Guan, R., and P. R. Wiles. 1997. Ecological impact of introduced crayfish on benthic fishes in a British lowland river. Conservation Biology 11(3):641-647.

Harvey, B. C., and A. J. Stewart. 1991. Fish size and habitat depth relationships in headwater

streams. Oecologia 87:336-342.

Herbert, M. E. 1999. Fish assemblage structure along environmental gradients in a coastal plain drainage: influences from a reservoir. MS Thesis, Texas A&M University, College Station, Texas.

Hill, A. M., and D. M. Lodge. 1994. Diel changes in resource demand: competition and predation in species replacement among crayfishes. Ecology 75(7):2118-2126.

Hobbs, H. H., Jr. 1989a. An illustrated checklist of the American crayfishes (Decapoda: Astacidae, Cambaridae, and Parastacidae). Smithsonian Contributions to Zoology 480.

Hobbs, H. H. Jr.. 1989b. A review of global crayfish introductions with particular emphasis on two North American species (Decapoda: Cambaridae). Crustaceana 56(3):299-316.

Hobbs, H. H., Jr. 1990. On the crayfishes (Decapoda: Cambaridae) of the Neches River Basin of eastern Texas with the descriptions of three new species. Proceedings of the Biological Society of Washington 103(3):573-597.

Hobbs, H. H., III. 1991. Decapoda. Pages 823-858 *in* J. H. Thorp and A. P. Covich (editors). Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego, California.

Huryn, A. D., and J. B. Wallace. 1987. Production and litter processing by crayfish in an Appalachian mountain stream. Freshwater Biology 18:277-286.

Keller, T. A., and P. A. Moore. 2000. Context-specific behavior: crayfish size influences crayfish-fish interactions. Journal of the North American Benthological Society 19(2):344-351.

Kerans, B. L., and J. R. Karr. 1994. A benthic index of biotic integrity (B-IBI) for rivers of the Tennessee Valley. Ecological Applications 4(4):768-785.

Kershner, M. W., and D. M. Lodge. 1995. Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*. Journal of the North American Benthological Society 14(3):414-422.

Kushlan, J. A. 1976. Environmental stability and fish community diversity. Ecology 7(4):821-825.

Larimore, R. W., W. F. Childers, and C. Heckrote. 1959. Destruction and re-establishment of stream fish and invertebrates affected by drought. Transactions of the American Fisheries Society 88:261-285.

Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129(2):271-280.

Lenat, D. R. 1993. A biotic index for the southeastern United States: derivation and list of

tolerance values, with criteria for assigning water-quality ratings. Journal of the North American Benthological Society 12(3):279-290.

Lodge, D. M., M. W. Kershner, J. E. Alod, and A. P. Covich. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology 75(5):1265-1281.

Lonzarich, D. G., J. M. L. Warren, and M. R. E. Lonzarich. 1998. Effects of habitat isolation on the recovery of fish assemblages in experimentally defaunated stream pools in Arkansas. Canadian Journal of Fisheries and Aquatic Sciences 55:2141-2149.

Lorman, J. G., and J. J. Magnuson. 1978. The role of crayfish in aquatic ecosytems. Fisheries 3(6):8-10.

Mather, M. E., and R. A. Stein. 1993. Direct and indirect effects of fish predation on the replacement of a native crayfish by an invading congener. Canadian Journal of Fisheries and Aquatic Sciences 50:1279-1288.

Matthews, W. J. 1983. Fish faunal structure in an Ozark stream: stability, persistence, and a catastrophic flood. Copeia 1986(2):388-397.

Matthews. W. J. 1987. Physiochemical tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. Pages 111-120 *in* W. J. Matthews and D. C. Heins (editors). Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, Oklahoma.

Matthews, W. J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York, New York.

McCormick, P. V. 1990. Direct and indirect effects of consumers on benthic algae in isolated pools of an ephemeral stream. Canadian Journal of Fisheries and Aquatic Sciences 47:2057-2065.

McCune, B. 1997. Influence of noisy environmental data on canonical correspondence analysis. Ecology 78(8):2617-2623.

McNeelly, D. L., B. N. Futrell, and A. Sih. 1990. An experimental study on the effects of crayfish on the predator-prey interaction between bass and sculpin. Oecologia 85:69-73.

Meador, M. R., and W. J. Mathews. 1992. Spatial and temporal patterns in fish assemblage structure of an intermittent Texas stream. American Midland Naturalist 127:106-114.

Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. Ecology 65(5):1525-1534.

Mitchell, D. J., and L. A. Smock. 1991. Distribution, life history and production of crayfish in the James River, Virginia. American Midland Naturalist 126:353-363.

Momot, W. T. 1966. Upstream movements of crayfish in an intermittent Oklahoma stream. The American Midland Naturalist 75(1):150-159.

Momot, W. T. 1995. Redefining the role of crayfish in aquatic ecosystems. Reviews in Fisheries Science 3(1):33-63.

Momot, W. T., H. Gowing, and P. D. Jones. 1978. The dynamics of crayfish and their role in aquatic ecosystems. The American Midland Naturalist 99(1):10-35.

Ott, R. L. 1993. An introduction to statistical methods and data analysis, fourth edition. Wadsworth Publishing Company, Belmont, California.

Page, L. M., and D. W. Schemske. 1978. The effect of interspecific competition on the distribution and size of darters of the subgenus *Catonotus* (Percidae: *Etheostoma*). Copeia 1978(3):406-412.

Peckarsky, B. L. 1983. Biotic interactions or abiotic limitations? A model of lotic community structure. Pages 303-324 *in* I. Thomas D. Fontaine and S. M. Bartell (editors). Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan.

Pianka, E. R. 1994. Evolutionary ecology. Harper Collins College Publishers, New York, New York.

Poff, N. L., and J. D. Allen. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76(2):606-627.

Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46:1805-1818.

Polis, G. A. 1984. Age structure component of niche width and intra-specific resource partitioning: can age groups function as ecological species? The American Naturalist 123(4):541-564.

Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, B. Statzner, and I. R. W. D. Badgen. 1988. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society 7(4):456-479.

Probst, W. E., C. F. Rabeni, W. G. Convington, and R. E. Marteney. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. Transactions of the American Fisheries Society 113:283-294.

Rabeni, C. F. 1985. Resource partitioning by stream-dwelling crayfish: the influence of body size. The American Midland Naturalist 113(1):20-29.

Rabeni, C. F. 1992. Trophic linkage between stream centrarchids and their crayfish prey.

Canadian Journal of Fisheries and Aquatic Sciences 49:1714-1721.

Rabeni, C. F., K. J. Collier, S. M. Parkyn, and B. J. Hicks. 1997. Evaluating techniques for sampling stream crayfish (*Paranephrops planifrons*). New Zealand Journal of Marine and Freshwater Research 31:393-700.

Rahel, F. J. 1989. Nest defense and aggressive interactions between a small benthic fish (the johnny darter *Etheostoma nigrum*) and crayfish. Environmental Biology of Fishes 24(4):301-306.

Rahel, F. J., and R. A. Stein. 1988. Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and a small benthic fish. Oecologia 75:94-98.

Reice, S. R. 1994. Nonequilibrium determinants of biological community structure. American Scientist 82(5):424-435.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43(1):223-225.

Robison, H. W., and T. M. Buchanan. 1988. Fishes of Arkansas. The University of Arkansas Press, Fayetteville, Arkansas.

Roell, M. J., and D. J. Orth. 1993. Trophic basis of production of stream-dwelling smallmouth bass, rock bass, and flathead catfish in relation to invertebrate bait harvest. Transactions of the American Fisheries Society 122:46-62.

Ross, S. T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 2:352-388.

SAS (Statistical Analysis System Institute). 1988. SAS/STAT User's Guide, 6.03 edition. Statistical Analysis System Institute, Inc., Cary, North Carolina.

Scheiner, S. M. 1993. MANOVA: multiple response variables and multispecies interactions. Pages 94-112 *in* S. M. Scheiner and J. Gurevitch (editors). Design and analysis of ecological experiments. Chapman and Hall, New York, New York.

Schlosser, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs 52(4):395-414.

Schlosser, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66(5):1484-1490.

Schlosser, I. J. 1987a. The role of predation in age- and size- related habitat use by stream fishes. Ecology 68(3): 651-659.

Schlosser, I. J. 1987b. A conceptual framework for fish communities in small warmwater streams. Pages 17-24 *in* W. J. Matthews and D. C. Heins (editors). Community and

evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Schlosser, I. J., and K. K. Ebel. 1989. Effects of flow regime and cyprinid predation on a headwater stream. Ecological Monographs 59(1):41-57.

Simonson, T. D., J. Lyons, and P. D. Kanehl. 1994. Quantifying fish habitat in streams: transect spacing, sample size, and a proposed framework. North American Journal of Fisheries Management 14:607-615.

Stein, R. A. 1976. Sexual dimorphism in crayfish chelae: functional significance linked to reproductive activities. Canadian Journal of Zoology 54:220-227.

Stein, R. A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. Ecology 58:1237-1253.

Stein, R. A., and J. J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. Ecology 57:751-761.

Stelzer, R. S., and G. A. Lamberti. 1999. Independent and interactive effects of crayfish and darters on a stream benthic community. Journal of the North American Benthological Society 18(4):524-532.

Taylor, R. C. 1983. Drought-induced changes in crayfish populations along a stream continuum. The American Midland Naturalist 110(2):286-298.

Taylor, R. C. 1988. Population dynamics of the crayfish *Procambarus spiculifer* observed in different-sized streams in response to two droughts. Journal of Crustacean Biology 8(3):401-409.

Taylor, C. A., J. M. L. Warren, J. J. F. Fitzpatrick, I. H. H. Hobbs, R. F. Jezerinac, W. L. Pflieger, and H. W. Robison. 1996. Conservation status of crayfishes of the United States and Canada. Fisheries 21(4):25-38.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67(5):1167-1179.

ter Braak, C. J. F. 1995. Ordination. Pages 91-173 *in* R. H. G. Jongman, C. J. F. ter Braak and O. F. R. van Tongeren (editors). Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, England.

ter Braak, C. J. F., and P. Smilauer. 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, New York.

ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57(3):256-289.

Whitledge, G. W., and C. F. Rabeni. 1997. Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotope analysis. Canadian Journal of Fisheries and Aquatic Sciences 54:2555-2563.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49(10): 2196-2218.

Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52(2):336-342.

Stream hydrology and locations of sites sampled for crayfish and fish within the Sam Houston National Forest, 1999-2000. Sites are listed according to river drainage. Locality descriptions contain abbreviations for road types: FR = National Forest Road, FM = farm to market road.

Stream name	Specific Locality	County	National Forest Compartment(s)	Hydrology
	Trinity			
Little Creek	Upstream of FR 217	San Jacinto	106	Perennial
Big Creek	Upstream of FR 217 in Big Creek Scenic Area	San Jacinto	106	Perennial
	East Fork San Jacinto			
Pea Creek	W of FR 207-A, where bend in road is close to stream	San Jacinto	83	Perennial
Winters Bayou	Upstream of FM 1375	Walker	84	Intermittent
Roark Creek	Downstream of FR 207	Walker	78	Perennial
Clear Creek	4 miles SW of Coldspring, access by oil lease road	San Jacinto	94	Perennial
Montague Creek	Upstream of FM 1725, 6 miles NW of Cleveland	San Jacinto	121	Intermittent
Un-named Creek	Upstream of the end of FR 261	San Jacinto	116	Perennial
East Fork Caney Creek	Upstream of FM 2693, 4 miles NW of Evergreen	San Jacinto	84	Intermittent
	West Fork San Jacinto			
West Sandy Creek	Downstream of north end of FR 208-A	Walker	24	Intermittent
Gum Branch	Upstream of FM 1375	Walker	52	Perennial
Smith Branch	Upstream of FR 222-A	Walker	50	Perennial
Sand Creek	Upstream of FM 1375, W of Lake Conroe	Walker	37	Perennial
Bay Branch	Downstream of FM 1791	Montgomery	18	Perennial
Caney Creek	Upstream of FM 1375, 4 miles W of Lake Conroe	Montgomery	17, 21	Intermittent
Big Chinquapin Creek	Upstream of Park Rd. 40, Huntsville State Park	Walker	57	Perennial

APPENDIX B

Number collected and relative abundance for all fish and crayfish sampled from streams of the Sam Houston National Forest, 1999-2000. Codes used in tables and figures area also listed.

Species	Species Code	*n*	Relative Abundance
Crayfishes			
Procambarus clarkii	Pclark	579	0.580
Procambarus kensleyi	Pken	236	0.236
Orcontectes palmeri longimanus	Opalm	173	0.173
Cambarus ludovicianus	Cludo	7	0.007
Procambarus acutus acutus	Pacu	3	0.003
Total		998	
Fishes			
Gambusia affinis	Gaff	623	0.194
Fundulus notatus	Fnot	343	0.107
Notropis atrocaudalis	Natr	284	0.088
Ichthyomyzon gagei	Igag	268	0.083
Lythrurus fumeus	Lfum	229	0.071
Aphredoderus sayanus	Asay	185	0.058
Lepomis megalotis	Lmeg	162	0.050
Fundulus olivaceous	Foli	112	0.035
Lepomis punctatus	Lpun	103	0.032
Noturus nocturnus	Nnoc	95	0.030
Lepomis young-of-year	LepYOY	82	0.026
Erimyzon oblongus	Eobl	79	0.025
Lepomis macrochirus	Lmac	75	0.023
Etheostoma parvipinne	Epar	71	0.022
Cyprinella venusta	Cven	70	0.022
Lepomis spp.	LepSP	70	0.022
Ameiurus natalis	Anat	65	0.020
Percina sciera	Psci	37	0.012
Etheostoma gracile	Egra	32	0.010
Lepomis cyanellus	Lcya	31	0.010
Etheostoma chlorosomum	Echl	30	0.009
Esox americanus	Eame	24	0.007
Elassoma zonatus	Ezon	23	0.007
Lepomis gulosus	Lgul	22	0.007
Micropterus salmoides	Msal	20	0.006
Lepomis marginatus	Lmar	17	0.005
Lepomis humilis	Lhum	12	0.004
Percina macrolepida	Pmac	12	0.004
Pimephales vigilax	Pvig	12	0.004
Fundulus chrysotus	Fchr	7	0.002
Minytrema melanops	Mmel	5	0.002

Appendix B. Continued.

Species	Species Code	n	Relative Abundance
Lythrurus umbratilis	Lumb	4	0.001
Noturus Gyrinus	Ngyr	3	0.001
Total		3212	

VITA

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Publications
- Healy, B. D., and D. G. Lonzarich. 2000. Microhabitat use and behavior of over-wintering juvenile coho salmon in a Lake Superior tributary. Transactions of the American Fisheries Society 129:866-872.
- Healy, B. D., and F. P. Gelwick. Native mussel assemblages of the Sam Houston National Forest of East Texas. Texas Journal of Science (In revision).
- Gelwick, F., B. Healy, N. Dictson, and R. Knipe. 2001. Fishes of Keechi Creek Wildlife Management Area. The Texas Journal of Science 53(1):13-18.
- Gelwick, F., B. Healy, N. Dictson, and J. Cathey. 2000. Fishes of Richland Creek Wildlife Management Area. The Texas Journal of Science 52(4):313-318.

Selected Presentations
- B. D. Healy and F. P. Gelwick. The effects of interactions between benthic fishes and crayfish on their distribution and abundance in streams. 48th Annual Meeting, North American Benthological Society, Keystone, Colorado, May 28-June 1, 2000.
- B. D. Healy and F. P. Gelwick. Distribution of benthic fishes and crayfishes in the Sam Houston National Forest. Joint meeting of the Arkansas, Texas, and Louisiana chapters of the American Fisheries Society, Bossier City, Louisiana, January, 23-25, 2000.