Primary Research Paper

The role of salinity in structuring fish assemblages in a prairie stream system

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Abstract

We used fishery surveys from 1954 to 1957 to determine the relationship between salinity and prairie stream-fish assemblage composition prior to the major drought of the 1950s and subsequent anthropogenic modifications. A total of 78,931 fishes were captured, representing 13 families and 44 species. Species were classified as having low, moderate, or high salinity tolerances based on k-means clustering of detrended correspondence scores. The proportion of species with high salinity tolerances was correlated positively (r = 0.74) with salinity, whereas the proportion of species with low (r = -0.69) or moderate (r = -0.36) tolerances was correlated strongly and negatively with salinity. Many of the low or moderate salinity tolerant species found in the 1950s were not collected in studies conducted 15 and 35 years later. Examination of these studies provides compelling evidence that salinity has been a dominant and persistent factor in affecting the structure of stream-fish assemblages for the past 50 years.

Introduction

Two major goals in stream-fish ecology are to characterize patterns in the distribution and abundance of coexisting species, and to identify processes responsible for establishing and maintaining those patterns. To these ends, numerous studies have examined biotic (Werner & Hall, 1976; Baker & Ross, 1981; Jackson et al., 1992; Douglas et al., 1994; Gilliam & Fraser, 2001) and abiotic (Gorman & Karr, 1978; Grossman & Freeman, 1987; Poff & Allan, 1995; Willis & Magnuson, 2000; Ostrand & Wilde, 2001; Bonner & Wilde, 2002) mechanisms that affect species richness, composition, and abundance in streamfish assemblages. In prairie streams of the Great Plains of central United States, biotic interactions play a role in structuring fish assemblages (Marsh-Matthews & Matthews, 2000), but abiotic factors such as hydrological regime, temperature, pH, and salinity often are believed to be more important (Smith & Hubert, 1989; Capone & Kushlan, 1991; Fausch & Bramblett, 1991; Ostrand & Wilde, 2001).

Prairie streams are characterized by highly variable discharge regimes that result in rapid changes in temperature, dissolved oxygen concentrations, and other parameters of water quality (Fisher et al., 1982; Minckley & Meffe, 1987; Ostrand & Wilde, 2002). The upper Red River drainage and its tributaries, which drain much of western Oklahoma and northern Texas, are characterized by such environmental variability (Ostrand & Wilde, 2001). Moreover, the headwaters of the Red River occasionally have salt concentrations approximating that of seawater (Matthews, 1998). Consequently, salinity should be important in structuring stream-fish assemblages in this drainage. Echelle et al. (1972) provided an initial assessment of the influence of salinity in structuring fish assemblages in the Red River drainage system by examining factors that limited the distribution and abundance of Red River pupfish, Cyprinodon rubrofluviatilis Fowler, which is an abundant and ecologically important species. They found that Red River pupfish were more common at sites with higher salinities, but provided limited insight regarding the potential influence of salinity in structuring the overall assemblage. Taylor et al. (1993) found salinity, followed by stream size, alkalinity, quantity of woody debris, and water clarity, to be among the factors that best accounted for patterns in the distribution of abundant members of stream-fish assemblages in portions of the Red River and its tributaries in Oklahoma. However, both studies (Echelle et al., 1972; Taylor et al., 1993) were conducted after one of the most severe droughts to affect the Great Plains (Woodhouse & Overpeck, 1998). In Texas, rainfall dropped by 40% between 1949 and 1951, and by 1953 approximately 75% of the state experienced below normal rainfall. The severity of this drought, coupled with anthropogenic modifications of stream ecosystems, resulted in localized extirpations of several species throughout the upper Red River drainage (G. R. Wilde, unpublished). Thus, it is unclear whether the results of Echelle et al. (1972) and Taylor et al. (1993) identify historic distributional patterns or patterns that result from changes in interspecific interactions (e.g., competitive release) associated with modifications in species composition that occurred after the drought.

Between 1954 and 1957, the Texas Game and Fish Commission conducted a number of fishery surveys in the Red River drainage of Texas (Lewis, 1957a, b, c; Lewis & Dalquest, 1957a, b). These surveys provide detailed information on both water quality and composition of the ichthyofauna of the Red River drainage prior to the drought of the 1950s. Therefore, the purpose of this paper is to synthesize the results of these surveys to: (1) provide an historic description of fish assemblages in the Red River basin of Texas, (2) determine the relationship between salinity and stream-fish assemblage structure prior to the drought of the 1950s, and (3) assess the persistence of salinity as a factor that structures contemporary fish assemblages.

Materials and methods

Data were obtained from fishery surveys conducted by Lewis (1957a, b, c) and Lewis & Dalquest (1957a, b). Their surveys focused on five tributaries of the Red River in Texas, including the Little Wichita River (LW), Wichita River (W), Pease River (P), Prairie Dog Town Fork of the Red River (PDTF), and the Salt Fork of the Red River (SF). Fish assemblages were sampled with the use of seines and gill-nets at several locations within each tributary, and each location usually was sampled monthly for one year. Sampling effort was reported to be approximately constant across sites and dates. However, three sites in the Salt Fork of the Red River were sampled only once because of drying of the streambed. Data included descriptions of the sampling sites, water quality measurements at each site, and monthly summaries of numbers and species of fishes at each site. From these data, we calculated several ecological indices of assemblage structure including species richness (S), species evenness (E), mean number of individuals per sample (Catch Per Unit Effort, CPUE), and the total number of individuals of each species for each site within each of the five rivers. We also used mean total dissolved solids (TDS), reported as parts per million, as an indirect measure of salinity at various sampling sites.

We used detrended correspondence analysis (MVSP for Windows, Version 3) on log-transformed abundance data with a downweighting of the rare species (those that occurred at fewer than 20% of the total number of sites occupied by the most common species) to extract patterns of variation in stream-fish assemblages (Hill & Gauch, 1980). We chose detrended correspondence analysis (DCA) over canonical correspondence analysis (Ter Braak, 1986; Palmer, 2002) because it provides an indirect assessment of the effects of environmental factors on patterns of variation in abundance by superimposing an external data set onto ordination axes. This was necessary because, other than TDS, we did not have access to a true environmental data set. Instead, we related patterns in species occurrence to TDS and ecological indices of assemblage structure (i.e., S, E, and CPUE). We chose to downweight rare species, rather than exclude them, because we wished to understand the effects of TDS on the entire fish assemblage. Moreover, we chose to define rare species as those occurring in less that 20% of the sites occupied by the most common taxa because we wanted to place more emphasis on widely distributed species to ascertain broad scale patterns in the role of salinity in structuring stream-fish assemblages and because we found little difference in the results when rare species were included versus excluded from the analyses.

To examine the influence of TDS, S, E, and CPUE on patterns of variation in stream-fish assemblages, we superimposed vector correlations between each of the variables and each of the first two DCA axes onto a scatter plot of species scores as a function of the first two DCA axes. The vector correlations were bootstrapped with 10,000 iterations to assess statistical significance, free from the underlying assumptions of traditional parametric tests (i.e., linearity, homoscedasticity, and bivariate normality of error terms). Correlation analyses also were performed on all combinations of TDS and ecological indices of assemblage structure. These too were bootstrapped with 10,000 iterations. Statistical significance was set at $\alpha = 0.05$ for all individual tests.

Following the work of Echelle et al. (1972) and Taylor et al. (1993), we wanted to classify fish into three groups that corresponded to species with low, moderate, and high TDS tolerances based on empirical distributional patterns. Although this decision was somewhat arbitrary (e.g., we could have chosen two groups corresponding to tolerant and intolerant species), we believed three groups would capture more of the variation in observed tolerance levels. Because TDS was so highly correlated with the first DCA axis, we used species scores on the first DCA axis and k-means clustering (Legendre & Legendre, 1998) to assign fish to these groups defined by TDS tolerance. We then determined the percentage of fishes that belonged to each tolerance group at each sample site. Log-linear regression and correlation analysis were performed on angular-transformed proportional abundance of each tolerance group and log-transformed TDS

to find a predictive relationship between group abundance and TDS.

Results

A total of 78931 fishes, representing 13 families and 44 species, occurred at 34 sites within the Red River drainage of Texas. Species richness at each site ranged from 3 to 27 (mean \pm SD = 13.5 \pm 7.7), species evenness (Shannon's index) ranged from 0.18 to 0.99 (0.622 \pm 0.176), and CPUE ranged from 10 to 840 (250.2 \pm 210.0; Table 1). Mean TDS ranged from 231 to 46552 ppm (6747.9 \pm 9406.1 ppm). These values translated into approximately 0.36 to 72.74 mS, assuming a dominantly sodium chloride component. LogTDS was correlated significantly with CPUE (r = 0.40, p = 0.020) and S (r = -0.36, p = 0.034), but not E (r = -0.21, p = 0.229).

The first two DCA axes accounted for 51.1% of the total variation in species abundance. Log-TDS was correlated significantly with each of the first two DCA axes (r = 0.75, p < 0.001 and r = -0.51, p = 0.002, respectively), S was correlated significantly with each of the first two DCA axes (r = -0.74, p < 0.001 and r = -0.35,p = 0.040), and CPUE was correlated significantly with only the second DCA axis (r = -0.43, p = 0.014). All other correlations were non-significant. Scores from DC1 and k-means clustering identified species that had low TDS tolerances, moderate TDS tolerances, and high TDS tolerances. The high TDS tolerant species group was noticeably separated from the other two groups, especially in terms of the TDS vector (Fig. 1). Loglinear regression and correlation analyses (Table 2) showed a similar trend between species with low TDS tolerances (F = 29.01, df = [1, 32], p < 0.001) and species with moderate TDS tolerances (F = 4.68, df = [1, 32], p = 0.038) in the way their distributions were affected by TDS. More specifically, the percentage of species at each site with low or moderate TDS tolerances decreased as TDS increased and in roughly the same manner (r = -0.69, p < 0.001 and r = -0.36,p = 0.032, respectively). Species with high TDS tolerances (F = 38.61, df = [1, 32], p < 0.001), on the other hand, responded quite differently than did the other two tolerance groups in that a

| Table 1. Mean salinity (TDS), species richness (S), Shannon's |
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| index of evenness (E), and catch per unit effort (CPUE) for each |
| site in the upper Red River drainage, Texas |

| Site | TDS | S | Е | CPUE |
|-------|--------|----|------|------|
| LW1 | 299 | 16 | 0.62 | 126 |
| LW2 | 231 | 25 | 0.68 | 181 |
| LW3 | 586 | 17 | 0.57 | 93 |
| LW4 | 895 | 21 | 0.64 | 121 |
| LW5 | 373 | 17 | 0.61 | 117 |
| LW6 | 2178 | 27 | 0.29 | 840 |
| W1 | 11,563 | 12 | 0.62 | 279 |
| W2 | 21,519 | 10 | 0.61 | 180 |
| W3 | 3734 | 17 | 0.66 | 230 |
| W4 | 17,278 | 11 | 0.59 | 310 |
| W5 | 14,932 | 14 | 0.64 | 238 |
| W6 | 1781 | 26 | 0.76 | 168 |
| W7 | 1806 | 27 | 0.72 | 118 |
| W8 | 3321 | 21 | 0.50 | 180 |
| W9 | 2366 | 27 | 0.61 | 251 |
| P1 | 3321 | 8 | 0.89 | 110 |
| P2 | 20,132 | 10 | 0.55 | 744 |
| Р3 | 7431 | 17 | 0.38 | 391 |
| P4 | 4075 | 24 | 0.48 | 483 |
| P5 | 6763 | 9 | 0.71 | 139 |
| P6 | 3490 | 17 | 0.59 | 200 |
| P7 | 3208 | 3 | 0.99 | 10 |
| PDTF1 | 3049 | 9 | 0.63 | 355 |
| PDTF2 | 20,375 | 4 | 0.57 | 194 |
| PDTF3 | 3594 | 3 | 0.89 | 94 |
| PDTF4 | 4278 | 3 | 0.51 | 37 |
| PDTF5 | 10,262 | 6 | 0.86 | 139 |
| PDTF6 | 46,552 | 5 | 0.18 | 794 |
| SF1 | 667 | 11 | 0.37 | 330 |
| SF2 | 590 | 5 | 0.93 | 85 |
| SF3 | 1320 | 6 | 0.52 | 38 |
| SF4 | 1739 | 7 | 0.83 | 63 |
| SF5 | 2730 | 13 | 0.56 | 380 |
| SF6 | 2992 | 11 | 0.59 | 489 |

Abbreviations for the rivers are provided in the text.

strong positive relationship existed between percent composition and TDS (r = 0.74, p < 0.001).

Discussion

Relatively few published studies document longterm trends in assemblage structure of prairie fishes (Cross & Moss, 1987; Chadwick et al., 1997; Bonner & Wilde, 2000) and none have been published for highly saline systems. Although our study is not truly a long-term assessment of assemblage structure, it does provide evidence that abiotic factors, such as salinity, are capable of structuring stream-fish assemblages for many decades. This is especially interesting considering the apparent loss of many salinity-intolerant species. The decrease in local species diversity throughout much of the upper Red River drainage is consistent with observed patterns in biodiversity from other regions of Texas (Anderson et al., 1995), which have been attributed to, or at least correlated with, disturbance (Hubbs et al., 1997). Thus, salinity, which often is associated with disturbed habitats, is not surprisingly a dominant factor that structures stream fish assemblages in a prairie system.

Our results are qualitatively similar to those of Echelle et al. (1972) and Taylor et al. (1993) in that salinity plays a prominent role in structuring fish assemblages throughout the Red River drainage. For example, Echelle et al. (1972) suggested there were three groupings among the 12 most commonly collected species within the Red River drainage system: (1) Red river pupfish and plains killifish (Fundulus zebrinus Jordan and Gilbert); (2) plains minnow (Hybognathus placitus Girard), Red River shiner (Notropis bairdi Hubbs and Ortenburger), emerald shiner (Notropis atherinoides Rafinesque), and speckled chub (Macrhybopsis aestivalis Girard); and (3) red shiner (Cyprinella lutrensis Baird and Girard), western mosquitofish (Gambusia affinis Baird and Girard), green sunfish (Lepomis cyanellus Rafinesque), longear sunfish (Lepomis megalotis Rafinesque), fathead minnow (Pimephales promelas Rafinesque), and bullhead minnow (Pimephales vigilax Baird and Girard). Their groupings are similar to those from this study, for we classify both of the members of their first group as having high salinity tolerances and most of their third group as having moderate salinity tolerances. Echelle et al. (1972), however, do not have an assemblage corresponding to species with low salinity tolerances. This might be the result of using only the 12 most abundant species, if the rare species are those with low salinity tolerances. Alternatively, it might be a true difference in



Figure 1. Scatterplot of detrended correspondence scores for each of the 44 species with vectors representing the correlations between TDS, S, E, and CPUE and detrended axes from the Red River drainage. The solid, dashed, and dotted lines are minimum convex hulls around the high, moderate, and low salinity tolerant species, respectively. The vector correlations are amplified 2.5 times to facilitate visualization.

assemblage structure between the 1950s and the late 1960s. The groupings of Taylor et al. (1993) also correspond to those in our study in that all members of their first group (i.e., plains minnow, speckled chub, Red River shiner, and chub shiner [Notropis potteri Hubbs and Bonham]) are classified by us as having high salinity tolerances. Their second group consists of two species with high salinity tolerances (i.e., Red River pupfish and plains killifish) and one species with low salinity tolerance (i.e., emerald shiner). Their third and fourth groups, on the other hand, are a mixture of species with moderate or low salinity tolerances. However, our classification scheme is based on surveys conducted some 35 years before and might yield slightly different results if the same procedures were used on current assemblage data.

In the 1950s, 91% of the low salinity tolerant species, 73% of the moderate salinity tolerant species, and 43% of the high salinity tolerant species exhibited relative abundances less than or equal to one percent of the total number of fishes collected at

Table 2. Results from log-linear regression and correlation analyses for each of the three salinity tolerance groups for the Red River drainage

| Tolerance groups | βο | β_1 | r | р |
|------------------|------------------|----------------|---------------|------------------|
| High Moderate | 124.39 102.52 | 21.71 -8.47 | 0.74 -0.36 | < 0.001 0.029 |
| Low | 121.87 | 13.24 | -0.69 | < 0.001 |

all rivers (Fig. 2). The less abundant species are those with lower salinity tolerances, or conversely, the more abundant species are those with high salinity tolerances. Using salinity tolerances of species collected in the 1950s, we estimated the percentage of each tolerance class that was not collected in Taylor et al. (1993). Although the study sites are not identical to those of Lewis and Dalquest, they are within the same drainage and provide insight into how species abundances and distributions might change over 35 years. Fifty-nine percent of the low salinity tolerant species, 60% of the moderate salinity tolerant species, and 14% of



Figure 2. Graphical depiction of the proportion of fishes at each collection locality with low, moderate, and high salinity tolerances in the Red River drainage.

the high salinity tolerant species from the 1950s were not collected in 1989 (Taylor et al., 1993). Thus, salinity tolerances appear to be related to the likelihood of persistence and may be a dominant factor in maintaining biodiversity in prairie stream systems.

tems. The implications of this study extend beyond the Great Plains of central United States. With many of the world's freshwater rivers and streams, particularly those located in arid and semi-arid regions, becoming increasingly salinized due to both natural and anthropogenic activities (Williams, 1987, 2001; Davies & Day, 1998), there is societal need to understand the ecological impact of salinization on freshwater biota. We demonstrate the importance of salinity as a persistent structuring mechanism in prairie stream-fish assemblages and suggest that salinity can differentially affect the ability of species to persist in environmentally harsh conditions over extended periods of time, leading to an overall loss in biodiversity in these disturbed habitats. We believe that more studies should examine the effects of salinity on stream-fish assemblages and more effort should be taken to minimize the salinization of many rivers and streams if adequate conservation is to be afforded to freshwater biota.

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References

- Anderson, A. A., C. Hubbs, K. O. Winemiller & R. J. Edwards, 1995. Texas freshwater fish assemblages following three decades of environmental change. Southwestern Naturalist 40: 314–321.
- Baker, J. A. & S. T. Ross, 1981. Spatial and temporal resource utilization by southeastern cyprinids. Copeia 1981: 178–189.
- Bonner, T. H. & G. R. Wilde, 2000. Changes in the Canadian River fish assemblage associated with reservoir construction. Journal of Freshwater Ecology 15: 189–198.
- Bonner, T. H. & G. R. Wilde, 2002. Effect of turbidity on feeding efficiency of prairie stream fishes: test of a hypothesis. Transactions of the American Fisheries Society 131: 1203–1208.
- Capone, T. A. & J. A. Kushlan, 1991. Fish community structure in dry-season stream pools. Ecology 72: 983–992.
- Chadwick, J. W., S. P. Canton, D. J. Conklin & P. L. Winkle, 1997. Fish species composition in the central Platte River, Nebraska. Southwestern Naturalist 42: 279–289.
- Cross, F. B. & R. E. Moss, 1987. Historic changes in fish communities and aquatic habitats in plains streams of

Kansas. In Matthews, W. J. & D. C. Heins (eds), University of Oklahoma Press, Norman, OK: 155–165.

- Davies, B. & J. Day, 1998. Vanishing Waters. University of Cape Town Press, Cape Town.
- Douglas, M. E., P. C. Marsh & W. L. Minckley, 1994. Indigenous fishes of western North America and the hypothesis of competitive displacement: *Meda fulgida* (Cyprinidae) as a case study. Copeia 1994: 9–19.
- Echelle, A. A., A. F. Echelle & L. G. Hill, 1972. Interspecific interactions and limiting factors of abundance and distribution in the Red River pupfish, *Cyprinodon rubrofluviatilis*. American Midland Naturalist 88: 109–130.
- Fausch, K. D. & R. G. Bramblett, 1991. Disturbance and fish communities in intermittent tributaries of a western Great Plains river. Copeia 1991: 659–674.
- Fisher, S. G., L. J. Gray, N. B. Grimm & D. E. Busch, 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecological Monographs 52: 93–110.
- Gilliam, J. F. & D. F. Fraser, 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. Ecology 82: 258–273.
- Gorman, O. T. & J. R. Karr, 1978. Habitat structure and stream fish communities. Ecology 59: 507–515.
- Grossman, G. D. & M. C. Freeman, 1987. Microhabitat use in a stream fish assemblage. Journal of Zoology 212: 151–176.
- Hill, M. O. & H. G. Gauch, 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42: 47–58.
- Hubbs, C., E. Marsh-Matthews & W. J. A. A. Matthews Anderson, 1997. Changes in fish assemblages in east Texas streams from 1953 to 1986. Texas Journal of Science 49: 67– 84.
- Jackson, D. A., K. M. Somers & H. H. Harvey, 1992. Null models and fish communities: evidence of nonrandom patterns. American Naturalist 139: 930–951.
- Legendre, P. & L. Legendre, 1998. Numerical Ecology. Elsevier Science, Amsterdam.
- Lewis, L. D., 1957a. Basic survey and inventory of species present, as well as their distribution in the Pease River, its tributaries and watershed within Wilbarger, Foard, Cottle, Motley, Floyd, and Brisco Counties, Texas. Federal Aid project Completion Report F-7-R-4, B-10.
- Lewis, L. D., 1957b. Basic survey and inventory of species present, as well as their distribution in the Prairie Dog Town Fork of the Red River, its tributaries and watershed within Childress, Hall, Brisco, Armstrong, Randall, and Deaf Smith counties, Texas. Federal Aid Project Completion Report F-7-R-4, B-11.
- Lewis, L. D., 1957c. Basic survey and inventory of species present, as well as their distribution in the Salt Fork of the Red River, its tributaries and watershed, lying within Collingsworth, Donley, and Armstrong Counties, Texas. Federal Aid Project Completion Report F-7-R-4, B-12.

- Lewis, L. D. & W. W. Dalquest, 1957a. A basic survey and inventory of species in the Little Wichita River in Northcentral Texas, lying in the counties of Baylor, Archer, and Clay. Federal Aid Project Completion Report F-7-R-3, A-3 and B-8.
- Lewis, L. D. & W. W. Dalquest, 1957b. A fisheries survey of the Big Wichita River system and its impoundments. IF Report Series, No. 2.
- Marsh-Matthews, E. & W. J. Matthews, 2000. Spatial variation in relative abundance of a widespread, numerically dominant fish species and its effect on fish assemblage structure. Oecologia 125: 283–292.
- Matthews, W. J., 1998. Patterns in Freshwater Fish Ecology. Kluwer Academic Publishers, Norwell, MA.
- Minckley, W. L. & G. K. Meffe, 1987. Differential selection by flooding in stream fish communities of the arid American southwest. In Matthews, W. J. & D. C. Heins (eds), University of Oklahoma Press, Norman, OK: 93–104.
- Ostrand, K. G. & G. R. Wilde, 2001. Temperature, dissolved oxygen, and salinity tolerances of five prairie stream fishes and their role in explaining assemblage patterns. Transactions of the American Fisheries Society 130: 742–749.
- Ostrand, K. G. & G. R. Wilde, 2002. Seasonal and spatial variation in a prairie stream-fish assemblage. Ecology of Freshwater Fish 11: 137–139.
- Palmer, M. W., 2002. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74: 2215–2230.
- Poff, N. L. & J. D. Allan, 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76: 606–627.
- Smith, J. B. & W. A. Hubert, 1989. Use of a tributary by fishes in a Great Plains river system. Prairie Naturalist 21: 27–38.
- Taylor, C. M., M. R. Winston & W. J. Matthews, 1993. Fish species-environment and abundance relationships in a Great Plains river system. Ecography 16: 16–23.
- Ter Braak, C. J. F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167–1179.
- Werner, E. E. & D. J. Hall, 1976. Niche shifts in sunfishes: experimental evidence and significance. Science 191: 404– 406.
- Williams, W. D., 1987. Salinization of rivers and streams: an important environmental hazard. Ambio 16: 180–185.
- Williams, W. D., 2001. Anthropogenic salinisation of inland waters. Hydrobiologia 466: 329–337.
- Willis, T. V. & J. J. Magnuson, 2000. Patterns in fish species composition across the interface between streams and lakes. Canadian Journal of Fisheries and Aquatic Sciences 57: 1042–1052.
- Woodhouse, C. A. & J. T. Overpeck, 1998. 2000 years of drought variability in the central United States. Bulletin of the American Meteorological Society 79: 2693–2714.