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Springs in time: fish fauna and habitat changes in springs over a 20-year interval

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ABSTRACT

1. Despite the range of threats to springs and the number of spring-endemic species, studies of temporal changes in the fauna of springs have rarely been reported. Changes in the fish of 22 Oklahoma (USA) springs were compared among surveys in 1981, 1982, and 2001.
2. Twenty-year assemblage differences were correlated with physical alteration of specific springs and stocking of native fish, which was made possible by past habitat changes that produced pools. Physical alteration of springs is a major ongoing threat to Oklahoma springs.
3. Variation in spring fish assemblages among the three surveys was apparently affected by fish movement in and out of springs, and the greater rain-induced connectivity between springs and streams during one year.
4. Although flow reduction is a commonly cited threat to springs, there was little evidence of flow reduction impacts in this study because Oklahoma springs may have been affected prior to 1981 and high-flow springs, which most often contain fish, were in areas with low groundwater water use.

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INTRODUCTION

Springs and their associated wetlands and brooks can be important habitats for fish, salamanders, invertebrates, vascular plants, and algae (Sweet, 1982; Aboal *et al*., 1998; Minckley and Unmack, 2000; Ashley *et al*., 2002; Fensham and Fairfax, 2003; Fensham and Price, 2004). Springs contain a diversity of generalist species (Glazier, 1991) and some springs also contain spring-specialized endemics (Hubbs, 1995, 2001; Fensham and Price, 2004).

Springs are especially susceptible to a variety of human disturbances because of their groundwater source and geographically small size. Flow from springs can be reduced by groundwater loss through extraction and affected springs may become intermittent or even dry completely. Polluted groundwater will discharge pollutants to associated spring waters (Delistraty and Yokel, 1999; Peterson *et al*., 2000). Spring habitats may be affected as sites are altered by excavation, the construction of spring houses, channelization of spring

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brooks, and damming (Matthews *et al*., 1985), and changes in local land-use can increase siltation and affect riparian shading. Fish stocking, invasion by exotic species, or habitat disturbance by large animals (e.g. cattle or feral pigs) can directly affect both spring habitats and the biota (Miller *et al*., 1989; Shepard, 1993; Fensham and Fairfax, 2003). Individual springs may be affected by more than one type of disturbance.

The combination of localized distribution of spring-specialists and human disturbance can lead to changes in the fauna of springs, including the loss or imperilment of specialists. For example, locally endemic or imperiled spring-specialist fish are known from Australia (Kodric-Brown and Brown, 1993), Europe (Persat *et al*., 1996), the USA (Peden, 1973; Hambrick and Robison, 1979; Matthews *et al*., 1985; Moyle and Williams, 1990), and Mexico (Miller *et al*., 1989).

Despite the diversity of threats to springs, there is very little information on temporal changes in spring biota, and the association of biotic changes with habitat changes in springs (Fensham and Fairfax, 2003). An exception is an extensive description of Texas springs that includes temporal patterns of discharge and notes on faunal changes in some springs (Brune, 2002). Other exceptions are a study over 30 years of changes in the macroinvertebrates of the spring-fed Doe Run Creek (Johnson *et al*., 1994) and studies tracking rare species in particular springs (the Devils Hole pupfish; Anderson and Deacon, 2001). In contrast, many faunal studies of springs have examined the distribution of the biota of springs (fish: Matthews *et al*., 1985; various invertebrate taxa: Forester, 1991; Gaskin and Bass, 2000; Orendt, 2000; Myers and Resh, 2002; Di Sabatino *et al*., 2003; Rudisill and Bass, 2005), effects of flow permanence on macroinvertebrates (Smith and Wood, 2002), and threats to springs (Shepard, 1993; Minckley and Unmack, 2000; Fensham and Fairfax, 2003).

Matthews *et al*. (1985) surveyed the fish and invertebrates in 50 Oklahoma springs (USA) in 1981 and again in 1982. This survey provided a basis for a recent survey, in which the same springs were re-visited in 2001 after an intervening period of 20 years. The objectives of this project were to document changes in the fauna of springs over time and to correlate these, where possible, with habitat or other environmental changes. Results for spring fish are presented here.

MATERIALS AND METHODS

Several of the 50 re-surveyed springs are concentrated in two areas of karst, the Arbuckle uplift in south-central Oklahoma and the Ozark Plateau in north-east Oklahoma (Figure 1). The remaining springs are widely dispersed and are associated with either smaller named non-karst aquifers or alluvial systems along major rivers.

By design, sampling methods were very similar to those of Matthews *et al*. (1985). Field work was done primarily in June and July 2001, which was consistent with the 1981/1982 study. Delays in getting landowner permission postponed sampling at four sites until as late as October. The numbering system for springs used by Matthews *et al*. (1985) was retained in this survey.

Fish were sampled using a 2 m wide, 3 mm mesh seine; fine-meshed dip nets (maximum mesh diameter 1.0 mm); and rarely by observation. Several passes with the seine were made in habitats large enough to seine. Because of the small size of most of the spring habitats, only voucher specimens were kept and most captured fish were immediately released. Thus, fish were not quantitatively sampled and fish data were limited to presence–absence information. Voucher specimens were initially preserved in formalin, and then transferred to 70% isopropanol. Collected fish were deposited in the Sam Noble Oklahoma Museum of Natural History at the University of Oklahoma.

In addition to biological sampling, habitat measurements included pH (Orion meter), water temperature, and conductivity (YSI meter). Discharge was calculated from a transect in an area with even flow and a regular cross-section, using several measurements of depth and velocity. Velocity was measured with a Marsh-McBriney meter. In the few springs with outflow through a pipe, discharge was measured as the time to fill a container of known volume. Local land-use and modifications to springs were noted.

Spring discharge was not measured in the 1981 and 1982 surveys, so direct comparison of discharge among years was not possible. Precipitation can be used as a surrogate measure of potential discharge differences among years because of the relationship between rainfall and discharge for springs (Bonacci, 1993; van der Kamp, 1995; Labat *et al*., 2002; Barfield *et al*., 2004). Indeed, rainfall has been used to estimate missing spring discharge values (Sepulveda, 2001); unfortunately, the discharge data were too scanty for such estimates. Cumulative May and June precipitation data were used as a measure of relative precipitation (and spring discharge) among years. Rainfall data were obtained from the Oklahoma Mesonet for 1981, 1982, and 2001 at four monitored sites near areas with surveyed springs: Tahlequah (Ozark Plateau sites), Tishomongo (Arbuckle sites), Norman (central Oklahoma), and Woodward (north-west Oklahoma) (Figure 1).

When possible, owners were interviewed or filled out a questionnaire about seasonal and long-term flow patterns and the perceived relationship of these patterns to rainfall, physical modifications to the springs, and land-use changes in the vicinity of springs. Similar information from 1981 and 1982 was included in the extensive field notes.

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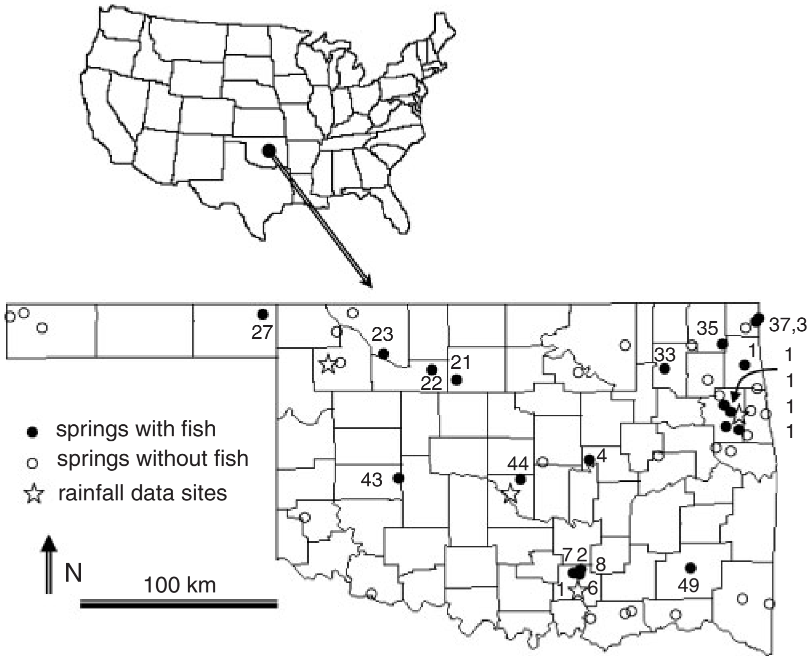

Figure 1. Location of sampled springs within Oklahoma (USA). Spring numbers are given for springs with fish. Concentrations of springs are in two karst areas, the Arbuckle Uplift in south-central Oklahoma and the Ozark Plateau in the north east, which are encircled with dotted lines. Rainfall data sites are indicated. Subdivisions within Oklahoma are counties.

RESULTS

In the three survey years, fish were found in 22 of the 50 springs (Matthews *et al*., 1985; this survey). Springs with fish were classified as karst aquifers, non-karst aquifers, or as alluvial springs (Table 1). Sampling in 2001 increased the known species richness of fish in these springs from 24 to 26, with the addition of the striped shiner *Luxilus chrysocephalus* and the redfin darter *Etheostoma whipplei*. Both added fish species probably originated from nearby streams; the springs with *L. chrysocephalus* had a sizable spring brook connecting to a stream and the spring with *E. whipplei* was located in a recently flooded floodplain of a stream.

Springs with fish had circum-neutral pH and a wide range of conductivity (Table 1). Water temperatures in 2001 were generally between 14.5 and 18.0°C. Most of the temperatures above 18.0°C were in springs discharging into pools, and the highest temperature of 29.1°C occurred in a pool of a drying stream and apparently dry spring at the site of a formerly flowing spring that was sampled in 1981 and 1982.

The presence of fish in springs was associated with both spring discharge and connectedness between springs and streams. Based on the 2001 data, the discharge of springs with fish averaged 43.6 $L\,s^{-1}$ (SE = 19.5 $L\,s^{-1}$, $n = 14$). Three

Table 1. Properties of springs with fish. Discharge is shown in Table 2

Spring	Spring type	Water temp. (°C)	pH	Conductivity ($\mu S\,cm^{-1}$)
1	karst aquifer	17.8	6.6	530
2	karst aquifer	*	*	*
6	karst aquifer	17.9	6.7	526
7	karst aquifer	21.6	6.7	572
8	karst aquifer	17.7	6.6	539
12	karst aquifer	22.5	6.8	288
16	karst aquifer	17.2	6.3	260
17	karst aquifer	15.5	6.2	135
18	karst aquifer	15.4	6.1	147
19	karst aquifer	16.0	6.5	443
21	alluvial spring	18.3	7.2	1920
22	alluvial spring	16.0	6.6	592
23	alluvial spring	17.0	7.0	420
27	non-karst aquifer	16.5	6.8	406
33	alluvial spring	29.1	6.8	315
35	karst aquifer	*	*	*
37	karst aquifer	15.6	6.5	208
38	karst aquifer	14.8	6.6	220
43	non-karst aquifer	21.0	6.9	1422
44	non-karst aquifer	14.5	5.9	213
46	alluvial spring	24.1	6.3	99
49	non-karst aquifer	20.2	7.6	652

*Indicates missing values.

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springs with discharge over $100\,\mathrm{L\,s^{-1}}$ greatly inflated this average and removal of these springs from consideration reduced the mean discharge to $9.34\,\mathrm{L\,s^{-1}}$ ($\mathrm{SE} = 4.53\,\mathrm{L\,s^{-1}}$, $n = 11$). Discharge of springs lacking fish averaged $1.8\,\mathrm{L\,s^{-1}}$ ($\mathrm{SE} = 0.7\,\mathrm{L\,s^{-1}}$, $n = 27$), which was significantly lower than the discharge of springs with fish (*t*-test: $t_{36} = 2.469$, $P = 0.018$). Most springs with fish were connected to streams; isolated springs were generally fishless. Twenty of the 22 springs with fish were connected either directly, or through spring brooks, to streams. Two springs with fish were isolated; one was excavated in a floodplain and the other was dammed. In contrast, nine of 23 springs without fish were isolated from streams.

Among-year comparisons

There was little among-year variation in the number of springs with fish and in the total number of fish species caught. Fish were found in 17 springs in 1981 and 1982, and in 18 springs in 2001. In total, 17 species of fish were recorded in 1981 and 2001, and 21 species in 1982. Three spring-specialist species occurred, the southern redbelly dace *Phoxinus erythrogaster*, the Arkansas darter *Etheostoma cragini*, and the least darter *Etheostoma microperca*. None of these three species is a strict spring endemic because they are found in larger streams with spring inputs.

In contrast to these summary counts, there was considerable variation in the among-year pattern of species' occurrences in individual springs. The total of 75 species × spring occurrences (Table 2) showed all possible present/absent patterns over the three survey years: a species present in one of the three years (a__, _b_, or __c in Table 2, where a = 1981, b = 1982, c = 2001), absent in one of the three years (_bc, a_c, or ab_), or present in all years (abc). A fish species was consistently present all years in a spring (= present/absent pattern of abc) 22 times, or 29.3% of the total species × spring occurrences. These 22 occurrences included 12 different species. Several were common stream fish that were found at multiple sites, including the central stoneroller *Campostoma anomalum*, the banded sculpin *Cottus carolinae*, and the western mosquitofish *Gambusia affinis*; and one was *P. erythrogaster*, the most widespread of the spring specialists. Other typical stream fish were found all three years in only a single spring (e.g. the red shiner *Cyprinella lutrensis*, the plains killifish *Fundulus zebrinus*, the green sunfish *Lepomis cyanellus*, and the sand shiner *Notropis stramineus*). The remaining four species were darters, including the rare spring-specialist, the Arkansas darter *E. cragini*.

Among-year differences in fish presence/absence patterns, especially year(s) with more species present or more absent than other years, were assessed by comparing the patterns of species occurrences across years (e.g. a__ versus ab_ versus abc in Table 2). The distribution of occurrences among all possible present/absent patterns was tested with chi square (Table 3, $P < 0.001$), using an even distribution among the seven possible patterns (i.e. with 75 springs × species occurrences/seven patterns = 10.6 occurrences/pattern) as the distribution expected by chance. Differences from the expected distribution highlighted the distinction between 1982 (year 'b') and the other sampled years. Differences were greatest for species present in 1982 only (_b_: more than expected); species present in 1981 and 2001 but absent in 1982 (a_c: fewer than expected); and species present in all three years (abc: more than expected; Table 3).

Rainfall was used as a surrogate for general interannual patterns of spring discharge. Indeed, many spring owners commented that their springs flowed more in rainy years and generally had increased flow after rains. Cumulative May to June precipitation across the four rainfall sites was greater in 1982 than in 1981 and 2001 (Figure 2; one-way ANOVA: $F_{2,8=}$ 4.46, $P = 0.05$). The high precipitation and higher spring discharges in 1982 correspond with the higher fish richness in that year's survey.

20-year comparisons

Differences in the occurrence of fish in 2001 compared with 1981 and 1982 were of special interest because these differences reflected potential changes over 20 years. Although the among-year pattern of occurrences did not indicate that 2001 was unique, there were 19 occurrences with disrupted patterns in 2001 (i.e. a species present only or absent only in a spring in 2001; patterns ab_ and __c in Table 2). Ten of the 19 occurrences resulted from variability in the occurrence of the three most common species of fish found in the survey: *L. cyanellus*; *G. affinis*; and *C. anomalum*, with five, three, and two occurrences, respectively. The other disrupted occurrences were distributed among seven species, including the two species collected only in 2001, *L. chrysocephalus* and *E. whipplei*.

The association between disturbance and changes in fish assemblages over the 20-year period was evaluated using comparisons of the observations and the 2001 questionnaires with 1981/1982 field notes, which included comments from owners. Several types of disturbance occurred, and these were broadly grouped into three categories: (1) fish stocking; (2) alteration of spring habitats; and (3) alteration of spring flows (Table 4).

Fish were stocked into three springs, and stocking was successful in two of these springs (Table 4). All three stocked springs had previous modifications that increased habitat area: a concrete enclosure that formed a rectangular pool at the spring source, submerged 208 L metal (55 gallon) drums in upwelling areas, and a pond formed by an earthen levy

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Table 2. Summary of fish occurrences in springs in the 1981, 1982, and 2001 surveys[a]. Presence in particular years is indicated by: a = 1981, b = 1982, c = 2001; _ = absent

			Spring								
			1	2	6[b]	7	8	12	16	17	18
Cyprinidae	*Campostoma anomalum*	Central stoneroller	a_c	abc	_bc		_b_				
Cyprinidae	*Cyprinella lutrensis*	Red shiner									
Cyprinidae	*Luxilus cardinalis*	Cardinal shiner									
Cyprinidae	*Luxilus chrysocephalus*	Striped shiner			__c						
Cyprinidae	*Notemigonus crysoleucas*	Golden shiner									
Cyprinidae	*Notropis stramineus*	Sand shiner									
Cyprinidae	*Phoxinus erythrogaster*	Southern redbelly dace	abc		abc	__c		_b_	a__		
Cyprinidae	*Pimephales promelas*	Fathead minnow									
Cyprinidae	*Semotilus atromaculatus*	Creek chub						_b_			
Ictaluridae	*Ameiurus melas*	Black bullhead									
Ictaluridae	*Ameiurus natalis*	Yellow bullhead									
Poeciliidae	*Gambusia affinis*	Western mosquitofish	abc	abc	_b_	a_c	_bc	ab_			
Atherinidae	*Labidesthes sicculus*	Brook silverside						_b_			
Fundulidae	*Fundulus notatus*	Blackstripe topminnow						_b_			
Fundulidae	*Fundulus zebrinus*	Plains killifish									
Centrarchidae	*Lepomis cyanellus*	Green sunfish	__c	_b_	_b_			ab_			__c
Centrarchidae	*Lepomis humilus*	Orangespotted sunfish									
Centrarchidae	*Lepomis macrochirus*	Bluegill						_b_			
Centrarchidae	*Lepomis megalotis*	Longear sunfish									
Centrarchidae	*L. cyanellus x macrochirus*	hybrid sunfish			_b_						
Centrarchidae	*Micropterus salmoides*	Largemouth bass									
Percidae	*Etheostoma cragini*	Arkansas darter									
Percidae	*Etheostoma microperca*	Least darter	abc			abc	_b_				
Percidae	*Etheostoma radiosum*	Orangebelly darter									
Percidae	*Etheostoma spectabile*	Orangethroat darter	abc	abc	abc	_bc		_b_		abc	
Percidae	*Etheostoma whipplei*	Redfin darter									
Cottidae	*Cottus carolinae*	Banded sculpin						__c			
number of species/spring			6	4	7	4	3	9	1	1	1
2001 discharge (L sec^{-1})			7.2	NA	136.2	29.0	136.0	NA	12.8	1.9	1.7

	Spring													
	19	21	22	23	27	33	35	37	38	43	44	46	49	#of springs
Central stoneroller			__c			_b_	ab_						abc	8
Red shiner		ab_	abc							__c				3
Cardinal shiner								_b_						1
Striped shiner														1
Golden shiner		_b_												1
Sand shiner			abc											1
Southern redbelly dace	abc							_b_						7
Fathead minnow		ab_				_b_				__c				3
Creek chub														1
Black bullhead		_b_												1
Yellow bullhead		a__												1
Western mosquitofish					__c		abc				a__	ab_		10
Brook silverside														1
Blackstripe topminnow														1
Plains killifish		a__	abc											2

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Table 2. *continued*

	Spring													
	19	21	22	23	27	33	35	37	38	43	44	46	49	#of springs
Green sunfish		ab_	_b_	__c								abc	_bc	10
Orangespotted sunfish		a__												1
Bluegill														1
Longear sunfish		ab_	_b_							_bc				3
hybrid sunfish														1
Largemouth bass				a_c										1
Arkansas darter							abc							1
Least darter														3
Orangebelly darter													abc	1
Orangethroat darter							_bc							7
Redfin darter												__c		1
Banded sculpin								abc	abc					3
# of species/spring	1	9	6	2	1	2	4	3	1	3	1	3	3	total = 75
2001 discharge (L sec^{-1})	1.8	1.1	2.6	4.3	9.7	0.0	0.2	46.9	236.1	NA	0.4	0.1	0.0	

[a] Data for 1981 and 1982 are from Matthews *et al*., 1985.
[b] In 1981, *C. anomalum* and *G. affinis* were found 1 mo after the initial survey; site was surveyed 2x in 2001 (no fish were found in the 1st survey).

Table 3. Patterns of species occurrence among sampling years. a = present in 1981, b = present in 1982, c = present in 2001, _ = absent in the corresponding year. The expected value assumed equal likelihood of each occurrence pattern

Occurrence pattern	Expected	Observed
a__	10.6	5
ab_	10.6	8
abc	10.6	22
_b_	10.6	20
_bc	10.6	6
__c	10.6	11
a_c	10.6	3

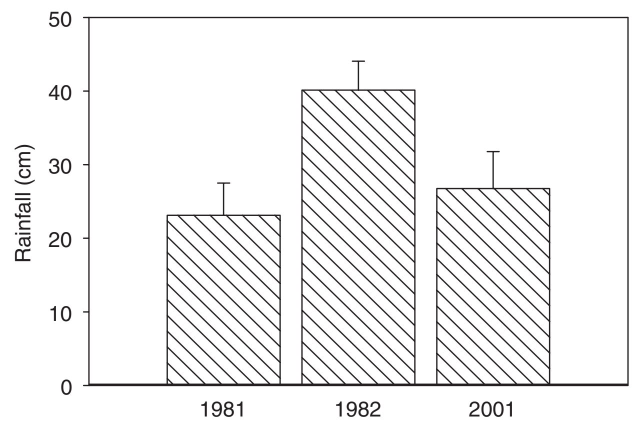

Figure 2. Mean (+1 SE) May and June rainfall recorded at four sites during each of the three survey years. Sites are listed in the text and the relative locations of rainfall and survey sites are shown in Figure 1.

blocking the spring brook. Stocked species were native to the area, but were not present in the springs prior to stocking. The small southern redbelly dace did not persist and may have escaped through the spring brook into the receiving stream, whereas the larger green sunfish and largemouth bass were confined to pools by the low flow of the respective spring brooks.

Between 1982 and 2001, major habitat alteration occurred at three springs and affected the fish in two of these (Table 4). A spring-brook pool and its fish were lost when the pool was drained and incorporated into the adjacent crop field. In contrast to this pool loss, damming of a temporary stream with a spring in its channel inundated the spring and formed a 600 m + long linear reservoir. Fish diversity increased with water permanence and increased habitat size and heterogeneity. A third alteration, the construction of a dam with culverts across a large spring, had no apparent effect on the composition of the fish assemblage.

Changing flows affected fish assemblages in three springs. Cessation of flow occurred in only one spring with fish. Spring

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Table 4. Summary of disturbances to 22 fish-containing springs between 1981 and 2001

Disturbance	Spring number	History	Species affected	Biodiversity effects
Fish stocking	16	concrete pool stocked in 1981; no fish in later surveys	Southern redbelly dace	species not established
Fish stocking	23	stocked in pond; present in 1981 and 2001	largemouth bass	species established*
Fish stocking	23	stocked in spring brook pond; present in 2001	green sunfish	species established
Fish stocking	18	stocked in two submerged 55 gallon drums; present in 2001	green sunfish	species established (2 individuals)
Draining	21	after 1982: field regraded and spring brook pool drained	several species	loss of fish
Submersion	43	inundated by a small reservoir between 1982 and 2001	several species	increased fish diversity
Construction	2	spring pool bisected by a dam with culverts	None	no measured effect
Loss of flow	33	flow from a pipe in 1982; a wet meadow by 2001	central stoneroller, flathead minnow	loss of all fish
Flooding	12	excavated spring in stream floodplain	several species	variable composition; 'stocked' by floods
Flushing flow	6	infrequently dammed and rapidly drained	up to 7 species	temporary reduction in fish diversity

*Temporarily lost by dam breakage in 1982.

flow at Spring 33 provided a refuge pool for fish in the adjacent temporary stream during the 1981 and 1982 surveys, but only a wet meadow and a couple of small warm fishless pools in the stream bed remained in 2001 (this was the pool with the highest recorded temperature). Variation in flow temporarily affected fish assemblages in one spring when the deep concrete swimming pool surrounding the spring was occasionally filled and rapidly emptied by the land owners. The resulting flush temporally removed all fish in the spring and adjacent brook. Storm-induced floods apparently inundated a spring located in the gravel floodplain of a flood-prone stream, and introduced stream fish. Excavation of this spring provided an expanded pool habitat.

DISCUSSION

Oklahoma is ecologically diverse and, consequently, there is geographical variation in the composition of fish assemblages across the state (Miller and Robison, 2004). This variation was reflected in the fish assemblages of the sampled springs. Twenty-six fish species were found in this spring survey; a more recent survey of 50 additional springs added only one species, the slough darter *Etheostoma gracile* (Bergey, unpublished). The 27 species amounts to 15% of the 176 fish species listed for the state (Miller and Robison, 2004). All species that were found in springs are native to Oklahoma and occurred within their usual ranges. Two of the species are used as bait (the golden shiner *Notemigonus crysoleucas* and the fathead minnow *Pimephales promelas*) and two are game species (the bluegill *Lepomis macrochirus* and the largemouth bass *Micropterus salmoides*), and it is possible that these species may have been locally stocked into some springs prior to the earliest survey in 1981. Although most of the spring fish are generalists that commonly occur in streams, three species are spring-associates: the southern redbelly dace *P. erythrogaster*; the least darter *E. microperca*; and the Arkansas darter *E. cragini*. The southern redbelly dace and the least darter have a conservation status of Secure (G5; NatureServe, 2006), although regional declines have been noted in some least darter populations (in Arkansas by Hargrave and Johnson, 2003). The Arkansas darter has a conservation status of Vulnerable (G3; NatureServe, 2006) and is a candidate for US Fish and Wildlife Service listing as threatened or endangered, primarily because of declines caused by the loss of spring habitats.

Several factors can influence year-to-year variation in assemblage composition in springs. Likely factors affecting these springs are variation in discharge, survey timing, and human disturbance at individual springs. The higher precipitation in 1982 than in 1981 and 2001 indicates higher spring discharge in 1982 and was associated with the highest yearly species richness. Springs with higher discharge have greater habitat area (Hubbs, 1995) and typically have higher fish abundance, and sometimes diversity, than springs with smaller discharge and area, partly because of greater habitat heterogeneity and greater diversity of resources in larger habitats (Kodric-Brown and Brown, 1993). Higher discharge also facilitates the movement of fish between streams and springs, via spring brooks and by overland flooding of isolated springs. Most Oklahoma springs containing fish are connected to streams directly or by spring brooks, which are conduits for fish dispersal. Probable mechanisms of the high species richness of the springs in 1982 were a combination of a temporary increase in habitat size and higher connectivity of

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springs with streams. An alternative explanation, that procedural differences caused the 1982 rise in richness, is not likely because the same field team, using the same procedures, sampled in 1981 and 1982.

The consequences of survey timing include the effects of year-to-year variation in rainfall-associated discharge discussed above and stochastic conditions, particularly the presence or absence of fish in springs at the time of sampling for species that move between springs and streams. Because fish are vagile, single collections of fish in springs may miss species that are not permanent residents of the individual springs. Support for this stochastic effect is the high frequency of common, widespread species (i.e. the green sunfish *L. cyanellus*, the western mosquitofish *G. affinis*, and the central stoneroller *C. anomalum*) among the fish that were either absent in one year or present in only one year in individual springs.

Matthews *et al*. (1985) found that almost one-half of the springs in the 50-spring survey had been physically modified before 1981 and identified future human disturbance as a concern for the springs. This concern was well founded. Between 1981 and 2001, further disturbance affected at least five (or 23%) of the 22 springs with fish. Fish populations were altered in four of the five springs affected, including complete faunal loss in two springs.

Disturbances included fish stocking, habitat alteration, and loss of spring flow. All fish-stocked sites had pre-1981 modifications that increased habitat area by forming pools in springs which might otherwise be too small to support fish (Kodric-Brown and Brown, 1993). Although these introductions were of native fish into fishless springs, they may have had an impact on invertebrate assemblages. Deliberate introductions and invasions by exotic fish have imperiled or extirpated fish and invertebrates from springs and are a continuing threat to the conservation of rare spring-dwelling endemics (Ponder, 1986; Persat *et al*., 1996).

Habitat alteration is an ongoing disturbance for springs in the area, and has taken a number of forms. Although only three springs with fish were modified in the last 20 years, many of the smaller fishless springs were affected. Recent changes among the larger pool of 50 springs include submersion of a spring by damming a stream, loss of spring pools by draining or leaks in above-ground tanks, enlargement of the spring pool, construction of a dam with culverts across a pool, use as a dump site, road construction over a spring, and various land-use changes including conversions from livestock pasture to yard and from pasture to a cattle-holding pen. Despite the number and range of modifications, effects on fish were minor; the only loss of fish from a spring resulted from draining a constructed spring-associated pool.

Reduction in spring discharge, including complete spring drying, has affected springs worldwide, often because of groundwater abstraction for irrigation (Brune, 2002) or, in Australia, watering livestock (Fensham and Fairfax, 2003). In this survey, springs with fish have been little affected by spring drying over the last 20 years. The single spring that ceased flowing emerged through a pipe and it is not known whether the loss in surface flow resulted from a change in the groundwater levels or simple removal of the pipe. Anthropogenically influenced flow reductions in some of these springs prior to 1981 are likely (Matthews *et al*., 1985).

Natural fish populations may occur in springs with a discharge above particular thresholds (Kodric-Brown and Brown, 1993). Consequently, in this survey the smaller springs contained only invertebrates. In Oklahoma, most of the larger springs and hence most of the springs with fish were associated with the Arbuckle–Simpson and Ozark Plateau aquifers. These two aquifers are substantial and have low groundwater use, primarily because they are little used for irrigation (Tortorelli, 2004; Bingham, 1969). Although threats from groundwater abstraction for irrigation are unlikely for the surveyed springs, groundwater levels in the Simpson–Arbuckle are threatened by a scheme for the large-scale sale of groundwater for distant urban use, which has the potential to reduce the flow of regional springs.

In conclusion, springs in the south-central USA continue to be affected by human activities. Habitat alteration is a major regional threat and can both directly affect spring fish and indirectly make spring habitats more conducive to the establishment of stocked or invasive species. Although most of the spring-dwelling fish in the area studied are widespread generalists, the high number of human alterations in spring habitats suggests that unprotected springs in other areas may be similarly threatened.

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