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Fish habitat associations in a spatially variable desert stream

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White sands pupfish *Cyprinodon tularosa* were sampled with minnow traps along the length of Lost River, a highly variable desert stream in New Mexico, to evaluate if their abundance, median standard length (L_S) and sex ratio values differed by microhabitat variables. Habitat measurements were made in a 4 m^2 area around the minnow trap. White Sands pupfish populations were primarily structured by L_S. As specific conductance and surface area increased, median size of fish decreased. Shallow areas with higher specific conductance were correlated with an increased number of fish.

Key words: *Cyprinodon tularosa*; fish length; habitat; pupfish; salinity; specific conductance.

INTRODUCTION

Organisms have varying abilities to tolerate abiotic conditions; consequently, abiotic factors can be a major determinant of biodiversity. Salinity and temperature are two factors that can influence community composition (Dunson & Travis, 1991; Lopes, 1994; Leland & Fend, 1998; Maes *et al*., 1998). High salinity and temperatures along with high variance in those factors are common features of many desert aquatic systems (Miller, 1981). Despite the severe conditions of desert aquatic systems and generally low biodiversity, primary productivity can be high (Cole, 1994). Organisms able to tolerate high salinity and temperatures can exploit habitats that are not available to less tolerant species (Bayly, 1972; Herbst, 2001). This paper investigates the habitat associations of a highly tolerant desert fish.

Pupfishes (*Cyprinodon* sp.) occur in isolated springs and streams throughout the south-western deserts of North America (Turner & Liu, 1977). Pupfishes are well known for their tolerances to environmental extremes (Brown & Feldmeth, 1971), occurring in habitats that often have unusually high temperatures

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(>40° C) and salinities (up to four times sea water) (Miller, 1948; Barlow, 1958; Bennett & Beitinger, 1997; Beitinger *et al*., 2000). Tolerances to high salinity allow pupfishes to occur in systems where they would be potentially excluded due to their poor competitive abilities. In mixed communities, pupfishes are often found only in areas of high salinity (Echelle *et al*., 1972; Martin, 1972; Kodric-Brown & Mazzolini, 1992).

In the absence of interspecific competition pupfishes are not restricted to marginal habitats. Variation in habitat or environmental factors, however, may result in spatial differences in pupfish population structure. Many desert systems containing pupfishes can have considerable spatial variation in salinity and temperature (Miller, 1948; Stockwell & Mulvey, 1998). Previous research has shown that pupfishes have an optimum temperature and salinity for growth and reproduction (Kinne, 1960; Gerking *et al*., 1979). Optimum conditions for pupfishes, however, may not be static (Kinne, 1960). Ontogenetic shifts in habitat use may be related to behaviours such as foraging (Nowak *et al*., 2004), predator avoidance (Dahlgren & Eggleston, 2000) and reproduction (Gerking *et al*., 1979). These behavioural choices can lead to population structuring (*e.g.* size or sex segregation) among habitats (Lomnicki, 1988).

Larger fishes generally attain greater reproductive success in territorial species such as pupfishes (Kodric-Brown, 1977, 1981; Loiselle, 1982; Ludlow *et al*., 2001). Larger individuals may exclude smaller fishes from optimum reproductive habitats (Kodric-Brown & Mazzolini, 1992). Territorial male pupfishes may also exclude females from breeding areas if females are not receptive to breeding (Barlow, 1961). Size structuring of populations can also occur as a result of predator avoidance (Dahlgren & Eggleston, 2000). Larger and more visible fishes may avoid shallow habitats to reduce the probability of predation by piscivorous birds (Steinmetz *et al*., 2003).

In spatially variable systems common to pupfish habitats, pupfish population structure, such as density, sex ratio and size, would be expected to correspond to certain habitat characteristics. The White Sands pupfish *Cyprinodon tularosa* Miller & Echelle occurs in spatially variable habits and can tolerate a wide range of salinities and temperatures (Stockwell & Mulvey, 1998; Rogowski, 2004). Previous work has shown an apparent correlation between size and salinity within White Sands pupfish systems (Rogowski, 2004). In this study the relationship between White Sands pupfish size and salinity was explored. Fish were sampled from a variety of habitats throughout an isolated desert stream to determine if fish size, sex ratio and abundance were associated with salinity, temperature, water volume, depth and other habitat variables.

MATERIALS AND METHODS

STUDY AREA

The White Sands pupfish is endemic to the Tularosa Basin of south-central New Mexico (Miller & Echelle, 1975). The White Sands pupfish can be found in salinities ranging from a low of 2·1 (3·2 mS cm^{-1}) to salinities three times that of sea water (*c.* 120 mS cm^{-1}) depending on the aquatic system (Rogowski, 2004). Two of the systems are saline riverine systems (Salt Creek and Lost River) where salinity fluctuates spatially and temporally (13 to *c.* 120 mS cm^{-1}) (Rogowski, 2004). Despite this wide variation in salinity, White Sands pupfish occur throughout both systems.

Lost River (Fig. 1) provides an ideal natural setting to investigate whether White Sands pupfish size or density is correlated with salinity and temperature. In Lost River salinity varies temporally and spatially, from a low of 15·9 to >88 (specific conductance ranges from 26·2 to 119·9 mS cm^{-1}). White Sands pupfish are the only aquatic vertebrate found within the river, and appear to be restricted only by the availability of water. Macroparasites (trematodes) do not occur in the system apparently because secondary gastropod hosts are excluded by the high salinity (Rogowski, 2004). High salinity also precludes the existence of large invertebrates, such as dragonfly larvae, dytiscids and belostomatids, which might prey upon White Sands pupfish. These invertebrates are present in habitats of lower salinity within the Tularosa Basin. Thus, the only predators of White Sands pupfish are probably piscivorous birds such as the great blue heron *Ardea herodias* (pers. obs.).

SAMPLING

Sample sites were established in 30 areas within Lost Creek over a 1 month period beginning on 6 July 2001. Temperature, salinity and variances in these metrics appear to be higher during this time of year (Rogowski, 2004). Small isolated pools were not sampled in this study. Areas were only sampled if there were at least 10 m of linear aquatic habitat and a water depth of at least 14 cm. Lost River was divided into four sections that at times of low flow are separated by dry streambeds, playas and road crossings. The sections are referred to as the upper, middle, mid-lower and lower sections with samples sizes of six, eight, four and 12, respectively (Fig. 1). The upper section is

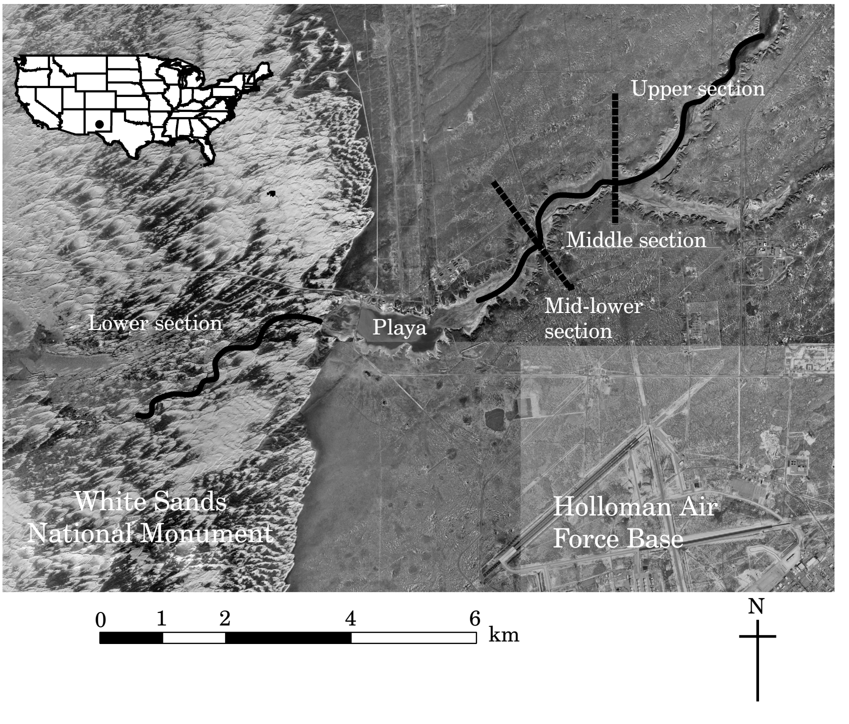

FIG. 1. Lost River, orthophotograph taken 4 January 2003, courtesy of the United States Geological Survey. The inset shows the relative location of Lost River in New Mexico, U.S.A.

characterized by a couple of small (<2 m diameter) spring fed pools (at Malone Draw) where water is apparently permanent. The middle section begins at a bluff and continues downstream to a road crossing. The road crossing delineates the upper end of the mid-lower section that terminates in a large playa. The section below the playa constitutes the lower section of Lost River.

Unbaited wire minnow traps (3 mm mesh) were used to sample fish. Traps were deployed for a minimum of 2 h. A 2×2 m square frame constructed of PVC pipe was situated over the river so that the minnow trap was at the centre. The width of Lost River was generally smaller than the width of the measuring frame. A scale drawing of the habitat enclosed within the 4 m^2 frame was made to estimate water surface area. Water depth was measured on a grid defined by the 4 m^2 sample site (at 0·5 m increments) to calculate a volume of water for the sample site. Temperature, specific conductance and salinity were measured with a portable instrument (Yellow Springs Instrument-YSI 85®).

Fish captured were sexed and measured for standard length (L_S, nearest mm). If <*c*. 150 fish were captured, all individuals were sexed and measured; otherwise, a random sub-set consisting of at least 150 fish was sexed and measured.

STATISTICAL ANALYSES

A polynomial redundancy analysis (pRDA) was used to determine if habitat variables could account for the number and size of White Sands pupfish present, as well as any potential differences between sexes. Fish number was used as a metric instead of fish density as density is dependent on volumetric measurements. The inclusion of density as response variable would have resulted in an inflated correlation with the predictor habitat measurements of surface area and volume. Fish density and size were investigated using regressions. The pRDA was conducted using polynomial RdaCca (Makarenkov & Legendre, 2001, 2002). Polynomial RDA is similar to a traditional RDA, but a polynomial function is used instead of a linear function. A polynomial function generally explains a greater amount of variation in biological data than linear functions (Makarenkov & Legendre, 2001, 2002). Polynomial RDA was used to investigate the relationship of L_S, sex and fish number to habitat measurements. There was no difference in median L_S of fish between males and females (Wilcoxon rank sum test, two-sample test, normal approximation $Z = 0·82317$, $P = 0·4104$), thus sexes were combined for the pRDA analysis. To determine if there was a difference in habitat preference based on sex, the percentage of female fish was included as a variable in the pRDA. The response matrix (Y) was composed of fish variables (fish number, median L_S and per cent female) with the explanatory matrix (X) composed of environmental variables (habitat measurements). Binary variables representing each of the stream sections were included in the explanatory matrix. In pRDA, variance in the response matrix is constrained by the environmental variables (explanatory). The response and explanatory variables were $\log_{10}(x + 1)$ transformed prior to analysis with the exception of the binary variables and the surface area to volume ratio variable (arcsine transformed).

A second pRDA was conducted specifically on sites from the lower section of Lost River to determine if there were any White Sands pupfish habitat associations on a smaller scale. The lower section is separated from the upstream sites by a relatively large playa. For most of the year fish movement is restricted by the dry playa.

RESULTS

Specific conductance ranged from 44–118 mS cm^{-1}, with temperatures ranging from 24–35° C. A summary of the habitat measurements is listed in Table I. Significantly more females were collected than males (Wilcoxon rank sum test, two-sample test, normal approximation $Z = -3·737$, $P = 0·0002$). In the pRDA, 88·62% of the variance in the response matrix White Sands (pupfish variables) was explained by habitat measurements (Table II). The percentage of

TABLE I. Range of site values for White Sands pupfish and habitat measurements in Lost River by area; sample sizes are in parentheses

	Upper (6)		Middle (8)		Mid-lower (4)		Lower (12)	
Measurements	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
White Sands pupfish variables								
Median L_S (mm)	24	31	18	29	26	34	33	42
Female (%)	50	100	50	96	26	91	54	84
Fish number per trap	1	340	16	723	90	840	27	291
Habitat variables								
Surface area (m^2)	1·67	4·0	2·55	3·81	2·36	3·50	0·90	1·86
Specific conductance (mS cm^{-1})	50·0	103·5	86·1	118·5	75·9	77·6	43·8	67·9
Temperature (° C)	25·1	29·8	29·8	35·9	27·4	31·1	24·2	31·5
Volume (m^3)	0·0069	0·0092	0·0019	0·0064	0·0021	0·0073	0·0026	0·0079
Surface area: volume	0·023	0·048	0·059	0·15	0·048	0·13	0·019	0·062
Maximum depth (cm)	30·0	72·0	20·0	44·8	17·0	35·0	18·0	46·0

L_S, Standard length.

TABLE II. Summary of a polynomial RDA of White Sands pupfish from Lost River

	Axis 1	Axis 2
Canonical eigenvalues	1·747	0·0572
Total variance of canonical axes (%)	85·547	2·803
Cumulative % of total variance	85·547	88·349
Cumulative % of canonical variance	96·531	99·694
White Sands pupfish response variables (normalized eigenvectors)		
Fish number	−1·3203*	−0·01045
Median L_S	0·05898	−0·2378*
Per cent female	0·0098	0·02391
Habitat variables (biplot scores)		
Volume	0·3923*	0·4205*
Surface area to volume ratio	−0·5472*	0·4378*
Specific conductance	−0·5147*	0·7075*
Maximum depth	0·4592*	0·2952*
Temperature	−0·2757*	0·4868*
Surface area	−0·4356*	0·6343*
Upper section[a]	1·1072	0·9209
Middle section[a]	−0·7537	0·9422
Mid-low section[a]	0·1692	−1·0054
Lower section[a]	−0·6610	−0·2496

[a]Binary variables, with values representing the centroid.
*Variables are significant at $\alpha = 0{\cdot}05$ (excluding binary variables).

variance in the response variables explained by the habitat variables was statistically significant. A permutation test provided in the programme, polynomial RDACCA, revealed a probability of 0·005 that the observed variance occurred by chance (999 permutations). A biplot of the results is presented in Fig. 2. Habitat variables explained a greater portion of the variance in fish number, than median L_S, based on their eigenvectors (−1·32 and 0·059, respectively). Of the habitat variables, specific conductance had the largest relative biplot score and thus explained a greater portion of the variance in the two response variables (fish number and median L_S). Habitat variables explained little of the variance in the percentage of females, indicating that there is no difference in habitat associations between male and female White Sands pupfish.

The number of fish was moderately and positively correlated with surface area to volume ratio, surface area and specific conductance. Fish number was negatively correlated with maximum depth and volume. The number of fish (per site) was not related to median L_S, however, a regression of median L_S and $\log_{10}$ fish density (fish number per volume) revealed a negative relationship (adjusted $r^2 = 0{\cdot}2075$, $F_{1,28}$, $P = 0{\cdot}0066$), while a regression of $\log_{10}$ fish density and $\log_{10}$ specific conductance revealed a positive relationship (adjusted $r^2 = 0{\cdot}2818$, $F_{1,28}$, $P = 0{\cdot}0015$). At the river section level the relationship between $\log_{10}$ fish density and L_S was positive for the middle section and negative for the mid-lower section (adjusted $r^2 = 0{\cdot}5918$, $F_{1,6}$, $P = 0{\cdot}0256$; adjusted $r^2 = 0{\cdot}9567$, $F_{1,2}$, $P = 0{\cdot}0145$, respectively).

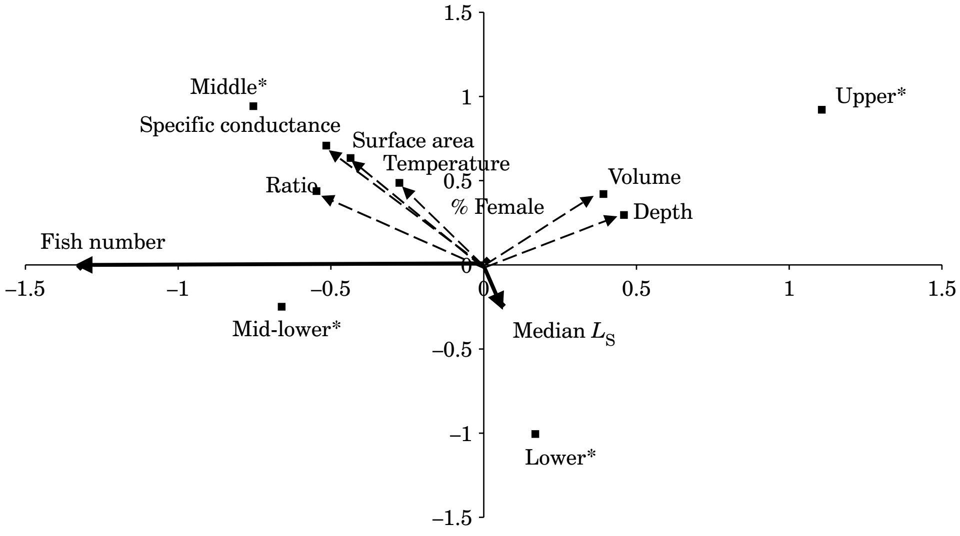

FIG. 2. A biplot based on a polynomial redundancy analysis of White Sands pupfish number, median standard length, per cent females and habitat measurements. ⟶, Biplot scores of response; – – →, biplot scores of habitat variables. ■, River sections (binary variables*) indicating the centroid for a particular river section and have no associated arrows. 'Ratio', the ratio of surface water area to water volume. The biplot score for % females was too small to represent with an arrow at this scale.

Centroids representing each of the four sections of Lost River were located in four separate quadrants in the biplot, indicating that each section had distinct characteristics (Fig. 2). Sites in the upper section of Lost River were characterized by having a greater volume of water and maximum depth, while the mid-lower section had the opposite characteristics. The middle section of Lost River was typified by having higher specific conductance, greater surface area and higher temperatures than the other sections. The lower section was associated with lower salinity, surface area and temperature.

The pRDA of the lower section of Lost River was not significant (4999 permutations; $P = 0{\cdot}0906$). Restricting the pRDA to two response variables (number of fish and median L_S) and three explanatory variables (volume, ratio and specific conductance) did not improve the model ($P = 0{\cdot}544$).

A regression was conducted to examine the relationship between specific conductance and L_S. In this regression, median L_S of female and male fish were pooled together. There was a significant negative correlation between White Sands pupfish L_S and $\log_{10}$ specific conductance (adjusted $r^2 = 0{\cdot}615$, $F_{1,29}$, $P < 0{\cdot}0001$; Fig. 3).

DISCUSSION

This study was conducted to determine if White Sands pupfish population structure in Lost River was related to habitat measurements, with particular reference to salinity. Fish populations were primarily structured by size and density, with no indication of segregation by sex. Larger fish were found in

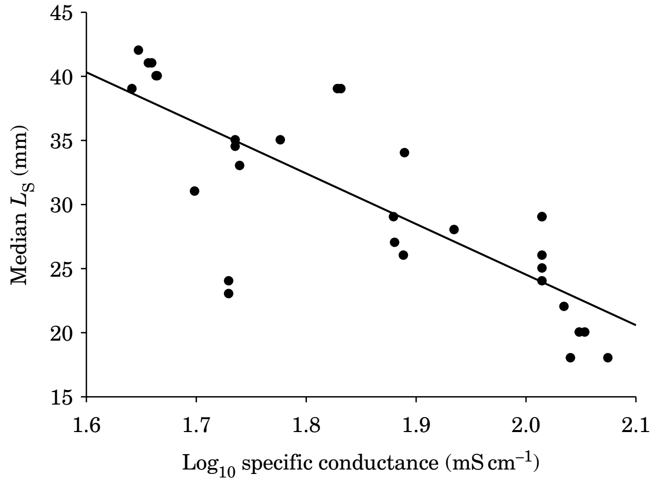

FIG. 3. Bivariate fit of median standard length of White Sands pupfish and specific conductance (log_{10} transformed). The curve was fitted by $y = 103{\cdot}4601–39{\cdot}466109x$.

areas of lower salinity. Surprisingly, more fish were found in areas of high salinity, high temperature, shallow water and low volume. There was no association with White Sands pupfish L_S and water depth, suggesting that larger fish were not selecting deeper areas to avoid avian predators.

The negative relationship observed between fish density and L_S suggests a density dependent effect. Pupfishes are known to emigrate (McMahon & Tash, 1988), and it is possible that pupfish populations maybe self-thinning due to intraspecific competition as shown in steelhead trout O*ncorhynchus mykiss* (Walbaum) (Keeley, 2003). It is unknown whether the apparent density dependent relationship is a result of competition for breeding territories, food resources or a combination of the two processes.

In pupfishes, ontogenetic shifts in salinity tolerance could lead to differences in habitat associations. In *Cyprinodon macularius* Barlow & Girard, growth is dependent on the interactions of age, temperature and salinity (Kinne, 1960). Energy conversion and growth in older fish were greater in lower salinities and temperatures, compared to juvenile fish. In addition, Kinne (1960) found that older fish also have a reduced ability to adjust to changes in salinity. Thus, lower salinity and temperature observed in the lower section of Lost River might be more optimal for White Sands pupfish growth than other sections, resulting in greater fish L_S for older individuals.

Larger pupfishes might also be associated with low salinity areas for reasons related to reproduction and fitness. Most pupfishes are territorial breeders with males defending territories (Kodric-Brown, 1977, 1981). An important factor in maintaining territories is male size. Larger males are more successful at defending territories (Kodric-Brown, 1977, 1978). Female twoline pupfish C*yprinodon bifasciatus* Miller prefer larger males (Ludlow *et al.*, 2001), and in *C. macularius*, males prefer larger females (Loiselle, 1982). As a consequence of increased breeding success of larger pupfishes and a preference for larger mates, it could be infered that areas containing larger fishes should be preferred pupfish habitat (Kodric-Brown, 1977, 1978, 1981).

Water permanence might also account for the correlation between larger White Sands pupfish and low salinity. Low specific conductance (salinity) might be indicative of greater groundwater influx and of more permanent water. Larger fishes are generally older fishes (Moyle & Cech, 2000) and the probability of survival is likely to be greater in areas where water is more permanent. The relationship between water permanence and longevity could account for the larger size of fish found in the lower section. Previous work has revealed that White Sands pupfish from the lower section tended to be older than fish collected from the middle or upper section (Rogowski, 2004). If the lower section is preferred habitat as a result of low salinity, however, then the absence of juvenile fish suggests that they are being excluded from the area, probably as a result of the territoriality of larger White Sands pupfish.

The method of sampling was biased towards larger fish. Due to the mesh-size, traps were not effective in capturing fish <18 mm. Small White Sands pupfish appeared to be more numerous in shallower areas, where it was not possible to sample adequately. It is likely that temperatures and salinity were even greater in shallow water. If shallow areas could have been sampled, there would probably be an even greater association of L_S with temperature and salinity.

Although river sections are not continuous, except during or after periods of precipitation, sections were not expected to be so well differentiated in the analysis. A more gradual gradient of habitat differences among river sections was expected, as Lost River is a fairly small system (14–20 km). It is possible that the habitat associations observed had an underlying association that was not related to the measured variables. There is, however, probably a strong negative relationship between salinity and L_S, as observed in the three White Sands pupfish systems (Lost River, Salt Creek and Malpais Springs) that have variable salinity (Rogowski, 2004).

In mixed communities pupfishes are often relegated to high salinity areas (Echelle *et al*., 1972; Martin, 1972; Kodric-Brown & Mazzolini, 1992). In a system without interspecific competition pupfishes still show signs of habitat segregation. This study provides evidence of ontogenic changes in White Sands pupfish habitat use, with smaller and presumably younger fish associated with shallower and more saline water. It is not known if juvenile fish prefer shallow or high salinity areas, or if it is a result of exclusion by larger territorial fish occupying low salinity habitats. This difference in habitat associations can have important conservation implications.

Most pupfishes are threatened and endangered (Williams, *et al*., 1985), with many conservation plans calling for translocations as a means of increasing the security of these threatened fishes. If there are truly differences in habitat use between adult and juvenile pupfishes, ignoring ontogenic habitat differences may compromise population viability and recovery efforts.

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