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Relation of desert pupfish abundance to selected environmental variables in natural and manmade habitats in the Salton Sea basin

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Synopsis

We assessed the relation between abundance of desert pupfish, *Cyprinodon macularius*, and selected biological and physicochemical variables in natural and manmade habitats within the Salton Sea Basin. Field sampling in a natural tributary, Salt Creek, and three agricultural drains captured eight species including pupfish (1.1% of the total catch), the only native species encountered. According to Bray–Curtis resemblance functions, fish species assemblages differed mostly between Salt Creek and the drains (i.e., the three drains had relatively similar species assemblages). Pupfish numbers and environmental variables varied among sites and sample periods. Canonical correlation showed that pupfish abundance was positively correlated with abundance of western mosquitofish, *Gambusia affinis*, and negatively correlated with abundance of porthole livebearers, *Poeciliopsis gracilis*, tilapias (*Sarotherodon mossambica* and *Tilapia zillii*), longjaw mudsuckers, *Gillichthys mirabilis*, and mollies (*Poecilia latipinna* and *Poecilia mexicana*). In addition, pupfish abundance was positively correlated with cover, pH, and salinity, and negatively correlated with sediment factor (a measure of sediment grain size) and dissolved oxygen. Pupfish abundance was generally highest in habitats where water quality extremes (especially high pH and salinity, and low dissolved oxygen) seemingly limited the occurrence of nonnative fishes. This study also documented evidence of predation by mudsuckers on pupfish. These findings support the contention of many resource managers that pupfish populations are adversely influenced by ecological interactions with nonnative fishes.

Introduction

The desert pupfish, *Cyprinodon macularius*, has decreased considerably in abundance over the past several decades, culminating in its listing by the federal government as an endangered species (USFWS 1986). Pupfish originally inhabited the lower Colorado and Gila rivers in Arizona and Baja California, the Salton Sea and its tributaries in California, and the Sonoyta River in northern Sonora, Mexico (Moyle 2002). Today, the last remaining natural habitats of this species include San Sebastian Marsh and San Felipe Creek on the southwestern edge of the Salton Sea, and Salt Creek on the northern shore (Steinhart[1]). Transplanted stocks of pupfish also inhabit ponds at Palm Canyon, the Anza-Borrego Desert State Park, the Living Desert Museum in Palm Desert, the Coachella Valley Preserve, and Oasis Springs near the Salton Sea.[1] In addition, field surveys by the California Department of Fish and Game have uncovered many heretofore undocumented

[1] Steinhart, P. 1990. California's wild heritage; threatened and endangered animals in the Golden State. California Department Fish Game, Sacramento, CA.

populations of pupfish in irrigation canals and drains flowing to the Salton Sea (Lau & Boehm[2], Sharon Keeney, California Department Fish and Game, personal communication).

The decline of desert pupfish populations has been attributed to loss of habitat and unfavorable changes in environmental conditions caused mostly by construction and operation of dams on major rivers, capping of springs, and flooding of springs and marshes during formation of the Salton Sea (Steinhart[1]). The introduction of western mosquitofish, *Gambusia affinis*, sailfin molly, *Poecilia latipinna*, and tilapias (mostly *Sarotherodon mossambica* and *Tilapia zillii*) – which possibly compete for food and space, and prey on eggs and juveniles – may have further depleted natural populations of pupfish (Steinhart[1] , Moyle 2002).

This study was conducted to assess the biological and physicochemical variables that influence abundance of desert pupfish populations in selected natural and manmade habitats of the Salton Sea Basin. Specific objectives of this study were as follows: (i) to determine whether relative abundance of pupfish varied among selected habitats; (ii) to characterize the abundance of co-habiting nonnative fish species; (iii) to quantify the gut contents of piscivorous longjaw mudsuckers, *Gillichthys mirabilis*; (iv) to document water quality and other environmental conditions; and (v) to relate pupfish abundance to abundance of nonnative fishes, predation by mudsuckers, and variations in environmental conditions. These variables and their interrelationships must be understood so that resource managers can protect remaining populations of pupfish.

Methods

Study area

We established sampling sites in Salt Creek (a natural habitat, 33°26′48″ N, 115°50′56″ W) and three agricultural drains (Avenue 84, 33°26′27″ N, 116°02′45″ W; County Line, 33°25′47″N, 116°02′37″ W; and Trifolium 20A, 33°06′30″ N, 115°45′51″ W) that historically contained desert pupfish (Figure 1). We visited sampling sites at least seasonally from February 2000 to December 2001 with more frequent visits during spring and summer when pupfish were expected to be most numerous.

Fish sampling

Within each sampling site, we fished 10 minnow traps (25.4 cm high × 25.4 cmwide × 43.2 cm long, 0.3 cm square mesh) baited with about 60 g of tuna-flavored cat food for approximately 4 hr, then pooled catches. We also collected supplemental fish samples for gut analysis of potentially piscivorous species by fishing with unbaited traps for 30 min and by hauling a small minnow seine. We identified and counted all captured fishes, then released desert pupfish in the capture vicinity. We

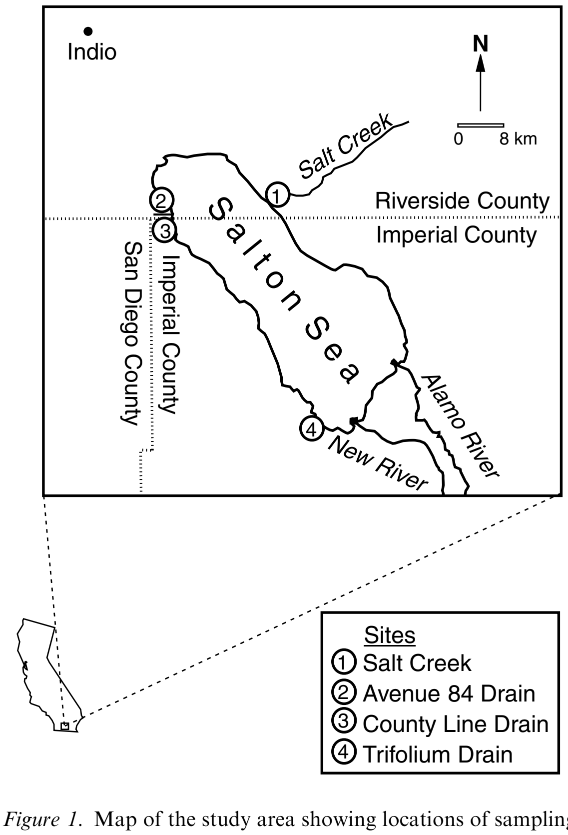


Figure 1. Map of the study area showing locations of sampling sites.

[2] Lau, S. & C. Boehm. 1991. A distribution survey of desert pupfish (*Cyprinodon macularius*) around the Salton Sea, California. Final report, Section 6 Project No. EF90XII-1, California Department Fish Game, Region 5, Long Beach, California.

preserved nonnative fishes in 10% formalin and, in the case of longjaw mudsuckers, analyzed them for gut contents. We removed gut contents of mudsuckers by dissection from the anterior end of the esophagus to the anus, identified items to the lowest taxonomic level possible by using standard keys (e.g., Usinger 1971, Merrit & Cummins 1978, Pennak 1978), then weighed each taxonomic category (wet biomass) to the nearest 0.00001 g.

Habitat characteristics

We recorded water quality (temperature, dissolved oxygen, pH, salinity, and turbidity measured with a Hydrolab DataSonde 3 attached to a Surveyor 4 display unit), water depth (measured with a meter stick), current velocity (measured with a Price AA current meter), stream width (measured with a fiberglass tape), and vegetation density (measured with a fiberglass tape along a line transect that crossed the width of the creek or drain) at each baited minnow trap when the traps were first fished. We recorded water quality again when traps were removed. In addition, we collected two samples of surface water in clean plastic screwtop bottles from upstream and downstream boundaries of each site, then acidified one upstream sample and one downstream sample with two drops of 5.25 N sulfuric acid for analysis of total ammonia. We retained the remaining samples for measuring total dissolved solids (TDS). Water samples were frozen until total ammonia and TDS could be determined in the laboratory. We also collected grab samples of bottom sediments from upstream and downstream boundaries of each site, placed them into clean plastic containers with snaptop lids, and froze them until they could be measured for particle size distribution. Sediment particle size distribution was determined by sieving thawed samples through a series of standard sieves (mesh diameters of 31.5, 9.5, 2.0, 1.4, and 0.053 mm), then measuring the dry weights of each sediment fraction and the filtrate passing through the 0.053-mm sieve. Schoklitsch's sediment factor (s) was calculated with a graphical procedure described by Bogardi (1974). According to Bogardi (1974), the value for s (which can assume any arbitrary positive value) increases as sediment material becomes coarser.

Data analysis

Raw data were stored as Excel files, then summarized using SAS software (SAS 1990) or statistical programs written by Ludwig & Reynolds (1988). Differences in fish species composition were assessed by using the chi-square test for homogeneity on numbers of fishes caught in baited minnow traps at each site. Species assemblages at various sites were compared by using Bray–Curtis resemblance functions. Fish species abundance and gut contents of longjaw mudsuckers were summarized with Lotus Freelance Graphics 97 software (Lotus Development Corporation Cambridge, MA). Fish species abundance and environmental variables were related to abundance of desert pupfish by using canonical correlation. Prior to conducting canonical correlation, raw data were either angular transformed if expressed as percentages or logarithmically transformed.

Results

Relative abundance of desert pupfish

We captured a total of 16885 fish represented by eight species with baited minnow traps (Table 1), with desert pupfish accounting for 193 (1.1%) individuals. Pupfish numbers varied seasonally and annually with most individuals captured during June–July (Table 2). Most pupfish were captured in Salt Creek (51.3%), with County Line Drain contributing 39.4% and Trifolium 20A Drain contributing 9.3% (Table 2). Although pupfish were not captured with baited minnow traps in Avenue 84 Drain, one individual was caught with an unbaited trap.

Relative abundance of co-habiting nonnative fishes

The numbers of nonnative fishes varied among sampling sites and times (Figure 2). The ratios of fish species differed significantly among the 4 sites ($\chi^2 = 21007$; df = 15; $p < 0.0001$). Porthole livebearers, *Poeciliopsis gracilis*, comprised 55% of fish caught during this study; however, all were captured in Avenue 84 Drain mostly during May–August (Figure 2). Tilapias were the second most numerous taxon (26.1%) with most captured in

Table 1. List of fish species, number caught, and relative contribution (%) to the total catch in baited minnow traps fished for 4-hr-intervals on 12 occasions between February 2000 and December 2001.

Family	Species	Common name	Number	%
Cichlidae	*Sarotherodon mossambica & Tilapia zillii*	Tilapias[a]	4403	26.1
Cyprinodontidae	*Cyprinodon macularius*	Desert pupfish	193	1.1
Gobiidae	*Gillichthys mirabilis*	Longjaw mudsucker	26	0.1
Poeciliidae	*Gambusia affinis*	Western mosquitofish	693	4.1
	Poecilia latipinnia & Poecilia mexicana	Mollies[a]	2290	13.6
	Poeciliopsis gracilis	Porthole livebearer	9280	55.0
Total			16885	100.0

[a] Judging from random samples of archived specimens, tilapias consisted mostly of *Sarotherodon mossambica* (403 of 510 fish, or 79%) whereas mollies consisted mostly of *Poecilia latipinnia* (222 of 285 fish, or 78%).

Table 2. Numbers of desert pupfish captured in baited minnow traps from Salt Creek (SC), Avenue 84 Drain (A84D), County Line Drain (CLD), and Trifolium 20A Drain (TFD) from February 2000 to December 2001. Pupfish were also captured from A84D in December 1999 and from the Salton Sea near the mouth of Salt Creek in October 2001.

Date	SC	CLD	TFD	A84D
February 2000	0	0	0	0
June 2000	37[a]	14	–[b]	0
July 2000	28[a]	40[a]	–[b]	0[a]
September 2000	0	0	0	0
April 2001	0	0	–[b]	0
May 2001	0	0[a]	0	0
June 2001	8[a]	0	0	0
July 2001	26[a]	15[a]	0	0
August 2001	0	4[a]	9[a]	0
September 2001	0	3[a]	9	0
October 2001	0	0	0	0
December 2001	0	0[a]	0	0
Total	99	76	18	0

[a]Additional pupfish (numbers not shown) were captured at these sites with unbaited minnow traps or minnow seines.
[b]No data.

Avenue 84, County Line, and Trifolium 20A drains during June–September (Figure 2). Mollies were less numerous (13.6%), with most captured at Avenue 84 and County Line drains during May–October (Figure 2). Western mosquitofish comprised 4.1% of the catch with most occurring in Salt Creek during June–July (Figure 2). Desert pupfish were relatively rare (1.1%), with most captured in County Line Drain and Salt Creek during June-July (Table 2, Figure 2). Longjaw mudsuckers were the least abundant species (0.1%), with most caught in Avenue 84 Drain during June–July (Figure 2).

As judged by Bray–Curtis resemblance functions, the species assemblage in Salt Creek differed considerably from those in the three drains (Table 3). Salt Creek and Avenue 84 Drain were least similar because fish captured in Salt Creek were mostly pupfish and western mosquitofish whereas fish captured in Avenue 84 Drain were mostly porthole livebearers. Among drains, species assemblages in County Line Drain and Trifolium 20A Drain were most similar and dominated by tilapias and mollies.

Gut contents of longjaw mudsuckers

Nineteen of 32 longjaw mudsuckers captured during this study had full guts. Over 78% of the biomass of gut contents consisted of fish, with desert pupfish contributing nearly 22% (Figure 3). Pupfish occurred exclusively in gut contents of mudsuckers from County Line Drain whereas porthole livebearers occurred exclusively in gut contents from Avenue 84 Drain and tilapias occurred exclusively in gut contents from Trifolium Drain. Miscellaneous aquatic invertebrates and insects comprised most of the remaining food items.

Water quality and other habitat variables

Water quality differed considerably between Salt Creek and the three agricultural drains (Figures 4 and 5). On average, Salt Creek contained the highest measurements of percent cover, pH,

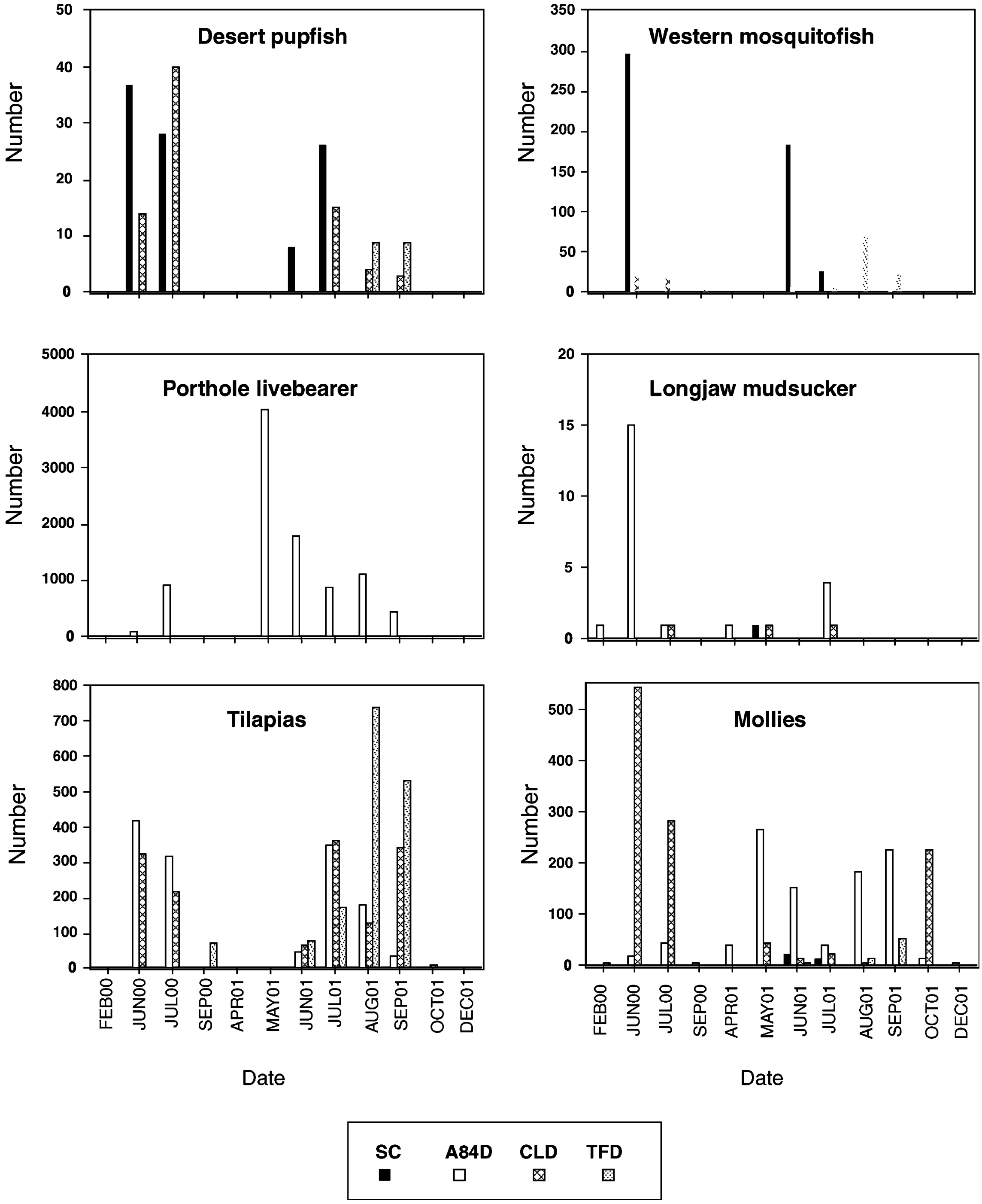
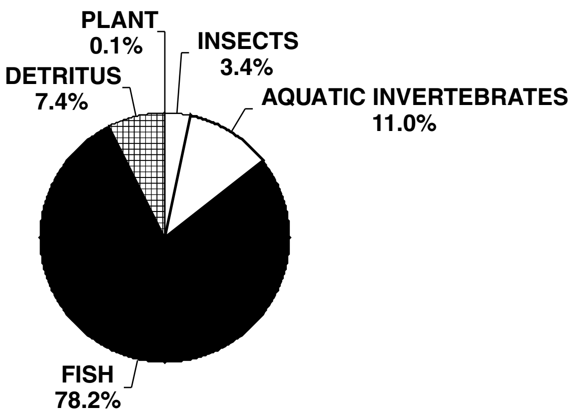


Figure 2. Numbers of fish caught with baited minnow traps from Salt Creek (SC), Avenue 84 Drain (A84D), County Line Drain (CLD), and Trifolium 20A Drain (TFD) on various *dates*.

Table 3. Comparison of fish species assemblages in Salt Creek (SC), Avenue 84 Drain (A84D), County Line Drain (CLD), and Trifolium 20A Drain (TFD). Values for pairs of sampling sites are Bray–Curtis resemblance functions expressed as dissimilarity indices. Values approaching 0 indicate similar assemblages whereas values approaching 1 indicate dissimilar assemblages.

	SC	A84D	CLD	TFD
SC	0.00	0.99	0.90	0.86
A84D	–	0.00	0.67	0.78
CLD	–	–	0.00	0.30
TFD	–	–	–	0.00



Unidentifiable fish remains	1.4 %
Tilapias	18.7 %
Desert pupfish	21.6 %
Porthole livebearer	36.5 %
Total fish	78.2 %

Figure 3. Gut contents of 19 longjaw mudsuckers. Percentages are based on wet weights of the combined gut contents.

salinity, and turbidity and the lowest measurements of sediment factor and dissolved oxygen. In Salt Creek, excessively high values for pH and salinity, and excessively low values for dissolved oxygen occurred during summer or early fall. By comparison, water quality variables in the drains did not exhibit excessive seasonal variations. In addition, Salt Creek was rarely disturbed by human activities whereas the drains were routinely subjected to mechanical removal of cattails during June–August, and barnacle bars blocking their mouths were artificially breached in September–October.

Relation of desert pupfish abundance to nonnative fishes and environmental variables

Canonical correlation analysis of fish species and environmental variables yielded only one significant canonical variable ($CC = 0.884$; $F = 2.02$; $df = 60$; $p = 0.0003$). The canonical variable was positively correlated with abundance of desert pupfish and western mosquitofish and negatively correlated with abundance of porthole livebearers, tilapias, longjaw mudsuckers, and mollies (Table 4). The canonical variable was also positively correlated with cover, pH, and salinity and negatively correlated with sediment factor and dissolved oxygen. These results indicate that pupfish numbers were high when mosquitofish were numerous, but pupfish numbers were low when porthole livebearers, tilapias, mollies, and longjaw mudsuckers were numerous. The results also indicate that pupfish numbers were higher when cover, pH, and salinity values were high and sediment factor and dissolved oxygen values were low.

Discussion

Anecdotal evidence suggests that desert pupfish populations have declined over the past 45 years in agricultural drains flowing into the Salton Sea. Barlow (1961) and Walker et al. (1961) reported that pupfish were extremely abundant in drains and shoreline pools during the early 1960s. In 1980, however, pupfish occurred in only 15 of 18 drains sampled by Black[3] and their numbers represented less than 5% of all fish captured. In 1983, Moore[4] (cited by Schoenherr 1988) captured just 6 pupfish in 40 drains and, in 1987, S.J. Montgomery (personal communication, cited by Schoenherr 1988) captured only 3 pupfish among 1128 fish in drains on the southeastern corner of the Salton Sea

[3] Black, G.F. 1980. Status of the desert pupfish, *Cyprinodon macularius* (Baird and Girard), in California. California Department of Fish and Game, Inland Fisheries Endangered Species Program Special Publication 80–1, Sacramento, California.

[4] Moore, K.E. 1983. Results of two fisheries surveys of the desert pupfish resources in and around the Salton Sea, Imperial and Riverside Counties. Memorandum to Fisheries Management, Region 5, California Department Fish and Game, 5 pp.

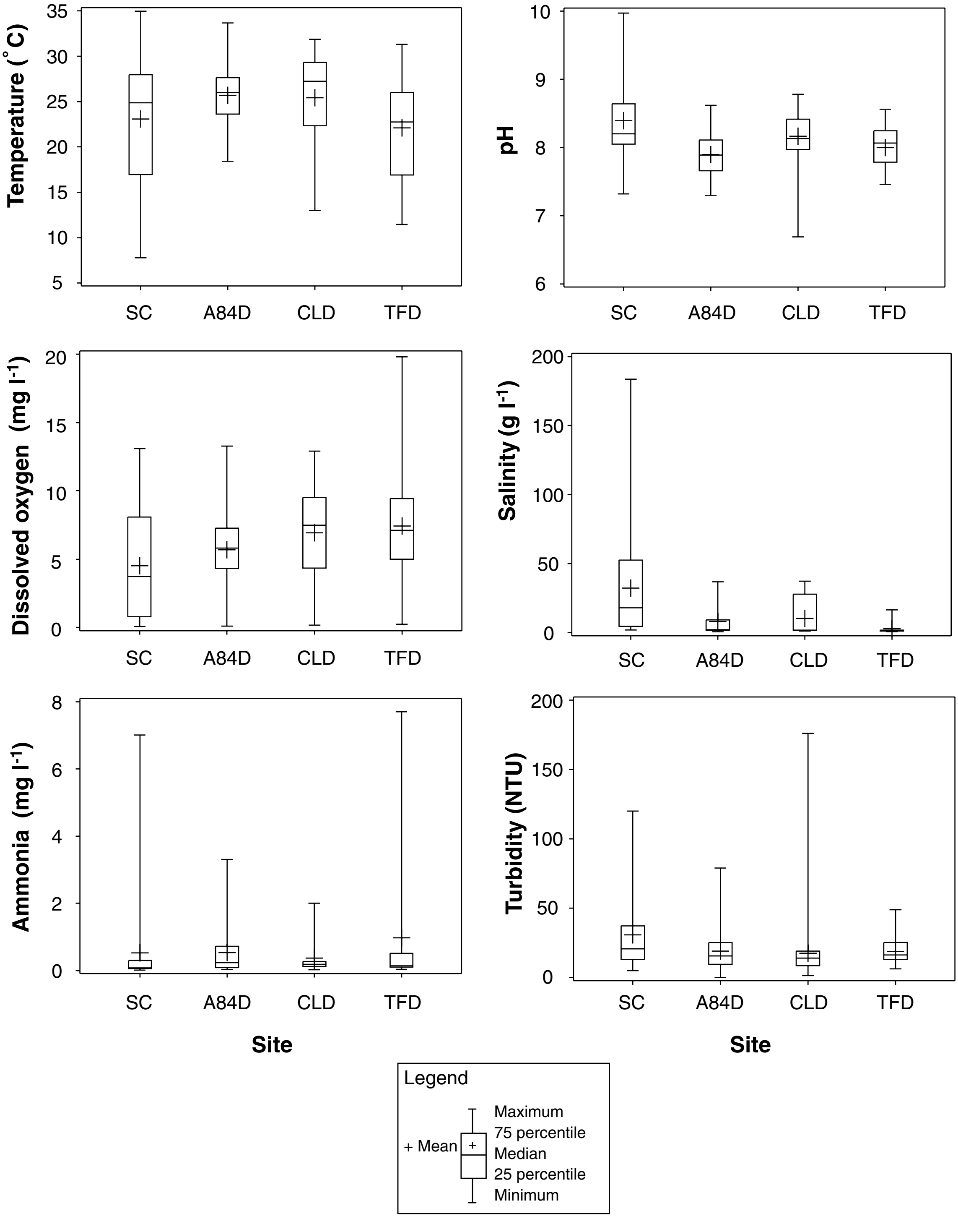


Figure 4. Boxplots of water quality variables measured on 12 occasions from Salt Creek (SC), Avenue 84 Drain (A84D), County Line Drain (CLD), and Trifolium 20A Drain (TFD).

Table 4. Canonical correlations for fish species abundance and selected environmental variables. A positive association exists between two variables when the product of their canonical correlations is positive whereas a negative (inverse) association exists when the product is negative. For example, a negative association exists between desert pupfish abundance and sediment factor whereas a positive association exists between pupfish abundance and salinity. Bold numbers indicate significant canonical correlations.

Variable	Canonical correlation
Fish species	
Desert pupfish	**0.5282**
Western mosquitofish	**0.6665**
Porthole livebearer	**−0.5398**
Longjaw mudsucker	**−0.3291**
Tilapias	**−0.4471**
Mollies	**−0.3206**
Environmental variables	
Sediment factor	**−0.6562**
Salinity	**0.5396**
Turbidity	0.0057
Dissolved oxygen	**−0.3283**
Velocity	−0.1126
Discharge	0.0226
NH_3	0.1238
Temperature	−0.0178
Cover	**0.5946**
pH	**0.5273**

near Niland. In spring 1991, pupfish numbers seemingly increased because Lau & Boehm[2] reported this species constituting 18.5% of 4546 fish captured in 45 of 70 sites (37 of 57 drain sites and 8 of 13 shoreline pools had pupfish). During our study, however, pupfish comprised only 1.1% of 16885 fish.

Desert pupfish are short lived fish that can complete their life cycle within a year and generally do not live beyond 2 years (Moyle 2002). Although they can breed year round if supplied with a constant warm environment, they typically breed from April to October, increasing their population numbers during summer months through an influx of juveniles (Schoenherr 1988). During our study, pupfish were captured mostly during summer when juveniles dominated the catch (Table 2). However, we also caught several pupfish at other times of the year, including an adult male in bright-blue breeding coloration at County Line Drain in May 2001. Several researchers (e.g., Cox 1966, Miller & Fuiman 1987, McMahon & Tash 1988) indicated that the Quitobaquito pupfish, *Cyprinodon macularius eremus*, which is closely related to desert pupfish, slows down its metabolism during winter in response to low water temperatures, sometimes burrowing into the substrate and becoming dormant. This behavior has also been reported in other pupfish species such as the Salt Creek pupfish, *Cyprinodon salinus*, the Amargosa pupfish, *C. nevadensis amargosae*, and the Big Spring pupfish, *C. n. pectoralis* (Miller 1948, Soltz 1974), and might explain why we captured few pupfish between fall and spring when cool water temperatures prevailed in our study area. Nevertheless, in the Death Valley system, Miller (1948) attributed the winter scarcity of Salt Creek pupfish to mortality from desiccation of streams and predation by natural enemies.

In our study area, the mouths of agricultural drains blocked by barnacle bars are often artificially breached during fall months to facilitate discharge of agricultural drainage, thus enabling desert pupfish to migrate into the Salton Sea. Outmigration from agricultural drains may explain our capture of a single juvenile pupfish in October 2001 from the Salton Sea near the blocked-off mouth of Salt Creek. Beginning in May 2003, the California Department of Fish and Game conducted monthly trapping surveys along selected shorelines of the Sea and pupfish were captured on several occasions. Although most pupfish were caught in close proximity to open mouths of drains, a few were also captured several kilometers from the nearest open drain (S. Keeney, personal communication).

In addition to seasonal variations, the abundance of desert pupfish differed among sites with most pupfish occurring in Salt Creek during our study (Table 2, Figure 2). The relatively high abundance of pupfish in Salt Creek may have been due to environmental conditions that favor survival of this species (Figures 4 and 5). Compared to agricultural drains, Salt Creek had the highest percent cover, salinity, pH, and turbidity, and the lowest sediment factor, and dissolved oxygen. Pupfish can tolerate excessively high temperatures (Lowe & Heath 1968, Brown & Feldmeth 1971, Schoenherr & Feldmeth 1991), high salinities (Barlow 1958, Kinne & Kinne

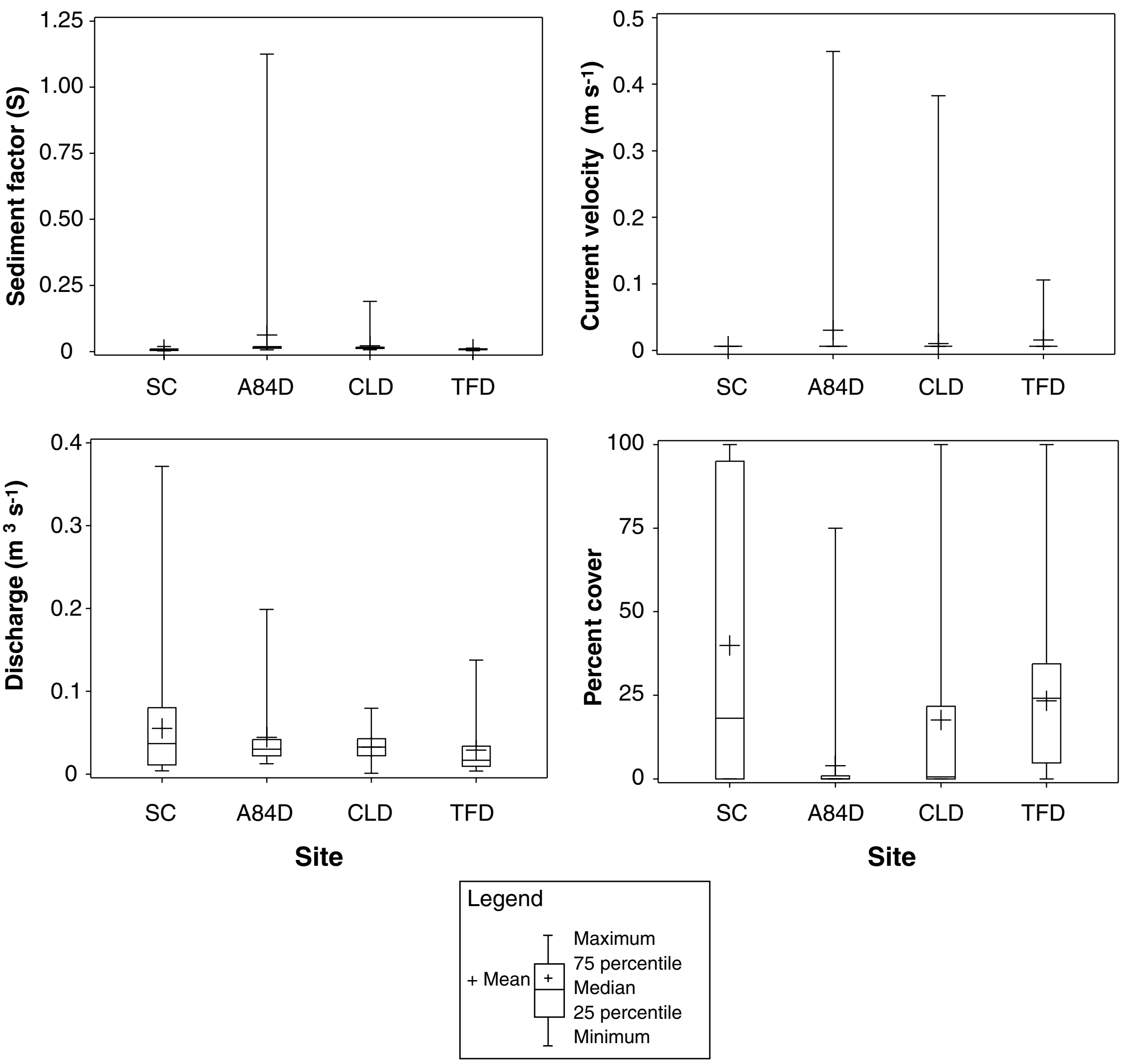


Figure 5. Boxplots of selected habitat variables measured on 12 occasions from Salt Creek (SC), Avenue 84 Drain (A84D), County Line Drain (CLD), and Trifolium 20A Drain (TFD).

1962), and low dissolved oxygen (Lowe et al. 1967), which allows them to survive in environments hostile to less hardy species. Our observations suggest that pupfish were most numerous in Salt Creek because high salinity and low dissolved oxygen especially during late summer or fall curtailed survival of most nonnative fishes. The high association between pupfish and western mosquitofish may reflect the high tolerance of both species to harsh environments (Moyle 2002). Mosquitofish are known to survive in waters with temperatures of 10–35°C, pH of 4.7–10.2, and salinity of 0–58 g l^{-1} (Swanson et al.[5]).

Schoenherr (1988) speculated that introduction of redbelly tilapia, *Tilapia zillii*, in 1973 may have contributed to the decline of desert pupfish populations in the Salton Sea drainage. Schoenherr (1981) also documented the displacement of

[5] Swanson, C., J.J. Cech, Jr. & R.H. Piedrahita. 1996. Mosquitofish: biology, culture, and use in mosquito control. Elk Grove, California: California Mosquito Vector Control Association.

pupfish by tilapias in a pond adjacent to the King Street Canal between 1978 and 1980. During our study, Salt Creek contained the fewest numbers of nonnative species (Figure 2), including tilapias and the piscivorous longjaw mudsucker (we captured only one mudsucker in Salt Creek). Although we did not examine gut contents of adult tilapias, large numbers of this life stage move into agricultural drains from fall through spring when the mouths of drains are open to the Salton Sea. Moyle (2002) reported that both redbelly tilapia and Mozambique tilapia, *Sarotherodon mossambica*, are capable of feeding on fish when the opportunity arises. Thus, predation by both adult tilapias and mudsuckers might account for low numbers of pupfish in drains.

Although beyond the scope of our study, desert pupfish in agricultural drains may also be adversely affected by reproductive interference from nonnative fishes and detrimental consequences associated with removal of cattails and other vegetation during routine ditchbank maintenance. Schoenherr (1988) attributed the decline of desert pupfish populations to poor reproductive performance exacerbated by aggressive behavior of breeding males towards large numbers of juvenile tilapia. Soltz (1974) noted that three male Big Spring pupfish spent over 50% of their time chasing mollies away from their territories, suggesting a negative effect on breeding activities of these pupfish. Mechanical removal of vegetation during summer can adversely affect reproduction because desert pupfish are known to use plants for egg deposition (Courtois & Hino 1979). Mire & Millet (1994) also observed spawning by Owens pupfish, *Cyprinodon radiosus*, on vegetation that included root mats, filamentous algae, and vertical plant stems. In addition, the harvesting of aquatic vegetation can physically remove pupfish entrapped in the vegetation and reduce or eliminate potential cover, thus exposing pupfish to higher rates of predation.

In summary, desert pupfish abundance was generally highest in habitats where water quality extremes (especially high pH and salinity, and low dissolved oxygen) seemingly limited the occurrence of nonnative fishes. Our study also documented predation by longjaw mudsuckers on pupfish. These findings support the contention of many resource managers that pupfish populations are adversely influenced by ecological interactions with nonnative fishes.

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References

Barlow, G.W. 1958. High salinity mortality of desert pupfish, *Cyprinodon macularius*. Copeia 1958: 231–232.

Barlow, G.W. 1961. Social behavior of the desert pupfish, *Cyprinodon macularius*, in the field and in the aquarium. Am. Midland Nat. 65: 339–359.

Bogardi, J. 1974. Characteristics of sediment and bed material. pp. 36–49. *In:* J. Bogardi (ed), Sediment Transport in Alluvial Streams, Akademiai Kiado, Budapest, Hungary. (translated by Z. Szilvassy)

Brown, J.H. & C.R. Feldmeth. 1971. Evolution in constant and fluctuating environments: Thermal tolerances of desert pupfish (*Cyprinodon*). Evolution 25: 390–398.

Courtois, L.A. & S. Hino. 1979. Egg deposition of the desert pupfish, *Cyprinodon macularius*, in relation to several physical parameters. California Fish Game 65: 100–105.

Cox, T.J. 1966. A behavioral and ecological study of the desert pupfish (*Cyprinodon macularius*) in Quitobaquito Springs, Organ Pipe Cactus National Monument, Arizona. Dissertation, University of Arizona, Tucson, Arizona, USA. 91 pp.

Kinne, O. & E.M. Kinne. 1962. Rates of development in embryos of a cyprinodont fish exposed to different temperature–salinity–oxygen combinations. Can. J. Zoo. 40: 231–253.

Lowe, C.H. & W.G. Heath. 1968. Behavioral and physiological responses to temperature in the desert pupfish *Cyprinodon macularius*. Physiol. Zool. 42: 53–59.

Lowe, C.H., D.S. Hinds & E.A. Halpern. 1967. Experimental catastrophic selection and tolerances to low oxygen concentration in native Arizona freshwater fishes. Ecology 48: 1013–1017.

Ludwig, J.A. & J.F. Reynolds. 1988. Statistical Ecology. John Wiley & Sons, New York. 337 pp.

McMahon, T.E. & J.C. Tash. 1988. Experimental analysis of the role of emigration in population regulation of desert pupfish. Ecology 69: 1871–1883.

Merrit, R.W. & K.W. Cummins (eds). 1978. An Introduction to the Aquatic Insects of North America, Kendall & Hunt Publishing Company, Dubuque, Iowa, USA. 441 pp.

Moyle, P.B. 2002. Inland fishes of California, University California Press, Berkeley, California. 502 pp.

Miller, R.R. 1948. The Cyprinodont Fishes of the Death Valley system of eastern California and southwestern Nevada. Miscellaneous Publications of the Museum of Zoology, University Michigan 68: 1–155.

Miller, R.R. & L.A. Fuiman. 1987. Description and conservation status of *Cyprinodon macularius eremus*, a new subspecies of pupfish from Organ pipe cactus national monument, Arizona. Copeia 1987: 593–609.

Mire, J.B. & L. Millett. 1994. Size of mother does not determine size of eggs or fry in the Owens pupfish, *Cyprinodon radiosus*. Copeia 1994: 100–107.

Pennak, R.W. 1978. Fresh-water invertebrates of the United States, 2nd edition, John Wiley & Sons, New York, NY USA. 628 pp.

SAS Institute Inc. 1990. SAS/STAT user's guide, version 6, fourth edition, Vol. 2, Cary, North Carolina, USA. 889 pp.

Schoenherr, A.A. 1979. Niche separation within a population of freshwater fishes in an irrigation drain near the Salton Sea, California. Bull. S. Calif. Acad. Sci. 78: 46–55.

Schoenherr, A.A. 1981. Replacement of *Cyprinodon macularius* by *Tilapia zillii* in an irrigation drain near the Salton Sea. Proc. Desert Fishes Council 13: 65–66.

Schoenherr, A.A. 1988. A review of the life history and status of the desert pupfish, *Cyprinodon macularius*. Bull. S. Calif. Acad. Sci. 87: 104–134.

Schoenherr, A.A. & C.R. Feldmeth. 1991. Thermal tolerances for relict populations of desert pupfish, *Cyprinodon macularius*. Proc. Desert Fishes Council XXIII (1991): 49–54.

Soltz, D.L. 1974. Variation in life history and social organization of some populations of Nevada pupfish, *Cyprinodon nevadensis*, Dissertation, University of California, Los Angeles, California, USA. 148 pp.

Usinger R.L. (ed). 1971. Aquatic Insects of California with Keys to North American Genera and California species, University of California Press, Berkeley, California, USA. 508 pp.

USFWS (U.S. Fish and Wildlife Service). 1986. Endangered and threatened wildlife and plants; determination of endangered status and critical habitat for the desert pupfish. Fed. Regist. 51: 10842–10851.

Walker, B.W., R.R. Whitney & G.W. Barlow. 1961. Fishes of the Salton Sea. pp. 77–91. *In*: B.W. Walker (ed), The ecology of the Salton Sea, California in relation to the sport fishery, Calif. Fish Game Fish. Bull. 113: 77–91.