PHYSIOLOGICAL RESPONSES OF A NATIVE AND AN INTRODUCED DESERT FISH TO ENVIRONMENTAL STRESSORS[1]

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Abstract. We compared the physiological responses of two similar cyprinids, the Mojave tui chub (*Gila bicolor mohavensis*) and the arroyo chub (*Gila orcutti*), to stressors common in their aquatic desert environment. The introduced arroyo chub has displaced the native Mojave tui chub from its fluctuating habitat, a desert river. In laboratory tests, the introduced species showed more appropriate resting-routine metabolic rate responses to increasing temperature and decreasing oxygen tension and better swimming performance responses to high water velocity conditions periodically typical of this habitat than did the native species. This result was expected as the introduced species has a longer evolutionary history in fluctuating stream habitats than does the native species. We concluded that these differences in adaptation contributed to replacement of Mojave tui chub by arroyo chub.

Key words: adaptation; endangered species; Gila bicolor mohavensis; Gila orcutti; *hybridization; hypoxia response; introduced species; metabolic rate; species interaction; swimming performance; temperature response.*

INTRODUCTION

An organism's response to abiotic factors and its interactions with other organisms determine whether or not it will continue to persist in an environment (Hutchinson 1957). When an introduced organism replaces a native organism (one with a long history of persistence in its environment), we assume that the interaction between them is responsible for the demise of the native organism. Recent research suggests that differential responses to abiotic factors may play a role in the outcome (displacement or coexistence) of biotic interactions (Dayton 1971, Levin and Paine 1974, Connell 1978, Sousa 1979, Baltz et al. 1982, Meffe 1984). We were interested in the interaction between two similar cyprinids, native Mojave tui chub (*Gila bicolor mohavensis*) and introduced arroyo chub (*Gila orcutti*), which resulted in displacement of the native species from its fluctuating habitat, the Mojave River. Previous authors assumed that the introduced species replaced the native species through competition and hybridization (Hubbs and Miller 1943, Hubbs 1955, Miller 1961, Moyle 1976, United States Fish and Wildlife Service 1984). The fluctuating nature of the river and the evolutionary histories of both fishes led us to predict that the introduced species would respond more appropriately to environmental stressors typical of the Mojave River than does the native species. Although we could not observe the interaction (as it took place 40 yr ago), we could test this prediction by comparing these fishes' physiological responses to abiotic stressors typical of desert rivers. If the introduced species proved better suited to conditions in the river, it would suggest

that differential responses to abiotic stressors set the stage for displacement and may have mediated the outcome of the biotic interaction. Our results suggest that the interplay of differential responses to abiotic factors and biotic interactions caused this displacement.

Habitat description

The Mojave River flows from the east side of the San Bernardino Mountains to its terminus in the usually dry Soda Lake bed in the center of the Mojave Desert, California (Courtois 1984). The river is subterranean throughout most of its length except where bedrock extrusions cause surface flow. This creates several disjunct stream habitats along the riverbed. The Mojave Desert region undergoes seasonal temperature extremes ($-6.7°$–$40.6°$C, Victorville data; NOAA 1983). This climate, along with the Mojave River's typically low flows, causes wide fluctuations in water temperature ($0.0°$–$36.0°$ yearly with $10°$–$15°$ variation monthly near Victorville; United States Geological Survey 1981). Under these conditions, community respiration can cause low oxygen conditions (Hynes 1970). Periodic years with high rainfall and the episodic nature of rainfall in the area (California Department of Water Resources 1981) cause torrential "flash" flooding. Subsequent rainless periods dry flooded areas and strand fishes. Since high temperatures, low oxygen availability, and high flow rates are periodic conditions in the river, we chose to compare the two species' responses to these abiotic stressors.

Faunal history

Mojave tui chubs (hereafter "tui chubs"), although native only to the Mojave River (Snyder 1919, Pister 1981), were restricted to stream habitats for a relatively

TABLE 1. Mean mass (±2 SE) of each temperature acclimation group (n = 12 fish) used in metabolic rate trials.*

Fish species	Acclimation temperature (°C)		
	10	20	30
	Mass (g)		
Mojave tui chub	2.65 ± 0.25	2.32 ± 0.32	2.00 ± 0.29
Arroyo chub	2.84 ± 0.84	1.96 ± 0.19	1.78 ± 0.19

* There were no significant pairwise differences among the mean masses of the acclimation groups except between the 10° and 20° arroyo chubs (ANOVA followed by Duncan's new multiple-range test, $P < .05$).

short period, as the river flowed into several large lakes until the end of the late Cenozoic ($\approx$8000 BP; Van Devender 1977). In addition, they are part of a subspecies complex found throughout a number of western drainages. All members of this complex live in lakes or sluggish rivers (Kimsey 1954, Moyle 1976, Cooper 1978). Arroyo chubs, which are native to streams of the Los Angeles Plain (Miller 1968), have had a longer history in stream environments similar to the Mojave River. These species distributions were separated by the San Gabriel, San Bernardino, and San Jacinto Mountains until arroyo chubs were introduced into Deep Creek, one of the headwaters of the Mojave River, before the 1930's (Hubbs 1955, United States Fish and Wildlife Service 1984, Castleberry 1985). Arroyo chubs soon replaced tui chubs in headwaters but were isolated from lower sections by areas of subterranean flow. Tui chubs persisted in lower sections of the river until heavy rainfalls in 1937 and 1938 caused torrential flows which spread arroyo chubs downstream; a decline in tui chubs followed (Hubbs and Miller 1943). Miller (1969) reported that by the early 1960's tui chubs could no longer be found in the Mojave River system.

METHODS

Fish collection

Collection sites were chosen so that experimental fish would closely represent genetic stocks that came together in the original arroyo chub introduction. This avoided possible genetic changes brought on by numerous hybridization events that plague both species in some parts of their ranges (Hubbs and Miller 1943, Greenfield and Greenfield 1972). Tui chubs were seined from Lark Seep on China Lake Naval Weapons Center, China Lake, California and arroyo chubs from Big Tujunga Creek in the San Gabriel Mountains, California. Fish were transported, soon after capture, to the University of California, Davis. They were held in 210-L insulated fiberglass tanks supplied with a continuous flow of air-equilibrated, unchlorinated well water at temperatures between 18° and 24°C and fed Oregon Moist Pellets, Tetramin dry flake food, and occasionally brine shrimp. All fish used in these experiments were reproductively mature.

Temperature acclimation

After at least 1 mo in laboratory holding facilities, we acclimated fish to experimental respirometry temperatures (10°, 20°, and 30°; all ± 0.2°) in groups of 20 held in 35-L insulated plastic containers. Fish stayed at their acclimation temperature for 5–8 wk before experimentation.

Metabolic responses

We measured resting-routine metabolic rates (defined as the metabolic rate for a quiescent fish whose spontaneous activity is confined by the design of the respirometer; Mitchell 1986) at acclimation conditions and at increased temperature and decreased oxygen (hypoxic) conditions to compare the species' metabolic responses to these stressors. To make these measurements, 12 fish were selected within a narrow size range (1.5–5.0 g) and weighed individually (Ohaus B 3000 D electronic balance accurate to ±0.01 g) (Table 1). We placed each fish into a 210-mL glass respirometry jar (see Castleberry 1985 for design details). We used 13 jars; 12 with fish (experimental) and 1 without fish (control). We attributed any oxygen consumed in the control jar to microbial respiration. We placed the respirometry jars in a temperature-controlled (±0.2°), ultraviolet-sterilized (Aquafine Corporation, Model SL-1) water bath contained in two 250-L insulated fiberglass tanks and covered the tanks. Respirometers received a continuous flow of respirometry tank water, which was pumped up into a stripping column and then into a manifold which provided separate flows to each of the respirometers (Cech et al. 1979). After a 3-h acclimation period (previously determined to be adequate for the fish to reach metabolic stasis) we shut off the flow to each respirometer and measured resting-routine metabolic rates as rates of oxygen consumption, using standard static respirometry methods as described by Castleberry (1985).

After this, we opened the inflow clamp to each respirometer and started nitrogen gas flowing through the stripping column to decrease the oxygen tension of the inflowing water to ≈ 5kPa in 0.5 h. Fish stayed at this lower or hypoxic oxygen tension for a 2-h acclimation period. After this period, we measured their metabolic rates to assess their response to decreased oxygen tensions.

Following the hypoxic measurements, fish were removed from their respirometers, placed in individual holding cages, returned to holding tanks, and fed Tetramin. Late the next day (24 h later), we increased their holding temperature 5° overnight. On the following morning (12 h later), we reweighed the fish, placed them into their respective respirometers, and repeated the previous normoxic and hypoxic metabolic rate measurements at the 5° higher temperature. This allowed assessment of the fishes' response to temperature increase and temperature increase coupled with de-

creased oxygen tensions. After the final hypoxic run, fish were returned to holding tanks.

This experimental regime yielded respiratory metabolic rate data on three groups of fish (one each acclimated to 10°, 20°, and 30°) at four conditions (two oxygen levels at two temperatures). We calculated metabolic rates as mass independent oxygen consumption rates $(mg \cdot kg^{-2/3} \cdot h^{-1})$ to remove variation due to differences in fish mass (Heusner 1984) and normalized these data using log transformations. We analyzed mass differences between groups and intraspecific metabolic rate differences under similar treatment conditions for each group using ANOVA (Snedecor and Cochran 1980). Within each group, we analyzed intraspecific metabolic rate differences using two-way ANOVA (Snedecor and Cochran 1980). We made pairwise comparisons within each ANOVA using Duncan's new multiple-range test (Steel and Torrie 1960). We analyzed interspecific metabolic rate differences under similar treatment conditions using t tests (Snedecor and Cochran 1980).

Swimming performance

We used a modified Blazka-type swimming apparatus (Castleberry 1985) to generate controlled water velocity conditions under which we could test for swimming performance differences between species. Although we could not accurately measure water velocity due to the operator's physical reaction time and equipment constraints, this system did provide consistent water velocity conditions under which we could compare the swimming performance of fish.

We chose one fish of each species and put them together in the swimming chamber of the apparatus to begin each trial. Fish that were tested simultaneously were chosen to be of equal size. We allowed fish 10 min to adjust to the swimming apparatus, an additional 10 min to train at a low swimming speed, and then increased the water velocity at a consistent (from run to run) rate until one fish was pinned against the back baffle. We recorded the first species pinned and analyzed species-specific differences using a sign test (Hollander and Wolfe 1973). We conducted 15 swimming performance trials, each on a separate pair of fish, in 20° (±0.5°) water. Behavioral observations also yielded information concerning species interactions during these events.

RESULTS

We first compared the two species' metabolic rate responses to temperature (Fig. 1). The 20°C acclimated fish of both species had significantly higher metabolic rates than 10°-acclimated fish held under the same dissolved oxygen conditions. The 30° fish of both species had significantly higher metabolic rates than 20°-acclimated fish under normoxic conditions, whereas only 30° arroyo chubs showed a similar difference under the
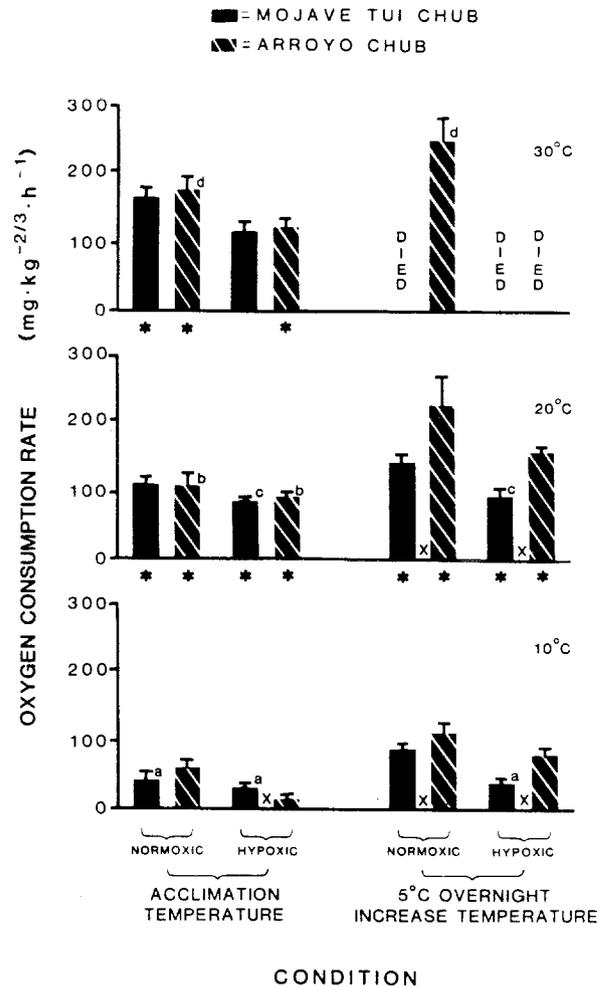

FIG. 1. Mean metabolic rates (shown as oxygen consumption rates), plus two standard errors (vertical T-bars), for three temperature acclimation groups of chubs (10°, 20°, and 30°C) at normoxic (21–17 kPa PP_{O_2}) and hypoxic (5 kPa PP_{O_2}) conditions both at acclimation temperatures and after a 5° overnight temperature increase. DIED: indicates fish died before they reached that condition. × indicates a significant difference between species' rates at that condition ($P < .05$, t tests). * indicates a significant difference between acclimation groups' rates at conditions above and below the asterisk ($P < .05$, ANOVA). Bars with common lowercase letters indicate a lack of significant intraspecific difference ($P > .05$, two-way ANOVA) within acclimation group. There were 12 fish in each temperature acclimation group for each species.

hypoxic condition. The 10° and 20° arroyo chub rates increased significantly with a 5° temperature increase (Fig. 1). Under normoxia, tui chubs showed a similar, but reduced, response with a 5° temperature increase. The 10° and 20°-acclimated tui chubs did not show this response under hypoxia. These differing responses to a 5° increase resulted in significant differences between species' metabolic rates under these conditions. The 30°-acclimated tui chubs did not survive the 5° temperature increase. Arroyo chubs survived this condi-

TABLE 2. Performance of the two chub species swimming in water of increasing velocity, and sizes of fish used in these trials.

Fish species	Number of times pinned first*	Fish sizes ($\bar{X} \pm 2$ SE)†	
		Mass (g)	Standard length (mm)
Mojave tui chub	12	4.0 ± 0.7	61 ± 4
Arroyo chub	3	4.2 ± 0.7	61 ± 4

* The two species' scores were significantly different from equal ($P < .05$, sign test).

† Masses and standard lengths of the two species were not significantly different nor were they correlated with individual trial outcomes.

tion but did so without a significant increase in their metabolic rates.

Both species showed slightly reduced metabolic rates in response to hypoxia (Fig. 1). This reduction was significant in four of five cases for both fish. The 10°-acclimated arroyo chubs' metabolic rate depression in response to hypoxia resulted in a significant difference between species. Arroyo chubs lost equilibrium at this condition but recovered as they were returned to normoxia. Exposure to hypoxia did kill 30°-acclimated arroyo chubs after a 5° temperature increase, but 30°-acclimated tui chubs died before the same temperature normoxic data could be collected.

We were careful to observe the activity level of respirometry fish at frequent intervals during experimentation. Both species were quiescent in the respirometers.

Tui chubs were pinned first in swimming performance trials significantly more often than were arroyo chubs (Table 2). Both species struggled under high-water-velocity conditions, often touching the back baffle, before becoming pinned. Pinned fish appeared exhausted and were unable to maintain position in the water current even under low-velocity conditions. These fish recovered after being returned to holding tanks.

DISCUSSION

Arroyo chubs were more tolerant and responded more appropriately to laboratory conditions simulating environmental stressors typical of desert rivers than tui chubs. This implies that arroyo chubs would survive environmental extremes in the Mojave River better, as we predicted based on the fluctuating nature of the river and the species' differing evolutionary histories.

Tui chubs showed less tolerance of high temperatures than did arroyo chubs. Tui chubs acclimated to 30°C did not survive an overnight temperature increase of 5° (Fig. 1). Arroyo chubs survived this increase, indicating they would have a survival advantage over tui chubs in high temperatures likely to occur under low water conditions.

Tui chubs showed less increase in metabolic rate to a 5° temperature increase than did arroyo chubs, re-

sulting in a significant difference between the species' metabolic rates after this increase (Fig. 1). A large metabolic rate increase in response to a temperature increase might help arroyo chubs to remain active in stream environments where rapid temperature increases are common. This response might also assist arroyo chubs in escaping stressful situations. Tui chubs, although they would use less energy under increasing temperature conditions, may be at a disadvantage in a fluctuating-temperature, flowing-water situation because they are unable to remain as active as arroyo chubs, thereby reducing their ability to capture prey, escape predators, and avoid stressful situations. This response would not be necessary in a fish adapted to a lake environment. Lake environments seldom undergo rapid and uniform increases in temperature (Wetzel 1975) and do not require high activity levels to satisfy metabolic demands (Washbourn 1936).

Tui chubs showed a greater tolerance of low temperatures, and especially low temperature hypoxia, than did arroyo chubs. Arroyo chubs experienced difficulty acclimating to the 10° acclimation temperature. Of the 20 fish acclimated to this temperature, 2 died while the temperature was being decreased. Since 10°, hypoxic-exposed fish experienced loss of equilibrium, we suspect that metabolic failure caused their decreased metabolic rates (Fig. 1), which could not be maintained for an extended period of time. Tui chubs did not experience problems acclimating to 10° or hypoxic equilibrium problems. This suggests that arroyo chubs would be at a survival disadvantage in a system that experienced low temperatures, especially if accompanied by hypoxic conditions. Low water temperature is a transient and short-lived condition in the Mojave River (United States Geological Survey 1981). Daily temperature variations typical of flowing water systems would provide a temporal refuge from temperature minima. Low temperature hypoxia is not a selective force in a flowing water environment because low temperatures are associated with high levels of dissolved oxygen (Hynes 1970). This difference between the species would not give tui chubs a selective advantage over arroyo chubs in the present Mojave Desert aquatic environment. Low temperature hypoxia is, however, a selective force in lake environments which stratify or freeze over (Greenback 1945, Tonn and Magnuson 1982). The tui chub's low temperature hypoxia tolerance would be an advantage in a lake environment that remained cold for long periods of time, such as might have been the case in pre-late Cenozoic Mojave Desert lakes.

The swimming performance of arroyo chubs (Table 2) conceivably puts them at a survival advantage over tui chubs. On a day-to-day basis, arroyo chubs would be expected to be better able to maintain position in a water current, giving them an advantage in capturing prey, escaping predators, and changing location. Arroyo chubs would also be better at maintaining stream

position in a flood situation. A fish that was unable to maintain stasis in a flood in the Mojave River would be washed downstream onto the desert playa where it would eventually perish. Although Courtois (1982) observed tui chubs moving downstream to avoid being stranded in an artificial desiccation event, this characteristic did not seem to serve tui chubs well in Mojave River floods. Thompson (1921) reported that a flood washed thousands of tui chubs out onto Soda Lake where they died as the lake evaporated. During the short period that tui chubs and arroyo chubs coinhabited the Mojave River, Hubbs and Miller (1943) observed a similar occurrence. As a result, arroyo chubs constituted a larger percentage of the fish Hubbs and Miller (1943) sampled in the river after the flood than they did in similar samples taken before the flood.

The results of our investigation support our prediction that arroyo chubs would respond more appropriately to environmental stressors typical of desert rivers than would tui chubs. Arroyo chubs, having spent the greater amount of time in stream environments similar to the Mojave River (Eigenmann and Eigenmann 1890, Miller 1942), seem better suited physiologically to these habitats. Tui chubs, having been lake-dwelling fishes until the late Cenozoic, are less well suited for inhabiting rivers but exhibit low temperature hypoxia tolerance, which might be adaptive in a lake environment. As is the case for many southwestern desert fishes, the tui chub's habitat apparently changed faster than did its ability to adapt (Smith 1981). Tui chubs are poorly adapted to the Mojave River but persisted there in the absence of similar fish.

Our laboratory information and observations by investigators working in the Mojave River area before the introduction of arroyo chubs (Thompson 1921) and shortly thereafter (Hubbs and Miller 1943) suggest that this lack of adaptation to extreme environmental situations caused population numbers of tui chubs to fluctuate widely. It is very likely that tui chub population numbers increased in the Mojave River during benign environmental periods and then decreased drastically with each period of environmental stress. Our laboratory comparisons suggest that arroyo chubs would not be as severely affected. Arroyo chubs' influence on tui chubs and the outcome of the interaction between these species may have pivoted on their differential responses to environmental stressors. Major floods occurred in 1937 and 1938 (United States Geological Survey 1981), shortly after the arroyo chub introduction.

The complete nature of the interaction between these species is unknown. It has generally been assumed that arroyo chubs replaced tui chubs through competition (competitive exclusion) and hybridization (Hubbs and Miller 1943, Hubbs 1955, Miller 1961). Other biotic interactions, such as predation and aggression (interference competition), were probably not important in this interaction as neither species is piscivorous nor

aggressive (Hubbs and Miller 1943, Vicker 1973, Moyle 1976, D. T. Castleberry, personal observation). Exploitation competition is a possibility, although no evidence of this interaction exists. The one well-documented interaction is hybridization (Hubbs and Miller 1943). Since hybrids seemed to show very low fertility (Hubbs and Miller 1943), hybridization would dilute the reproductive effort of the parent species. The effect on tui chub population numbers would be strongest where a selective abiotic disturbance, such as a flood or high water temperatures, decreased tui chub : arroyo chub population ratios so that arroyo chubs were more numerous than tui chubs. Hubbs and Miller (1943) had the opportunity to observe many hybrids and concluded that in their morphological adaptation to flowing water environments, they were intermediate to the parent species. This suggests that hybrids were also selected against. Since environmental stressors could be expected to remove tui chubs and tui chub-arroyo chub hybrids selectively, the interplay of differential responses to abiotic factors (high temperatures and floods) and biotic interaction (hybridization) might result in arroyo chubs displacing tui chubs. This replacement could take place without invoking competition as a causative factor.

We are not the first to suggest that abiotic factors play a role in mediating the outcome of biotic interactions between fishes in fluctuating streams. Meffe (1984, and papers by Minckley cited therein) found that native fishes were better adapted to floods than introduced predators, and that flooding, if frequent and moderate, might supersede deterministic outcomes of predation (extirpation of native species) by reducing populations of introduced predators. In our study and those just mentioned, fish with longer evolutionary histories in fluctuating stream environments had a selective advantage over fish with histories in lake or sluggish river environments. The differing outcomes of the interactions discussed here and by Meffe (1984) (displacement vs. coexistence, respectively) are the result of the nature of the biotic interaction and the effect that abiotic factors have on that interaction. In our study, high temperatures and flooding presumably accentuated the effect hybridization (or competition) had on the native species, resulting in displacement, while Meffe (1984) found that flooding minimized the effect of predation on the native species, allowing coexistence. These examples underscore the role that abiotic factors play in the outcome of biotic interactions.

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