

Differences in swimming ability and behavior in response to high water velocities among native and nonnative fishes

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Synopsis

We conducted swimming performance tests on native and nonnative fishes commonly found in Arizona streams to evaluate the extent of differences in swimming ability among species. Fishes with similar mean lengths were subjected to stepwise increases in water velocity in a laboratory swim tunnel until fish could no longer maintain position. Nonnative fathead minnows *Pimephales promelas* and red shiners *Cyprinella lutrensis* exhibited swimming abilities similar to native longfin dace *Agosia chrysogaster*, speckled dace *Rhinichthys osculus* and spikedace *Meda fulgida*. Nonnative mosquitofish *Gambusia affinis* exhibited swimming ability similar to native Gila topminnows *Poeciliopsis occidentalis*. Desert suckers *Catostomus clarki*, bluehead suckers *Catostomus discobolus* and speckled dace exhibited behavioral responses to high water velocities that may confer energetic advantages in swift water. Differences in swimming ability do not appear to adequately explain the disproportionate removal of nonnative fishes via flooding. Behavioral responses to high flows are more likely the mechanism that allows native fish to persist in streams during flood events.

Introduction

Many native fishes in the southwestern United States have experienced dramatic declines in number and distribution because of interactions with nonnative species (Moyle et al. 1986, Minckley & Douglas 1991). In canyon-bound streams, flooding may be responsible for the persistence of some native species in the presence of established nonnative fish populations. Floods can dramatically alter the structure of fish assemblages in streams (Harrell 1978, Harvey 1987, Collins et al. 1981). Minckley & Meffe (1987) sampled southwestern streams in canyon areas before and after flood events and documented a change in species composition from a mixture of native and nonnative species before flooding to predominantly native species after these flood events. They hypothesized that lower

displacement of native fishes during floods corresponds to an evolutionary history in streams where fishes were subject to wide fluctuations in discharge and velocity. The mechanism by which nonnative fishes appear to be disproportionately removed is not clearly understood. Differences in swimming ability or behavioral responses to high water velocities may be the mechanism responsible for observed patterns of differential removal.

Laboratory swimming performance tests were conducted on eight native and four nonnative fish species (Table 1) that are commonly found in Arizona streams. Literature on the swimming ability of many fishes exists, but testing procedures are variable, which makes comparisons among species difficult. Results often can be influenced by the testing methods used (Farlinger & Beamish 1977, Beamish 1978) and by differences in

Table 1. Number, status, total length, start velocity and swimming duration of fish tested in a laboratory swim chamber.

Species code Scientific name	Status	Number	Total length (mm)		Start velocity cm s ⁻¹	Swim duration Mean (min)
			Mean	Range		
GAAF <i>Gambusia affinis</i>	Nonnative	22	41.6	37.5–44.9	22	33.08
POOC <i>Poeciliopsis occidentalis</i>	Native	22	40.5	36.6–42.0	22	30.36
AGCH <i>Agosia chrysogaster</i>	Native	22	69.2	61.2–79.5	46	52.28
CACL <i>Catostomus clarki</i>	Native	17	69.7	70.3–74.8	54	61.47
CADI <i>Catostomus discobolus</i>	Native	16	71.3	61.5–81.5	54	42.01
CAIN <i>Catostomus insignis</i>	Native	23	71.3	62.2–79.8	46	25.18
CYLU <i>Cyprinella lutrensis</i>	Nonnative	26	68.9	62.7–75.3	54	41.39
MEFU <i>Meda fulgida</i>	Native	21	60.6	55.2–64.7	54	35.50
LECY <i>Lepomis cyanellus</i>	Nonnative	20	70.2	63.0–79.2	30	32.40
PIPR <i>Pimephales promelas</i>	Nonnative	23	68.7	65.2–73.2	54	30.78
RHOS <i>Rhinichthys osculus</i>	Native	19	68.4	61.0–83.0	46	43.64

fish size or water temperature (Bams 1967, Otto & Ohararice 1974, Ward et al. 2002b). We conducted our swimming tests at similar sizes and temperatures; so relative swimming ability among species could be compared. The objectives of this study were to evaluate physiological and behavioral differences in swimming ability that may explain the differential displacement of fishes during floods.

Methods

We used a backpack electrofishing unit to capture fish from the Colorado, Gila, Little Colorado, Verde and Santa Cruz Rivers in Arizona from September 2001 to January 2002. We transported 16–22 individuals of each species (Table 1) to the Environmental Research Laboratory in Tucson, Arizona, and held them in 0.5 m³ recirculating tanks at 20°C (±2°C). We held all fish for at least 24 h to recover from capture and transport. Fish tested were of similar length (mean = 70 mm TL), except for Gila topminnow *Poeciliopsis occidentalis* and mosquitofish *Gambusia affinis*, which differed in length from other species, but were similar in length to

each other (mean = 41 mm TL). We tested fish within 72 h of capture because Ward et al. (2002b) found that fish held in captivity for extended periods of time had reduced swimming ability. We tested all fish at 20°C (±1°C), which is within the normal thermal range for all of the selected species (Valdez & Carothers 1998).¹

We used a recirculating swim tunnel (Ward et al. 2002a) to assess swimming ability. A centrifugal pump circulated water between two 150 l reservoirs through a 50 × 7.5 cm² clear acrylic tube that formed the swim chamber. We controlled flow with a gate valve on the pump outlet. A flow meter, fixed near the exit of the swim chamber measured water velocity to within 1 cm s⁻¹. We tested two fish of the same species at one time because Bulkley et al. (1981)² found no difference in swimming ability among native Colorado River fishes tested singly or in pairs. We initiated tests

¹ Valdez, R.A. & S.W. Carothers. 1998. The aquatic ecosystem of the Colorado River in Grand Canyon. SWCA Inc., Environmental Consultants, Flagstaff, AZ.

² Bulkley, R.V., J.C.R. Berry, R. Pimental & T. Black. 1981. Tolerance and preference of Colorado River endangered fishes to selected habitat parameters. Final completion report. Utah Cooperative Fishery Research Unit, Logan. 83 pp.

by placing two fish of the same species into the swim chamber for 10 min at 75% of the average failure velocity determined from several pilot trials. This 10 min period allowed fish to recover from handling and acclimate to the swim chamber. We used a stepwise increase in water velocity of 4 cm s^{-1} every 5 min until failure occurred or the maximum swim tunnel velocity of 96 cm s^{-1} was reached. Fish that became pinned against the downstream screen and remained motionless for 10 s were scored as a failure and removed. Our methods ensured that all fish swam for about 30 min within the swim chamber (Table 1). We measured the total length (TL) of each fish after testing and noted behaviors associated with ability to resist high water velocities. We used two sample *t*-tests to compare lengths and mean failure velocity between *Gila topminnow* and mosquitofish. We used analysis of variance, with a Tukey–Kramer procedure to control for multiple comparisons, to compare lengths and mean failure velocities among all other species tested.

Results

Mean TL length of mosquitofish (41.6 mm TL) and *Gila topminnows* (40.5 mm TL) were not significantly different ($p = 0.136$). Mean length of spinedace *Meda fulgida* (60.9 mm TL) was smaller than the other species tested. All other species tested had similar mean length (70 mm TL) ($p > 0.05$, Table 1). Mean failure velocity was similar for *Gila topminnows* (36.5 cm s^{-1}) and mosquitofish (38.5 cm s^{-1}) ($p = 0.185$, Figure 1).

Mean failure velocity for nonnative red shiners *Cyprinella lutrensis* (77.5 cm s^{-1}) and fathead minnows *Pimephales promelas* (69.1 cm s^{-1}) were similar to failure velocities for native longfin dace *Agosia chrysogaster* (73.5 cm s^{-1}), speckled dace *Rhinichthys osculus* (70.4 cm s^{-1}) and spinedace (75.3 cm s^{-1} , Figure 2). Green sunfish *Lepomis cyanellus* had significantly lower failure velocity (46.2 cm s^{-1}) than native longfin dace, speckled dace, spinedace and Sonora suckers *Catostomus insignis* (55.9 cm s^{-1}).

Catostomids exhibited large differences in their ability to withstand high water velocities (Figure 2). Mean failure velocity of desert suckers *Catostomus clarki* (93.1 cm s^{-1}) and bluehead suckers *C. discobolus* (86.62 cm s^{-1}) were significantly higher than Sonora suckers and failure velocities reported for flannelmouth suckers *C. latipinnis* (45.8 cm s^{-1}) (Ward et al. 2002b). Our estimates of the ability of desert suckers and bluehead suckers to withstand high water velocities were

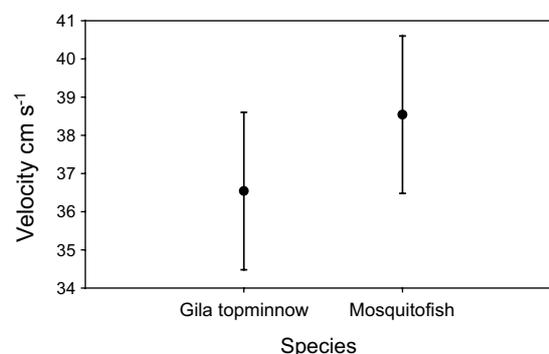


Figure 1. Relative swimming ability of *Gila topminnow* and mosquitofish of similar size. Each point is the mean velocity for which that species failed to maintain position in laboratory swimming tests. Error bars indicate 95% confidence intervals around the mean failure velocity.

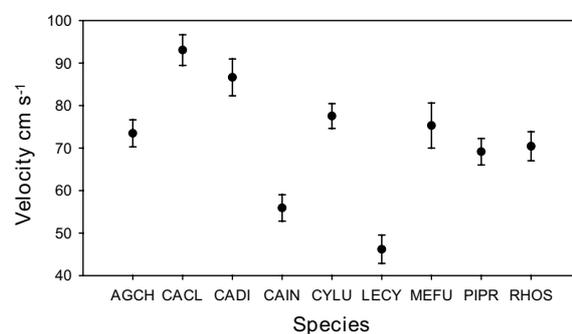


Figure 2. Relative swimming ability of six native and three non-native fish species of similar size commonly found in Arizona streams. Each point is the mean velocity for which that species failed to maintain position in laboratory swimming tests. Error bars indicate 95% confidence intervals around the mean failure velocity. See Table 1 for species code abbreviations.

low because 88% of desert suckers and 31% of bluehead suckers tested did not fail at the maximum velocity of our swim tunnel (96 cm s^{-1}), so data for desert suckers and bluehead suckers did not represent true failure velocities.

The reported velocities for desert suckers, bluehead suckers and speckled dace were not measures of swimming alone, but a combination of swimming and specialized behavior. All of the desert suckers that we tested and 81% of the bluehead suckers tested repeatedly used their mouths to suction onto the tunnel bottom and avoid swimming as water velocities increased. Of the 19 speckled dace tested, 47% were observed to

position their pectoral fins so that water passing over them would push them against the tunnel bottom and allow them to maintain position within the tunnel for several seconds at a time without swimming.

Discussion

Our velocity tests were not meant to mimic all the characteristics of a natural flash flood, but these tests do indicate relative differences in physiological ability to withstand high water velocities during flood events. Our results also provided insight into behavioral mechanisms that may be responsible for observed patterns of differential displacement and habitat partitioning among stream dwelling fishes.

Red shiners, fathead minnows and green sunfish often are reduced in number during flood events in southwestern streams (Harrel 1978, Minckley & Meffe 1987, Schultz et al. 2003). However, our results indicated that red shiners and fathead minnows had equal or greater swimming ability than many of the native species tested. A mechanism other than low swimming ability might be responsible for the disproportionate removal of these fishes during flooding. Despite the low ranking of green sunfish in our tests, they have been able to persist in numerous unregulated southwestern streams, including certain canyon-bound reaches (Dudley & Matter 1999).

We noted no physiological differences in swimming ability between Gila topminnow and nonnative mosquitofish. Meffe (1984) and Minckley & Meffe (1987) observed that Gila topminnows quickly oriented to high flows and held position in low velocity areas in response to simulated flash floods, whereas mosquitofish often ventured into midstream areas and were displaced. The observations of Meffe (1984) and Minckley & Meffe (1987) further indicate behavioral responses to high flows and not differences in physiological swimming ability likely are responsible for differential displacement of mosquitofish over Gila topminnow.

Although, in general, failure velocity of nonnative and native fishes of similar size was comparable in our study, differences in swimming ability related to fish size may play a role in the pattern of disproportionate removal of nonnative fish during flooding. Harvey (1987) found that susceptibility to displacement rapidly declined as fish size increased, and that the effects of floods on stream fish communities can depend on

small differences in the timing of reproduction and fish size.

Morphology significantly influences swimming capabilities among fish species (Peake et al. 1997). Desert suckers and bluehead suckers used their mouths to suction onto the bottom of the swim chamber and avoid loss of position. This behavioral response to elevated water velocities allowed them to withstand significantly higher velocities than other species that were tested. The suctioning behavior in bluehead suckers has been observed in natural populations while snorkeling in Havasu Creek in Grand Canyon National Park, Arizona. Desert suckers and bluehead suckers are commonly found in higher velocity areas than many other species (McAda 1977, Rinne & Stefferud 1996, Holden & Abate 1999).³ Desert suckers and bluehead suckers have disc-shaped lips and cartilaginous sheaths on the jaws for grazing algae and diatoms from rocks (Minckley 1973, Sublette et al. 1990). These mouth structures in combination with bodies that are rounded above and flattened below may permit desert and bluehead suckers to maintain position and feed in high velocity areas that would require large energy expenditures for other species.

Speckled dace avoided swimming at high water velocities by positioning their pectoral fins against the bottom of the swim tunnel, allowing them to maintain position for several seconds at a time without swimming. Many benthic fishes use body and fin shape to increase downward friction and hold position (Adams et al. 1997, 1999, Webb et al. 1996). Fingerling Atlantic salmon *Salmo salar* also anchor themselves in stamina tests by keeping pectoral and anal fins in contact with the tunnel bottom (Peake & McKinley 1998, Brett 1967). Use of pectoral fins to press against the bottom and a streamlined body shape may permit speckled dace to utilize high velocity areas and avoid displacement during flood events. This behavior did not allow speckled dace to withstand significantly higher velocities than other species in our laboratory tests but may confer energetic advantages on natural substrates.

Strong selection pressure to maintain position during floods and exploit high velocity areas, may have resulted in the behaviors and morphological adaptations seen in desert sucker, bluehead sucker and speckled dace. The lack of large physiological

³ Holden, P.B. & P.D. Abate. 1999. Fisheries survey of the lower Virgin River, Beaver Dam Wash, Arizona to Lake Mead, Nevada. Bio/West, Inc., Logan, UT.

differences in swimming ability in the other species we tested support Meffe's (1984) conclusion that behavioral differences between native and nonnative species is the mechanism primarily responsible for the observed patterns of differential removal of native and nonnative fishes during floods. Some species may have adaptive behavioral mechanisms we were unable to observe within the confines of a laboratory setting. Observations of fish behavior in the field during actual or simulated flood events may reveal additional behaviors native fishes use to avoid displacement during floods.

Variations in hydraulic conditions during flood events often restructure fish communities only temporarily. Nonnative fishes often quickly re-invade systems from which they have been displaced (Minckley et al. 1977, Meffe 1984). Where differential displacement of native and nonnative fishes naturally occurs, the creation of barriers to upstream fish movement may reduce recolonization of nonnative species. Dam outflows on regulated streams could also be manipulated to mimic natural flood events and displace nonnative fishes. The effects of such releases would depend on the magnitude and timing of the release as well as downstream channel characteristics (Minckley & Meffe 1987). Although flooding may impart only short-term advantages to native fishes it may still be useful as a conservation tool.

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