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12. Differential Selection by Flooding in Stream-Fish Communities of the Arid American Southwest

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Abstract

Nonnative fishes introduced into unregulated streams of arid, mountainous regions in Arizona and New Mexico are unable to resist flooding and are significantly reduced in numbers or destroyed. Native fishes show little if any response to such events; species composition and population sizes are similar before and following major floods. Differential responses reflect differences in evolutionary histories. Native faunal elements have long been subjected to vagaries of flashflooding in constrained channels and have capabilities to withstand such disturbances. Introduced alien fishes that evolved in mesic lowlands of other regions apparently do not.

Native ichthyofaunas of North America west of the Rocky Mountain axis are depauperate and unique, consisting largely of geographic relicts, monotypic genera, and endemic species (Miller, 1959). Relatively few fishes have become adapted to the natural rigors of aquatic systems in this region. The vast, rugged area between the Rockies and the Sierra Nevada, south of the Columbia and Klamath rivers and north of the U.S.-Mexico boundary, supports only about 75 species of native fishes; 43 (57%) of these are endemic to a single drainage, and 18 (21%) are at one locality each (Minckley et al., 1986). Although the area with which we are specifically concerned, Arizona and New Mexico west of the Continental Divide, has only 37 recognized species and subspecies, 4 are members of monotypic genera, and 14 (38%) are endemic (Minckley, 1973, 1985). Surviving species are (1) those that have evolved generalizations that promote remarkable resistance to extinction, (2) specialized inhabitants of long-existing habitats such as thermal springs or highly erosive streams, or (3) those suited for particular modes of life through preadaptation to factors such as high temperature or salinity (Hubbs, 1941; Miller, 1959, 1961; Deacon and Minckley, 1974; G. R. Smith, 1978, 1981; M. L. Smith, 1981; Minckley et al., 1986).

Habitat alteration and an influx of introduced fishes are resulting in reduction or extirpation of much of this native southwestern fauna (Miller, 1961 et seq.; Minckley and Deacon, 1968; Deacon, 1968, 1979; Miller and Pister, 1971; Minckley, 1973, 1985; Moyle, 1976a; Pister, 1974 et seq.; Soltz, 1979; Deacon et al., 1979; Williams, 1981; Meffe, 1983, 1985; Meffe et al., 1983; Rinne and Minckley, 1985;

Williams et al., 1985). At least four species and six subspecies of fishes in six genera have become extinct in the last 40 years as a result of human-induced disturbance (Pister, 1981). Of 67 fishes in the United States listed as threatened or endangered, 45 (67.2%) live in arid zones (James E. Johnson, U.S. Fish and Wildlife Service, pers. comm.). The insular nature of the distributions of native desert fishes, with restricted ranges and few to no colonization pathways between populations (e.g., MacArthur, 1972), makes them particularly susceptible to local extinction.

On the other hand, more than 140 fish species have been successfully established outside their native ranges in North America for sport, forage, biological control, aquaculture, and hobby interests and by accident (Moyle, 1976b, 1985). We apply terminology for nonnative fishes recommended by Shafland and Lewis (1984) where appropriate; most of these in the American Southwest would be considered transplants, originating in the Mississippi or other mesic lowland drainages of the United States, but others are exotics from Eurasia, Central America, and Africa (Minckley, 1973; Moyle 1976a; Courtenay et al., 1984). The terms "introduced" or "nonnative" are applied to both these categories. Many of these animals have been dispersed by humans and thus are less restricted than native forms by natural or artificial barriers. As a result, southwestern stream-fish communities have been and are being transformed from native faunas to mixed native-nonnative associations, or in some cases to entirely introduced assemblages (Minckley, 1973, 1979a, 1982, 1985; Moyle and Nichols, 1973, 1974; Moyle,

1976a, b; Taylor et al., 1984; Marsh and Minckley, 1982, 1985; Moyle et al., in press).

Successful introductions are usually associated with construction of artificial habitats, particularly creation of lentic conditions in impoundments and regulation of rivers by dams that change violent, flood-prone systems to calm, mildly fluctuating lakes with stabilized downstream flows. Regulation of the Colorado and other western rivers not only reduces fluvial habitats for native fishes but also enhances an amazing diversity of introduced groups, including clupeids, salmonids, cyprinids, catostomids, ictalurids, poeciliids, centrarchids, percichthyids, percids, and cichlids (Minckley, 1973, 1979a; Moyle, 1976a, b, in press). Mainstream impoundments and lesser lentic habitats, including recreational lakes and livestock ponds, also act as refuges for these fishes, from which they move both upstream and downstream.

Replacement of native species occurs most often and rapidly in impoundments. Moyle (1976b) noted that reservoirs are "hard on the native [California] fish fauna because they favor lake-adapted introduced species over native stream-adapted forms." Native Sacramento squawfish (*Ptychocheilus grandis*) and hardhead (*Mylopharodon conocephalus*) tend to "disappear from reservoirs after an initial five or ten years of abundance." He also noted a few native species that were enhanced by reservoirs, a situation not yet seen in the Colorado River system. With minor exceptions native fishes have not colonized Arizona impoundments. Certain markedly long-lived forms, razorback sucker (*Xyrauchen texanus*), bonytail chub (*Gila elegans*), and Colorado squawfish (*Ptychocheilus lucius*), persist for as long as 30 or more years without successful recruitment in reservoirs of the lower Colorado system and then decline toward local extinction (Miller, 1961; Minckley, 1983; McCarthy, 1986).

Variations on Trends of Species Replacement

Unlike predictable patterns in highly altered habitats, substantial variations exist both in extent and rapidity with which nonnative fishes replace indigenous forms in relatively natural southwestern drainages. Often environmental factors exclude introduced fishes and thus protect natural faunal elements. For example, temperatures greater than 36°C and dissolved oxygen less than 1 mg/l in some Nevada springs exclude nonnative forms but are tolerated by endemic springfishes (*Crenichthys baileyi*, *Crenichthys nevadae*) (Hubbs and Hettler, 1964; Hubbs et al., 1967; Deacon and Wilson, 1967; Courtenay et al., 1985). Similarly, moapa (*Moapa coriacea*) and desert dace (*Eremichthys acros*) live in water hot enough (more than 34°C) to be avoided by most introduced fishes (Hubbs and Miller, 1948; Nyquist, 1963; Deacon and Bradley, 1972). Desert pupfish (*Cyprinodon macularius*) were formerly abundant in the Salton Sea, California (Coleman, 1929; Cowles, 1934; Barlow, 1961), where they successfully occupied shore pools (Barlow, 1958a) in which salinities of 80 to 90 gm/l excluded other species. Their ova develop and hatch (with various rate and structural consequences) in salinities up to 70 gm/l, depending somewhat on temperature (Kinne, 1960; Kinne and

Kinne, 1962a, b; Sweet and Kinne, 1964). Such extremes in salinities, as well as temperatures varying more than 20°C in a single day and to maxima greater than 38°C (Barlow, 1958a, b), until recently shielded the species from interactions with introduced forms. However, equally tolerant sailfin molly (*Poecilia latipinna*) and exotic cichlids (*Oreochromis* sp., *Tilapia zilli*) are now abundant. Desert pupfish have virtually disappeared (Crear and Haydock, 1971; Fisk, 1972; Schoenherr, 1979; Black, 1980) and are proposed to be listed as endangered (U.S. Department of the Interior, 1984).

More difficult to explain are situations where little or no replacement has occurred over decades in natural or semi-natural streams, while dominance by introduced fishes was achieved in nearby regulated watercourses in only a few years. Natural flooding provides the most evidence for slowing or precluding establishment of aliens. Unique characteristics of stream segments also seem to affect species replacement. Native fishes persist in canyon-bound segments of both regulated and unregulated systems far longer than in other reaches. Species differences further exist, with river-adapted nonnative species enjoying more success than others.

We document that nonnative fishes that evolved under lowland, mesic conditions as a rule do poorly under natural southwestern flooding regimes and argue that this is due to fundamental differences in runoff patterns as contrasted with those of mesic lowlands. This phenomenon is attributed to differences in selective pressures associated with historic conditions of flooding over evolutionary time.

Contrasts in Flood Hydrology

Floods of southwestern arid lands differ qualitatively and quantitatively from those of lowland mesic regions owing to fundamental differences in geology, physiography, and climate (Hoyt and Langbein, 1955; Leopold et al., 1964; Fogel, 1981; Crosswhite and Crosswhite, 1982). The American Southwest is geologically active and mountainous, and watercourses are strongly influenced by local and regional relief. Watersheds are large, sparsely vegetated, and discretely divided, occupying steep valleys cut through uplifts and high plateaus. Precipitation is in the form of rainfall except at the highest elevations in winter and, although low in average amount, often falls as a few major storms a year.

High-intensity precipitation of summer monsoons can particularly result in abrupt and almost complete runoff into stream channels, increasing discharge by three or more orders of magnitude in seconds or minutes (Burkham, 1970, 1976a). A clearly defined frontal wave often leads a flash-flood, followed by high and variable discharges that last from a few minutes to several hours and rapidly subside. A channel is transformed almost instantaneously from a dry wash or intermittent stream to a torrent, returning to its former state almost as quickly (Ives, 1936; Wooley, 1946; Jahns, 1949; Lewis, 1963; Deacon and Minckley, 1974; Cooley et al., 1977; Harrell, 1978; Fisher and Minckley, 1978; Collins et al., 1981; Fisher et al., 1982). Geographically generalized and protracted winter precipitation results in scouring floods

only when it is of unusual magnitude, as when augmented by warm rains melting snowpacks or falling on saturated land surfaces (Forbes, 1902; Olmstead, 1919; Burkham, 1970, 1976b).

Floods passing over impermeable bedrock and constrained by steep canyon walls cannot dissipate energy through overflow, infiltration, or straightening and widening of alluvial channels, and their destructiveness is amplified (Leopold and Maddock, 1955; Bull, 1979, 1981). Degradation and removal of terraces and mobilization and transport of large quantities of inorganic material, often of boulder size, are characteristic (Jahns, 1949; Kesseli and Beaty, 1959; Melton, 1965; Thomson and Schumann, 1968). Accompanying phenomena are transport of organic materials ranging from fine-ground detritus to mature riparian trees (Forbes, 1902; Rinne, 1975; Burkham, 1976b; Minckley and Clark, 1984; Minckley and Rinne, in press), sudden decreases in water temperature by 15°C or more (Deacon and Minckley, 1974), and rapid fluctuations in other physical and chemical parameters (Fisher and Minckley, 1978; Minckley, 1981; Rampe et al., 1985).

In contrast, most mesic watersheds have low relief, deep soils, and dense vegetative cover. **Drainage** channels meander, have low gradients, and are far less distinct, and broad floodplains extend laterally many times the widths of streams (Leopold, 1962). **Floods** are cumulative discharge events that take hours or days to peak and an equally long time to subside. Floodplain river lakes (Welcomme, 1979) or smaller pools (Halyk and Balon, 1983) are formed behind natural levees, in depressions, and in oxbows and serve as refugia for fishes escaping high discharges. Canyon and bedrock constraints are absent or minimal. High discharges spread and infiltrate with reduced energy over and into adjacent floodplains (Hoyt and Langbein, 1955; Leopold et al., 1964).

We chose for hydrologic comparison 5 unregulated **Arizo-**

Table 12.1. Geographic Relief of Some Mesic- and **Arid-Zone** (Arizona) Streams

Locality	Maximum Relief* (m)	Gradients (m/km)
Mesic zones:		
Mississippi River, near Saint Francisville, La.	4.6	0.03
White River, White River National Wildlife Refuge, Ark.	43.1	0.06
Saint Francis River, near Widener, Ark.	61.5	0.08
Mississippi River, Ky.	90.1	0.06
Licking River, near Visalis, Ky.	146.2	0.18
Marais des Cygnes River, near Ottawa, Kans.	270.8	0.52
Des Moines River, near Boone, Iowa	273.8	0.39
Wakarusa River, near Wakarusa, Kans.	297.3	0.84
Neosho River, near Neosho Falls, Kans.	292.3	0.52
Little Blue River, near Hanover, Kans.	360.0	0.51
Arid zones:		
Sycamore Creek, near Ft. McDowell, Ariz.	541.5	8.83
Salt River, above Lake Roosevelt, Ariz.	701.5	3.09
Aravaipa Creek, near Klondyke, Ariz.	873.2	14.58
Bonita Creek, near Gila River, Ariz.	1,009.2	8.67
Eagle Creek, near Morenci, Ariz.	1,156.9	5.14

*Maximum vertical distance from river surface at median discharge to highest adjacent terrain at area measured.

na streams and 10 streams of the Mississippi River basin. Data for each, including stream gradients, channel widths, and canyon profiles, were derived from appropriate U.S. Geological Survey topographic maps. The term *channel* denotes that part of the system scoured of perennial vegetation by flooding, while *floodplain* includes nonscoured alluvial fill (Burkham, 1972). *Stream* includes the channel portion occupied by water during modal discharge.

Gradients of southwestern streams are one to two orders of magnitude greater than in those of mesic lowlands (table 12.1). Overall relief is also far greater as a result of rugged terrain. Channel cross sections (fig. 12.1) illustrate the con-

Figure 12.1. Representative channel cross sections from North American mesic and arid-zone streams; scales for the latter have been enlarged for clarity. Vertical notches indicate boundaries of channels.

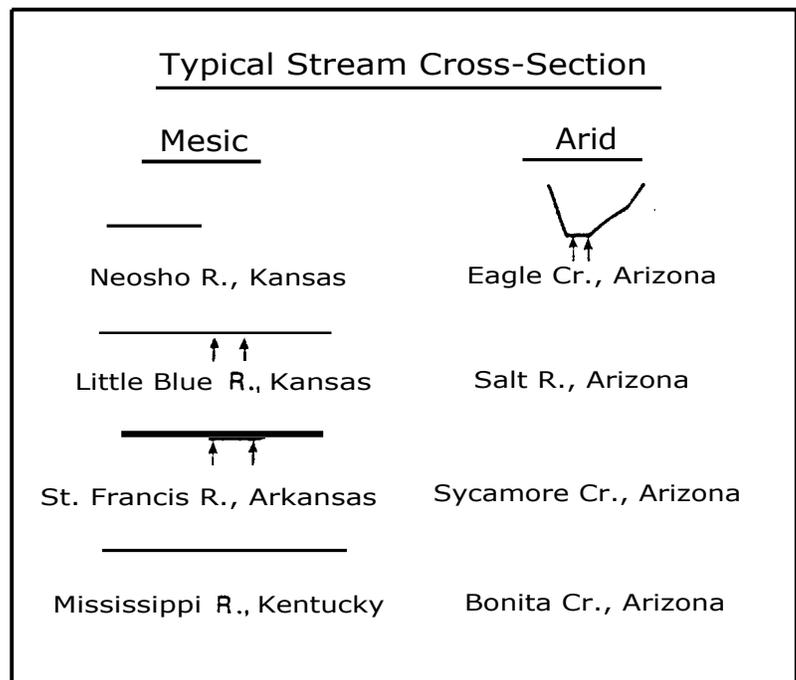


Table 12.2. Summary of Gross Characteristics of Southwestern Arid-Land and Mesic Streams

Zone	Cross Section	Stream Gradient	Substrate	Competency	Flood Onset	Permanency	Available Refugia
Mesic zones	Generally unconstrained, broad floodplains	Low	Fine-grained, organic	Generally low	Slow—hours, days	Highest downstream	Floodplains, extensive interconnections with marshlands
Arid lands	Constrained by canyon walls	High	Coarse-grained, inorganic, or bedrock	Often high	Rapid—seconds, minutes	Highest in mid-reaches	Streamsides, eddies behind obstructions

strained nature of these systems, with an almost complete lack of floodplains, particularly in canyon-bound reaches. Other contrasts and a summary of discharge differences appear in table 12.2.

We also compared discharge patterns of several Arizona watercourses and three streams of the Suwannee River drainage of Florida and Georgia, the last chosen on the bases of "typical" mesic characteristics, similarity of watershed areas to Arizona systems, and record availability. Records for the following streams were examined (years of record and watershed areas in parentheses): Arizona—Santa Cruz River near Lochiel (1950-75; 213 km²), Aravaipa Creek near Mammoth (1920, 1932-42, and 1967-75; 1,401 km²), Gila River near Safford (1941-46 and 1957-65; 20,451 km²); Florida—Santa Fe River near Graham (1971-81; 246 km²), Santa Fe River at Worthington Springs (1971-81; 1,507 km²), and Suwannee River at Ellaville (1971-81; 17,742 km²). Data reported as mean instantaneous discharge per day in ft³/sec were converted to m³/sec. A set of these records is included as fig. 12.2 to illustrate seasonal patterns of flashflooding. Such means obviously tend to minimize peak flows, particularly in southwestern systems where floods are rapid and of short duration; a massive 10-min flow may be almost unrecognizable. The data are thus conservative with respect to discharge extremes.

Mean annual discharge patterns were developed by summing numbers of days at each discharge level on a log scale. For example, total days a stream flowed at or less than 0.003, 0.006, 0.009, ..., 0.03, 0.06, 0.09, ..., 0.3, 0.6, 0.9, ..., 3, 6, 9, ... etc., m³/sec were tallied. An index of total volume discharged was computed by multiplying number of days at a

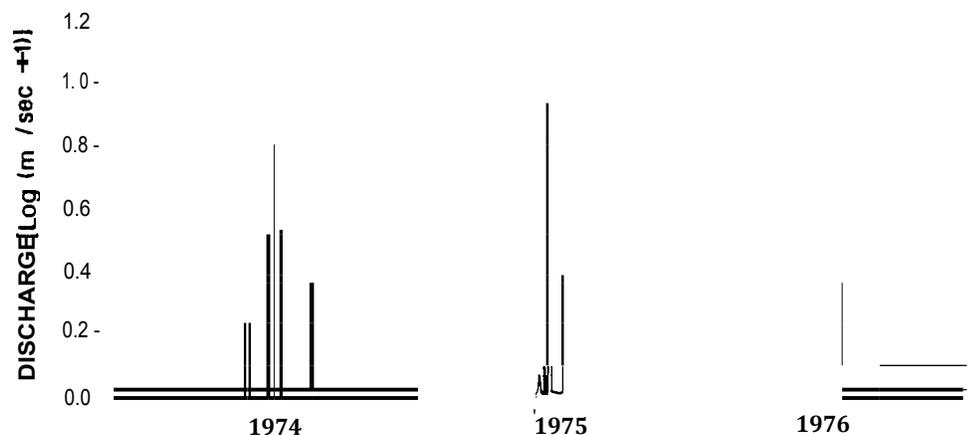
given discharge by the latter and summing over the period of record. Cumulative curves of number of days at each discharge level and total runoff (total water yield of the watershed per unit time) owing to a particular discharge were developed and contrasted for arid land and mesic watersheds of comparable size (fig. 12.3). The more widely two curves are separated, the greater the unevenness of discharge for a given watershed.

In aggregate these curves demonstrate a prevalence of high discharges producing most of the annual water yield in brief periods of time in southwestern systems, while low discharges produced a far greater proportion of total yield from mesic watersheds. For example, discharge 38% of the time was 0.03 m³/sec in the Santa Cruz River, Arizona, which accounted for only ca. 0.5% of total water yield. Discharge 0.3 m³/sec almost 84% of the time accounted for only 9% of the total. The upper 50% of total water yield occurred at greater than 7.5 m³/sec in only 0.6% of the total time. In contrast, the two curves for Santa Fe River near Graham, Florida, are nearer together. The upper 50% of total water yield occurred in 9% of the time, 15 times greater than that necessary for an equivalent percentage of total yield in the arid-land system.

Selective Pressures on Riverine Fishes

It is reasonable to suspect from fundamental differences between arid-zone and lowland mesic streams that biotic elements are under contrasting hydrologic selection pressures. It is established that fishes of mesic drainages make use of inundated floodplains during floods, either to avoid

Figure 12.2. Discharge in the Santa Cruz River, Arizona, from 1974 through 1976. Data are daily instantaneous means and illustrate the seasonal and "flashy" nature of arid-land stream discharge.



Differential Selection by Flooding in Stream-Fish Communities

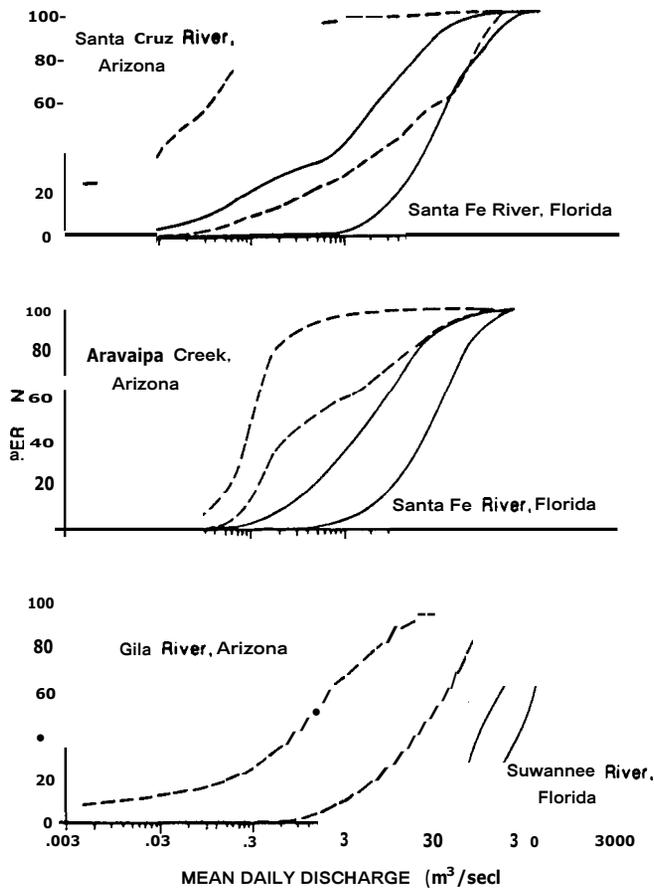


Figure 12.3. Cumulative discharge patterns for selected North American arid-land (dashed line) and mesic (solid line) streams of different discharges but similar watershed sizes. The lower curve for each watercourse is cumulative percentage of total yearly discharge owing to each daily discharge rate; the upper curve is cumulative total percentage time flowing at each daily discharge. Compiled from U.S. Geological Survey (published periodically). See text for further explanation.

physical conditions of the channel or for feeding, reproduction, and nursery areas (Guillory, 1979; Welcomme, 1979; Halyk and Balon, 1983; Ross and Baker, 1983). Even those fishes that remain in flooded channels and do not resist transport are merely moved to larger, more permanent, and perhaps more stable downstream habitats (Horton, 1945; Starrett, 1951; Strahler, 1957; Hynes, 1970; Horwitz, 1978; Vannote et al., 1980), which provide refuge during environmental extremes (Paloumpis, 1956, 1958). Strong selection for lowland mesic fishes to maintain position at discharges greater than the mode should therefore be minimal.

In contrast, arid-zone fishes often cannot avoid high discharges by movement onto floodplains, particularly in reaches constrained by bedrock canyons. Furthermore, there is evidence that native fishes concentrate in canyons in summer despite dangers of high water, presumably to avoid elevated water temperatures in shallower, unshaded segments (Siebert, 1980) and to take advantage of greater permanency in bedrock pools. It is sorely disadvantageous for

these fishes to move or be carried downstream, as many arid land watercourses desiccate long before reaching master streams except in periods of major runoff (John, 1964; Deacon and Minckley, 1974; Constantz, 1981; Minckley, 1981; Minckley and Brown, 1982). High-volume, short-term floods produce downstream discharges for only a relatively few moments in time. Such spates percolate into coarse alluvial fans of smaller systems or finer-grained but extensive deposits of larger rivers. Infiltration coupled with spreading over terminal alluvial deposits or into saline waters of intermontane basins (Deacon and Minckley, 1974) and evapotranspiration that often exceeds 2 m/y cause floodwaters to disappear in minutes or hours (Burkham, 1976c). Fishes transported or swimming downstream are stranded and die. Substantial selection pressure must therefore exist for southwestern stream-dwelling organisms to maintain position during high discharges.

Apparent morphological adaptations of some fishes to swift and/or turbulent flow may reflect this phenomenon. Several cyprinids and catostomids that inhabit larger, severely flooding waters have depressed skulls and keeled or humped napes, huge buttressed fins, narrow caudal peduncles, slim bodies, and reduced scales, all of which tend to reduce drag and presumably improve swimming ability in fast and turbulent currents (Hubbs, 1941; Vogel, 1981; Minckley, 1973). Other aquatic animal groups in the region have comparable adaptations in morphology, behavior, and/or life-history characteristics (Bruns and Minckley, 1980; Gray, 1980, 1981; Fisher et al., 1982; Gray and Fisher, 1981; Jackson, 1984).

Flood Effects on Southwestern Fishes

Native fishes resist floods by maintaining position in or adjacent to channel habitats, persisting in microrefugia, or rapidly recolonizing if displaced. Nonnative fishes that evolved under regimes of mesic lowlands respond to flooding in their natural habitats by movement into floodplain or other refugia or downflow movement or transport. In erosive western streams the latter are frequently displaced and destroyed. Data supporting these claims are of three types: (1) a series of samples before and after major floods of known magnitudes that illustrate differential removal of alien fish species in Arizona and New Mexico streams, (2) detailed analyses of flood effects on two interacting Arizona fishes, one native and one transplanted, and (3) inferences from present distributional patterns of native and nonnative species elsewhere in the region.

Differential Effects of Flooding

Fish populations in seven unregulated and three regulated streams or stream reaches (fig. 12.4) were sampled before and after major floods in the period 1964 through summer 1985. Part of this information has been published or reported in agency documents (Barber and Minckley, 1966; Minckley and Clarkson, 1979; Minckley, 1981; Propst et al., 1985a, b), but a substantial proportion has not appeared elsewhere. Collections to be contrasted were chosen on the bases of (1) a substantial period (greater than six months) that did not

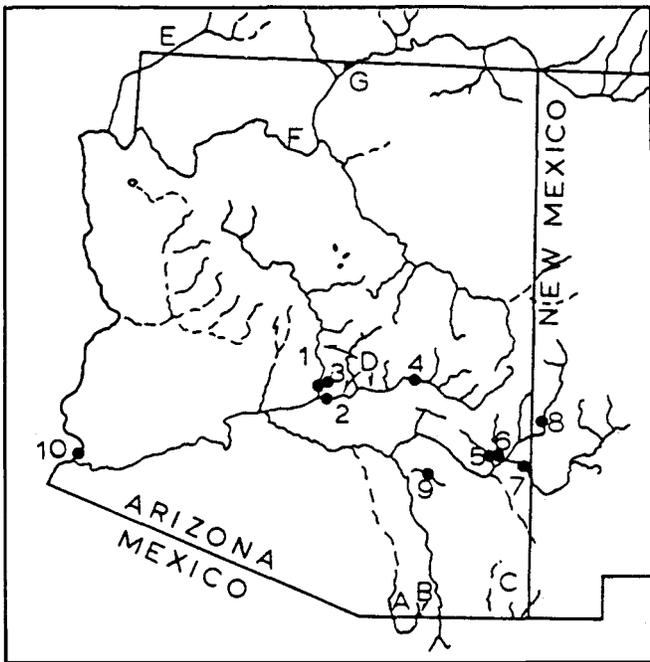


Figure 12.4. Map of Arizona and western New Mexico with major drainages. Sampling localities are 1: Verde River; 2: Salt River (regulated below controlling dams and above inflow of Verde River; 3: Sycamore Creek; 4: Salt River (unregulated, upstream from dams); 5: Bonita Creek; 6: Eagle Creek; 7: Gila River; 8: San Francisco River; 9: Aravaipa Creek; 10: lower Colorado River. Other localities mentioned in text include A: Santa Cruz River; B: Sharp Spring; C: Chiricahua Mountains; D: Salt and Verde river reservoirs; E: Virgin River; F: Grand Canyon of the Colorado River; G: Lake Powell.

include flooding before the first sample and (2) a short period of time (less than six weeks) between a flood event and a second sample from the same reach. Early examples (before 1975) were largely fortuitous in distribution relative to flooding, but for the past 10 years such events have been specifically evaluated for their **faunal** impacts. Floods were defined by their maximum instantaneous flows relative to mean discharges, as follows:

$$\text{Index of magnitude} = \frac{\text{Maximum instantaneous discharge,}}{\text{Mean discharge}}$$

where maximum discharges for individual events and means over the period of record ending in 1982 were those given by U.S. Geological Survey records (published periodically). When an event was extended with multiple peaks, the largest was used for computation of an index of magnitude.

The largest unregulated streams are Salt River, Arizona, and Gila and San Francisco rivers, Arizona and New Mexico (in part Brown et al., 1981; Minckley, 1985), upstream from major water-control structures. Perennial, intermediate-size streams include Eagle and Aravaipa creeks, in Arizona (Minckley, 1979b, 1981; Silvey et al., 1984). The last two

streams in the sample set are Bonita and Sycamore creeks, which are locally intermittent (Heindl and McCullough, 1961; Thomson and Schumann, 1968). All these watercourses are constrained by canyons through a substantial portion of their lengths. All support one or more native and introduced fishes. Regulated streams include the Salt and Verde rivers, in Arizona, downstream from impoundments, and the mainstream Colorado River, in Arizona-California (Minckley, 1979a, 1982, unpub. data; Marsh and Minckley, 1985).

Collections were by seines; gill, trammel, and hoop nets of various lengths and meshes; and electrofishing in all available habitats. Data for the Salt, Verde, and Colorado rivers are least reliable because of large habitat sizes. Pools greater than 10 m in depth and rapids with velocities greater than 1.5 m/sec defy effective sampling. Smaller streams were blocked and fishes removed and enumerated (Minckley, 1981). Fishes were identified (table 12.3) and released or preserved for later identification; representative specimens are in the Arizona State University Collection of Fishes. Samples before and after floods were compared for faunal composition and relative abundance. Terms for abundance when absolute numbers were not recorded in field notes were quantified for present purposes as follows: dominant = comprising 50% of a sample; abundant = 25%; common = 15%; scarce = 5%; and rare = 1%.

Fish faunas of canyon-bound reaches of unregulated streams invariably shifted from a mixture of native and nonnative species to predominantly, and in some instances exclusively, native forms after floods approaching or exceeding two orders of magnitude greater than mean discharge (table 12.3; fig. 12.5). Intermediate-size floods (those near one order of magnitude) depleted but rarely destroyed nonnative populations. Floods of less than one order of magnitude greater than mean discharge had no discernible effect on fish populations. Relationships between percentage increase in relative abundance of native species (declines in numbers of nonnative fishes) and declines in numbers of nonnative species were correlated with increasing magnitude of flooding; both are highly significant, while changes in native species with flood magnitude are not significant (fig. 12.5). Wider stream, channel, and/or floodplain segments often accumulate both native and nonnative fishes presumably displaced from canyons by major flooding, and the latter tend to persist in such places (Propst et al., 1985a). It is obvious from composition of samples taken before floods that drought periods and periods of "normal" flow separating flood events were characterized by increased incidence of nonnative fishes, resulting from reintroduction, redispersal, local reproduction by survivors, or other manner of appearance.

Among nonnative forms common carp (*Cyprinus carpio*) populations are substantially reduced by high-intensity flooding. This ubiquitous species is rarely abundant in unregulated systems, but large adults tend to be widespread. Red shiners (*Notropis lutrensis*) also are depleted or removed by flooding but rapidly reestablish substantial populations through survivors, reinaders from protected habitats such as reservoirs, or direct reintroduction. Red shiners are aggressively spreading (or being spread), despite restrictions on their use as baitfish and the existence of substantial deter-

Table 12.3. Differential Effects of Floods of Contrasting Magnitudes on Native Versus Nonnative Fishes in Some Unregulated and Regulated Streams of Arizona and New Mexico

No. Obs.	Magnitude of Flood Maxima	Native Fishes				Introduced Fishes	
		No. Species		% Total Fauna		No. Species	
		Before	After	Before	After	Before	After
Unregulated Reaches							
Salt River above Roosevelt (mean discharge [69 yr] 24.7 m ³ /sec)							
2	5.9 ± 1.21 (4.2-9.5)	5.5 ± 0.29 (5-6)	5 ± 0.17 (4-6)	67.5 ± 8.50 (50-90)	68.8 ± 10.78 (50-95)	4.3 ± 0.48 (4-6)	5.3 ± 0.48 (4-6)
7	29.7 ± 8.60 (11.6-78)	4.7 ± 0.18 (4-5)	4.9 ± 0.26 (4-6)	67.9 ± 7.30 (40-95)	72.9 ± 6.97 (45-90)	4 ± 0.44 (2-5)	2.4 ± 0.48 (1-4)
2	106.2 ± 3.65 (103-110)	4.5 ± 0.50 (4-5)	4	72.5 ± 7.50 (65-80)	100	4 ± 0.44 (3-5)	0
Gila River Near Safford (mean discharge [58 yr] 12.8 m ³ /sec)							
1	5.6	3	3	20	25	7	8
5	30 ± 9.10 (11.6-47.8)	2.2 ± 0.37 (1-3)	2 ± 0.32 (1-3)	19 ± 2.45 (10-25)	64 ± 12.39 (30-95)	5.2 ± 0.37 (4-6)	4 ± 0.55 (3-6)
1	221	1	2	15	95	5	3
San Francisco River at Clifton (mean discharge [58 yr] 5.58 m ³ /sec)							
4	22.5 ± 8.60 (12.8 -48.2)	3 ± 0.41 (2-4)	3	21.4 ± 2.39 (15-25)	32.5 ± 5.95 (20-45)	5.5 ± 0.29 (5-6)	3.8 ± 0.85 (2-6)
1	284.9	4	3	25	95	6	1
Eagle Creek at Morenci Pump Station (mean discharge [38 yr] 1.45 m ³ /sec)							
3	5.7 ± 1.41 (3.7-8.4)	4 ± 0.58 (3-4)	3.7 ± 0.33 (3-5)	31.7 ± 4.41 (25-40)	33.3 ± 7.31 (20-45)	5.3 ± 0.33 (5-6)	6 ± 0.58 (5-7)
4	37.35 ± 12.27 (13.5-66)	3.8 ± 0.25 (3-5)	3.5 ± 0.29 (3-4)	36.3 ± 5.54 (30-50)	48.8 ± 9.87 (20-65)	5.8 ± 0.48 (5-7)	4 ± 0.91 (2-6)
1	479	4	5	35	100	4	0
Aravaipa Creek near mouth (mean discharge [27 yr] 0.85 m ³ /sec)							
4	6.6 ± 1.02 (4.8-9.4)	6.5 ± 0.29 (6-7)	6.5 ± 0.29 (6-7)	98.8 ± 1.25 (95-100)	100	0.3 (0-1)	0
5	49.9 ± 12.94 (14.6-78)	6.4 ± 0.24 (6-7)	6.2 ± 0.20 (6-7)	98.0 ± 1.22 (95-100)	100	0.2 (0-1)	0
3	358.5 ± 102.4 (185.6-540)	6.3 ± 0.33 (6-7)	6	96.7 ± 1.67 (95-99)	100	(0-1) (0-1)	0
1	1,999.2	7	7	99	100	1	
Sycamore Creek near Fort McDowell (mean discharge [21 yr] 0.84 m ³ /sec)							
6	6.8 ± 1.08 (3.4-9.7)	1.5 ± 0.70 (1-3)	1.33 ± 0.21 (1-2)	87.5 ± 2.81 (75-95)	91.7 ± 2.47 (80-95)	1.5 ± 0.34 (1-3)	1.3 ± 0.21 (1-2)
3	39.3 ± 6.30 (30-51.3)	1.7 ± 0.67 (1-3)	1.7 ± 0.67 (1-3)	91.7 ± 3.33 (85-95)	99.33 ± 0.67 (98-100)	2 ± 0.58 (1-3)	0.3 (0-1)
4	397.7 ± 89.92 (174-504)	1.4 ± 0.24 (1-2)	1.6 ± 0.40 (1-3)	87 ± 2.63 (77-92)	99.2 ± 0.58 (97-100)	2.6 ± 0.24 (2-3)	0.6 (0-2)
Bonita Creek near mouth (estimated mean discharge [un gauged during study] 0.50 m ³ /sec)							
4	6.5 ± 1.40 (3.2-9.9)	4.3 ± 0.25 (4-5)	4.5 ± 0.29 (4-5)	68.3 ± 6.37 (60-75)	66.3 ± 6.25 (55-80)	4.3 ± 0.33 (4-5)	3.8 ± 0.63 (4-5)
4	62.5 ± 14.68 (24-90)	4.8 ± 0.25 (4-5)	4.3 ± 0.48 (4-5)	75 ± 2.35 (70-80)	93.3 ± 2.17 (85-100)	4.8 ± 0.25 (4-5)	2 ± 1 (1-5)
1	250	4	4	75	100	4	0
Regulated Reaches							
Salt River below Stewart Mountain Dam (mean discharge [52 yr] 26.2 m ³ /sec)							
5	3 ± 0.72 (1.6-5.8)	2.6 ± 0.24 (2-3)	2.8 ± 0.20 (2-3)	81.8 ± 2.60 (75-90)	84.6 ± 5.22 (70-95)	5 ± 0.32 (4-6)	4.8 ± 0.37 (4-6)
4	55.8 ± 14.3 (16-81.3)	2.3 ± 0.25 (2-3)	2.5 ± 0.29 (2-3)	72.5 ± 5.20 (60-85)	86.0 ± 4.56 (78-99)	7.5 ± 1.94 (5-13)	2.5 ± 2.10 (1-7)

Table 12.3. *Continued*

No. Obs.	Magnitude of Flood Maxima	Native Fishes				Introduced Fishes	
		No. Species		% Total Fauna		No. Species	
		Before	After	Before	After	Before	After
Verde River below Bartlett Dam (mean discharge [94 yr] 19.2 m ³ /sec)							
3	3.1 ± 0.89 (1.5-4.6)	3.7 ± 0.33 (3-4)	3.3 ± 0.33 (3-4)	61.7 ± 4.41 (55-70)	65 ± 0.86 (50-75)	6.7 ± 0.86 (5-8)	6.7 ± 1.67 (5-10)
1	149	3	4	65	97	11	3
Colorado River below Laguna Dam (mean discharge [12 yr] 9.10 m ³ /sec)							
1	>100	1	1	1.3	0.5	17	15

Note: Means are followed by ± one standard error; ranges are in parentheses. See text for further explanation.

*Discharges in regulated reaches normally depend on releases to satisfy domestic, irrigation, and/or power-generation demands; maximum instantaneous discharges of higher magnitudes are from uncontrolled or emergency releases.

†Data are from two sampling periods (November 1982, February 1983) immediately before a high-discharge event and two periods (August and November 1983) following; information for May 1983, a time of transition from low to high discharges, was excluded (Marsh and Minckley, 1985).

rence in the form of dams, naturally or artificially dried channels, and other barriers. Both golden shiners (*Notemigonus crysoleucus*) and fathead minnows (*Pimephales promelas*) are typically removed by floods, and rarely reappear unless reintroduced. Catfishes, with the exception of flathead catfishes (*Pylodictis olivaris*), are depleted by large floods. The stream-adapted flathead is, however, rapidly expanding its range and populations, despite physical impacts of flooding, barriers, and other factors. Poeciliid fishes (*Gambusia affinis*, *Poecilia latipinna*, and others) are decimated by flooding. Their high reproductive potentials allow rapid recovery, especially by mosquitofish, if some survive or are reintroduced. Mosquitofish are widely used by public health agencies in the control of pestiferous insects and often are stocked immediately following high waters. Centrarchids (largemouth and smallmouth basses [*Micropterus salmoides*, *M. dolomieu*] and green and bluegill sunfishes [*Lepomis cyanellus*, *L. macrochirus*]) seem highly susceptible to displacement in Arizona streams (see also Schlosser, 1985). Smallmouth bass and green sunfish are in part stream-adapted, however, and usually reappear in a few weeks. Exotic cichlids introduced into unregulated streams have invariably disappeared (Minckley, 1973; Barrett, 1983). A number of common nonnative species with direct access to unregulated portions of one or more larger rivers have rarely or never been taken there, perhaps because of lack of flood resistance. Included are threadfin shad (*Dorosoma petenense*), buffalofishes (*Ictiobus bubalus*, *I. cyprinellus*, *I. niger*), redear sunfish (*L. microlophus*), black crappie (*Pomoxis nigromaculatus*), and yellow bass (*Morone mississippiensis*). Some are, however, displaced or disperse downflow through regulated stream reaches from reservoirs during major flooding into delivery and irrigation canals (Minckley, 1973; Marsh and Minckley, 1982).

Depletions of native fishes, when they occurred, were in the most constrained streams or stream reaches, but no consistent patterns were evident. In no instance was a native species extirpated by high discharges, although differential displacement susceptibilities are undoubtedly reflected in recorded changes in species composition not reported here. Harrell (1978) similarly recorded some native west Texas

species as more "flood-adapted" than others. When reductions in population sizes were detected, they typically involved relatively greater losses of young-of-the-year than adults, as has been reported elsewhere (John, 1963; Seegrist and Gard, 1972; Schlosser, 1982, 1985). One massive discharge in Sycamore Creek, Arizona, destroyed young and substantially reduced adults of longfin dace (*Agosia chrysogaster*) (Deacon and Minckley, 1974). Nonnative fishes were eliminated by that event. John (1963) recorded similar reductions in populations of speckled dace (*Rhinichthys osculus*) in streams of the Chiricahua Mountains, Arizona. A comparable flood in Eagle Creek in 1984-85 numerically reduced the entire native fauna of six species (in part, Propst et al.; 1985b), while a remarkably large flood in Aravaipa Creek in 1983 (almost 2,000 times mean discharge) had no discernible impacts on seven native fish species (D. A. Hendrickson, Arizona State University, pers. comm.). That stream is especially notable since no major changes in fish-community structure were demonstrable over a period of almost four decades for which data were available to Meffe and Minckley (1987), despite documented occurrences of many major floods.

Samples from regulated systems indicate relatively few or no changes in species composition of predominantly nonnative faunas as long as releases from upstream dams are of low, controlled volumes. However, emergency releases, some of which must have equaled flashflooding of the past, had major impacts in canyon-bound reaches of the Salt and Verde rivers (table 12.3) equivalent to those in unregulated systems. Native catostomids (*Catostomus insignis*, *Catostomus clarkii*) and a few longfin dace remained. Nonnative forms were essentially destroyed, introduced fishes entrained from upstream impoundments were abundantly skewered on riparian trees, and a number of alien species formerly abundant in downstream wastewater ponds have not been found again (Minckley and Deacon, 1968; Minckley, 1973; Deacon and Minckley, 1974; Marsh and Minckley, 1982). On the other hand, similar emergency release of water into the lower Colorado River, which rose to flood over a locally broad valley, had little if any influence on nonnative or the single remaining native species (table 12.3).

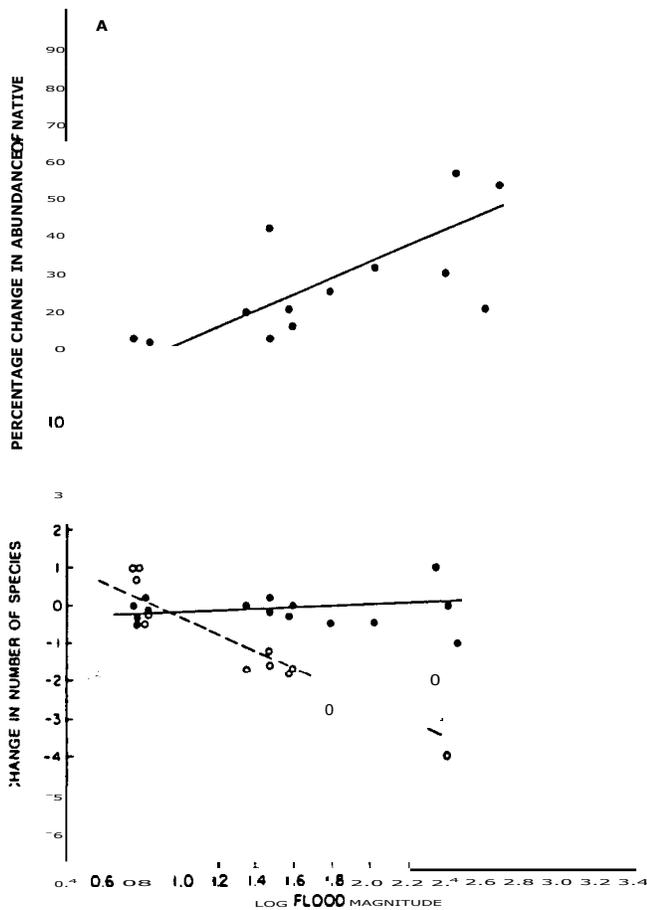


Figure 12.5 Change in percentage abundance of native fishes (transformed by arc sine square root) and change in number of native and introduced fish species as a function of log-transformed flood magnitude. Solid circles = native species; open circles = introduced forms. Percentage data are in part a result of arbitrary assignment of values to qualitative expressions for abundance (see text) and thus may reflect errors of 10% or more. Data for Aravaipa Creek (table 12.3) were excluded because of the consistently low occurrence of nonnative species in that system. Regression equations; (A) $Y = -10.319 + 21.62X$, $r = 0.773$, $P < 0.01$; (B) native: $Y = -0.0374 + 1.98X$, $r = 0.273$, $P > 0.05$ (NS); introduced: $Y = 1.952 - 2.275X$, $r = -0.873$, $P < 0.01$.

A Quantified Example

The most definitive example of maintenance of a native species through influences of flooding involves instances of coexistence of native Sonoran topminnows (*Poeciliopsis o. occidentalis*) and mosquitofish. The latter was transplanted to Arizona in the 1920s (Miller and Lowe, 1964) from an extensive natural range centered in the lower Mississippi River valley (Rosen and Bailey, 1963). Its regional colonization was accompanied by extirpation of topminnows through predation (Meffe, 1985). This pattern has been repeated throughout the United States range of the Sonoran topminnow, resulting in its endangered status (Minckley et al., 1977; Meffe et al., 1983; U.S. Fish and Wildlife Service, 1984).

Coexisting populations were studied in Sharp Spring, Arizona, from 1979 through 1983, and flood impacts were quantified (Meffe, 1984). The spring system consisted of 18 perennial pools connected by reticulate channels flowing through a 600-m reach of marshland within a moderately incised arroyo (Meffe et al., 1982). Approximately 2 km of intermittent pools and marshes below this section led to the Santa Cruz River floodplain.

Sampling with a variety of nets and seines was performed between August 1979 and early 1981. Adult fish were enumerated and released alive. Numbers of the two species were inversely related after prolonged low discharge (fig. 12.6A), and the numbers of topminnows declined as mosquitofish expanded their population. Fishes were again sampled in late July and September 1981 after a series of flashfloods, two of which were observed (Meffe, 1984) and at least one of which (not observed) scoured the system. Both species crowded along stream margins and in eddying currents until discharge crested during the first flood, but mosquitofish ventured into midstream at first signs of recession while discharge remained high and turbulent. Topminnows remained tightly along shorelines until discharge returned to pre-flood levels. Reductions in mosquitofish populations were greater than 98%, while topminnows suffered only a 75% decline (fig. 12.6B). Of the apparent loss of topminnows, thousands were found in newly filled pools a few hundred meters downstream, in position for recolonization of the permanent reach. Only three mosquitofish were collected from the downstream section, indicating that they were mostly transported from the habitat.

Behaviors of these two fishes were compared in a laboratory flume designed to provide water surges simulating flash-flood conditions. Sonoran topminnows consistently maintained their positions in strong and pulsing currents by moving against walls of the flume. The behavior appeared genetic since it was well developed and effective in one-day-old individuals. By comparison, mosquitofish repeatedly failed; young fish in particular did not maintain position and were killed in the experimental system.

Distributional Inferences

Most native southwestern fishes persist in substantial numbers in streams that (1) are distant from human population centers or protected by Indian reservations or other reserves,

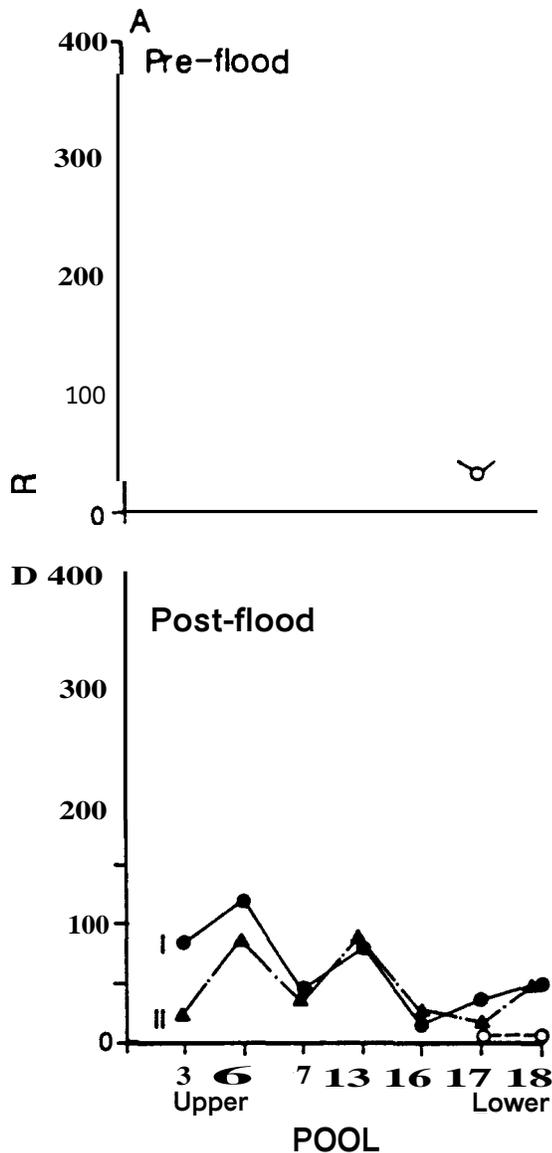


Fig. 12.6. Numbers of adult fishes (solid circles and triangles = native *Poeciliopsis occidentalis*; open circles = transplanted *Gambusia affinis*) captured in each of seven pools in Sharp Spring, Arizona, **A**, before, and **B**, after a series of major floods. Pools were numbered upstream to downstream. Consecutive roman numerals in **B** refer to two postflooding samples about five weeks apart. Modified from Meffe, 1984.

(2) act as delivery systems for water from montane watersheds and thus are unmodified because of their natural utility, and/or (3) are located in rugged terrain and thus are undisturbed because of poor access, tend to be precipitous, and are canyon-bound (Minckley, 1985). These patterns are discernible in Arizona and New Mexico, as well as in recent accounts of centers and patterns of abundance and persistence of native fishes elsewhere in the region.

Moyle and Nichols (1974) recorded abundant native minnows syntopic with scattered, large adults of green sunfish in unmodified streams of the Sierra Nevada foothills of California, whereas modified reaches were often dominated by the transplanted centrarchid. In the Virgin River, Arizona-Utah-Nevada, endangered woundfin (*Plagopterus argentissimus*) and other native cyprinoids are absent from or rare in modified downstream reaches, whereas the native fauna (two catostomids and four cyprinids, including woundfin) remains as recorded in the 1930s, and normative fishes are rare in canyon-bound, highly fluctuating, and often hot and saline middle portions of the stream (Cross, 1975; U.S. Fish and Wildlife Service, 1985).

This situation also obtains for fishes of special concern in the upper Colorado River basin. With the exception of Colorado squawfish, which still range widely (Miller et al., 1983a, b; Tyus, 1985), most are now restricted to habitat enclaves in reaches characterized by or associated with deep, swift water or other special conditions in canyons (Upper Colorado River Biological Subcommittee, 1984). Miller et al. (1982) summarized findings of the extensive Colorado River Fisheries Project in Utah and Colorado, reporting 10 native and 21 nonnative fish species upstream from Lake Powell. They commented on impacts of regulation in the system as follows:

Sediment entering the rivers is accumulating in sand bars and filling the main river channel. There are now more silt/sand areas, braided channels, and aggradation of the main river channel with a reduction of deep runs, clear gravel/rubble areas, and the frequency and duration of overbank flows. A shallower, wider, and warmer river has resulted which fluctuates less seasonally but substantially more on a daily basis. These changes seem to benefit the introduced (exotic) fishes while having detrimental effects on the endemic endangered species. [Miller et al., 1982]

They specifically noted that humpback chub (*Gila cypha*) persisted in deep, canyon areas "too harsh for exotics." In the Colorado River itself Valdez et al. (1982a) found native fishes most abundant upstream and transplanted fishes dominant downstream in a 460-km reach. They forwarded no explanation for this pattern, but proximity to Lake Powell and a relatively greater number of backwater and eddy habitats almost certainly enhanced nonnative fishes in the lower reach, while the upper consisted largely of rapids, runs, and main-channel pools. Tyus et al. (1982) reported the Green River portion of the upper Colorado Basin dominated by transplanted species. However, they also observed that "endemic suckers and chubs were more common in canyon areas where exotics are less abundant. Although more stressful environmental conditions occur in canyons, these endemics appear to be more adapted to them." Comparisons of tributaries in the Gunnison and Dolores rivers corroborated

conditions in the larger main stems Valdez et al., 1982b). Both are modified and regulated, but the former far less so than the latter. Of all fishes taken, 88% in the Gunnison River and 27% in the Dolores River were native.

Conclusions

Declines in the Native Western Ichthyofauna

Native southwestern fishes have persisted in highly fluctuating and violently flooding river systems for millions of years (Minckley et al., 1986) and have obviously succeeded until recently at coping with the rigors of such hydrologic regimes. As pointed out by Minckley (1983), geologic changes have likely caused far more local and regional alterations in aquatic habitats than have human activities of the last century. Major differences are that humans altered these aquatic systems with remarkable rapidity, disallowing genetic adaptation, and that physical changes were accompanied by pressures from hordes of invading forms.

Losses of native fishes attributable in part to establishment of nonnative and exotic species have been noted and demonstrated in western North America for more than half a century (Miller, 1946, et seq.; Minckley, 1984; Moyle, 1984). Interactions identified in declines of native fish populations include competition, predation, reproductive inhibition, hybridization, associated parasites and disease, environmental effects, or any combination of the above (Moyle and Li, 1979; Li and Moyle, 1981; Schoenherr, 1977, 1981; Taylor et al., 1984; Welcomme, 1984; Moyle, 1985; Moyle et al., in press). Of these, the first two seem most important in southwestern waters, although the remainder have not been studied on an other than local basis (see in part Werner, 1980, 1984).

Role of Natural Flooding

It is clear that the more "natural" stream habitats support the greatest proportion of native fishes and that greater modifications lead to fewer native forms. Even in modified systems, reaches most similar to the original state e.g., erosive, canyon-bound segments where higher flows of regulated streams cause conditions similar to those before modification support the largest proportions of native forms.

It is further demonstrable that such generalizations apply to other life forms besides fishes. A parallel, for example, exists in relationships among "naturalness" of streams, riparian vegetation, and bird populations. Ornithologists have long regarded native riparian plant communities as essential to maintenance of diverse avifaunas in western North America (Carothers et al., 1974; Stevens et al., 1977). Invasion by exotic saltcedar *Tamarix chinensis* has a negative impact on population sizes of many riparian birds (Carothers, 1977; Cohan et al., 1978). Minckley and Clark (1982, 1984) pointed out that diverse native vegetation persists most luxuriantly in canyon segments of Arizona streams, especially in unregulated reaches, while nonnative saltcedar becomes dominant along regulated or otherwise modified segments

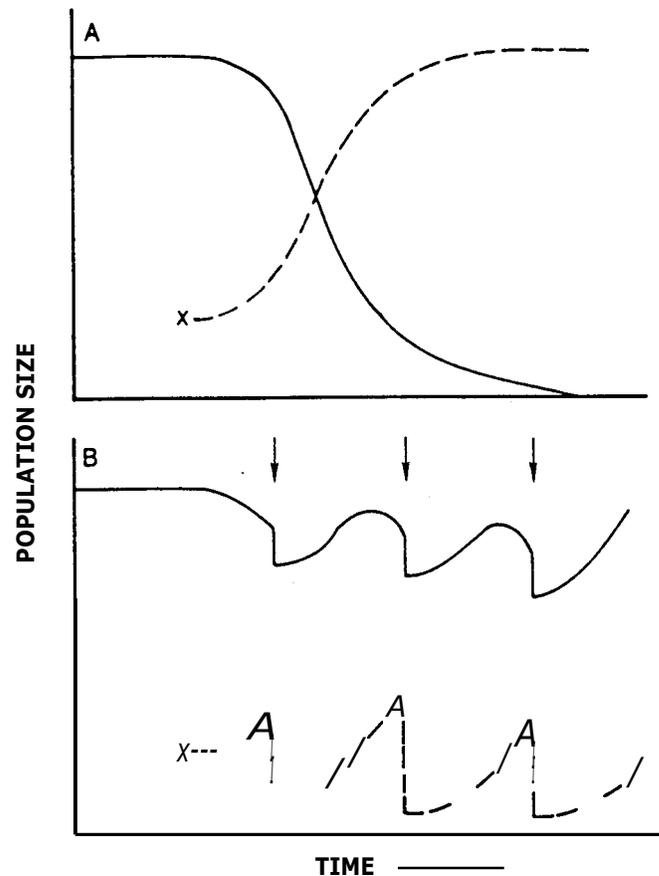


Fig. 12.7. Graphic model of suggested dynamic equilibrium between native and nonnative fishes in unregulated arid-land streams. A: In an artificial or regulated system native fishes (solid line) typically decline and disappear upon introduction (x) of nonnative fishes (dashed line). B: In a free-flooding system, native fishes similarly decline after nonnatives appear, but flooding (arrows) reduce the latter to levels that permit recovery of native fishes. During interflood periods, nonnative fishes again expand populations and ranges and negatively impact native species until the next flood. If flooding occurs frequently enough, long-term coexistence may occur. carrying capacity.

and on man-disturbed floodplains (Robinson, 1965; Haase, 1974; Horton, 1977).

Habitat changes that accrue from damming are profound (Simons, 1979), and certainly are far more complex and widespread than normally recognized. Because natural stream channels represent an average condition, tending toward a steady-state balance between average supply and removal of water and sediments by adjustment of the geometry of the system itself (Chorley, 1962), alterations in amounts of water or quantity and quality of sediments elicit complex sequences of compensatory changes (Hendrickson and Minckley, 1985). A river channel represents the most efficient geometric form that can accommodate means and extremes of discharge occurring throughout its history (Curry, 1972). Thus water removal from the upper Colorado River basin results in aggradation of the middle portion of the system (Miller et al., 1982), removal of sediments by deposition in

Lake Powell results in degradation of sandbars and other alluvial deposits in Grand Canyon (Dolan et al., 1974), bottoms become armored by remaining larger gravel and boulders, while regulated flow allows even more accumulation of coarse sediments from tributaries that block the river and create greater rapids than before (Leopold, 1969; Dolan et al., 1974), and so on. All are compensatory waves of physical change resulting from alteration of dynamic equilibria (Chorley, 1962; Curry, 1972; Bull, 1979, 1981), and similarly dynamic waves pass through associated biological systems.

Floods maintain the unique nature of erosive western streams on which native biotas depend. Flooding furthermore alters fish-community structure by differential removal of lentic adapted nonnative species, forcing the system back toward a natural coevolved state and allowing lotic-adapted native species to persist. Differential capacities to persist in free-flooding southwestern streams have thus become important determinants of community structure, allowing persistence of native species that are otherwise eliminated by introduced predators and competitors. If floods occur with sufficient regularity, recovery of native species is permitted before they are driven to extinction, and a dynamic equilibrium of the two opposing faunas may be maintained (fig. 12.7). Such a cycle may continue if flooding is regular and strong. If floods are curtailed by damming, nonnative fishes typically increase in numbers to approach 100% of the fauna.

Implications for the Future

Implications of the apparent requirement for flooding to maintain native western fish faunas are critical to consider if indigenous species are to be perpetuated. Trends in rapidly developing arid lands are toward maximal exploitation of water resources. Maintenance of any surface water at all, let alone a natural regime of annual discharge, may border on the impossible.

Attempts to accomplish this have involved estimations of minimum, maximum and "optimal" **instream** flows required to perpetuate fish and wildlife resources (Stalnaker and Arnette, 1976; Bovee and Milhous, 1978; Stalnaker, 1979; Bovee, 1981; Orth and Maughan, 1982). Data are

generated for probability-of-use or preference curves, species by species for depths, current velocities, and substrate types (Bovee and Cochnauer, 1977; Orth et al., 1983). Such information is used in mathematical models that estimate volumes of discharge required to satisfy these preferences and allow the species to persist after streams are altered for human use. Instream flow techniques were developed primarily for salmonids (Bovee, 1978), and there are problems and concerns about their applicability to warmwater species (Orth and Maughan, 1982; Moyle and Baltz, 1985; Alley and Reed, in press). Such technology may succeed in streams where near-average flows produce a major proportion of water yield (e.g., mesic systems in fig. 12.3) and where fish faunas are adapted to that moderate regime as in mesic zones, but may fail in arid land systems. We do not discourage attempts to apply these techniques in our region but hesitate to accept that southwestern systems will respond with maintenance of indigenous faunas unless major floods are allowed.

We conclude that regulation of natural streams that includes an end to flooding will result in extirpation of native fish species adapted to what appears to humans to be a severe and unpredictable aquatic system. We recommend that managers dealing with endangered native faunas seek, define, and perpetuate naturalness in southwestern stream habitats despite their superficial appearances of violence and uninhabitability when in flood, rather than attempt to improve on nature through control and manipulation of discharge.'

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