OVERVIEW OF THE EFFECTS OF FLOODING ON THE AQUATIC BIOTA IN LOTIC SYSTEMS IN THE ARID WESTERN UNITED STATES

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INTRODUCTION

The purpose of this paper is to review the current state of knowledge on the effects of flooding on the aquatic biota in lotic systems in the arid western United States, and to specifically identify the response and subsequent time of recovery of periphyton, aquatic invertebrates, and fish in these arid regions. This review provides a number of ecological concepts important to interpretation of data collected as part of the Arid Lands Habitat Characterization Project.

This review focuses on stream systems covering portions of ten states (Arizona, California, Colorado, Idaho, Nevada, New Mexico, Oregon, Texas, Utah, and Wyoming) representing nine ecoregions (Sierra Nevada, Snake River Basin/High Desert, Northern Basin and Range, Southern Basin and Range, Wyoming Basin, Colorado Plateaus, Arizona/New Mexico Plateau, Arizona/New Mexico mountains, and the Southern Deserts) (Omernik 1987).

An extensive literature review was conducted on case histories from the region and papers that provided a theoretical framework that predicts or helps explain patterns of response. Papers that provided descriptions of flood characteristics of the region, physical characteristics of streams in the region, and life history characteristics of the biota of the region were also reviewed in order to help clarify the nature of disturbance and subsequent recovery by the biotic community. References from outside the region were also included if they supported more general findings on the effects of floods on aquatic organisms, had similar disturbance and/or recovery patterns, or to contrast differences between the arid western United States and other regions of the world.

THE THEORETICAL FRAMEWORK

The role of disturbance in streams has become a major theme in stream ecology in recent decades. Current understanding of stream ecology suggests stream communities are structured differently by biotic and abiotic controls along some type of environmental gradient (Peckarsky 1983, Ross *et al.* 1985, Schlosser 1987, Power *et al*.1988, Resh *et al*. 1988). Even the task of developing a unifying definition of disturbance has generated much discussion (Resh *et al*. 1988, Reice *et al*. 1990, Poff 1992, Townsend and Hildrew 1994, Townsend *et al*. 1997), and studies documenting recovery from disturbance have used variable endpoints to

indicate recovery (Niemi *et al*. 1990). Perhaps the best definition to bridge the various nuances is provided by Townsend and Hildrew (1994). They define disturbance as "any relatively discrete event in time that removes organisms and opens up space or other resources that can be used by individuals of the same or different species." Implicit in the discussion of disturbance is that various components of the biota will perceive disturbance differentially. A flow that scours macroinvertebrates from gravel may have no effect at all on an adult pool-dwelling fish. Because of these potential differential responses, disturbance for three communities (periphyton, aquatic invertebrates, fish) of the lotic biota will be treated separately.

As a result of the concept that disturbance plays a constraining role in the patterns and processes observed in streams, a new generation of models have emerged that attempt to characterize the spatial and temporal variability in streams and use these characterizations as templates to match the biota to the environment (Poff and Ward 1989, Townsend and Hildrew 1994, Poff and Allen 1995). The culmination of these various models is the idea that as one moves from a frequently disturbed, unpredictable environment to an infrequently disturbed, predictable environment there will be a predictable change in the attributes of the biotic community. Aquatic communities in "harsh" environments are expected to be trophically simple, have relatively low species richness, and be stable and persistent in the face of disturbance, due to the dominance of flood and/or drought resistant taxa (Poff and Ward 1989, Recie *et al*. 1990). Communities in more "benign" environments are expected be trophically complex, have intermediate or high species richness, and decreased persistence and stability in the face of unpredictable disturbances (Peckarsky 1983, Poff and Ward 1989).

Expanding upon the concept of grouping streams based on temporal variability of discharge parameters, the logical extension is that such parameters would group regionally (Poff and Ward 1990). Such grouping lends itself to the suite of landscape classification systems that have been devised for aquatic biological assessment across the United States (Hughes and Larsen 1988). Such classifications are based on the assumption that attributes of the aquatic community can be predicted based on known environmental features (Hawkins and Norris 2000). If this assumption holds true, then classification of streams based on hydrological variability and other known environmental variables would help predict expected life history attributes and the response of the aquatic biota to disturbance and predict the subsequent recovery.

APPLYING THE THEORETICAL FRAMEWORK TO THE ARID WEST

Flood predictability, frequency, degree of intermittency, and flow predictability can not be generalized across the entire arid region of the western United States, but some rather broad scale characterizations can be made. For the most part, streams in the arid west fall in the more harsh, unpredictable ranges in the disturbance models discussed previously. Lowland streams in the desert southwest are generally characterized by low flows, with violent flash floods occurring occasionally throughout the summer as the result of localized thunderstorms falling on sparely vegetated landscape into down cut channels. More prolonged, less-severe floods are seen during the winter as a result of larger weather systems (Fisher and Minckley 1978, Rampe *et al*. 1985, Minckley and Meffe 1987). Flooding on the western Great Plains is similar to summer patterns in the southwest, little winter flooding, and generally some flooding as a result of spring snowmelt (Fausch and Bramblett 1991). More coastal regions (Sierra Nevada, cold desert regions) experience little summer precipitation, but often have heavy snows and/or winter rains resulting in high frequency and fairly high predictability of flooding (Erman *et al*.1988, Poff and Ward 1989, Pearsons *et al*. 1992). In the interior mountain ranges, the spring snowmelt flood is highly predictable and flood frequency and flow variability are low (Poff and Ward 1989).

Macroinvertebrate assemblages of lowland arid regions west of the Continental Divide generally consist of southwestern, Rocky Mountain, and widespread faunas (Gray 1981). Assemblages east of the Continental Divide often include eastern faunas, as well as southwestern, Rocky Mountain, and widespread faunas (Bramblett and Fausch 1991). These faunal assemblages are expected to be composed of species with small body size, accelerated and asynchronous development, and behavioral avoidance to floods (Poff and Ward 1989). Higher elevation faunas across the regions are characteristic of the Rocky Mountain fauna (Molles 1985) and have life history adaptations that indicate higher flood predictability, such as increased developmental synchrony with emergence and reproduction temporally cued to floods.

The zoogeography of fishes of the arid west have been discussed in great detail by Smith (1978) and Minckley *et al*. (1986) for areas west of the Rocky Mountains, and by Cross *et al*. (1986) for areas east of the Rocky Mountains. Fish assemblages in lowlands west of the Rocky Mountains are characterized by being depauperate and unique, and have survived by evolving general life history strategies (e.g., fathead minnows), or by becoming specialized in long existing habitats (e.g., Devils Hole pupfish), or having a pre-adaptation to

particular modes of life, like high temperatures and high salinity (e.g., razorback sucker) (Minckley and Meffe 1987). Fish assemblages in lowlands east of the Continental Divide are also characterized as depauperate faunas, but do not exhibit the high degree of endemism due to connections with the Mississippi, Missouri, and Red River basins (Fausch and Bramblett 1991). Fishes from this larger species assemblage would be expected to demonstrate "pioneering" characteristics. One would expect them to be small, vagile, early maturing species with broad tolerances to both flooding and desiccation. The community should be depauperate and trophically simple with weak interspecific interactions and demonstrate high persistence (Poff and Ward 1989, Fausch and Bramblett 1991). Coldwater assemblages at higher elevations across the region would be expected to demonstrate stronger interspecific interactions because of higher flood predictability (Poff and Ward 1989).

EFFECTS OF FLOODS ON THE BIOTA

Periphyton Assemblages

Fisher *et al*. (1982) describes succession of the periphyton assemblage in Sycamore Creek, Arizona. Sycamore Creek has a modal summer flow of 0.03 m^3/s and discharges of approximately 1 m^3/s are sufficient to cause some disturbance to the benthic environment. After one severe summer flood (7 m^3/s), diatoms dominated the periphyton assemblage for one month, but the assemblage had recovered to pre-flood conditions within two months. The original species diversity was established within five days after the flood. Recolonization was attributed to "seeding" from the sediment.

Grimm and Fisher (1989) documented periphyton assemblage resistance and resilience over a three-year period that contained 35 spates in Sycamore Creek, Arizona. Resilience was studied for 21 sequences (time between disturbances). Flows of 1-2 m^3/s were found to basically remove all filamentous algae and cyanobacteria. Diatoms were evident within hours and standing crop returned to pre-flood levels in 9 to 97 days. Gray (1980) had previously recorded recovery of the periphyton community in 35 days after a single flood event. Recovery time took longer during the winter when flood events were longer in duration. Resistance was found to be quite low, but resilience was very high. Grimm and Fisher (1986) had previously hypothesized nutrient availability would strongly influence recovery time, but not standing crop. They indicated the system was nitrogen limited. Spates may provide needed nitrogen for rapid recolonization.

Bruns and Minckley (1980) reported times to recovery in Aravaipa Creek, Arizona, in their study of distribution and abundance of benthic invertebrates. While diatoms recovered immediately, filamentous algae did not reach pre-flood levels for six months and remained slightly depressed in shaded canyon reaches. Sampling was conducted every six weeks, therefore recovery time may have been overestimated. In earlier studies on Aravaipa Creek, Minckley (1981) documented recovery within 16 to 45 days after flooding events. The infrequent sampling of the latter study potentially missed the rapid recovery shown earlier on Aravaipa Creek and longer recovery times may have been an artifact of natural depression of algal biomass later in the year.

In other areas, rapid recovery of periphyton from floods has also been documented. Power and Stewart (1987) documented algae at 66% of study sites 24 to 26 days after a severe flood (compared to 81% of study sites before the flood) and restored distributional patterns of two algae species with different resistance capabilities to flooding. Lamberti *et al*. (1991) found chlorophyll *a* levels equivalent to a control reach eight months after a catastrophic flood and debris flow in a Cascade Mountain stream in Oregon. Although pre-flood levels were not reported, Scrimgeour *et al*. (1988) reported recovery of periphyton based on total organic carbon analysis to be 23 days after a severe flood in an unstable New Zealand River. Niemi *et al*. (1990) reported periphyton recovery (density, biomass, or productivity) was rapid, taking anywhere from 4 to 30 days.

In their review of recovery of lotic periphyton from disturbance, Steinman and McIntire (1990) indicated that very little experimental data existed on periphyton recovery from disturbance. They were able to make the following generalizations based current knowledge of the effects of floods on periphyton. First, floods act as disturbances on periphyton assemblages in streams through dislodgement from substrates by direct shear stress, and abrasion by sediments. Second, good dispersal abilities, high production rates, short generation times, and flexible life history strategies should allow for rapid recolonization and recovery after floods. They also hypothesized that periphyton in stable environments (e.g., pools, backwaters) would be more susceptible to dislodgement than assemblages from areas with swift flow. Peterson (1987) found that mucilage production remaining after disturbance accelerated recovery by periphyton communities following restoration of normal conditions.

The limited data on periphyton recovery in the arid west indicate rapid recovery from floods. Although periphyton assemblages generally have low resistence to flood events and are easily scoured away, recovery was fairly rapid, taking 5 to 97 days depending on the season and the endpoint used to define recovery. Longer recovery times were generally associated with prolonged winter floods, or may have been artifacts of infrequent sampling.

Macroinvertebrate Assemblages

The preponderance of work on macroinvertebrate recovery following floods in the arid west has been conducted on Sycamore Creek, Arizona. Sycamore Creek is a lowland Sonoran Desert stream subjected to intense flash floods in the summer time, and less intense, prolonged winter floods. The system has an average of six floods per year, but have as few as one and as many as 16 (Gray 1981).

Grey (1980, 1981) first reported recovery times for macroinvertebrates as 7 to 21 days after single flood events and 35 to 49 days to recovery following frequent flooding. Floods were documented to remove 80 to 100% (mean = 86%) of the benthic fauna. Life history characteristics that allowed persistence and rapid recovery in this system included continuous reproduction, extremely rapid development, and lack of dormant stages. Those species without these adaptations exhibited behavioral avoidance to floods by flying out or swimming to protected microhabitats (e.g., riparian vegetation, stream edge). Gray (1981) believed the rarity of dormancy was related to the extreme flow regime that can scour the substrate up to depths of one meter. Gray and Fisher (1981) reported nearly 67% of the taxa recolonized by aerial pathways with drift and upstream movements being of secondary importance. They discounted any significant recolonization from vertical movement due to the severe scour of the substrate which often occurs during these flow events. Palmer *et al*. (1992) also discounted the hyporheic zone as a refuge and recolonization source in unstable substrates, but Poole and Stewart (1976) observed downward migration of some species following a flood on the Brazos River, Texas, indicating that it is a behavioral response in at least some species. Jackson (1988) verified the importance of aerial pathways in Sycamore Creek, but reported that some taxa must depend heavily on egg survival or drift following floods that occur during extremely hot weather when the already short lived aerial adults experience increased mortality.

Fisher *et al*. (1982) described succession of the macroinvertebrate community in Sycamore Creek, Arizona. Sycamore Creek has a modal summer flow of 0.03 m^3/s and discharges of approximately 1 m^3/s are sufficient to cause some disturbance to the benthic environment. After one severe summer flood (7 m^3/s), numbers and biomass of macroinvertebrates was reduced by 98%. The greatest losses occurred among immature nymphs and larvae with lower losses for species with aquatic adult stages such as hemipterans and beetles. Within 13 days, macroinvertebrate biomass was at 50% of pre-flood levels and equal to pre-flood levels in 35 days. The rapid recolonization was attributed to aerial adults (aquatic adults capable of flight and aerial adults which had emerged prior to flooding).

Grimm and Fisher (1989) studied macroinvertebrate resistance and resilience over a three-year period that contained 35 spates in Sycamore Creek, Arizona. Spates of 2-3 m^3/s were found to move coarse sand and, therefore, qualify as a disturbance for the benthic macroinvertebrate community. Pre-flood numbers recovered within 13 to 52 days. Like their findings on algal assemblages, recovery took longer during winter. Resistence was found to be low and resilience quite high. Boulton *et al*. (1992) verified these findings of low resistence and high resilience, but also identified seasonal variations in assemblage structure that were relatively unaffected by flood events. Seasonal changes may confound detection of recovery and should be taken into account.

Meffe and Minckley (1987) looked at a long-term data set (1966 to 1983) on Aravaipa Creek, Arizona, to determine persistence and stability in the Sonoran Desert stream. The stream has a modal summer discharge of 0.14 to 0.28 m^3/s. During the period reviewed, at least ten flows exceeding 30 m^3/s were reported and seven of those were winter floods were >100 m^3/s. No precise recovery data was reported (see Bruns and Minckley 1980 below), but the authors indicated recovery was "rapid" and reestablished within a few days after single flood events or several weeks to a few months during periods of high flood frequency despite losses of up to 99% of macroinvertebrate numbers. Persistence was very high throughout the monitoring period. Numbers were depressed during periods of frequent flooding in 1977 and 1978, but relative abundance ranking of benthic invertebrates was very stable. The authors concluded that both short-term and long-term persistence was very high.

Bruns and Minckley (1980) studied the distribution and abundance of benthic invertebrates in Aravaipa Creek, Arizona. During this study, five spates of >1.5 m^3/s occurred. This discharge was of

sufficient intensity to move the substrate and, therefore, act as a disturbance on the benthic community. Densities of most species were severely reduced, and returned to pre-flood levels within 120 to 150 days. Simulliid larvae showed no decrease, and *Tricorythodes* spp. and *Ochrotrichia* spp. had not returned to pre-flood levels at the end of the study (180 days after last spate). There are two main reasons for the extended recovery times reported. First, macroinvertebrates were only sampled every six weeks to detect seasonal changes in the fauna, and were not trying to directly measure the resilience of the assemblage. Second, the authors' record of when each individual taxa returned to pre-flood levels would be confounded by seasonal variation in species abundances. This was confirmed by Minckley (1981) when he indicated that overall macroinvertebrate numbers returned to pre-flood levels within 15 days, and pre-flood biomass was achieved within 45 days after flooding on the same stream. Rapid recovery was also reported for another Sonoran Desert stream by Collins *et al*. (1981) for Tule Creek, Arizona, after a March flood of approximately 570 m^3/s (modal discharge 0.02 m^3/s), but no exact recovery time was given.

Molles (1985) monitored the recovery of a stream invertebrate assemblage from a flash flood on Tesuque Creek, New Mexico. The creek is a high elevation (2960-3010 m at the study site) tributary to the Rio Grande River. The discharge of the flood was unknown, but erosion of up to 1 m of stream bed was recorded. The mid-August storm was localized and only disrupted one fork of Tesuque Creek, allowing for a before and after impact assessment with a control site. Numbers and biomass indicated recovery of overall invertebrate production after 12 months. Oligochaetes were little affected and dipterans recovered within 60 days. Ephemeropterans and plecopterans took nearly a year, while trichopterans varied in recovery time from 12 to 24 months. Species richness, evenness, and diversity paralleled recovery of biomass and took around 12 months. Very little difference was detected between the before and after, and flooded to undisturbed comparisons. The author concluded this system recovered like a typical high elevation Rocky Mountain stream generally flooded once a year from melting snow, and did not have the extremely rapid recovery reported for more southern lowland desert streams.

Cushing and Gaines (1989) ruled out drift, upstream migration, hyporheic (groundwater-streamwater interface in streams) refugia, and oviposition by aerial adults as significant sources of recolonization following winter spates in endorheic (surface flow does not leave the basin) cold desert spring-streams in Washington. Recovery is difficult to measure, because species composition of this naturally depauperate fauna is often quite different after disturbance. This contrasts to the relatively species rich exorheic

(tributaries to larger streams) cold desert or high plains streams of Colorado that show more stable temporal variation in community structure (Gray *et al*. 1983).

In the winter flood-prone foothills of the Sierra Nevada range, Siegried and Knight (1977) documented initial reductions of 85% in macroinvertebrate numbers at the onset of winter floods in early November and a 96% reduction by mid-January after eight severe floods. While no direct measure of recovery was reported, the authors stated that numbers and biomass increase in May as the rains end and algae blooms occur. If the patterns they report are typical, then recovery for various taxa ranges from <1 month to six months and is dependent on newly hatched eggs and autochthonous energy sources.

In other areas, Lamberti *et al*. (1991) found macroinvertebrate densities equal to a control reach within six months and species diversity equal to a control reach within nine months after a catastrophic flood and debris flow in a Cascade Mountain stream in Oregon. Cobb *et al*. (1992) demonstrated significant losses of benthic macroinvertebrates after spates, but densities began recovery immediately and returned to pre-flood levels after 120 days, even after the largest observed flood. Scrimgeour *et al*. (1988) reported density, biomass, and number of taxa recovered to pre-flood levels in 132 days after major reductions from a severe flood in an unstable New Zealand river. They attributed the high persistence and resilience of this unpredictable flood-prone system to highly developed refuge seeking behaviors, occurrence of non-synchronized, flexible life histories, and the ability to recolonize empty substrates rapidly (Scrimgeour and Winterbourn 1989). Niemi *et al*. (1990) reviewed 698 different data sets, and concluded that 90% of macroinvertebrate communities recovered (total density, total biomass, and/or species richness) within a maximum of 12 months from a variety of disturbances in a variety of areas.

In his review of recovery of macroinvertebrate assemblages from disturbance, Wallace (1990) pointed out that endpoints of restoration (either functional or taxonomic) will quite likely give different time frames to restoration. Despite varying measures of recovery in the literature, his assessment of the literature agrees with the studies presented above that recovery in frequently flooded systems in arid regions can recover in approximately 2 months, while more temperate regions require >4 months to a year to recover. Niemi *et al*. (1990) indicated resilience to be related to 1) persistence of impact, 2) life history of the organism, 3) time of year, and 4) distance to recolonization source.

The case studies presented above indicate that macroinvertebrate assemblages recover from flooding in arid southwestern streams anywhere from 7 to 52 days, depending on flood frequency and season. Studies from other areas with more predictable flood regimes indicate that recovery from an unpredictable flood usually takes less than 120 days, but may take up to two years. Life history characteristics, such as prolonged reproductive periods, rapid development, and flood avoidance behavior, all facilitate recovery in unpredictable environments.

Fish Assemblages

Minckley and Meffe (1987) listed resistance mechanisms by fishes to floods in the arid southwest as 1) maintaining position in or adjacent to channel habitat, 2) persisting in refugia, or 3) rapid recolonization. While no recovery data is presented, they do indicate that the native fauna of the southwest is very persistent in unaltered habitats that are subjected to these severe flow regimes. Conversely, introduced species from more temperate, wet regions usually do not persist in these unaltered environments. Several authors have addressed adaptations of fishes in arid regions, and the threats posed by introduced species as a result of more benign, regulated environments (Deacon *et al*. 1964, Barber and Minckley 1966, Deacon 1968, Moyle and Nichols 1973, Deacon and Minckley 1974, Moyle and Nichols 1974, Pister 1974, Schoenherr 1977, Schreiber 1978,Soltz and Naiman 1978, Deacon 1979, Schreiber and Minckley 1981, Courtenay *et al*. 1985, Meffe 1985, Minckley and Meffe 1987). These native fishes have evolved several adaptations to maintaining position during floods, as floodplain refuge is often lacking and displacement in intermittent stream means becoming stranded and dying. Morphological adaptations include depressed skulls, keeled or humped napes, large fins, narrow caudal peduncle, slim bodies, and reduced scales. Many species also have physiological tolerances to sudden changes in temperatures during floods and to high salinities, high temperatures, and low dissolved oxygen when stranded in temporary pools.

Deacon and Minckley (1974) reported that flash floods "seldom" extirpated populations of native species, although some accounts were known from canyon areas with no refuge areas. In most instances, when follow up work was conducted, recovery was rapid with newly hatch fish and migrating adults present in canyon reaches. Severe flood data from northern Mexico indicated recovery to pre-flood abundances within eight months. Another example listed by the authors indicated that flood gates on a reservoir on the Salt River, Arizona, increased flows from 0.5 m^3/s to 2000 m^3/s in a few hours and persisted for days.

Subsequent sampling indicated that introduced threadfin shad and sunfish were decimated, while native suckers remained abundant.

Meffe (1984) demonstrated persistence in the Sonoran topminnow in Sharp Spring, Arizona. A flood of approximately 4 m^3/s reduced topminnows by 75% and reduced introduced mosquitofish by 98%. During smaller floods of <2 m^3/s, densities of topminnows increased indicating they were recolonizing from downstream pools while mosquitofish did not increase until natural reproduction had occurred. This pattern was also seen in Sabino Creek, Arizona, (Dudley and Matter 1999) when a flood removed a population of introduced mosquitofish. The native Gila chub was able to maintain and increase its range in the stream despite the persistent presence of introduced green sunfish. Greenfield *et al*. (1970) also reported removal of mosquitofish after a severe flood in the Santa Clara River, California, while the native Santa Ana sucker recovered completely in five months. A fourth example occurred from the Santa Ana River, California, where six non-native species collected in 1991 and/or 1995 were not collected in 1996 following recent severe winter flooding (Chadwick Ecological Consultants, Inc. 1996).

Minckley (1981) reported that the relative abundance of native fish species had remained remarkably consistent when reviewing data sets on Aravaipa Creek, Arizona, from 1943 to 1979. He noted that spatial segregation of species reduced intraspecific competition and that there was no evidence that floods had any effect on abundance or movement patterns of native fishes. Introduced populations of green sunfish were consistently wiped out by flooding and populations of other introduced species within the watershed never established in the stream. A study of movements of fishes in Aravaipa Creek indicated that fish remained in canyon reaches during summer floods, and either quickly returned or never moved following prolonged winter floods (Siebert 1980).

Meffe and Minckley (1987) looked at a long-term data set (1966 to 1983) on Aravaipa Creek, Arizona, to determine persistence and stability of fish assemblages in the Sonoran Desert stream. The stream has a modal summer discharge of 0.14-0.28 m^3/s. During the period reviewed, at least ten flows exceeding 30 m^3/s were reported and seven of those were winter floods >100 m^3/s. Persistence of species and relative abundance rankings were high during this period. No native species became extinct and no exotic species became established. Data indicated only minor fluctuations in species richness, and short- and long-term persistence appeared to be high. No direct measures of recovery were given, but in one extreme event during

October of 1983, discharge peaked at 1,982 m^3/s, with water levels 15 m above base flow. All substrate except for boulders was mobilized, and more than 50% of the riparian forest was destroyed. Fish surveys conducted only two weeks later showed quantitatively similar assemblage structure (i.e., all species were present and in the same proportions as before the flood).

Collins *et al*. (1981) records one of the few instances of a flood in the arid southwest causing an extinction of a native fish species. The population in question was the endangered Sonoran topminnow that had been *transplanted* to the creek ten years earlier. The flood that eliminated the population was a >100-year event (approximately 570 m^3/s vs. a modal discharge of 0.02 m^3/s) that caused major changes to the channel and riparian area. The population was isolated by dams, other water development structures, and drainages with introduced competitors and predators that had already caused the extinction of the topminnow in the area. These factors had eliminated the natural immigration corridors that had historically existed for recovery after extreme flow events.

Gido *et al*. (1997) evaluated the variability of fish assemblages in secondary channels of the San Juan River in New Mexico and Utah. During high spring flows the fish assemblage was dominated by native species resistant to flooding. After high spring flows subsided, species that were uncommon or absent during runoff returned to the system. Secondary channels seemed to offer refuge to the native fauna from extreme flows. Secondary channels are generally dominated by introduced species during periods of lower flows. Flooding appears to allow the coexistence of native and introduced species in the system. Persistence of the native fish fauna despite severe floods and potential colonization by introduced species was also reported in a small Sierra Nevada stream in California (Moyle and Vondracek 1985).

Effects of flood disturbance on the fish community in the Purgatorie River and its tributaries in southeastern Colorado are described by Fausch and Bramblett (1991) and Bramblett and Fausch (1991). While persistence of fish communities has been reported from arid southwest streams (as a result of a highly endemic fauna adapted to harsh flow regimes) and central plains and Ozark streams (more perennial flow and developed flood plains ameliorating the disturbance), the effects of flash floods on the western Great Plains had not been examined. The high degree of endemism found in the southwest is not present in this region due to connections with the Mississippi and Red River basins. The authors sampled fish from pools during periods of zero flow in tributary streams and found persistence to be linked to deep pools with complex

habitats. When habitats were simple, recolonization by more "pioneering" species was observed. The authors believed that intense flash floods displace or destroy juvenile fish and displace some adults from pools with simple habitats, and that some adults of flood-resistant species maintain position in deep pools with complex habitats. Recolonization of adjacent pools from refuge pools occurs during times of subsiding flood flows and brief periods of flow between pools. Recovery time for the entire system is then dependent on timing of flows between pools, but persistence in these flashy tributaries is high. No introduced species have become established in this system despite introductions into reservoirs in the area.

Complexity of habitat, and resistance and resilience of the fish assemblage was also positively associated in the high desert of John Day Basin in Oregon (Pearsons *et al*. 1992). Recovery took only three months after severe spring floods associated with higher than normal rain events. Assemblage similarity between pre- and post-flood communities converged quickest in the more complex habitats.

Lamberti *et al*. (1991) found slow recovery in a Cascade Mountain stream in Oregon, with fish densities equal to a control reach two years after a catastrophic flood and debris flow. Recovery was attributed to immigration of 1+ trout during the first year and enhanced recruitment of fry in subsequent years. Recovery for fish was also slow in the Sierra Nevada Mountains after a flood in a channel constrained by snow during a heavy rain-on-snow event, when age 0 brook trout and Paiute sculpin mortality was high due to bed-material transport (Erman *et al*. 1988).

Niemi *et al*. (1990) evaluated 412 data sets, and concluded that systems with recolonization sources either upstream or downstream generally recovered in <1-year (range = 0.33-2 years). Smaller cyprinids, darters, and younger age classes moved back into disturbed areas more quickly. Timing relative to spawning was also shown to be important when flood predictability was high. Flooding prior to spawning generally results in the most rapid recovery of the assemblage, while disturbance during and after spawning can result in loss of eggs from the substrate or loss of newly hatched fish that cannot maintain position or find refuge due to lack of swimming ability. The reduction in year class strength will often result in longer recovery time. Areas with refugia available recovered quickly, while disturbances that resulted in changes to the physical habitat exhibited characteristically longer recovery times.

Very little data was found on actual recovery times for fish following flooding. Fish are more limited in their recolonization pathways (i.e., they must either remain in place or recolonize from upstream or downstream sources). Fish that have evolved in systems with highly unpredictable flow regimes and limited refuge often have morphological and behavioral adaptations to help them remain in place during high flows. In these cases, species assemblages may experience decreases in numbers, but relative proportions remain the same. Often, biomass losses can be assumed to be negligible, since only the smallest individuals probably fail to remain in place. In cases where recovery is dependent upon recolonization from upstream or downstream sources, recovery time is dictated by when adequate flow allows movement.

CONCLUSIONS

In their overview of recovery of lotic communities from disturbance, Yount and Niemi (1990) indicated that aquatic communities recovered quite rapidly if 1) life history characteristics allowed rapid recolonization, 2) availability of upstream and downstream colonizers or refuge in the affected area, 3) natural disturbance history favoring taxa with flexibility or adaptability to the disturbance. While the variability of flooding regimes over the entire range of the arid west is great, the vast majority of the fauna has evolved with rather unpredictable flood regimes. The fauna has evolved accordingly by either possessing morphological, behavioral, or life history adaptations that allow them to recovery very quickly from floods.

Periphyton communities appear to be the most easily disturbed from shear stress and scouring, but studies that have closely monitored recovery seldom report recovery times longer than one month once seasonality factors are taken into account. Periphyton communities appear to be the most easily disturbed from sheer stress and scouring, but studies that have closely monitored recovery seldom report recovery times longer than one month once seasonality factors are taken into account. Periphyton exhibit good dispersal abilities, short generation times, and flexible life history strategies that all allow rapid recolonization from floods. Studies in the arid west indicate that recovery can take as little as five days and up to three months, depending on the season and frequency of flood events.

The life history characteristics of macroinvertebrates in unpredictable flood environments demonstrate very rapid development times and prolonged reproductive periods (year round when temperatures are moderate during winter). Despite varying measures of recovery, the literature suggests that

recovery in frequently flooded systems in arid regions can occur in approximately two months. Values in the literature range from 7 to 52 days, depending on flood frequency and season. In more predictable flood regimes, timing of disturbance may prolong recovery due to decreases in recolonization pathways. Reported times of over four months are uncommon, but some taxa may take up to two years to recover.

Fish are the most limited in their ability to recolonize disturbed areas. Fish must either remain in place (characteristic of the southwestern fauna and their morphological adaptations to high discharge) or return from undisturbed upstream and/or downstream sources (characteristic of the small cyprinid assemblages of the western plains). Both recolonization pathways are probably important during most flooding events. Species composition generally remains the same, but numbers may be reduced until individuals move in from upstream and/or downstream areas, or successful reproduction takes place. In some cases, recovery time may be dependent on when adequate flows (e.g., subsiding of flood flows, reconnection of flow to permanent pools) allow movement.

It appears that the resilience of aquatic communities in the arid west is very high. Unpredictable disturbance regimes have developed faunas that can rapidly recolonize disturbed areas after disturbance. This type of variability appears to be an important component in predicting community structure and one that is often not directly incorporated into the regionalization methods used in biological assessments. While its importance has been recognized and is implicit in the habitat template models (Poff and Ward 1989, Poff and Ward 1990, Townsend, and Hildrew 1994, Muhar and Jungwirth 1998), it has generally not been employed as a variable to help discriminate a more fine scale approach. Given the apparent poor performance of using ecoregions to predict community structure in western aquatic systems (Gerritsen *et al*. 2000, Hawkins and Vinson 2000), it appears that additional levels of stratification are needed that incorporate spatial and temporal heterogeneity components.

ANNOTATED BIBLIOGRAPHY

Barber, W.E., and W.L. Minckley. 1966. Fishes of Aravaipa Creek, Graham and Pinal Counties, Arizona. *Southwestern Naturalist* 11:315-324.
Notes: Gives species accounts of seven native fishes of Aravaipa Creek, Arizona, and discusses the habitat preferences and adaptations to flow regime.

Boulton, A.J., C.G. Peterson, N.B. Grimm, and S.G. Fisher. 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* 73:2192-2207.

Notes: The authors studied macroinvertebrate assemblages from Sycamore Creek and monitored assemblages following eight flood events to assess macroinvertebrate assemblage stability in the system. The authors describe seasonal changes in the macroinvertebrate assemblage structure that was not significantly altered by spates. This observation points out the importance of accounting for seasonal variation when trying to detect recovery in aquatic ecosystems. Assemblage resistence to disturbance was variable, but resilience was generally high.

Bramblett, R.G., and K.D. Fausch. 1991. Fishes, macroinvertebrates, and aquatic habitats of the Purgatorie River in Piñon Canyon, Colorado. *Southwestern Naturalist* 36:281-294.

Notes: Fish and macroinvertebrates were sampled from the Purgatorie River and its tributaries in southeastern Colorado. The Purgatorie River has perennial, but highly variable flow while its tributaries are intermittent and consist of a series of permanent pools. The macroinvertebrate fauna is relatively depauperate. The fish fauna is also depauperate consisting of six cyprinids, one catostomid, two ictalurids, one cyprinodontid, and one centrarchid. All species are native. The authors identified three associations: 1) main river, 2) small perennial, and 3) generalist. All species generally lacked specialized ecological requirements.

Bruns, D.A., and W.L. Minckley. 1980. Distribution and abundance of benthic invertebrates in a Sonoran Desert stream. *Journal of Arid Environments* 3:117-131.

Notes: In a study of the distribution and abundance of benthic invertebrates in Aravaipa Creek, Arizona, the authors were able to roughly quantify recovery time for the algal and macroinvertebrate assemblages due to five spates >1.5 m^3/s that occurred during the 16 months of this study. Algal standing crop had recovered to pre-flood levels within six months, and nearly all macroinvertebrates had recovered with four to five months.

Chadwick Ecological Consultants, Inc. 1996. *Aquatic Biological Survey Santa Ana River Basin, 1996.* Draft report prepared for the Santa Ana River Discharges Association.

Notes: Fish sampling data from 1991, 1995, and 1996 indicated green sunfish, Mozambique tilapia, goldfish, black bullhead, channel catfish, and sailfin molly were not present at the time as they had been previously. Fish densities were down overall, but seemed to have the greatest effect on non-native species.

Cobb, D.G., T.D. Galloway, and J.F. Flannagan. 1992. Effects of discharge and substratum stability on density and species composition of stream insects. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1788-1795.

Notes: In a study of the effects of discharge and bedload movement on the density and species composition of a stream macroinvertebrate assemblage in a Manitoba stream, the authors measured assemblage responses to summer spates and spring runoff. Spring runoff caused the most dramatic changes in density, but recovered within four months. Despite being much lower in magnitude, spates caused measurable effects in densities and recovery took one to two months.

Collins, J.P., C. Young, J. Howell, and W.L. Minckley. 1981. Impact of flooding in a Sonoran desert stream, including elimination of an endangered fish population (*Poeciliopsis o. occidentalis*, Poeciliidae). *Southwestern Naturalist* 26:415-423.

Notes: The authors studied the effects of a severe flood (approximately 570 m^3/s) in an intermittent stream in the Sonoran Desert. The flood removed an introduced population of the endangered Sonoran topminnow, caused extensive channel erosion and channelization, and introduced the canyon treefrog and saltceder to the study site. The isolated nature of the study site hindered any chance of natural reestablishment of topminnow populations.

Courtenay, W.J., Jr., J E. Deacon, D.W. Sada, R.C. Allan, and G.L. Vinyard. 1985. Comparative status of fishes along the course of the pluvial White River, Nevada. *The Southwestern Naturalist* 30:503-524.
Notes: Documents declines in several species in the White River drainage of Nevada. "Unpredictable" water manipulations were attributed to maintaining some native populations whereas introduced species were displacing native species in most regulated and modified environments.

Cross, F.B., R L. Mayden, and J.D. Stewart. 1986. Chapter 11. Fishes in the western Mississippi basin (Missouri, Arkansas, and Red Rivers). Pages 363 -412. IN: Hocutt, C.H., and E.O. Wiley (eds.). *The Zoogeography of North American Freshwater Fishes*. John Wiley and Sons, New York.
Notes: Presents a fairly detailed description of the geologic history of the region detailing major drainage development and connections. Review of hypothesized preglacial stream fauna and present composition of the fauna in the major drainages in the western Mississippi basin.

Cushing, C.E. and W.L. Gaines. 1989. Thoughts on recolonization of endorheic cold desert spring streams. *Journal of the North American Benthological Society* 8:277-287.
Notes: The authors rule out most major recolonization routes for benthic macroinvertebrates in endorheic cold desert-spring streams in Washington because of the severity and timing of winter spates. They suggest that egg survival and survival of mobile adults could play an important role in recovery, but notes that species persistence can be low and that the fauna is often significantly different than the pre-flood community.

Deacon, J.E. 1968. Endangered non-game fishes of the west: Causes, prospects, and importance. *Proceedings of the Annual Conference of the Western Association of State Game and Fish Commissions*. 48: 534-549.
Notes: Gives a brief overview of the status of several species that were believed to be extinct, rare, endangered or in need of more study at the time.

Deacon, J.E. 1979. Endangered and threatened fish of the west. *Great Basin Naturalist Mem*. 3:41-64.
Notes: Describes the fish fauna of the western United States in terms of its relatively low diversity, high endemism, limited distribution, high tolerance to physical extremes, and low tolerance to biological interactions. Major threats such as habitat modification, disease and parasitism, biological interactions with introduced species, and restricted ranges are also discussed. Also discusses periods of most severe periods of species reductions.

Deacon, J.E., C. Hubbs, and B.J. Zahuranec. 1964. Some effects of introduced fish on the native fish fauna of southern Nevada. *Copeia* 1964:384-388.
Notes: Documents the extirpation of several native southwestern fishes as the result of introductions of alien species.

Deacon, J.E., and W.L. Minckley. 1974. Chapter VII: Desert Fishes. Pages 385-488. IN: Brown, Jr., G.W. (ed). *Desert Biology,* Volume II. Academic Press, New York.

Notes: The authors give a detailed account of severe disturbances encountered by desert fishes as the result of violent floods and periodic desiccation. The authors review life history, behavioral, morphological, and physiological adaptations of desert fish species. Several case studies from the southwestern United States and northern Mexico are given as examples of the resilience of these species.

Dudley, R.K. and W.J. Matter. 1999. Effects of a record flood on fishes in Sabino Creek, Arizona. *The Southwestern Naturalist* 44: 218-221.

Notes: A record flood on Sabino Creek, Arizona (365 m^3/s) eliminated a population of mosquitofish that had persisted in the reach for at least 10 years. Native Gila chub distribution and abundance increased in post-flood surveys. The continued presence of introduced green sunfish was not influenced by the flood and Gila chub densities remained lower where the species overlapped than in reaches where the Gila chub occurred alone.

Erman, D.C., E.D. Andrews, and M. Yoder-Williams. 1988. Effects of winter floods on fishes in the Sierra Nevada. *Canadian Journal of Fisheries and Aquatic Sciences* 45:2195-2200.

Notes: A severe winter flood in a snow-constrained channel caused large reductions in age 0 brook trout and Pauite sculpin abundance. The constrained channel caused increased shear stress that resulted in higher mortalities than the predicable and less constrained floods associated with spring floods.

Fausch, K.D., and R.G. Bramblett. 1991. Disturbance and fish communities in intermittent tributaries of a western Great Plains river. *Copeia* 1991:659-674.

Notes: A survey of fishes was conducted on the intermittent tributaries of the Purgatorie River in southeastern Colorado. Habitats consisted of isolated pools during long periods of now flow that are subjected to intense flash floods during summer thunderstorms. Of 11 native species, five penetrated and maintained populations to near the headwaters of the tributaries and five other species were found only 0.3-1.0 km from the mainstem. Persistence was enhanced by the complexity and deepness of the pools, but simpler pools were recolonized during periods of receding flood waters and rare instances of flow between pools.

Fisher, S.G., L.J. Gray, N.B. Grimm, and D.E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52:93-110.

Notes: The authors studied succession of algal and macroinvertebrate assemblages in a desert stream following three consecutive summer flash floods. Diatoms dominated the assemblage for the first month after flooding, but species diversity was established within five days. Pre-flood conditions were restored within 60 days. Macroinvertebrate biomass and abundance were reduced by 98%, but had recovered in 35 days. Rapid recolonization was attributed to aerial pathways.

Fisher, S.G., and W.L. Minckley, 1978. Chemical characteristics of a desert stream in flash flood. *Journal of Arid Environments* 1: 25-33.

Notes: The authors give a description of the physical and chemical characteristics of a flash flood on Sycamore Creek, Arizona. They documented large increases in particulate materials. Nitrate and phosphate generally increased while total dissolved substances declined regularly due to dilution.

Gerritsen, J., M.T. Barbour, and K. King. 2000. Apples, oranges, and ecoregions: On determining pattern in aquatic assemblages . *Journal of the North American Benthological Society* 19:487-496.

Notes: The authors present statistical exploratory techniques as an alternative to using a priori classification systems such as ecoregions based on data from Wyoming. Clustering separated macroinvertebrate communities better than ecoregions, but clusters showed strong ecosystem affinities. They suggest that an iterative process that includes hypothesis generation, exploratory data analysis, and evaluation and modification of hypotheses is likely to produce robust classifications.

Gido, K.B., D.L. Probst, M.C. Molles, Jr. 1997. Spatial and temporal variation of fish communities in secondary channels of the San Juan River, New Mexico and Utah. *Environmental Biology of Fish* 49:417-434.

Notes: Authors hypothesized that habitat heterogeneity and presence of refugia would enhance stability and reduce variability in fish assemblage of the San Juan River, New Mexico and Utah. Spring floods reduced numbers of introduced species and assemblage was dominated by native species (e.g., speckled dace, flannelmouth sucker, bluehead sucker). During lower flows, introduced species were more abundant in sampling and dominated the composition of secondary channels that were most likely historically dominated by larval and juvenile fish of native species. The native fauna is morphologically and physiologically better adapted to withstand high flows and therefore capable of persistence.

Gray, L.J. 1980. *Recolonization Pathways and Community Development of Desert Stream Macroinvertebrates*. Ph.D. Dissertation. Arizona State University, Tempe, AZ. 176 pages.

Notes: The author collected 99 taxa of aquatic insects from Sycamore Creek, Arizona. Many species showed very rapid development and continuous reproduction. Floods contributed to the rarity of dormancy. In the absence of dormancy, aerial adults became the life stage resistant to disturbance. Rapid recolonization occurred primarily from aerial pathways. Recovery was complete in 7-21 days following a single flood and 35-49 days following multiple floods.

Gray, L.J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream . *American Midland Naturalist* 106:229-242.

Notes: Publication resulting from Gray (1980). The paper lists life history strategies for the aquatic macroinvertebrate fauna of Sycamore Creek, Arizona. Flood resistant life history characteristics include continuous reproduction, extremely rapid development, and lack of dormant stages. Those species not having rapid development (e.g., hemipterans, aquatic beetles) demonstrated behavioral avoidance to floods. Macroinvertebrate assemblage recolonization and recovery are determined by the availability of adults that left the stream prior to flooding.

Gray, L.J., and S.G. Fisher. 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream . *American Midland Naturalist* 106:249-257.

Notes: The authors review recolonization pathways of aquatic macroinvertebrates and their relative importance to a desert stream community prone to flash floods. Aerial movements were used by 67% of the taxa for recolonization. Downstream drift was also an important pathway, but not to the extent demonstrated in studies on permanent streams. Upstream movement was also of secondary importance. While vertical movement from the substrate had been shown to be important in some intermittent streams, it was discounted as insignificant in this system where flash floods can scour the unstable substrate up to 1 m deep.

Gray, L.J., J.V. Ward, R. Martinson, and E. Bergey. 1983. Aquatic macroinvertebrates of the Piceance Basin, Colorado: Community response along spatial and temporal gradients of environmental conditions. *Southwestern Naturalist* 28:125-135.

Notes: This study analyzes spatial and temporal variation in macroinvertebrate assemblages of the Piceance Basin, Colorado. Four distinct assemblages were found along a longitudinal gradient that varied in flow constancy and temperature. Assemblage structure was more stable temporally near direct sources of groundwater discharge.

Greenfield, D.W., S.T. Ross, and G.D. Deckert. 1970. Some aspects of the life history of the Santa Ana sucker, *Castostomus (Pantosteus) santaanae* (Snyder). California Fish and Game 56:166-179.

Notes: A life history study on the Santa Ana sucker was conducted on the Santa Clara River, California. Spawning activity, fecundity, egg characteristics, and habitat characteristics were reported. Adaptations to flooding were also discussed.

Grimm, N.B., and S.G. Fisher. 1986. Nitrogen limitation in a Sonoran desert stream. *Journal of the North American Benthological Society* 5:2-15.

Notes: Nutrient enrichment bioassay experiments in Sycamore Creek, Arizona, indicated nitrogen limitation and proposed that nitrogen limitation was common in desert streams. Hypothesized that recolonization rates would vary depending on nitrogen supply.

Grimm, N.B., and S.G. Fisher. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8:293-307.

Notes: Resistence and resilience were evaluated for algal and macroinvertebrate communities in Sycamore Creek, Arizona, from 1984 to 1987. During this period, 35 rain spates took place, well over the mean of six per year. Both periphyton and macroinvertebrates were found to have low resistence to spates over 2 m^3/s, but were very resilient. Algal standing crop recovered in 9-97 days depending on season. Macroinvertebrate numbers recovered in 13-52 days, depending on the season.

Hawkins, C.P. and R.H. Norris. 2000. Performance of different landscape classifications for aquatic bioassessments: Introduction to the series. *Journal of the North American Benthological Society* 19:367-369.

Notes: The authors touch on the history of regional classifications systems and state that such classifications "are a priori classifications that represent hypotheses regarding how large-scale suites of environmental features directly or indirectly influence aquatic biota." This paper serves as an introduction to a series of papers that look to test the underlying hypotheses of regional classification systems.

Hawkins, C.P., and M.R. Vinson. 2000. Weak correspondence between landscape classifications and stream invertebrate assemblages: Implications for bioassessment. *Journal of the North American Benthological Society* 19:501-517.

Notes: The authors examined different a priori landscape classifications to assess variation in stream invertebrate assemblages from the western United States. All a priori classification performed poorly in explaining variation in the data. They suggested that classifications that explicitly recognize biological gradients associated with running waters would fair better.

Hughes, R.M., and D.P. Larsen. 1988. Ecoregions: An approach to surface water protection. *Journal Water Pollution Control Federation* 60:486-493.

Notes: The authors review the development of ecoregions (Omernik 1987) as a means to stratify aquatic chemistry and biota. The authors viewed an ecoregion approach as a compromise between national standards and site specific criteria.

Jackson, J.K. 1988. Diel emergence, swarming and longevity of selected adult aquatic insects from a Sonoran desert stream. *American Midland Naturalist* 119:344-352.

Notes: Study of emergence of aquatic insects of Sycamore Creek, Arizona, showed short nocturnal emergence periods followed by mating, oviposition, and death, all within 12 hours. Some taxa were longer lived (>24 hours), but showed reduced daytime activity. During cool periods of the year, adults are always present after flood waters recede; but, due to increased mortality during very hot times of the year, some adults of some taxa may not be present after a flood. In this case, the taxa must depend on egg survival or drift for recolonization.

Lamberti, G.A., S.V. Gregory, L.R. Ashkenas, R.C. Wildman, and K.M.S. Moore. 1991. Stream ecosystem recovery following a catastrophic debris flow. *Canadian Journal of Fisheries and Aquatic Sciences* 48:196-208.

Notes: Recovery of periphyton, macroinvertebrates, and fish were monitored after a basin-wide flood and subsequent catastrophic debris flow in a stream in the Cascade Mountains of Oregon. Chlorophyll *a* levels equivalent to a control reach eight months after the flood and facilitated macroinvertebrate recovery, with densities being equal to the control reach in nine months with some changes in assemblage structure remaining into the second year. Fish densities recovered in two years, but the authors warned that the magnitude of physical changes in the system could lead to prolonged ecosystem instability.

Meffe, G.K. 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology* 65:1525-1534.

Notes: A study conducted on Sharp Springs, Arizona, documented the differential effects of flooding a native topminnow and the introduced mosquitofish. Small floods (<2 m^3/s) had no effect on either species, but a flood of approximately 4 m^3/s reduced topminnow populations by 75% and mosquitofish populations by 98%. Increases in topminnow numbers after rain events indicated movement upstream from isolated pools, while no increase in mosquitofish numbers indicated they had been removed from the system. Severe flood events help native species persist with introduced species because of adaptations to the severe flood regime. In regulated systems, native species have been greatly diminished or become locally extinct, while introduced species have become established and flourish.

Meffe, G.K. 1985. Predation and species replacement in American southwestern fishes: A case study. *The Southwestern Naturalist* 30:173-187.

Notes: A study investigating the mechanisms by which introduces mosquitofish replace the native Sonoran topminnow. Predation of juveniles was demonstrated to be the most likely cause.

Meffe, G.K., and W.L. Minckley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. *The American Midland Naturalist* 117: 177-191.

Notes: Review of persistence and stability of fish and macroinvertebrates from a long-term data set on Aravaipa Creek, Arizona. The authors indicate that persistence and stability of the fish assemblage is very high as no native species have gone extinct, no alien species have become established, and relative rankings have change very little between surveys. Macroinvertebrates showed some temporary local extinctions after severe floods, but later recolonization maintained long-term persistence and stability.

Minckley, W.L. 1981. *Ecological Studies of Aravaipa Creek, Central Arizona, Relative to Past, Present, and Future Uses*. Final Report, U. S. BLM, Safford, AZ. 362 p.

Notes: The author provides a general description of the watershed and a synopsis of studies conducted on Aravaipa Creek, Arizona. He suggests that discharges of >2.83 m^3/s are sufficient to be considered disturbances to all components of the biota. Algal communities generally recovered 16-45 days following a single flood event, while macroinvertebrate numbers and biomass recovered in 16-45 days except in canyon reaches where recovery took 46-90 days. Relative abundance of fish species had been very consistent between data sets collected from 1943 until 1979. Floods had not had any detectable effects on abundance or movement patterns of native species. Flooding had consistently destroyed populations of green sunfish. Populations of yellow bullhead, largemouth bass, and mosquitofish had never become established despite their presence in the watershed.

Minckley, W.L., D.A. Hendrickson, C.E. Bond. 1986. Chapter 15, Geography of western North American freshwater fishes: Description and relationships to intracontinental tectonism. Pages 519 -613. IN: Hocutt, C.H., and E. O. Wiley (eds). *The Zoogeography of North American Freshwater Fishes*. John Wiley and Sons, New York.

Notes: This book chapter discusses the past hydrology, past climate, and geological processes that have formed the current fauna of western North America west of the Continental Divide. The high degree of endemism is attributed to barriers separating faunal areas as the result of tectonic activity. Similar species are attributed to those that presently or in the past were able to pass through salt water.

Minckley, W.L. and G.K. Meffe. 1987. Differential selection by flooding in stream-fish communities of the arid American southwest. Pages 93-104. IN: Matthews, W.J., and D.C. Heins (eds.). *Community and Evolutionary Ecology of North American Stream Fishes.* University of Oklahoma Press, Norman, OK.

Notes: Authors review adaptions of the depauperate and unique fish fauna of the arid southwest that allows their persistence in harsh environments. They review morphological, behavioral, and physiological adaptations. Conversely, introduced species from more mesic environments have not become established in the few relatively unaltered watersheds in the region. Unfortunately, the high incidence of regulated flow on many of these systems has resulted in more stable environments that allow alien species to persist and often out compete the native fauna.

Molles, M.C., Jr. 1985. Recovery of a stream invertebrate community from a flash flood in Tesuque Creek, New Mexico . *Southwestern Naturalist* 30:279-286.

Notes: The author assessed the effects and recovery of the benthic macroinvertebrate assemblage in a high elevation New Mexico stream following a severe flood during mid-August. The localized storm did not affect one fork of the stream so the author could monitor an undisturbed site as well as the disturbed site. Pre-disturbance data was available for both forks of the creek. Recovery

was generally complete in a year, but some taxa took nearly two years to recover. The stream responded like a typical high elevation Rocky Mountain stream as opposed to the more rapid recovery seen in lowland desert streams.

Moyle, P.B., and R. Nichols. 1973. Ecology of some native and introduced fishes of the Sierra Nevada foothills in Central California. *Copia.* 1973:478-490.
Notes: Analysis of fish assemblage structure revealed that introduced species increased where impoundments decreased flow variability and increased pool habitat. Introduced species were also associated with increased organic pollution, increased algal growth, and increased turbidity and siltation.

Moyle, P.B., and R. Nichols. 1974. Decline of the native fish fauna of the Sierra Nevada foothills, cental California. *American Midland Naturalist* 92:72-83.
Notes: Describes adaptations that have allowed persistence of native species in the more harsh reaches of streams in the Sierra Nevada foothills. Adaptations include ability to burrow into substrate during floods and high tolerances to high temperatures and low dissolved oxygen to remain in stagnant pools during times of low flows.

Moyle, P.B., and B. Vondracek. 1985. Persistence and structure of the fish assemblage in a small California stream. *Ecolog*y 66:1-13.
Notes: The fish assemblage of a small, Sierra Nevada stream was monitored for five years. The basic assemblage was present every year despite severe winter floods and high spring flows. Numbers and biomass showed considerable variation, but relative (or rank) abundances remained fairly constant.

Muhar, S., and M. Jungwirth. 1998. Habitat integrity of running waters - assessment criteria and their biological relevance. *Hydrobiologia* 386:195-202.
Notes: The authors suggest that habitat assessments will help assess ecological integrity by measuring the degree of anthropogenic alterations to the physical environment. They propose a detailed description of discharge regime, morphological character; lateral connectivity; and the longitudinal corridor are necessary to achieve this.

Niemi, G.J., P. DeVore, N. Detenbeck, D. Taylor, A. Lima, J. Pastor, J.D. Yount, and R.J. Naiman. 1990. Overview of case studies on recovery of aquatic systems from disturbance. *Environmental Management* 14:571-587.
Notes: The authors reviewed 150 case studies that reported some sort of resilience from disturbance in aquatic system. Recovery was measured in various ways making synthesis and comparisons difficult. Often, recovery was measured by the first reappearance of the species, return to predisturbance densities, or return to predisturbance average size. Recovery time across a wide range or organisms from a wide range of disturbances was less than three years. Exceptions included disturbances resulting in physical alteration of the habitat, residual pollution in the system, and systems with isolated populations.

Omernik, J.M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* 77:118-125.

Notes: Paper and map supplement describing regions of the United States based on land-surface form, vegetation, land use, and soils.

Palmer, M.A., A.E. Bely, and K.E. Berg. 1992. Response of invertebrates to lotic disturbance: A test of the hyporheic refuge hypothesis. *Oecologia.* 89:182-194.
Notes: Authors tested the hyporheic refuge hypothesis by using meiofaunal invertebrates from sand channel streams in northern Virginia . While downward migration was observed during increased flows, the movement was not sufficient to avoid scouring. Suggested that hyporheic zone may act as a refuge in more complex substrates not as susceptible to erosion.

Pearsons, T.N., H.W. Li, and G.A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries Society* 121:427-436.
Notes: Fish assemblage structure in a high desert stream in Oregon was surveyed before and after a summer flash flood and two spring floods. Hydraulically complex reaches lost fewer fish, had higher fish diversity, and had higher similarity than more simple reaches. Fish assemblages were resilient.

Peckarsky, B.L. 1983. Biotic interactions or abiotic limitations? A model of lotic community structure. Pages 303-323. IN: Fontaine III, T.D., and S.M. Bartell (eds). *Dynamics of Lotic Ecosystems*. Ann Arbor Science, Ann Arbor, MI.
Notes: This book chapter discusses the relative roles of biotic and abiotic factors in structuring benthic macroinvertebrate communities in streams using case studies from Wisconsin and Colorado. Streams are places on a continuum from "harsh" to "benign" physical characteristics. Biotic structuring of communities is hypothesized to be unimportant as harsh conditions would remove predators and maintain low levels of prey populations. As conditions become benign, biological interactions may increase in importance because of physical limitations on distribution of species. Predation and/or competition may then become the overriding factor determining community composition.

Pister, E.P. 1974. Desert fishes and their habitats. *Transactions of the American Fisheries Society* 103:531-540.
Notes: Discussion on the status and threats to the fishes of arid southwestern United States and adjoining areas in Mexico. The author gives general descriptions of the aquatic habitat types of the desert and several examples of unique species. The main focus is on impoundment and cyprinodontid fishes.

Peterson, C G. 1987. Influences of flow regime on development and desiccation response of lotic diatom communities. *Ecology* 68:946-954.
Notes: Diatom communities from sheltered or direct-current habitats in the Colorado River below Lake Mead were subjected to short-term desiccation. Direct-current assemblages had lower cell accumulation rates, but were more resistant to desiccation. Mucilage production after desiccation enhanced diatom immigration success. Mucilage production could be inferred to enhance recovery from flood disturbances as well.

Poff, N.L. 1992. Why disturbances can be predictable: A perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society* 11:86-92.

Notes: In a response to Resh *et al*. (1988), the author discusses perceived flaws in defining disturbance as unpredictable. He argues that disturbances can be predictable and that responses to disturbance may be constrained by evolutionary adjustments of the biota if the disturbance regime is highly predictable.

Poff, N.L., and J.D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecolog*y 76:606-627.

Notes: Fish assemblage data and long-term hydrological records were used from 34 streams in Wisconsin and Minnesota to test the hypothesis that fish assemblage structure could be predicted by the hydrological variability of the system. Assemblages could easily be predicted based on being hydrologically stable or variable. Species from variable flow regimes were characterized by having generalized feeding strategies, were associated with silt and general substrates, preferred slow velocities and were tolerant to silt. Stable streams had faunas demonstrating more specialized traits.

Poff, N.L., and J.V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805-1818.

Notes: Authors attempted to provide a quantitative description of the variability and temporal predictability of stream flow conditions. This was done in order to provide a context for delineating the range of physical environmental variability in lotic habitats. The data set included long-term discharge data for 78 streams in the continental United States. The data were analyzed to characterize streamflow variability and predictability. Streams were grouped based on degree of intermittency, flood frequency, and flood predictability. Grouping resulting in nine distinct groups and a conceptual model was developed that predicted population traits for fish, invertebrates, and overall community structure.

Poff, N.L., and J.V. Ward. 1990. Physical habitat template of lotic systems: Recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14:629-645.

Notes: Based on the authors' previous work (Poff and Ward 1989), the authors suggest that the hydrologic variability template can be used for developing a regional based model that provides a means to predict recovery from disturbance of stream communities, based on the historical pattern of spatiotemporal heterogeneity.

Poole, W L., and K.W. Stewart. 1976. The vertical distribution of macrobenthos within the substratum of the Brazos River, Texas. *Hydrobiologia* 50:151-160.

Notes: Authors studied the vertical distribution of macroinvertebrates in the substrate of the Brazos River, Texas. They documented movement of *Cheumatopsyche* and *Neochoropterpes* to lower levels following a large flood, suggesting a behavioral avoidance to scouring.

Power, M.E., and A.J. Stewart. 1987. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *American Midland Naturalist* 177:333-345.

Notes: Algae were monitored before and after a severe flood in an Oklahoma stream. A total of 81% of study sites had algae prior to a severe flood. Only 26% had algae four days after the flood. After 24-26 days, 66% of the sites had algae and distributional patterns were restored to pre-flood conditions.

Power, M.E., R.J. Stout, C.E. Cushing, P.P. Harper, F R. Hauer, W.J. Matthews, P.B. Moyle, B. Statzner, and I.R. Wais De Badgen. 1988. Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* 7:456-479.

Notes: The authors give an excellent review of the basic theories and evidence for each regarding biotic and abiotic controls in lotic environments. They discuss key areas of research needed in order to better define the role of each. The consensus of the group is that the idea of biotic "versus" abiotic factors is a dead end line of investigation, and that researchers need to examine the relative role that each plays in structuring stream communities.

Rampe, J.J., R.D. Jackson, and M.R. Sommerfeld. 1985. Physiochemistry of the upper Gila River watershed: II. Influence of precipitation runoff and flood events on the San Francisco River. *Journal of Arizona-Nevada Academy of Science* 19(1984):115-120.

Notes: Describes the physical and chemical changes during severe flood events on the San Francisco River, Arizona. Ambient levels of ammonia, nitrate, and phosphate increased.

Reice, S R., R.C. Wissmar, and R.J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. *Environmental Management* 14:647-659.

Notes: The authors contend that disturbance regime is a critical feature structuring stream communities. They disagree with equilibrium models and those who have tried to explain patterns and processes of stream communities in this way. They also suggest that the more harsh and frequently disturbed the environment, the faster the rate of recovery should be.

Resh, V.H., A.R. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace, and R.C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433-455.

Notes: The authors provide a fairly comprehensive review of studies of disturbance in lotic systems. They add a statistical component to their definition of disturbance in order to point out that disturbance should be unpredictable by definition. They find that most research has supported the dynamic equilibrium model of disturbance, but examples where the intermediate disturbance model and the equilibrium model are also presented. The authors go on to say that comparable hydrologic regimes and comparable geomorphology are the two most important factors to consider when choosing streams for comparative studies.

Ross, S.T., W.J. Matthews, and A.A. Echelle. 1985. Persistence of stream fish assemblages: Effects of environmental change. *American Naturalist* 126:24-40.

Notes: The authors evaluated stability and persistence of two fish populations in two streams in Oklahoma. One population in a temporally stable system had high persistence and stability. The other population in a more variable system (prone to intermittent and low flow) was persistent, but was not stable in terms of abundance.

Schlosser, I.J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17-24. IN: Matthews, W.J., and D.C. Heins (Eds.). *Community and Evolutionary Ecology of North American Stream Fishes.* University of Oklahoma Press, Norman, OK.

Notes: Based on previous work on Jordan Creek, Illinois, a gradient of biotic vs. abiotic structuring of stream fish assemblages is based on habitat heterogeneity (spatial variability) and flow fluctuation (temporal variability). Shallow, simple habitats are dominated by small cyprinids and

juvenile fish subjected to variable densities. Deeper, more complex habitats are dominated by larger, adult fish where predation plays a more substantial role in structuring the fish assemblage.

Schoenherr, A.A. 1977. Density dependent and density independent regulation of reproduction in the Gila topminnow, *Poeciliopsis o. occidentalis* (Baird and Girard). *Ecology*.58: 438-444.
Notes: Describes reproductive of Gila topminnow. Behavior included asynchronous cycles for individuals that allowed reproduction at the population level to continue all year and recruitment of young fishes occurred regardless of season. Fertility, fecundity, and brood size increased as density decreased. This adaptation to harsh lotic environment would allow persistence even after severe disturbance.

Schreiber, D.C. 1978. *Feeding Interrelationships of Fishes of Aravaipa Creek, Arizona*. M.S. Thesis. Arizona State University, Tempe, AZ. 59 pages.
Notes: A study of food habits of native fishes of Aravaipa Creek, Arizona, demonstrated a dramatic shift in the food habits of fish in July coincident with declines in certain macroinvertebrate taxa as a result of summer flooding. Changes were interpreted as opportunistic feeding behavior of each fish species within its respective habitat. Return to pre-flood food items in three months indicate recovery of macroinvertebrate densities.

Schreiber, D.C., and W.L. Minckley. 1981. Feeding interactions of native fishes in a Sonoran Desert stream. *Great Basin Naturalist* 41:409-426.
Notes: Synthesis of work described in Schreiber 1978.

Scrimgeour, G.J., R.J. Davidson, and J.M. Davidson. 1988. Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand River. *New Zealand Journal of Marine and Freshwater Research* 22:337-344.
Notes: Benthic macroinvertebrates and stone surface organic layers were monitored for 132 days following a severe flood in an unstable, New Zealand river. Both assemblages recovered rapidly despite smaller floods during the period.

Scrimgeour, G.J., and M.J. Winterbourn. 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand River. *Hydrobiologia* 171:33-44.
Notes: Significant decreases in biomass, primary production, and respiration of the epilithic community were seen after severe floods. Benthic invertebrate densities were also greatly reduced. Ability for rapid recovery and persistence of invertebrates attributed to refuge seeking behaviors, flexible life histories, and effective recolonization mechanisms.

Siebert, D.J. 1980. *Movements of Fishes in Aravaipa Creek, Arizona*. M.S. Thesis. Arizona State University, Tempe, AZ. 49 pages.
Notes: A mark-recapture study was conducted in Aravaipa Creek, Arizona. A total of 2,100 native minnows and suckers were tagged and then movement recorded upon recapture. Floods had little influence on movement patterns. Approximately six floods of varying discharges occurred during the study. Fish remained in the confined canyon reach even through summer floods and appeared to remain in the canyon reach or returned quickly during prolonged winter floods despite one 60-year event in the winter.

Siegfried, C.A., and A.W. Knight. 1977. The effects of washout in a Sierra foothill stream. *The American Midland Naturalist* 98:200-207.

Notes: A single riffle was monitored from May 1973 through April 1974 in a Sierra foothill stream. During this time, no fewer than nine severe winter floods occurred. Repeated washouts occurred in the study riffle. Initial decreases in macroinvertebrate numbers were 85%, and had increased to 96% by mid-January. No recovery data is presented, but the authors note recovery begins as rains subside in May and attached algal blooms occur.

Smith, G.R. 1978. Biogeography of intermountain fishes. *Great Basin Naturalist Memoirs* 2:17-42.

Notes: Detailed description of 83 species bounded by the Sierra Nevada, Grand Canyon, Rocky Mountains, and Snake River Plain. Discusses the development of current distributional patterns as the result of faulting, volcanism, and uplift.

Soltz, D.L., and R.J. Naiman. 1978. The natural history of native fishes in the Death Valley system. *Natural History Museum of Los Angels County, Science Series* 30:1-76.

Notes: Details the history and evolution of fish species found in one of the world's harshest environments. Gives detailed life history information on all extant and recently extinct species of the region. Provides information on life history, behavior, physiology, and morphological adaptations to extreme flow and desiccation.

Steinman, A.D., and C.D. McIntire. 1990. Recovery of lotic periphyton communities after disturbance. *Environmental Management* 14:589-604.

Notes: The authors assess the validity of using periphyton assemblages for assessing recovery of lotic ecosystems after disturbance. Recovery from floods, desiccation, organic enrichment, and toxic metal exposure are discussed. Data is very limited and no recovery times are reported. The authors conclude that because of fast growth, short generation time, flexible life history strategies, and good dispersal ability, periphyton assemblages have the ability to recover rapidly from disturbance.

Townsend, C.R., S. Doledec, and M.R. Scarsbrook. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: A test of habitat template theory. *Freshwater Biology* 37:367-287.

Notes: Using data from New Zealand streams, the authors indicate that insects from frequently disturbed streams should be small in size, high adult mobility, and have general habitat requirements (resilience characteristics). Also, they should have clinging mechanisms, be streamlined and/or flattened, and have two or more life stages outside the stream (resistance mechanisms). They conclude that bed movement and discharge pattern are the most appropriate measures for disturbance for aquatic macroinvertebrates.

Townsend, C.R. and A.G. Hildrew. 1994. Species traits in relation to a habitat template for river systems. *Freshwater Biology* 31: 265-275.

Notes: The authors present a model in which temporal heterogeneity (frequency and magnitude of disturbance) and spatial heterogeneity (physical and chemical habitat and its ability to act as refugia from disturbance) predict the traits of the organisms that inhabit the environment. The authors point out that the scale of environmental perturbation varies widely and the scale at which spatial heterogeneity can buffer the effects of disturbance is equally variable. The authors

also discuss predictability of disturbance, recovery patterns, resistance, resilience, and recolonization potential.

Wallace, J.B. 1990. Recovery of lotic macroinvertebrate communities from disturbance. *Environmental Management* 14:605-620.

Notes: The authors note that discrepancies among various definitions of disturbance and the various endpoints used to measure recovery has confounded attempts to characterize recovery in lotic systems. Disturbances can have extremely long-term effects when persistent toxic agents are present, physical changes occur to the habitat, and/or energy inputs are altered. The ability of macroinvertebrates to recolonize disturbed streams varies, depending on regional life histories and dispersal abilities. Aerial recolonization appears to be very important in small headwater streams, while drift may dominate in mid- to large-order streams.

Yount, J.D., and G.J. Niemi. 1990. Recovery of lotic communities and ecosystems from disturbance-a narrative review of case studies . *Environmental Management* 14:547-569.

Notes: The authors review the literature on recovery from disturbance and contrast arid and mesic regions. They distinguish between pulse and press disturbances and the differences in recovery times to these significantly different types of disturbance.