Resistance and resilience of Grand Canyon basal aquatic communities

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Dams have the ability to drastically alter river ecosystems, as they affect flow regime as well as water characteristics like temperature and turbidity (Webb et al. 1999). The Colorado River has not been exempt from this threat, particularly the stretch of river that cuts through the Grand Canyon. In 1966, Glen Canyon Dam was constructed to hold back much of the river before it has the chance to enter the Grand Canyon. This disturbance provided scientists an opportunity to monitor human- induced changes across the roughly 400 km segment bounded on the South end by Lake Mead. Out of all the food web components, scientists and decision makers should be particularly interested in studying how the base of the aquatic food web has responded. Basal aquatic communities, consisting of phytoplankton, zooplankton, and macroinvertebrates, are central to the functioning of the ecosystem as they are the main food source for not only larger aquatic consumers like trout and native fish, but also contribute to terrestrial food webs when larvae metamorphose into flying adults (Blinn 1991).

This paper aims to answer two questions. First, using knowledge of the river during pre-dam and post-dam conditions, have basal aquatic communities of primary producers and consumers been able to resist changes caused by Glen Canyon Dam? In other words, do post-dam communities overlap with pre-dam communities in their species composition, the diversity or total number of species, and the amount of biomass produced? Second, more recent data has been collected after high flow experiments, also known as test floods, which are meant to mimic historic fluctuations in flow. Using the recently collected data, are basal aquatic communities resilient? That is, do the communities recover to the pre-dam state, and if so, how quickly do they return? For both of these questions, I paid special attention to how far downstream from the dam a community is and whether it is influenced by the input of nearby tributaries.

Pre-dam

Phytoplankton

Determining what the basal aquatic communities looked like prior to dam construction is difficult, due to the lack of sampling efforts directed at the main channel of the Colorado River in the region of the Grand Canyon. The most relevant survey of which algae taxa lived in the Colorado River and its tributaries was collected by Flowers in 1959 and is hidden within a larger volume about the flora and fauna in Glen Canyon. While the author did not make a distinction as to which species were found in the main channel, there was a total of 53 taxa of chlorophytes and diatoms recorded (Flowers 1959). The best record of the quantity of algae in the river comes from samples taken from the Colorado River near Page, AZ, the closest city to Glen Canyon Dam. On average, samples contained 1512 total algal cells per mL of which 1219 were diatoms (Williams and Scott 1962). This study also describes the three dominant taxa collected at that site: *Synedra ulna, Navicula viridula*, and *Diatoma vulgare*.

Macroinvertebrates

In a review of aquatic invertebrates in the Grand Canyon, Blinn (1991) comments that the "best comparable material" is from a survey done by Musser (1959), even though there is again the problem that not all species are recorded with a description of whether they were found in the main river or a tributary. Musser (1959) lists 92 aquatic invertebrate species in over thirty families. However, the list only identifies species as common or rare, failing to provide any quantitative measure of density.

To provide a sense of the likely high diversity, I compiled some of the species Musser (1959) noted as widely distributed and/or found in the main river: *Heptagenia elegantula* and *Baetis sp*. (mayflies), *Argia emma* (damselflies), *Gerris remigis* and *Microvelia americana* (water striders), *Corydalus sp*. (dobsonflies), *Potamvia sp*. (caddisflies), *Simulus sp*. (black flies), *Calopsectra exigua* (midges), and *Hamerodromia sp*. (dance flies). Paradoxically, the checklist does not have a record of *Gammarus sp.* scuds, even though Blinn mentions they had been intentionally introduced to the river in 1932 to provide a food source for trout (Blinn 1991). The checklist also lacks any mention of zooplankton; a clear gap exists in our understanding of which and how many zooplankton existed in the Colorado River prior to 1966.

Post-dam

Phytoplankton

To determine if communities are resistant to the drop in temperature, reduction and increased consistency in flow, reduction in turbidity, and other changes associated with the dam, I considered the results of studies conducted after 1966. A survey by Crayton and Sommerfeld (1978) found 127 species of phytoplankton floating in the water, a much higher number of species than found prior to the dam being built. However, only a fraction of these species were present at a given time. Crayton and Sommerfeld (1978) found over half the species were diatoms, the rest were members of Chrysophyta, Chlorophyta and Cyanophyta. In my opinion the most likely explanation for the increased diversity is an increase in sampling intensity. Another possible explanation is that phytoplankton were under more stressful and reduced light conditions in the turbid water of the past, but that doesn't seem to be the case given a reduction in overall cell count in the more recent data. This study recorded a maximum density of 3000 organisms per liter, which is roughly 500 times lower than the density recorded by Williams and Scott (1962).

The most common phytoplankton species found were *Rhoicosphenia curvata*, *Cocconeis pediculus, and Diatoma vulgare*, which was also common in the pre-dam community (Crayton and Sommerfeld 1978, Williams and Scott 1962). Not surprisingly, there is a large overlap in the community in Lake Powell, behind Glen Canyon Dam, and in the river below the dam. It is unknown if species carried into the river from the dam are reproducing within the river; there is turnover in which diatom species are found perhaps because of the increase in suspended sediment farther downstream. In the tailwaters of Glen Canyon Dam, the phytoplankton community is dominated by a single species, *Cladophora glomerata* (Usher 1986, Stevens et al. 1997). According to Arizona Dept. of Game and Fish, *C. glomerata* colonized in 1967 and spread downstream until the intersection with the Paria River tributary. *C. glomerata* is a filamentous alga that prefers to grow on stable rock surfaces and in clear water. Sometimes the alga detaches because of daily dam releases and floats downstream in drift packets, but energy contained in the drift packets declines with distance from the dam (Shannon et al. 1996). It provides a refuge for fish and provides habitat for diatoms, like *Cocconeis pediculus*, which is a food resource for fish (Blinn et al. 1986). It supports a biofilm of diatoms that is nutritious for grazers (Furey et al. 2012). However, stable isotope analysis reveals C. glomerata itself is not edible to macroinvertebrates or fish (Pinney 1991, Angradi 1994). *C. glomerata* is also positively associated with the common macroinvertebrate *Gammarus sp*. (Blinn 1991). Blinn and colleagues (1986) also hypothesize that warm water releases, such as those proposed to help native fish populations, would lead to a decrease in upright diatoms, the preferred food source of *Gammarus*.

Macroinvertebrates

Not only has there been a disruption in the macroinvertebrate community due to the dam, but also due to many intentional stocking events. In 1967, 10000 mayflies, 10000 snails, 5000 leeches, and 2000 crayfish were introduced into the river (Stone and Rathbun 1969). Twice, in 1965 and again in 1968, *Gammarus*, commonly known as scuds, were introduced to supplement the diet of trout (Blinn 1991). Despite these introductions there are relatively few species in the main river compared to the high diversity that existed pre-dam.

The community of macroinvertebrates living in the channel is described as "depauperate" and lacks any members of the EPT (Ephemeroptera, Plecoptera and Trichoptera) group—commonly used to measure the health of a waterway—composed of mayflies, stoneflies, and caddisflies (Stevens et al. 1997). So, it seems as though none of the 10,000 introduced mayflies founded a population. This could be because certain species of mayflies must experience warm water to cue the progression of developmental stages. The temperature in Steven and colleagues' (1997) samples ranged from 9-13^{0}C, whereas previously it fluctuated between 9-26^{0}C (nps.gov/glca/learn/nature/hydrologicactivity.htm). The historically seasonal temperatures allowed mayflies and other temperature cued taxa to develop and complete their life cycle during warm summer months. Another reason certain species of mayflies and other taxa are precluded is because of their egg-laying behavior. Daily hydropeaking of the river means that asynchrony between dusk, the time when eggs are laid along the river's edge, and the time of minimum flow causes those eggs to experience desiccation and high mortality (Kennedy et al. 2016).

There are two dominant species: scuds *Gammarus lucustris*, in the tailwaters of the dam, and black flies *Simuliium articum*, further downstream after turbid tributaries join the main river (Stevens et al. 1997). The section of the river between the dam and the Paria River contained taxa associated with *C. glomerata*: *Gammarus*, a few Chironomidae species, Pysella snails, and Lumbricidae worms (Stevens et al.1997). Another survey of macroinvertebrate drift in the tailwaters near Lee's Ferry found individuals belonging to Chironomidae were more abundant than *Gammarus* (McKinney et al. 1999). After the turbid Paria River joins the main channel, the base phytoplankton changes to *Oscillatoria spp*. and macroinvertebrates change to be *Simuliium articum* and lumbriculoid worms, with other species composing less than 0.1% of dry standing biomass (Stevens et al. 1997). As the gravel below Lee's Ferry continues to be washed away, this is creating better habitat for *S. articum* larvae (Kondold et al. 1989, Blinn 1991). Another study showed that the dietary link between algae and invertebrates is strong just below the dam, but downstream beyond tributary inputs invertebrates switch to terrestrial-based resources like fallen leaf matter (Wellard et al. 2013). This makes sense given that tributaries add turbidity to the water, which makes for less light and reduced phytoplankton populations.

Overall, macroinvertebrate community structures have not resisted changes caused by Glen Canyon Dam. Instead, they have become amalgamations of native and exotic species. In most places they have shifted to be dominated by only a few species adapted to cold temperatures, clear water, and consistently low flow. It is unclear whether *Gammarus* was a part of the community prior to the dam, because there is a record of introduction (Blinn 1991) but it is not included in Musser's (1959) checklist. Musser (1958) listed several species in the family Chironomidae and two species in the genus Simuliium, but with the comments "three young larval specimens were found" and that they were in "tributary streams as Warm Spring Creek", suggesting that they were not nearly as abundant in pre-dam communities.

Zooplankton

Zooplankton in the Colorado River are often overlooked by investigators interested in aquatic invertebrates. A couple of early surveys were conducted in 1980 and 1985 which sampled between Glen Canyon Dam and Diamond Creek, plus a few tributaries (Haury 1986). The key findings were: (1) The majority of the 33 species found were derived from Lake Powell. Because the river zooplankton came from the lakes, this suggests that most were not in the river prior to the river being dammed. (2) The community consists of mostly copepods, the dominant calanoids being *Skistodiaptomus pallidus* and *Leptodiaptomus ashlandi* and the dominant cyclopoid being *Diacyclops thomasi*, compared to the number of cladocerans, the dominant species being *Daphnia geleata*. The exception to this is when water comes down spillways from the lake and in the more protected backwaters of the river. (3) Surprisingly, the abundance of zooplankton is constant along the stretch of the river between the dam and Diamond Creek, but with increasing distance from the dam came increasing numbers of individuals that Haury considered "poor in condition". Because some of the individuals are found with eggs or with spermatophores, Haury (1986) thinks populations could be reproducing and is possible they can sustain themselves in backwaters and terminal pools. Benenati and colleages (2001) found a contrasting result in their surveys from 1995-1999; zooplankton are more abundant further downstream from the dam, perhaps because of the increase in detrital matter. Also, they are more abundant near shore, as it is a more stable habitat compare to the middle channel (Benenati et al. 2001). Stable isotope analysis reveals zooplankton stemming from Lake Powell make up a large part of the diet of trout despite their low relative abundance (Angradi 1994). Further research should be done to detect how populations are maintained in the river, as zooplankton are good food sources for fish, particularly *Daphnia* because of their slower swimming abilities compared to copepods.

High Flow Experiments

It seems as though Blinn (1986) made an accurate prediction that high flow releases would negatively impact the food source of Gammarus. In 1996, researchers ran a high flow experiment through the Grand Canyon, releasing of 45,000 ft^3 of water per second from the dam in hopes of building up sandbars and possibly helping native fish. A study sampled sites spanning from just below the dam to Lava Falls post-flood (Shannon et al. 2001). Their results showed: (1) Total dry biomass increased after the flood. This suggests some level of recovery to pre-dam quantities. (2) The dominant algae in downstream turbid waters, *Oscillatoria spp.,* increased in abundance. However, the dominant clear water algae, *C. glomerata* decreased and dominance shifted to other miscellaneous algae species. (3) The mass of the dominant macroinvertebrate *Gammarus* was reduced. The flood removed silt, a habitat for Chiromonidae which explains why they were found in reduced numbers in pools. The initial wave from the flood swept away most of the zooplankton, and contrary to Haury's (1988) findings, densities declined downstream. The authors describe how the "collections for primary consumers during the post-flood trip of June of 1996 included some of the highest biomass values and most diverse fauna ever recorded during a six-year monitoring program" (Shannon et al. 2001).

Another high flow experiment occurred in 2008, under a similar protocol to the experiment in 1996. The impact on the macroinvertebrate community was similar to the earlier flood. Sometime after the 1996 flood, another alien species known as the New Zealand mud snail, *Potamopyrgus antipodarum*, invaded below Glen Canyon Dam and dominated the biomass of tailwaters (Cross et al. 2010). The biomass of *Gammarus* and *P. antipodarum*, declined immediately after the 2008 flood and in months following (Rosi-Marshall et al. 2010). The shifting away from *P. antipodarum* represents a shift towards more digestible food for secondary consumers like fish (Rosi-Marshall et al. 2010). Floods reduce the dominant species, allowing for other species to fill the community. However, there is little evidence that the invertebrates directly compete with each other. A more likely possibility is that the dam caused more physical exclusion rather than biological. Floods remove silt from in between the gravel beds on the bottom of the river (Melis et al. 2012), clearing out space for invertebrates to hide from fish predators. One reason the diversity increased following these floods, but did not return to the exact pre-dam assemblage, is that the flood water is taken from the base of the dam, and after most particles have settled out. The flood water is therefore much colder and less turbid than the original water flowing through the canyon.

Importance of tributaries

How did the main channel of the Colorado River increase in diversity? Where did the species come from? One possibility is that lower main stem flows lead to a relatively greater influence from the dozens of tributaries intersecting the Colorado River below Glen Canyon Dam. Oberlin and colleagues (1999) surveyed the aquatic life in ten tributaries from the Paria River to Diamond Creek. They found that miscellaneous species of macroinvertebrates, including members of EPT, make up a large portion of biomass in most of the tributaries. In contrast to the main channel, Oscillatoria biomass was lower than other miscellaneous primary producers and detrital biomass.

The source of water feeding each tributary influences what aquatic organisms can survive there. The tributaries fed by large watersheds like the Paira River, Little Colorado River, and Kanab Creek had low diversity and biomass, housing only chironomids, a hydropsychid caddisfly, and gastropods (Oberlin et al. 1999). The watershed fed tributaries experience both dry periods and sediment filled floods, making them inhospitable to many species. Conversely, the authors found high diversity and biomass in the more consistently flowing spring fed tributaries like Vasey's Creek and Spring Creek. For example, trichopterans, ephemeropterans, and megalopterans each dominate Bright Angel Creek at a different time of year (Whiting et al.

2014). However, until test floods are modified to release warm water from the top of Lake Powell and the daily hydropeaking is reduced, the Colorado River will not be recruiting temperature cued hemimetabolous insects or river-edge-egg-laying insects like mayflies from these tributaries.

Conclusion

Following the construction of Glen Canyon Dam, the Colorado River basal aquatic community was not able to resist the changes in flow, temperature and sedimentation. The phytoplankton assemblage below the dam shifted to dominance by *C. glomerata*, and downstream shifted towards dominance by *Osclillatoria spp*. The macroinvertebrate assemblage shifted towards dominance by three taxa, *Gammarus*, *P. antipodarum*, and *S. arcticus,* which thrive in the new physical regime. The dam also brought in a new zooplankton community, stemming from Lake Powell (Haury 1986).

High flow experiments mimicking historic flooding caused a reduction in biomass of dominant species, and increased overall diversity (Shannon et al. 2001, Rosi-Marshall et al. 2010). These patterns indicate the pre-dam communities are resilient. If the historic regime were to return, refuge populations maintained in tributaries could colonize the main river (Oberlin et al 1999). However, a full recovery will be dependent on two changes: the release of water from the warm, top layer of Lake Powell, as opposed to the cold base layer released during current high flow experiments and the reduction in daily hydropeaking which would prevent wave-induced egg mortality for river-edge laying species (Kennedy et al. 2016).

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