

Response of fish biota to dams in the Lower Colorado River Basin: empirical findings and utility for predicting responses to climate and water use change

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Abstract

The biologists have done their jobs. We know the life cycles and habitat requirements of endangered western fishes. . . [A] successful management program could be devised and implemented for the Grand Canyon region. [But, c]urrent politics stand in the way, just as surely as politics of the 1960s aided and abetted our efforts to learn enough to save this fauna. - W. L. Minckley 1991

Development of water resources in the Colorado River Basin over the past century has changed a dynamic, seasonal river into a highly managed system. Conversion of lentic habitat to reservoirs has altered seasonality of flow, temperature, and turbidity. These changes have played out in the fish fauna, where native fish species have declined and non-natives have increased. Relative to the past, the key aspect of the new environment is competition and predation, especially at juvenile stages, which is likely mediated by more stable flow regimes and increased resource limitation from reduced floodplain-river interactions. A dataset (SONFISHES) assembled by W. L. Minckley and covering 150 years of fish occurrence in the Lower Colorado River (below Glen Canyon Dam) has enabled characterization of patterns in extirpations and range contractions among native fishes and expansions among non-native fishes. Several studies have combined these data with measures of extinction risk to explain how range fragmentation and species traits correlate with observed or threatened extinctions in native species. Another study analyzed range shifts within a strategy-space of potential fish life histories (originally introduced by K. O. Winemiller and K. A. Rose) to understand how human activity has created and removed ecological niches. Together, these studies support the view that alterations to the river environment have caused observed changes. Although there is a convincing link between changes in the fish biota and the modified environment, I argue that additional work is needed to make this knowledge useful for predicting responses to further modification. In particular, to predict future changes in fish biodiversity requires a model that quantitatively relates alterations in environmental factors to persistence in the strategy-space of fish life histories. Only with such a model can we know the expected magnitude of change in fish fauna for a projected change in environmental conditions. Unfortunately, even without such a model we can *qualitatively* predict the fates of threatened “big-river” fishes in the absence of political will to intervene. As the quotation above suggests, this will has been lacking since at least the 1990s.

Goals of the paper

Reviewing changes to the fish fauna of the Lower Colorado Basin over the last 150 years through the ecological lenses of niche and life history theory, I explain how these views of the data not only support the view that alterations to the river environment have caused observed changes, but suggest mechanisms. I argue that despite this progress more work is needed to make quantitative predictions of responses to further modification (either intentional or associated with climate change). In particular, we must develop models that quantitatively relate environmental variability to ability of species to persist in life-history space. Such models would relate documented shifts in fish fauna to changes in environmental variables, providing essential estimates of effect size and giving managers a chance to predict responses.

Literature synthesis

I briefly discuss changes to the abiotic environment and fish biota of Lower Colorado over the past 150 years. Our understanding of changes to the fish fauna over this timescale owes mostly to the work of the late W. L. Minckley, who worked tirelessly to compile an occurrence dataset spanning these years (the SONFISHES dataset; Fagan *et al.* 2002). Finally, I summarize changes in the fish biota within the context of ecological niche and life-history theory to yield insights into ecological aspects of the invasion and extirpations in fishes of the Lower Colorado Basin.

The Lower Basin of the Colorado River, defined as the portion below Glen Canyon Dam, is impeded by six major dams before reaching the Gulf of California. These dams have resulted in major alterations to sediment supply, temperature, and flow within the mainstem Colorado (Gloss *et al.* 2005). Downstream of Glen Canyon Dam, two tributaries (the Paria and Little Colorado Rivers) contribute the vast majority of present day fine sediments (greater than 90% Cross, Topping), but these inputs represent a 84% decrease relative to pre-dam conditions (Topping *et al.* 2000). With the exception of experimental floods, timing of discharge from Glen Canyon Dam is now dependent on irrigation and electricity demand (Cross *et al.* 2013; Topping *et al.* 2003). Together, these changes have vastly altered patterns of natural variability (e.g., in Figure 1 the hydrograph below Lee's Ferry, AZ the 1964 closure of Glen Canyon Dam is clearly visible).

Resulting alterations to seasonality of flow, temperature, and turbidity within lentic habitats have played out in the fish communities, where native fish species have declined and non-natives have increased. Changes to the variability in the abiotic environment have consequences for a native fish biota adapted to such patterns (Lytle & Poff 2004). Further, although non-native taxa had begun to establish and spread long before establishment of major dams (Minckley 1991) that have essentially removed disturbances at seasonal (e.g., flooding due to spring run-off) timescales and substantially reduced variability due at finer timescales (e.g., due to weather systems). Even in river canyons subject to irrigation and power-generating flows, changes create stable habitats that can be resource-limited. For example, Cross *et al.* (2013) characterized food webs along the Lower Colorado from Glen Canyon Dam to Lake Mead, finding evidence for food limitation except for near the mouths of large tributaries. If food limitation in these habitats is a phenomenon of the modern Colorado, it may stem from reduced floodplain-river interactions (Olden *et al.* 2006). Reduced lentic habitat and altered variability combined with competition and predation from non-natives has imperiled the fish fauna of the Lower Colorado (Minckley 1991).

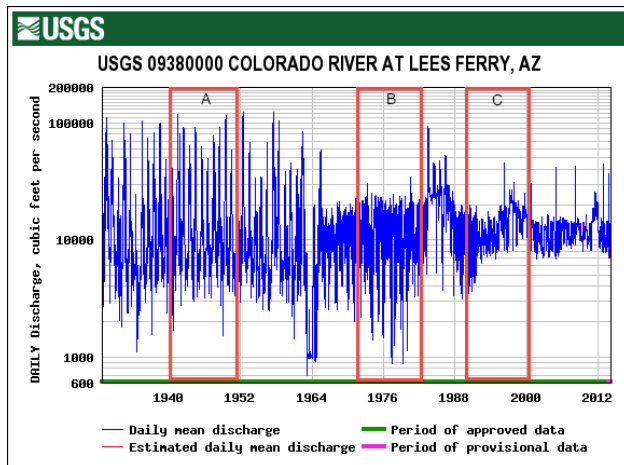


Figure 1: Discharge measured by USGS Gauge at Lee’s ferry. Boxed regions relate to both dam and biota: pre-dam and pre-breakpoint (A), post-dam and pre-breakpoint (B), post-dam and post-breakpoint (C). See Conclusions for discussion. (Data from waterdata.usgs.gov, plot modified from same source.)

expansion of non-natives, we turn to a 150-year occurrence dataset compiled by W. L. Minckley and coworkers.

The SONFISHES database, extirpation, and expansion

The SONFISHES database describes distributions on native and non-native species throughout the Sonoran Desert ecoregion over 160 years of museum collections, peer-reviewed literature, and technical reports (“gray” literature) (Fagan *et al.* 2002). The data comprise occurrence locations referenced in space and time: 19,396 for native species (n=28) and 16,339 for non-native species (n=49) (Unmack 2002). As seen in Figure 2, spatial coverage extends to portions of five states and northwest Mexico, totaling 25,970 km of reach draining 331,500 km² (Fagan *et al.* 2002)

The SONFISHES database has been used to characterize pattern of expansion in non-natives and range contraction in natives (Fagan *et al.* 2002; Olden & Poff 2005). Fagan *et al.* (2002) examined fragmentation and extinction risk in native fishes, breaking the occurrence dataset into pre- and post-1980 periods. After developing a scale-independent measure of rarity, these workers found that fragmentation before 1980 predicted extinction risk independently of the number of occurrences. Species with the most fragmented historical range were five times more likely to have suffered local extirpations, a finding which was insensitive to the 1980 breakpoint (Fagan *et al.* 2005). Examining changes in distribution of both non-native and native fishes, Olden & Poff (2005) determined that rates of spread for non-natives introduced after 1950 were slower than those introduced earlier, consistent with reduced human-mediated dispersal. Further, a strong correlation between early declines and later imperilment in natives suggested that proactive conservation approaches are necessary for these taxa (Olden & Poff 2005). More recent work has collated the observed distributional changes with data on species traits and analyzed resulting patterns in the context of ecological theory.

The fish fauna of the Colorado is depauperate but special. It consists of just 32 indigenous species in 5 families (Minckley 1991). In particular, the “big-river” fishes of families Cyprinidae (minnows) and Catostomidae (suckers) inhabiting the mainstem share several unique features: large body sizes, very long lives, leathery skin essentially without scales, and streamlined body plans—often featuring tiny heads and large keels or pre-dorsal humps (Minckley 1991). Of these, Cyprinids are the most endangered in the Colorado: two (Round-tail chub *Gila robusta* and Colorado squawfish *Ptychocheilus lucius*) are extirpated from the Lower Basin, with another (Bonytail *Gila elegans*) restricted to reservoirs of Lake Mohave and Havasu (Minckley 1991; Minckley *et al.* 2003). To understand the patterns of extirpations in these and other native fishes, and the

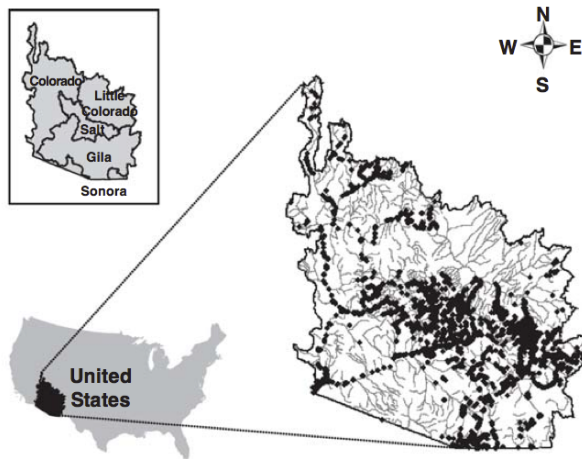


Figure 2: Spatial coverage of the SONFISHES database in the Lower Colorado River Basin. The inset shows major drainages and black dots are occurrence records (reproduced from Olden & Poff (2005)) used without permission).

size vs. number) define level sets of a fitness surface; locations in this multi-dimensional trait space are sometimes termed “life-history strategies”. For fish, K. O. Winemiller and K. A. Rose introduced a three-endpoint life-history strategy space (hereafter the “W–R” model) (Winemiller 1992; Winemiller & Rose 1992). This theory, illustrated in Figure 3, envisions strategies selected for based largely on the predictability and variability of resources (Winemiller 2005).

Niche theory posits that species have fundamental environmental requirements. The “fundamental niche”, where persistence is possible, is the subspace of a multi-dimensional environmental space where abiotic aspects of these requirements are met. Theory draws a distinction between the fundamental and “realized” niches, the latter is where the species actually occurs. The difference between the realized and fundamental niches of species is explained by limited dispersal and, more importantly, biotic interactions of competition and predation. As in life-history theory, the fundamental and realized niches are also envisioned to depend on traits—not only life-history but morphology, behavior, physiology, and trophic position. In relating these ideas to species invasions, a distinction has been made between factors based on how they affect the niche of potential invaders: “biotic resistance” operates on the realized niche, whereas “environmental resistance” affects the fundamental niche. Areas of where there is little resistance of either type have been termed “niche opportunities” (Shea & Chesson 2002).

In an effort to understand changes to the fish fauna of the Lower Colorado Basin through the context of life-history and niche theory, Olden *et al.* (2006) associated patterns of extirpation

Changes to fish fauna in life-history and niche space

Viewing patterns of extirpations and invasions through the lenses of ecological life history and niche theories may help to (1) understand species invasions more generally, and (2) infer mechanism for observed patterns.

In ecology and evolution, “life history” refers to traits such as age-at-maturity and age-specific fecundity or survival (Roff 2002). Thus, life-history theory is the study of how evolutionary and ecological factors affect these traits. Generally, the theory uses mathematical analysis to ask questions like, “how does the age at first reproduction affect individual fitness and population growth?” A basic notion in life-history theory is that tradeoffs between traits (e.g., egg

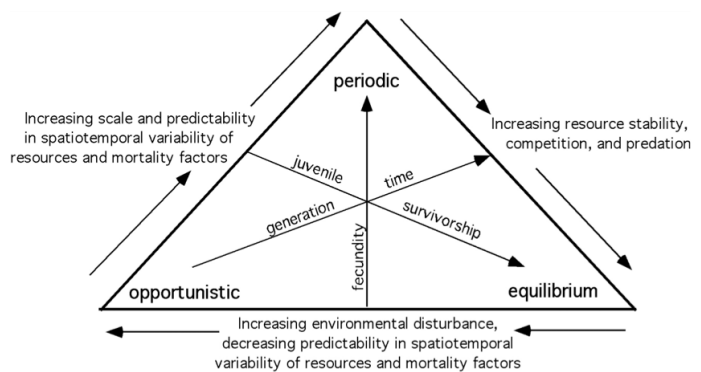


Figure 3: The Winemiller-Rose triangular model for fish life history envisions strategies defined by optimization of generation time, juvenile survivorship or age-specific fecundity relative to the predictability and variability of the environment and resources (reproduced from Winemiller (2005); used without permission).

and invasion from the SONFISHES dataset with a laboriously-compiled database of life-history, morphological, behavioral, physiological, and trophic traits. This trait-based approach provides useful context and potential mechanism for the findings mentioned above that range fragmentation influences extirpation risk (i.e., Fagan *et al.* 2002, 2005). In particular, in the Lower Colorado, extinction risk and fragmentation are both associated with a synergistic suite of “slow” life history traits (large body size, long lifespan, late age-at-maturity), low parental care, and specialized feeding (Olden *et al.* 2008). Although these traits are related to population growth in general, there are also weaker context-dependent indications that traits directly related to weak dispersal (i.e., high “swim factor”) are associated with higher extinction risk providing a more direct mechanism for fragmentation.

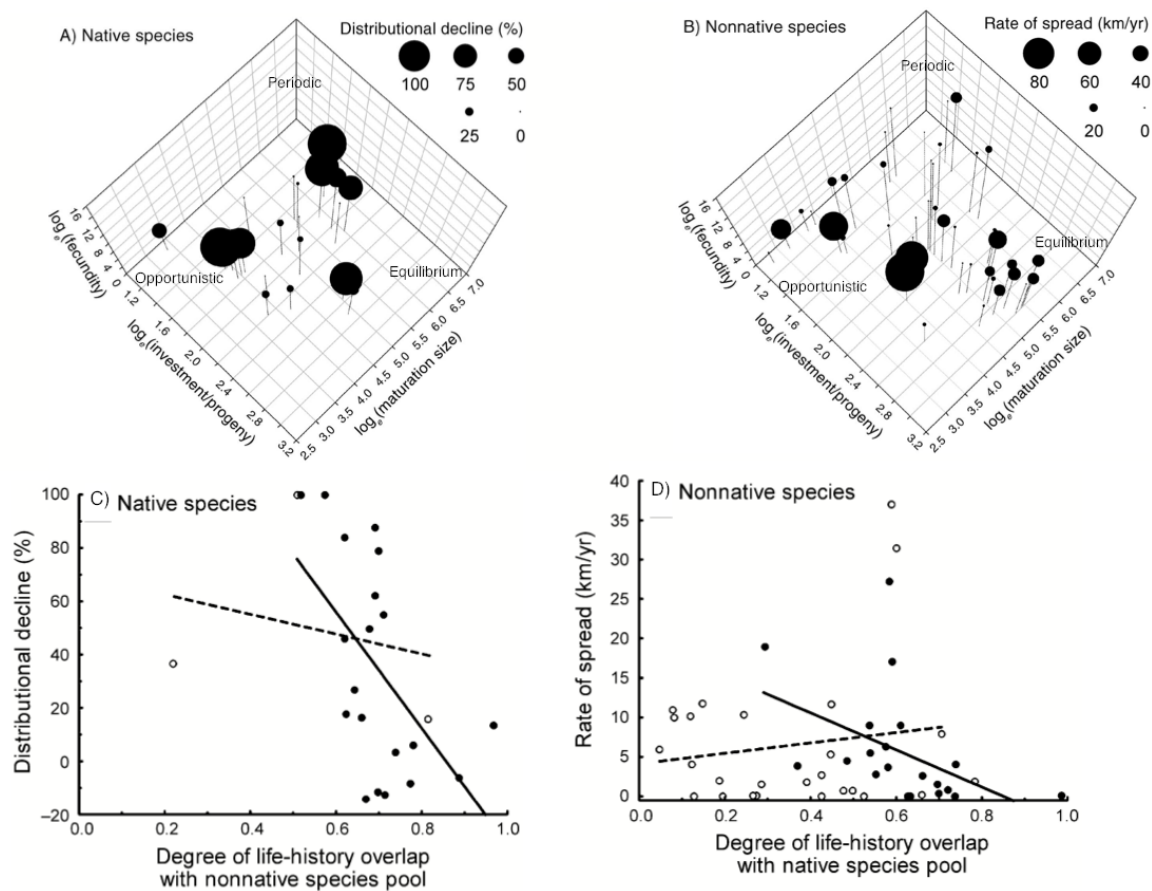


Figure 4: Distributional decline in native species (A,C) and spread in non-native species (B,D) plotted against axes consistent with the Winemiller-Rose life-history strategy space (A,B) with “opportunistic”, “periodic”, and “equilibrium” end-point strategies labeled. Point sizes give percentage distributional decline (A) for natives and rate of expansion in km/year (B) for non-natives (B). Also plotted against overall niche overlap (C,D). Open circles and dashed lines represent species that prefer slow-moving water, while closed circles and solid lines represent those preferring moderate or fast water (Modified from Olden *et al.* (2006) used without permission; see that paper for details of methods.)

Associating patterns of extirpation and expansion with species traits shows how human modification of the environment has created and removed ecological niches, and exemplifies how both biotic interactions and environmental conditions may mediate species invasions. In particular, the analysis by (Olden *et al.* 2006) of patterns within the W–R model revealed (Figure 4A-B) that

rapidly spreading invasives lie along a line connecting the opportunistic and equilibrium end-point strategies. Further, rapidly declining native species either overlap with non-natives along this line, or display a periodic strategy likely not adapted to modified environments.

Olden *et al.* (2006) also examined the potential for context-dependence in biotic resistance. This involved computing the total niche overlap (i.e., all traits) with non-natives (for native species) or natives (for non-natives) and separately examining species that prefer lentic (fast and medium moving water) from those preferring lotic (slow moving water) habitats more prevalent in the modern basin. Figure 4C-D illustrates the results, which show that expansion of non-natives declines with overlap of the native species pool in lentic but not lotic environments indicating biotic resistance in habitats more like the historic river. Thus, rapidly expanding non-native species take advantage of niche opportunities that are either created by human modification (i.e., lotic habitats), or inherent gaps in the niche space occupied by the depauperate native fauna within remaining lentic habitats.

Olden *et al.* (2006) demonstrates utility of trait-based approaches in ecology of invasions and conservation biology providing support for the niche-opportunity hypothesis both generally and within the context of the W–R model. These findings exemplify how both modified environmental conditions and biotic interactions mediate species invasions and support the view that alterations to the river environment have caused observed changes in species distribution. They also suggest two distinct patterns for extirpations of native fauna and appearance of invasives. In pattern 1, native fishes inhabiting the periodic end-point of the W–R model have life histories that are disadvantageous due to changes to the scale and predictability of environmental variation. In pattern 2, along the axis between opportunistic and equilibrium end-points non-native fishes have increased and native fishes have also declined. Although this work clearly suggests that pattern 1 is explained by changes in the abiotic environment, the extent to which pattern 2 owes to abiotic versus biotic factors (competition and predation between natives and non-natives) is unclear. Further, the analysis summarized here does not quantify changes in the river environment and so has no predictive utility for forecasting effects of future abiotic changes.

Conclusions

In the Lower Colorado Basin, native fishes, particularly those adapted to the variable pre-dam environment, have declined, and non-native species have increased (Minckley 1991; Fagan *et al.* 2002; Olden *et al.* 2006, 2008) Further development in the basin is constrained not only by actual water resources, but by legislative constraints imposed on human uses by the need to manage for threatened and endangered species. Faced with a changing climate, and rising demand for water resources, there is urgent need to understand effects of planned and unplanned changes both on species already at risk and those that are currently common. Although the conclusions of Olden *et al.* (2006), i.e., patterns 1 and 2, are relatively clear, to predict we need to understand quantitatively the strength of relationships between changes in abiotic environments and persistence of fishes within life history space.

Thus we require a model that quantitatively relates alterations in environmental factors to persistence in the strategy-space of fish life histories. I propose a three step approach to accomplish this elaboration on the ecological story of Lower Colorado Fishes: (1) develop a model based on the theory of life histories in variable environments that quantitatively relates environmental variation to persistence in life history space, (2) determine the change in variability of environmental

covariates, and (3) determine how much mortality variation needs to be due to the covariates to explain observed timescales of changes in range in life history space (i.e., Olden *et al.* 2006) based on the model from 1.

It would seem that the W–R model accomplishes step 1. In fact, while it provides intuition (which may be empirically supported at large biogeographic scales; see Mims & Olden 2012), it does not *quantitatively* incorporate variability in environments into persistence in life history space (Winemiller 1992; Winemiller & Rose 1992; Winemiller 2005). On the other hand, a large body of work in general theoretical biology (e.g., Tuljapurkar 1990; Orzack & Tuljapurkar 1989) has made such quantitative connections (much of it summarized in Caswell 2001). Only recently have general models in this field combined multiple dimensions of traits consistent with Winemiller (1992) with inputs based on environmental variability. For example, Tuljapurkar *et al.* (2009) combines generation time, a measure of iteroparity (demographic dispersion), and a measure of competitive ability (within-year variances in vital rates) in the context of environment-driven between-year variation. Although this work is in early stages, there is evidence of multiple strategies consistent both with the ideas of Winemiller (1992), and with earlier work on life histories in variable environments (Tuljapurkar 1990; Orzack & Tuljapurkar 1989).

So, while the first step is feasible, the second requires data on patterns of variability in environmental covariates over the past 150 years. Ideally, one would collate data on hydrologic regime before during and after extirpation, respectively A-C in 1. Unfortunately, stream gauges with long records are rare, and especially so in the Southwest USA (Poff *et al.* 2007; Mims & Olden 2012). Moreover, there is no source of hydraulic data that can match the spatial scope of the SONFISHES occurrence data. Thus, it will be necessary to make assumptions based on stream type which may weaken the strength of overall conclusions. Despite this issue, I argue strongly that this type of quantitative work is necessary for further ecological understanding. Only with such a model can we know the expected magnitude of change in fauna for a projected change in environmental conditions (under pattern 1 or 2), or hope to tease apart the relative strength of mechanisms in pattern 2.

Finally, I caution that the research proposed is *not* a necessary first step for conservation of native fishes in the Lower Basin. Rather, as suggested by Minckley (1991), it is well understood that non-natives have major effects on native fishes. Yet, while this understanding has led to massive investment in predator control, it tragically has not resulted in understanding of interaction strength between native and non-native fishes (Mueller 2005). Thus, we essentially waste time and money on a strategy of unknown efficacy. Policymakers, managers, and ultimately citizens must commit to scientifically evaluating management strategies, whether current or future. The large scale investment necessary to continue predator control militates against much budget for research. On the other hand, Minckley *et al.* (2003) put forward a plan for restoration of small-scale off-channel habitats, and protection of these habitats from non-native fishes, which would simultaneously allow for research on the strength of interactions with non-native fishes. This plan, however, has languished (Mueller 2005). In my opinion, the first step should be to implement Minckley's plan. After all, the biologists have done their jobs (Minckley 1991).

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