DISSERTATION

FISH FAUNA HOMOGENIZATION OF THE UNITED STATES, LIFE-HISTORY CORRELATES OF NATIVE EXTINCTIONS AND NON-NATIVE INVASIONS IN THE AMERICAN SOUTHWEST, AND THE BI-DIRECTIONAL IMPACTS OF DAMS IN THE AMERICAN SOUTHEAST

Submitted by

Julian David Olden

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JULIAN DAVID OLDEN ENTITLED FISH FAUNA HOMOGENIZATION OF THE UNITED STATES, LIFE-HISTORY CORRELATES OF NATIVE EXTINCTIONS AND NON-NATIVE INVASIONS IN THE AMERICAN SOUTHWEST, AND THE BI-DIRECTIONAL IMPACTS OF DAMS IN THE AMERICAN SOUTHEAST BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

Committee on Graduate Work

Paul L Angermeier

Paul L. Angermeier

Michael E. Douglas

Michael E. Douglas

Kurt D. Fausch

Kurt D. Fausch

N LeRoy Poff

N. LeRoy Poff (Advisor)

Dan Binkley

Dan Binkley (Department Head)

ABSTRACT OF DISSERTATION

FISH FAUNA HOMOGENIZATION OF THE UNITED STATES, LIFE-HISTORY CORRELATES OF NATIVE EXTINCTIONS AND NON-NATIVE INVASIONS IN THE AMERICAN SOUTHWEST, AND THE BI-DIRECTIONAL IMPACTS OF DAMS IN THE AMERICAN SOUTHEAST

The conservation of biodiversity and preservation of biological integrity are at the forefront of scientific thought and research. An important aspect of the current biodiversity crisis is the manner by which the compositions of biological communities are changing in time and space, and the specific mechanisms responsible for these changes.

In the first section of my doctoral dissertation I explore the process of biotic homogenization, by which formerly-distinct native communities become more similar as a result of native species extinctions and the establishment of cosmopolitan, nonnative species. I identify three forms of homogenization (genetic, taxonomic and functional) and explore the immediate and future impacts of each on ecological and evolutionary processes. Next, I present a conceptual model that describes a number of potential scenarios by which species invasions and/or extinctions can lead to various trajectories of biotic homogenization or differentiation (i.e., decreased community similarity). I use a simulation approach to explore the model's predictions and then validate the model using empirical data for freshwater fish faunas in the United States at three spatial scales: the entire continent, zoogeographic provinces in California, and watersheds within these provinces.

In the second section of my doctoral dissertation I examine the fish faunas of the Colorado River Basin, where environmental degradation and the proliferation of non-native fish species threaten the endemic, native faunas, making them especially susceptible to biotic homogenization. Using fish occurrence data for the past 160 years I quantify long-term changes in fish distributions and use a comprehensive suite of morphological, behavioural, physiological and life-history traits to identify specific life-histories strategies that are associated with the greatest loss of native species and spread of non-native species.

In the third section of my doctoral dissertation I report on research conducted in the Upper James River Basin that considers one of the primary causes of native extirpations and non-native introductions in aquatic systems; namely the regulation of rivers by dams and diversions. Specifically, I examine how environmental disturbance gradients that occur below a flood-control dam structure (i.e., altered flow regime, water temperatures, substrate composition, and macroinvertebrate biomass) influence the structure of downstream fish assemblages.

Julian David Olden
Graduate Degree Program in Ecology
Colorado State University
Fort Collins, CO 80523
Fall 2004

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Preface

My doctoral research is concerned with understanding the patterns and processes shaping fish communities at different temporal and spatial scales in different regions of the United States. A re-occurring theme in the current biodiversity crisis is that locally-distinct native fish communities are being replaced by nonnative-dominated communities composed of cosmopolitan fish species via a process called biotic homogenization. The first 3 chapters of my dissertation explore various aspects of biotic homogenization, with respect to its ecological and evolutionary implications (Chapter 1), the specific mechanisms involved (Chapter 2) and the spatial extent by which it has occurred for fish faunas across the United States (Chapter 3). A primary finding from this work is that fish homogenization is a complicated process, which can only be understood by exploring temporal patterns and causes of change in native and non-native fish species' distributions. The next 3 chapters of my dissertation explores these issues with respect to the endemic fish faunas of the Colorado River Basin by quantifying temporal changes in native and non-native fish distributions (Chapter 4), comparing functional trait differences between native and non-native species' pools (Chapter 5) and determining life-history correlates of native species' rarity, probability of extirpation and extinction risk. Shifts in the functional characteristics of fish communities in the Colorado River emphasize the critical role of river regulation in modifying environmental conditions and favouring non-native species over native species. The last chapter of my dissertation (Chapter 7) explores these issues in the Upper James River Basin by examining how fish

communities recover spatially to downstream and upstream disturbance gradients caused by river regulation.

Table of Contents

Chapter 7

Other Preliminaries

For the purposes of the rapid dissemination of my dissertation research and to appropriately acknowledge the intellectual contributions of my co-authors I have opted to prepare each chapter according to journal submission guidelines. Below I provide relevant publication and co-author information for each chapter.

Chapter 1: Olden, Julian. D., Poff, N. LeRoy, Douglas, Marlis. R., Douglas, Michael. E., and Kurt. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19:18-24.

Chapter 2: Olden, Julian. D., and N. LeRoy Poff. 2003. Toward a mechanistic understanding and prediction of biotic homogenization. *American Naturalist* 162:442-460.

Chapter 3: Olden, Julian. D., and N. LeRoy Poff. 2004. Ecological mechanisms driving biotic homogenization: testing of a mechanistic model using fish faunas. *Ecology* 85:1867-1875.

Chapter 4: Olden, Julian. D., and N. LeRoy Poff. In press. Long-term trends in native and non-native fish faunas of the American Southwest. *Animal Biodiversity and Conservation* 28(1):0000-0000.

Chapter 5: Olden, Julian. D., Poff, N. LeRoy, and Kevin R. Bestgen. Comparative life-history strategies of native and non-native fish faunas of the Colorado River Basin: linking ecological niche theory with rates of invasions and extirpations over the past century.

Chapter 6: Olden, Julian. D., Poff, N. LeRoy, and Kevin R. Bestgen. Living on the edge: species trait synergisms and the predisposition of endemic fishes to rarity, extirpation and extinction.

Chapter 7: Olden, Julian. D., Poff, N. LeRoy, and Paul. L. Angermeier. Upstream and downstream recovery of fish faunas to multiple dam-induced disturbance gradients.

Importantly, while I recognize the role of my co-authors, colleagues and anonymous journal reviewers in this work (see Acknowledgments of individual chapters), I stress that the entire dissertation is the sole product of my (Julian David Olden) creative efforts.

Chapter

1

Ecological and Evolutionary Consequences of Biotic Homogenization

Abstract

Biotic homogenization, the gradual replacement of native biotas by locally expanding non-natives, is a global process that diminishes floral and faunal distinctions among regions. Although patterns of homogenization have been well studied, their specific ecological and evolutionary consequences remain unexplored. We argue that our current perspective on biotic homogenization should be expanded beyond a simple recognition of species diversity loss, towards a synthesis of higher-order effects. Here, we explore three distinct forms of homogenization (genetic, taxonomic and functional), and discuss their immediate and future impacts on ecological and evolutionary processes. Our goal is to initiate future research that investigates the broader conservation implications of homogenization and to promote a proactive style of adaptive management that engages the human component of the anthropogenic blender that is currently mixing the Earth's biota.

Introduction

Anthropogenic environmental alterations and human-assisted dispersal of exotic species have sparked widespread changes in the global distribution of biota. The resulting modifications have predominantly been in two directions: range expansions of cosmopolitan, non-native species and range contractions of regional and endemic native species. This replacement of specific native forms by generalist non-natives in space and time has mixed the taxonomic composition of once disparate biotas, an occurrence termed 'biotic homogenization' (McKinney and Lockwood 1999).

Biotic homogenization is not a new phenomenon in the Earth's history. Episodic mixing of historically isolated taxa has occurred throughout the paleontological record (Vermeij 1991). More recently, humans have accelerated this process by facilitating biotic exchange among regions, as was first noted by Elton (1958) who observed a breakdown of Wallace's Faunal Realms due to global commerce. But only in the past decade has interest and concern regarding biotic homogenization been rekindled. Recent studies have either discussed or documented increased similarity in the composition of communities across an array of taxonomic groups (plants (Rooney et al. 2004), birds (Lockwood et al. 2000), reptiles and mammals (Wilson 1997), insects (Blair 2001), fish (Rahel 2000), mussels and amphibians (Duncan and Lockwood 2001), marine algae (Carlton 1996) and snails (Cowie 2001)). In fact, this global erosion of regional distinctiveness has ushered in a new era, aptly dubbed 'The Homogecene' that is creating in turn 'The New Pangaea' (Rosenzweig 2001a).

Lockwood and McKinney (Lockwood and McKinney 2001) recently emphasized the importance of identifying and understanding present-day patterns of biotic homogenization for establishing proactive conservation goals aimed at reducing its future ecological effects. While many investigations have provided considerable insight into empirical patterns of homogenization (Carlton 1996, Wilson 1997, Lockwood et al. 2000, Rahel 2000, Blair 2001, Cowie 2001, Duncan and Lockwood 2001, Rooney et al. 2004), the specific ecological and evolutionary consequences of this process still remain unexplored. Obviously a loss of species diversity carries ecological (Kinzig et al. 2002), evolutionary (Moritz 2002) and economic (Ehrlich and Ehrlich 1992) costs, yet to deepen our understanding of biotic homogenization, a distillation of broader and more globally significant perspectives is required. Why has this been slow to emerge? Higher-order implications may be much more subtle and difficult to grasp than, say, those associated with a simple gain or loss of species (Collins et al. 2002). This is particularly so given the broad spatial and temporal milieu within which biotic homogenization operates. It is clearly a more distinct and complex phenomenon than previously thought, and one whose consequences warrant explicit and extensive investigation.

Here, we identify three forms of homogenization (genetic, taxonomic and functional) and explore the immediate and future impacts of each on ecological and evolutionary processes. Our goal is to elucidate conservation implications of biotic homogenization, particularly as they relate to human dimensions, with the hope that directed research and an emerging synthesis will define not only the manner in which this process threatens global biotas, but also the proactive management scenarios required to suppress it.

Causes and consequences of genetic homogenization for species and populations

Genetic homogenization reduces the spatial component of genetic variability within a species or among populations of a species (Box 1.1). It can occur through a variety of mechanisms: (a) intentional translocation of populations from one part of the range to another; (b) intentional introductions of species outside of their normal ranges; and (c) extirpation of local or regional faunas. Genetic homogenization is a serious but often less recognized threat to the integrity of endemic gene pools, and can have a number of important implications.

Translocation of population(s) would enhance the potential for intraspecific hybridization, with the end result being the assimilation of previously differentiated gene pools (Stockwell et al. 1996, Storfer 1999). Introductions of species outside of their original range(s) could result in a founder effect and yield reduced levels of genetic variability, as well as setting the stage for interspecific hybridization (Rhymer and Simberloff 1996). And finally, if extirpations were a cause for faunal homogenization, then one consequence might be bottleneck(s) in local populations of the impacted species, along with lowered effective population size(s) (Lee 2002). This would occur directly via removal of individuals from source populations, or indirectly by habitat modifications. In relevant sections below, we explain these considerations in greater detail.

Intraspecific hybridization

Intraspecific hybridization can homogenize the unique characteristics of geographically distinct populations (Daehler and Carino 2001), as well as compromise the fitness of individuals by disrupting local adaptations (Storfer 1999). Intentional intraspecific introductions (either to replace or to supplement declining or extirpated populations) often result in an overt loss of genetic variability (Stockwell et al. 1996), resulting from founder effects, bottlenecks, and the resulting low genetic variability they engender (e.g. Quattro et al. 2002). For example, global stocking of cutthroat trout *Oncorhynchus clarki* from a single source region has yielded substantial genetic homogenization, and in at least one instance has played a primary role in the loss of a genetically distinct subspecies (Behnke 1992). As above, widespread aquaculture practices are often the catalyst for such homogenization in many fish species, yet ramifications are only now being unraveled (Douglas and Brunner 2002).

Genetic homogenization of populations can also influence the capacity of a species to expand its distribution. Mixing of locally adapted populations (e.g. peripheral with central) can impede species expansion because phenotypes favoured in central areas may be maladapted for conditions encountered at the distributional periphery (Lenormand et al. 1999, García-Ramos and Rodríguez 2002). Similarly, intraspecific hybridization and subsequent breakdown of regional distinctiveness can also increase vulnerability to invasion, and conversely, may enhance the success of hybrid competitors (Lee 2002). It may even promote expansion and ultimate success of the invading species. An interesting example of the latter involves the Argentine ant *Linepithema humile*. Here, spatial segregation of nests is determined genetically by innate aggression against non-nestmates

(Tsutsui et al. 2000). However, recently invading populations in California experienced a genetic bottleneck due to founder effects that resulted in widespread genetic similarity among populations. This, in turn, reduced intraspecific aggression and promoted formation of aggressive super-colonies that significantly impacted community- and ecosystem-level processes (Holway et al. 2002). Development of single, large colonies might be unstable over the long term (Tsutsui and Case 2001), yet a more immediate solution was sought to enhance recovery of invaded ecosystems. One solution was to introduce new alleles into the invasive populations so as to reduce genetic homogeneity and eliminate widespread development of super-colonies (Tsutsui et al. 2000). Clearly, genetic consequences of homogenization, particularly with regard to invader and resident, are only now beginning to be understood. This is as much a function of technological developments (such as application of single nucleotide polymorphisms to population-level problems; Brumfield et al. 2003), as it is of theoretical development.

Interspecific hybridization

Hybridization between genetically distinct species can create new adaptive systems, and thus, new ecological niches (Anderson and Stebbins 1954). This is particularly evident in aquatic ecosystems, where human-mediated dispersal has promoted numerous and dramatic hybridization events (Perry et al. 2002). Fishes provide the best examples, due simply to their external mode of fertilization coupled with weakly developed reproductive isolating mechanisms (Hubbs 1955). The situation becomes exacerbated when the introduced fish has evolved allopatrically, yet is closely related to the indigenous one. The poster children for this phenomenon are indigenous salmonid fishes of North America (Behnke 1992).

We posit that mechanisms driving genetic homogenization are actually synergistic, and that human interventions (as above) simply amplify the potential for hybridization within a given system. Human-mediated, long-distance dispersal and colonization events, for example, elevate the probability that pair-wise interactions between species will yield hybrids, while human-provoked environmental disturbances will likewise provide habitats suitable for hybrid progeny (Ellstrand and Schierenbeck 2000). This human dimensions aspect enhances the probability that 'hybrid swarms' will genetically extirpate native taxa (Rhymer and Simberloff 1996). Although such events are thought to occur over many years, even decades (as with trout, above), examples do exist where genetic swamping has occurred within quite abbreviated time frames. For example, within a scant four-year period following its introduction, the exotic pupfish *Cyprinodon variegatus* was involved in a large-scale introgressive hybridization event with the endemic *C. pecosensis* across 430 km of the Pecos River, New Mexico (Echelle and Connor 1989). Genetic swamping can occur relatively rapidly and over extended distances, and the seriousness of this phenomenon cannot be underestimated simply because its effects are deemed slower than, say, overt predation.

In summary, in spite of a limited number of studies, it is apparent that a great deal of uncertainty remains regarding the ecological consequences of genetic homogenization. This topic clearly deserves further investigation. Indeed, genetic homogenization may gain greater attention in the future given the emergence of field of landscape genetics

(Manel et al. 2003) and the importance of population diversity for ecosystem services (Luck et al. 2003).

Causes and consequences of taxonomic and functional homogenization for communities and ecosystems

To date, scientific research on homogenization has been pursued largely from a phylogenetic perspective (Lockwood and McKinney 2001, Rahel 2002) where the term 'taxonomic homogenization' is used to describe an increase in the compositional similarity among communities owing to the successful invasion of 'winning' species and the extirpation of 'losing' species (McKinney and Lockwood 1999, Box 1.1). Accounting for taxonomic change in communities is important and relatively easily achieved (Olden et al. 2003, Chapter 2); however, ecologically profound functional changes may occur in homogenized communities that are largely independent of taxonomic identity. Thus, a more subtle ecological examination of homogenization is required.

Species contribute individually and collectively to the functional stability of communities and ecosystems. Winners and losers in the homogenization lottery are not randomly distributed taxonomically; rather, invasion success and extirpation vulnerability are primarily defined by the interaction between intrinsic species traits and extrinsic environmental characteristics (McKinney and Lockwood 1999). Ecological implications of biotic homogenization might be more profitably examined by considering 'functional diversity', i.e. the composition of and variation in community traits, and its spatial distributed across landscapes (Box 1.1). Modifying the functional diversity of a community may result in functional homogenization involving the replacement of ecological specialists by the same widespread generalists. Although functional diversity is recognized as a determinant of ecosystem processes (Díaz and Cabido 2001), the importance of functional homogenization has received inadequate attention.

We present a conceptual model to assess the manner in which species introductions/extirpations can lead to functional homogenization with subsequent changes in overall community function and a reduction in ecosystem resilience (Box 1.2). Modifications to within- and between-community trait compositions will likely impinge upon community and ecosystem function, and resistance to environmental change. A decrease in functional diversity might reduce overall community and ecosystem functioning (Tilman et al. 1997), stability (Sankaran and McNaughton 1999), and resistance to environmental change by simply narrowing the available range of species-specific responses (Stachowicz et al. 2002). Consider a severe drought (the disturbance oval; Box 1.2, Fig. 1B) that strongly affects a subset of species in a community that possesses (or lacks) a particular suite of functional traits. Historical communities, with much greater breadth in functional space, should exhibit higher resistance or resilience when compared to homogenized communities (Box 1.2, Fig. 1B).

The functional homogenization of all local communities within a region (i.e. meta-communities) can increase vulnerability to large-scale environmental events by synchronizing local biological responses across individual communities. This in turn would reduce variability among communities in their response to disturbance, and would compromise the potential for landscape- and regional-level buffering. Because community composition defines the range of functional traits that influence ecosystem functions (such as nutrient retention or energy flow; e.g. McGrady-Steed et al. 1997), biotic homogenization might jeopardize ecosystem function by limiting the pool of species that can compensate for local extinctions (i.e. reduce spatial patterns in functional redundancy). Homogenized communities might therefore exhibit a decreased resilience to environmental disturbance because elevated similarities among-communities may damp or eliminate potential recolonizations by species with locally extirpated trait(s). Susceptibility of homogenized communities to environmental alteration might be particularly high in areas such as urban ecosystems that experience more frequent and severe disturbance events (Rebele 1994).

Although our model for functional homogenization (Box 1.2) is clearly hypothetical, it offers a methodological framework for future studies. Knowledge of the functional characteristics of spatially distinct biological communities could be used with observational and experimental data to explore the functional implications of community changes in trait types and frequencies that result from homogenization. An exploration of community similarities in multidimensional functional space should advance our understanding of biotic homogenization and its long-term ecological consequences, including the potential effects of homogenization on food-web structure and community susceptibility to species invasions (Box 1.3).

Evolutionary consequences of biotic homogenization

An evolutionary dimension to the current biotic crisis was perhaps best expressed by Soulé (1980) who stated: 'Death is one thing, an end to birth is something else'. We believe the potential evolutionary impacts associated with species invasions (Mooney and Cleland 2001) and endemic extirpations (Moritz 2002) are a useful framework within which the evolutionary implications of biotic homogenization can be addressed.

Speciation is a result of numerous ecological and evolutionary processes, which arguably act on the same biological template: the species. Rosenzweig (2001b) recently suggested that the future of speciation is intricately linked with the future of species diversity. Although we agree, we further expect biotic homogenization to provide a critical context within which speciation can occur, because future spatial variability in species diversity and composition is likely to be reduced greatly. A common component of most proposed mechanisms of speciation is that geographical isolation of sister populations (co-adapted gene complexes) is required for allopatric speciation, the putative source of most new species. Human facilitation of population dispersal across natural biogeographical barriers has diminished geographical isolates necessary for eventual allopatric speciation, thereby limiting future potential species diversity. Furthermore, the source of future biodiversity might also be restricted through the fusion of incipient evolutionary lineages via hybridization and introgression (Perry et al. 2001).

Alternatively, there is some possibility that biotic homogenization will promote the origin and diversification of new species, as invasive species evolve in new environments, or as greater hybridization opportunities create new species (Abbott 1992, Lee 2002). Species diversification may indeed be likely given the many examples of contemporary evolution (i.e. evolutionary changes observable over less than a few hundred years) involving invasive species (Stockwell et al. 2003). The question of whether homogenization will actually promote diversification via novel genetic convergences in new environments requires additional studies, perhaps using 'home and away' comparisons of invasive species with respect to energetics and life-cycle dynamics (e.g. Chess and Stanford 1998), behaviour and population genetics (e.g. Tsutsui et al. 2000), and habitat and resource use (e.g. Lohrer et al. 2000).

The widespread use of captive and genetically modified stocks to supplement dwindling wild populations will continue to cause mixing of formerly isolated populations. Immediate consequences of these events would be a compromise in disease or parasite resistance for the hybrid population, and a disruption of its capacity for local adaptation. Local adaptation and drift contribute to the genetic variability of isolated populations that helps assure that species respond evolutionarily to environmental change. Long-term consequences thus depend on the capacity for adaptation to environmental change (Levins 1968), which is a function of genetic background. Accordingly, homogenized genetic and/or functional variation might jeopardize the future resilience of biological communities by increasing the chances of species extirpations via reduced adaptive capacity. Indeed, paleontological evidence suggests that mass extinctions have never entirely reset the evolutionary clock because enough taxa (and therefore, functional diversity) survived to seed the recovery process without the origin of new phyla (Erwin et al. 1987). However, the extent to which extensive homogenization might constrain genetic or functional diversity and limit recovery in the face of future extinction events is uncertain.

In addition, the introduction of new species into new regions will result in multiple founder effects and could lead to novel selection pressures not previously observed (Mooney and Cleland 2001). This has the potential to alter evolutionary trajectories, irrespective of the extirpation of native species. Interestingly, although homogenization might facilitate novel species interactions, the number and breadth of these interactions are likely to be limited, owing to the taxonomic and functional simplification of the communities via common species invasions and extirpations. These simplifications in biotic interactions could lead to weaker selection pressures in the homogenized communities, and biotic mixing could therefore even endanger the long-term success of species that are seemingly the 'winners' in the homogenization process.

Conclusion

Homogenization is now considered one the most prominent forms of biotic impoverishment worldwide. To date, we have begun to understand patterns in biotic homogenization in both aquatic and terrestrial ecosystems; however, we are still unable to predict the consequences of these events, particularly for the provisioning of environmental goods and services. We believe that elucidating the future ecological and evolutionary threats of biotic mixing requires expanding our focus beyond isolated cases of species invasions and extinctions to the accumulation of multiple events that collectively occur across the entire landscape over time. Because the biotic homogenization process operates at larger spatial and temporal scales, we must incorporate this broader context into our thinking if we wish to quantify and understand the risks of genetic, taxonomic and functional homogenization to various levels of biological organization. Moreover, there is a growing need to expand the dimensions of biotic homogenization to include the abiotic context of global environmental homogenization, which promotes biotic simplification. It is in these areas that research will most effectively contribute new knowledge on the ecological and evolutionary implications of biotic homogenization. This will be a challenge given that continued growth and expansion of the human population will result in large-scale environmental upheaval, and subsequent pressures on regional biotas. However, we must place a premium on this research, and on the adaptive management scenarios that it will produce, to ensure that the Earth's ecosystems retain their resilience and sustainability in the face of this anthropogenic blender.

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Box 1.1. Measuring genetic, taxonomic and functional homogenization

Biotic homogenization, whether referring to genetic, taxonomic or functional, is defined as an increase in the spatial similarity of a particular biological variable over time, and is usually evaluated by comparing the average pair-wise similarity of the variable calculated at two discrete times.

Genetic homogenization can be quantified using a variety of genetic characteristics, such as the allelic composition of a particular locus or set of loci (i.e. identity of genotypes), their frequencies (i.e. relative abundance of genotypes), or by one of many metrics derived from the above parameters, such as percent polymorphic loci, mean number of alleles per locus, and mean heterozygosity. In addition, levels of population divergence can also be assessed by indices of genetic similarity such as F_{st} or using a variety of cluster analyses (e.g. Bayesian inference). These measures of genetic diversity are usually assessed in a comparative spatial framework (i.e. introduced versus source population, or disturbed versus non-disturbed populations), but they are rarely examined in a temporal framework (i.e. pre- and post- disturbance), simply because no genetic baseline data were collected prior to the homogenization event. It is in this temporal context where research is needed to elucidate genetic consequences of homogenization. Furthermore, choice of genetic markers (i.e. level of resolution) is crucial to detect the potential subtle genetic differences inherent to homogenization.

Taxonomic homogenization is calculated using species presence or absence data to examine the degree of similarity in community composition, and can be quantified using any one of a suite of similarity indices, diversity indices, cluster analyses or ordination approaches. Of the many similarity indices used in ecology for quantifying community similarity, Jaccard's coefficient (based on presence/absence data) is employed almost exclusively in homogenization studies. Other approaches include using diversity to quantify spatial turnover of species, comparison of species similarity based on cluster membership of communities, and the examination of position and distance between communities in reduced, species-ordination space.

Functional homogenization can be calculated in a similar fashion by first calculating the site-by-trait matrix (in the simplest case calculated as the product of the species-by-site matrix and the trait-by-species matrix) and then examining community similarity using one of the same approaches for taxonomic homogenization. Community similarity in functional characteristics could be assessed based on the presence or absence of species traits or the frequency distribution of traits in the community. Whether the species traits are discrete (binary or multi-state) or continuous will dictate the choice of similarity coefficient or multivariate statistical approach.

Box 1.2. A conceptual, trait-based framework for assessing the potential ecological consequences of functional homogenization

The occurrence and relative abundance of functional traits contributed by constituent species determines the functional diversity of a biological community. Fig. 1.1 presents a conceptual framework where each functional trait is represented by a single axis, and the collection of functional traits contributed by all species of the community defines the *n*-dimensional hypervolume in functional space occupied by the community (analogous to the species-specific functional niche of Rosenfeld (2002) extended to the entire community). For each single functional trait, species occupy some tolerance range along the environmental axis defined relative to that trait. The cumulative distribution of the trait states of all species represents the aggregate environmental tolerance for the community; therefore, an alteration of species composition (e.g. by invasion or extinction) can modify the overall community tolerance to the environmental condition. Figure 1.1A illustrates the effects of homogenization on a distribution of a single functional trait (i.e. one-dimensional trait space) for three hypothetical communities. The replacement of species possessing unique trait states (e.g. via the extirpation of rare species) by species possessing similar trait states (e.g. via the introduction of generalist species) during the homogenization process will truncate the tails of the trait distribution and compress the overall trait range for the community. Consequently, historical differences in the trait distribution among the three communities may be lost, causing them to become homogenized in functional space, i.e. current trait distributions converge toward some common central tendency.

In Figure 1.1B this conceptual framework is extended to a suite of species traits represented in multi-dimensional functional space for the same three hypothetical communities. It shows how the replacement of native species with unique trait states by introduced species with common trait states results in reduced breadth (i.e. trait variation) of the current or homogenized communities in functional space compared to the historical communities. Furthermore, the locations of the communities in functional space are shifted toward a common central tendency, as indicated by greater overlap in the three community trait polygons (Fig. 1.1B), an indication of functional homogenization. Note that because the 'winners' in biotic homogenization are often generalist species (McKinney and Lockwood 1999), the introduction of non-native species will result in reduced within-community functional diversity. However, if specialist, non-native species are introduced (i.e. species with trait combinations that do not exist in the recipient communities), the within-community functional diversity is expected to increase; however, greater between-community trait similarity is still expected to occur because the same species (and therefore traits) are introduced to the communities.

Box 1.3. Effects of homogenization on food-web structure and future species invasions

Simplification of food-web structure

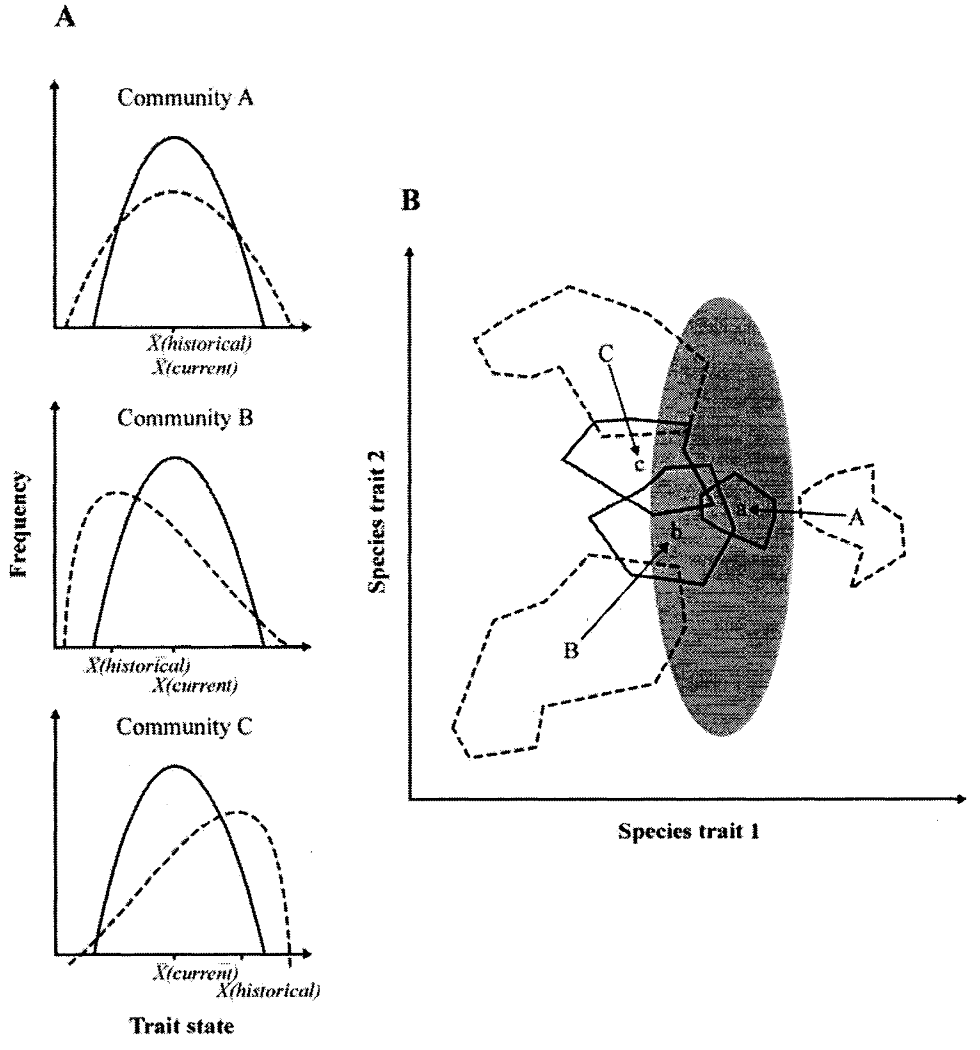
Given that species invasions and extirpations are acting in concert at all trophic levels, biotic homogenization could affect any of the myriad processes in communities that vary in space and time, such as spatial subsidies and food-web dynamics, and thereby have cascading effects elsewhere on the landscape. For example, increased spatial similarity in the species identity of predators and competitors could have direct and indirect effects on species at lower and higher trophic levels by increasing extirpation rates via intensified species-specific interactions (i.e. functionally similar species might utilize the same resources). In a recent study, Beisner et al. (2003) showed that the invasion of rainbow smelt *Osmerus mordax* into 2 north temperate lakes resulted in fish community homogenization through the spread of invaders, as well as the homogenization of zooplankton community structure via direct predation effects of smelt and indirect effects acting through competitive interactions among zooplankton. Therefore, positive feedback mechanisms of homogenization might exist where the simplification of one trophic level leads to increased simplification of other interconnected trophic levels (cf. Fausch et al. 2002). Investigations of biotic homogenization across multiple trophic levels will therefore become increasingly important for understanding the relationship between biotic mixing and food-web structure and dynamics. We believe that research examining how food-web dynamics are influenced by invasive species introductions (e.g. Woodward and Hildrew 2001), invasive species removal (e.g. Zavaleta et al. 2001), keystone native species (e.g. Power et al. 1996) and rare species (e.g. Lyons and

Schwartz 2001), and how changes in food-web structure influence ecosystem processes (e.g. Setälä 2002) could shed important insight into our understanding of the food-web consequences of biotic homogenization.

Increased susceptibility of communities to species invasions

Simplification via homogenization might also play a significant role in influencing the rate of species spread and community resistance to future invasions. García-Ramos and Rodríguez (2002) found that the speed of species invasion increased with environmental homogenization, which points to the importance of spatial heterogeneity in reducing population expansion of invasive species. Further, fluctuating resource theory (Davis et al. 2000) describes how species deletions are accompanied by resource release, which might make a community susceptible to further invasions. The loss of rare species from systems (a pattern commonly associated with homogenization; e.g. Rahel 2002) might substantially facilitate future species invasions and their associated ecological impacts (e.g. Lyons and Schwartz 2001). In addition to individual rare species, the simplification of the taxonomic and functional composition of entire communities could have important implications for future invasions and their ecological impacts. For example, grassland communities with low functional diversity exhibit decreased resistance to species invasions (Dukes 2002). Communities with low functional diversity are also more likely to exhibit similarities in temporal patterns of resource use, which ultimately translate into synchronized dynamics in species abundances. Temporal synchrony in population dynamics and the lack of complementary use of resources in time could increase the probability that resources are available to facilitate species invasions (e.g. Stachowicz et al. 2002).

Figure 1.1. A conceptual model of functional homogenization. (A) The effects of homogenization on a distribution of a single functional trait (i.e. one-dimensional trait space) for three hypothetical communities (A-C), where Trait state can refer to the value of a continuous trait or the category of a discrete trait and Frequency can refer to the frequency of species or individuals in the community that possess particular trait values or categories. $\bar{X}_{\text{historical}}$ and $\bar{X}_{\text{current}}$ represent the mean trait states for the historical (dashed line) and current or homogenized (solid line) communities, respectively. (B) The effects of homogenization on a set of species traits that are represented in multi-dimensional functional space (shown in two-dimensions for simplicity but can be readily extended to *n*-dimensions) for communities (A-C). Upper-case letters and dashed trait polygons represent historical communities, and lower-case letters and solid trait polygons represent current or homogenized communities. The shaded area represents a hypothetical environmental disturbance that affects a limited set of species in a community that possess (or lack) a particular suite of functional traits (indicated by the degree of overlap between the community polygons and the disturbance oval in functional space), and shows the relative resilience of the homogenized communities to future disturbances.



Chapter

2

Toward a Mechanistic Understanding and Prediction of Biotic Homogenization

Abstract

The widespread replacement of native species with cosmopolitan, nonnative species, is homogenizing the global fauna and flora. While the empirical study of biotic homogenization is substantial and growing, theoretical aspects have yet to be explored. Consequently, the breadth of possible ecological mechanisms that can shape current and future patterns and rates of homogenization remain largely unknown. Here, we develop a conceptual model that describes 14 potential scenarios by which species invasions and/or extinctions can lead to various trajectories of biotic homogenization (increased community similarity) or differentiation (decreased community similarity); we then use a simulation approach to explore the model's predictions. We found changes in community similarity to vary with the type and number of nonnative and native species, the historical degree of similarity among the communities, and to a lesser degree the richness of the recipient communities. Homogenization is greatest when similar species invade communities, causing either no extinction or differential extinction of native species. The model predictions are consistent with current empirical data for fish, bird and plant communities, and therefore may represent the dominant mechanisms of contemporary homogenization. We present a unifying model illustrating how the balance between invading and extinct species dictates the outcome of biotic homogenization. We conclude by discussing a number of critical, but largely unrecognized, issues that bear on the empirical study of biotic homogenization, including the importance of spatial scale, temporal scale, and data resolution. We argue that the study of biotic homogenization needs to be placed in a more mechanistic and predictive framework, in order for

homogenization studies to provide adequate guidance in conservation efforts to maintain regional distinctness of the global biota.

Introduction

Human-assisted dispersal of nonnative species and the modification of natural habitats have sparked widespread changes in the global distribution of organisms. Geographic modifications in patterns of species occurrences have predominantly been in two directions: the range expansion of cosmopolitan, nonnative species and the range contraction of rare, often endemic, native species. The gradual transition to nonnative-dominated communities has resulted in increased spatial and temporal similarity in the taxonomic characteristics of once disparate biotas, a phenomenon termed biotic homogenization (Vitousek et al. 1996, 1997; Bright 1998; Lockwood and McKinney 2001).

While of great contemporary concern, biotic homogenization is not a new phenomenon in the Earth's history. The paleontological record is replete with examples of episodic mixing of biotas that were historically isolated, such as the Great American Interchange resulting from the formation of the Panama isthmian land bridge, and the opening of transpolar interchange between Pacific and Atlantic (Vermeij 1991). Recognition of faunal mixing traces at least back to Charles Elton (1958), who discussed the breakdown of Wallace's Realms by global commerce. Even more recently, humans have greatly accelerated the mixing process through activities such as canal building (Por 1978), international commence (Carlton and Gellar 1993), recreation (Fuller et al. 1999), aquaculture (Naylor et al. 2001) and horticulture (Reichard and White 2001). As a result, humans have helped dissolve natural biogeographic barriers that once separated indigenous populations, causing the homogenization of the Earth's biota to an extent unseen by any previous natural episodes. Consequently, we are now entering a period characterized by an unprecedented rate of biotic homogenization, appropriately dubbed 'The Homogecene', in a place appropriately called 'The New Pangaea' (Rosenzweig 2001).

In the wake of continued human enhancement of species invasions and extinctions, the study of biotic homogenization is a rapidly emerging area in biology. For example, in the preface of a recent synthesis, McKinney and Lockwood (2001) emphasize the importance of identifying and understanding present day patterns of homogenization that may lead to proactive conservation goals aimed at reducing biotic mixing. Almost all research to date has focused on documenting patterns of homogenization for particular taxonomic groups, e.g., plants (McKinney and Lockwood 2001), trees (Rooney et al. 2001), birds (Lockwood et al. 2000), insects (Blair 2001), fish (Radomski and Goeman 1995; Rahel 2000; Marchetti et al. 2001; Scott and Helfman 2001), reptiles and mammals (Wilson 1997), mussels and amphibians (Duncan and Lockwood 2001a), snails (Cowie 2001) and marine algae and invertebrates (Carlton 1996). Of this research, quantitative estimates of biotic homogenization have been mainly limited to freshwater faunas (Rahel 2002).

In contrast to empirical advances, the invasion and extinction mechanisms underlying biotic homogenization have yet to be explored, as have the more subtle ecological and evolutionary consequences of homogenization (Olden et al. 2004, Chapter 1). Because a narrow focus on patterns of biodiversity loss may shed little insight into the potential consequences of biotic homogenization (Collins et al. 2002), a premium should be placed on understanding how the processes of species invasion and extinction contribute to the homogenization process. A necessary first step in understanding biotic homogenization and its ecological consequences is the development of theory that identifies the breadth of possible mechanisms that may drive current and future patterns and rates of homogenization. Ultimately, a sound theoretical foundation to the study of biotic homogenization is needed to assist in the development of future studies, as well as to aid in the analysis and interpretation of existing data.

Driven by the need for theory, our primary goal in this paper is to develop a theoretical framework that provides a mechanistic basis for understanding current and predicting future patterns of biotic homogenization. We propose a conceptual model that describes 14 unique scenarios through which different combinations of species invasions and extinctions can drive the homogenization process. These scenarios reflect the possible ecological outcomes resulting from interactions among nonnative species, native species, and habitat loss and fragmentation. Using a simulation approach, we apply the conceptual model to generate predictions of homogenization for each scenario as a function of differential patterns and numbers of nonnative species invasions and native species extinctions, the historical degree of compositional similarity among the communities, and the species richness of the communities. Based on the simulation results we present a unifying model for biotic homogenization that provides explanatory and predictive insight into the relative roles of different invasion and extinction processes that may be shaping currently observed patterns of homogenization in aquatic and terrestrial ecosystems. We conclude by discussing a number of important topics that require careful consideration in future studies of biotic homogenization, including issues associated with the influence of spatial and temporal scales on the investigation of homogenization, the importance of data resolution and the various approaches to quantifying homogenization, and the potential influence of species richness on observed patterns of homogenization. Our overarching goal is to provide a coherent and robust theoretical basis for the study of biotic homogenization. We hope this framework will help guide the collection, analysis and interpretation of empirical data, as well as ultimately enhance our understanding and prediction of future losses of regional distinctiveness in both space and time.

Mechanisms driving biotic homogenization – 14 scenarios of species invasions and extinctions

Conceptual model of biotic homogenization

Biotic homogenization, defined as an increase in species similarity among a set of communities through time, is quantified simply as the change in the pair-wise community similarity between two time periods. Homogenization can arise through many ecological mechanisms that represent specific, and often quite different, interactions among native species, nonnative species and the environment. Two distinct processes drive biotic homogenization: extinction of resident species (referred to as the losing species) and invasion of species (referred to as the winning species) into new areas (McKinney and Lockwood 1999; Lockwood and McKinney 2001). Here, we use the term extinction to denote the local loss (i.e., extirpation) of a species from a community. While it is true that invasion and extinction are required to fuel biotic homogenization, it is not generally appreciated that the magnitude and even the direction of change in community similarity can vary greatly depending on: (1) the relative numbers and taxonomic identities of the winning and losing species (defined by the differential impacts of nonnative species on the recipient communities and the differential response of native and nonnative species to habitat modification), (2) the historical compositional similarity among the communities, and (3) the species richness of the communities. Variation in these factors can result in very different magnitudes of increased community similarity (biotic homogenization), or even decreased community similarity (which we will refer to as biotic differentiation).

Below, we propose 14 scenarios depicting different pathways or mechanisms by which species invasions and extinctions can drive biotic homogenization and differentiation (illustrated in Fig. 2.1 and summarized in Table 2.1). We quantitatively illustrate patterns of community change associated with each of these scenarios using two hypothetical communities (referred to as site 1 and 2) with an initial community similarity of 50% based on an initial pool of 4 species (a, b, c and d); and using Jaccard's coefficient to quantify changes in community similarity (Fig. 2.1). This example is only illustrative. Later, we expand this example to consider how patterns in homogenization change when the numbers of winning and losing species are varied, when initial community similarity is varied, and when the assumption of fixed species richness is relaxed.

The 14 scenarios are divided into 3 groups, depending on whether the process is driven by species invasion (scenarios I1-I2), species extinction (scenarios E1-E4), or both invasions and extinctions (scenarios IE1-IE8). Because changes in community similarity are assessed in a pair-wise manner between two biological communities, we can derive each of the 14 scenarios from the combination of answers to the following dichotomous questions (represented as splits in Fig. 2.1): (1) Do nonnative species invade and successfully establish in both recipient communities?; (2) If nonnative species integration occurs, do the same or different invasive species establish in the recipient communities?; (3) In addition to the invasion, does the extinction of a native species in the recipient communities occur?; (4) If extinction occurs, is it bilateral (i.e., occurring in both sites) or unilateral?; (5) If bilateral extinction occurs, do the same or different native taxa go extinct?; (6) If unilateral extinction occurs, does a shared (i.e., originally occurring in both sites) or an unshared native species (i.e., originally occurring in only one site) go extinct?; and (7) Conversely to questions 2 – 6, in the absence of a species invasion, does unilateral/bilateral extinction of the same/different or shared/unshared native species occur? It is important to note that the invasion and extinction events in questions 2 – 6 do not necessarily imply that the invading species causes the extinction of the native species. Rather, these situations can equally arise from the introduction and extinction events being independently facilitated by anthropogenic disturbances, such as habitat loss or fragmentation. In summary, the questions above reflect the possible ecological outcomes resulting from the interactions between invading species, the resident species of the native communities, and environmental conditions. Although these scenarios are not completely exhaustive, they represent a broad array of possible outcomes associated with species invasions and extinctions, which are well supported by empirical evidence. Each of these scenarios is discussed below with reference to general and specific examples from the aquatic and terrestrial literature.

The 14 scenarios of species invasions and extinctions

Species invasion only (Scenarios I1 and I2)

Numerous studies in the literature have suggested that species invasions are often not accompanied by local extinction of native species (e.g., Simberloff 1981; Ebenhard 1988; Williamson 1996). In an extensive review, Simberloff (1981) reported that in 79% of studies (examining a large number of vertebrate and invertebrate species) the introduced species caused no extinction of native species. Consequently, species invasions may result in community augmentation where species are added to rather than subtracted from the communities. This may be especially true for plant communities where large numbers of native and nonnative species coexist at landscape scales (Stohlgren et al. 1999, 2003) and where the number of invasions has been show to exceed extinctions on islands across the globe (Sax et al. 2002). In aquatic ecosystems, the introduction of small-bodied fish species via bait bucket releases provides good support for scenario I1 driving homogenization (i.e., same species invade: Fig. 2.1). In North America, particular fish species are used preferentially for bait (Litvak and Mandrak 1993), and given that repeated introductions generally increase the probability of successful establishment (e.g., Forsyth and Duncan 2001) and bait fishes are small and non-piscivorous, we might expect that bait bucket releases will result in the introduction of the same species across the landscape without the extinction of resident fish species. In contrast, the intentional release of aquarium fish (Courtenay and Stauffer 1990) supports the importance of scenario IB for driving differentiation (i.e., different species invade: Fig. 2.1). In this case, many different species are introduced to multiple sites (likely due to the large pool of fish species common in the aquarium trade), again with no or little associated extinction pressure on the resident species.

Species extinction only (Scenarios E1 - E4)

Species extinctions without associated species invasions can play a large role in homogenization and differentiation, and may arise from at least three processes. First, increased modification and fragmentation of natural habitats have increased the rates of imperilment and extinction of many taxa (Saunders et al. 1991; Kerr and Currie 1995). Second, nonnative species may drive native species to extinction when invading a community, but ultimately fail to successfully establish. For example, while attempting to establish, an invasive species could reduce the abundance of particular resident species (e.g., prey species) and drive the resident to extinction, thereby contributing to its own eventual disappearance from the community because of lack of sufficient resources. This has been termed indirect failure by Case (1991), and although we are unaware of a published study documenting this phenomenon (likely due to our limited ability to observe this event) it has clear implications for community stability (Case 1995). Third, species invasions outside the focal taxonomic group can have significant impacts on native species in the communities in which homogenization is being studied and quantified. Examples include (but are not limited to): the extinction of native bird species by the Australian brown tree snake (Savidge 1987), and extinction of island reptiles by a variety of mammalian predators (Case and Bolger 1991), the loss of amphibian populations by fish introductions (Blaustein and Wake 1990), the effects of riparian plant invasions on aquatic macroinvertebrate biodiversity (Bailey et al. 2001), and the effects of browsing herbivores on native avifauna by modifying native habitats and consuming native plants (Diamond and Veitch 1981).

Of the three processes discussed above, the conversion of natural habitat into land dominated by agriculture and other anthropogenic activities is likely the primary mechanism causing species extinctions. The vulnerability of a species to extinction is primarily defined by the interaction of intrinsic individual characteristics, which determine survival and reproduction, and the degree of habitat modification (Pimm et al. 1988). Therefore, spatial patterns in species extinctions are expected to depend on species-specific vulnerability to different sources of habitat modification (influencing whether the same or different species go extinct in scenarios E1 and E2), and on the distribution of the species across the landscape and the spatial configuration and magnitude of habitat loss and fragmentation (influencing whether the extinction species was originally shared or unshared between the communities in scenarios E3 and E4).

Species invasion and extinction (Scenarios IE1 - IE8)

Invasive species may cause local extinctions of resident populations, or even cause global extinction of spatially-restricted fauna via direct (e.g., predation, grazing, competition, habitat alteration) and indirect pathways (e.g., alteration to fire regimes, nutrient cycling, hydrology, energy budgets) (Mack et al. 2000). Extreme examples include (but are not limited to) the ecological effects of the Argentine ant (Holway et al. 2002), rosy wolfsnail (Hadfield 1986), African crystalline ice plant (Vivrette and Muller 1977), spiny South American shrub (Braithwaite et al. 1989), Nile perch (Witte et al. 1992) and zebra mussel (Ricciardi et al. 1998). The probability of species extinction is expected to depend on the extinction vulnerability of the native species to species invasions (e.g., birds: Owen and Bennett 2000; plants: Lonsdale 1999), and the environmental template upon which these biotic interactions occur.

In addition to the potential biotic mechanisms driving species extinctions in these scenarios, both invasions and extinctions can independently be facilitated by natural and human-induced alteration to native habitats. For example, the modification of natural streamflow and thermal regimes in riverine ecosystems throughout the United States has presumably resulted in both the invasion of numerous exotic fish species and the loss of native fish species (Richter et al. 1997). Similarly, alterations to forest ecosystems have independently and interactively led to the successful invasion and extinction of bird species around the globe (Case 1996). As such, although it is useful to examine the conceptual model in Figure 2.1 in a causal manner, we emphasize that scenarios IE1-IE8 do not necessarily imply a direct mechanistic link between species invasion and extinction in recipient communities. The empirical literature amply shows that habitat modification independently facilitates species invasions and extinctions (Elton 1958); however, for the purposes of this paper, we restrict our focus to highlighting the empirical evidence supporting the scenarios where species invasions result directly in the extinction(s) of native species.

Scenarios IE1 and IE2 – There are many instances where ubiquitous introductions of species (i.e., the same species invading many sites) result in significant local extinctions (see references above). Whether the same species (scenario IE1: Fig. 2.1) or different species (scenario IE2: Fig. 2.1) are driven to extinction by the invader will depend primarily on the extinction vulnerability of the native species and the species-specific impacts (e.g., prey selectivity, competitive dominance) of the invader(s). High prey selectivity will likely result in the extinction of the same species across sites (scenario IE1) because the invader will selectively target particular native species, as in the case of a species-specific pathogen or predator. In contrast, low prey selectivity has a greater chance of causing the extinction of different native species across sites (scenario IE2). The probability that the same invasive species will be established and that the same native species will go extinct in multiple sites (i.e., scenario IE1) is supported by fact that winning and losing species involved in the homogenization process are not randomly distributed among taxonomic categories (McKinney 1997; Russell et al. 1998; McKinney and Lockwood 1999). Furthermore, evidence is accumulating to support the notion that invasion- and extinction-prone species traits are phylogenetically constrained, including among birds (Lockwood et al. 2000), fish (Duncan and Lockwood 2001b), mammals (Russell et al. 1998), and plants (Pyšek 1998).

Scenarios IE3 and IE4 – The introduction of the same species into multiple sites may lead to unilateral patterns of species extinctions, resulting in either the loss of a shared (i.e., originally occurring in both sites – scenario IE3: Fig. 2.1) or an unshared species (i.e., originally occurring in only one site – scenario IE4: Fig. 2.1). Unilateral extinction could occur when species only go extinct at sites lacking potential source populations to support rescue effects (*sensu* Brown and Kodric-Brown 1977) or lacking refugia from predation (Huffaker 1958). Similarly, species invasions associated with habitat disturbance may lead to greater chances of extinction compared to sites that are not subjected to this additional environmental stress (e.g., Ruiz et al. 1999). For instance, Moyle (1986) contended that for the eastern United States the local fish faunas appear to have adjusted to nonnative invasions without much loss of native species, whereas for more environmentally-disturbed ecosystems in the western United States and Florida, introduced species appear to have greater negative impacts on native communities. Unilateral extinction, coupled with the fact that species invasions may occur in communities that initially exhibit varying degrees of similarity in their species composition, supports the notion that an invading species may cause the extinction of a shared (scenario IE3) or an unshared species (scenario IE4).

Scenarios IE5 and IE6 – The invasion and establishment of different nonnative species across sites can influence community similarity by causing the bilateral extinction of the same (scenario IE5: Fig. 2.1) or different species (scenario IE6: Fig. 2.1). The global transport of nonindigenous marine organisms in ship ballast waters provides a powerful example where a large number of different species can be introduced into a region (e.g., Carlton and Geller 1993). After establishment, we might expect different invaders to cause the bilateral extinction of the same native species if, for example, they exhibit similar species-specific impacts (e.g., same prey preference and/or feeding mode: scenario IE5), or the extinction of different native species if they have dissimilar impacts (scenario IE6).

Scenarios IE7 and IE8 – Similar to scenarios IE3 and IE4, species invasions may result in the loss of a native species in one site but not another, an outcome that is again dependent on the occurrence of source populations to support recolonization events and the availability of refugia from predation. Different invaders can cause unilateral extinction (i.e., one invasive species causes an extinction, whereas the other species does not) via differential predation or competition pressures on the native species of the recipient communities. Moreover, given differences in the initial species compositions of the recipient communities, it is possible that the species driven to extinction may (scenario IE7: Fig. 2.1) or may not (scenario IE8: Fig. 2.1) be originally shared by the communities.

Simulation experiments – Exploring biotic homogenization under the 14 scenarios of species invasions and extinctions

Biotic homogenization is quantified by comparing the degree of similarity in community composition between two sites based on two points in time. Concordance in community composition across space can be quantified using any one of a suite of similarity indices, cluster analyses or ordination approaches (see Rahel 2002). Jaccard's coefficient of similarity (Jaccard 1900) is one of the most commonly used methods in ecology for quantifying community similarity and is employed almost exclusively in homogenization studies (e.g., Radomski and Goeman 1995; Rahel 2000; Marchetti et al. 2001; Rahel 2002). We used Jaccard's coefficient to measure similarity and estimate the degree of biotic homogenization and differentiation in our simulated communities. Jaccard's coefficient ranges from 0 (no species in common) to 1 (identical species composition), and is calculated simply as:

$$J(x_1 x_2) = \frac{a}{a+b+c} \tag{1}$$

where x_1 and x_2 represent two sites, a is the total number of species present in both x_1 and x_2, b is the number of species present in x_1 and absent in x_2, and c is the number of species absent in x_1 and present in x_2.

A deterministic simulation approach was used to examine how changes in community similarity differed among the 14 invasion-extinction scenarios. We restricted our simulations to reflect deterministic events because we wished to pursue a systematic exploration of the expected range of potential trajectories of biotic homogenization and differentiation resulting from interactions between native species, nonnative species, and environmental change. While stochastic dynamics are likely to be important in nature, they are difficult to infer from the "snapshot" data presented in the literature. Moreover, the ecological processes we simulate are common in nature and can be argued to have strong deterministic elements, and therefore our simulation approach is informative.

The simulation experiments involved generating 25 pairs of communities representing different levels of species richness (s = 4 to 100 species; increasing by increments of 4 species), for each of three different historical or initial community similarities (J_{initial} = 0.25, 0.50 and 0.75). The species composition of each pair was simulated to ensure the initial community similarity by increasing the value of a by $s \times J_{\text{initial}}$, and the sum of b and c by $s \times (1 - J_{initial})$ in equation (1) for each incremental increase of 4 species in the recipient community, e.g., $J_{initial} = 0.25$, species richness = 4 ($a = 1$, $b+c = 3$); $J_{initial} = 0.25$, species richness = 8 ($a = 2$, $b+c = 6$); $J_{initial} = 0.50$, species richness = 4 ($a = 2$, $b+c = 2$); $J_{initial} = 0.50$, species richness = 8 ($a = 4$, $b + c = 4$). Simulations were started at a species richness of 4 because this is the lowest value that community similarity could be set to the $J_{initial}$, as well as change via species extinction(s) or invasion(s). The simulation protocol predicted percent community similarity for each of the 75 simulated communities (i.e., 25 different initial levels of species richness and 3 different initial community similarities) following the mechanisms defined by each of the 14 scenarios for all possible combinations of the number of winners and losers. For all simulations the number of winners ranged from 0 (i.e., scenario E1-E4) to s (i.e., all other scenarios), whereas the possible number of losers was constrained by the number of species that the communities shared or did not share and the number of species that were available to become extinct, and therefore varied depending on the initial community similarity and particular scenario. In total, the simulations were completely exhaustive in that they generated predictions of community similarity under each invasion-extinction scenario for a range of species richness, initial community similarity, and numbers of winners and losers.

Percent change in community similarity (hereafter referred to as Δ_J) was calculated as the change in Jaccard's coefficient (expressed as a percent) between the predicted community similarity (generated from the simulation experiment) and the initial community similarity, i.e., predicted similarity minus the initial similarity of the communities. A positive Δ_J represents biotic homogenization and a negative Δ_J

represents the biotic differentiation. All simulations were conducted using computer macros in the MatLab® programming language written by J.D. Olden.

Predictions of biotic homogenization – The influence of species richness, initial community similarity, and species invasions and extinctions

The results from the simulations show that patterns in Δ_J are a function of the species richness of the recipient communities being invaded, the historical or initial degree of compositional similarity among the communities, the type of invasion-extinction scenarios, and the ratio of winning (invasive) to losing (extinct) species.

We examined the relationship between species richness of the recipient communities and Δ_J for each of the 14 invasion-extinction scenarios and for the 3 levels of initial community similarity (averaged across all combinations of the numbers of winners and losers.). Relationships were consistent among the different levels of initial community similarity, and therefore for the sake of brevity we only present the results for $J_{initial} = 0.50$ (Fig. 2.2). The effects of species richness on Δ_J for all scenarios were greatest at low species richness, but beyond a species richness of 20 patterns of community similarity became independent of richness. Although extinction-only scenarios (E1-E4) showed the strongest relationships with richness, in general, predicted Δ_J for all scenarios were insensitive to species richness. Further, this general pattern did not change in response to varying ratios of winners to losers (results not shown). Based on these findings, all subsequent examinations of changes in community similarity were averaged across all levels of species richness.

For all combinations of the number of winners and losers, relative patterns of Δ_J across the scenarios were similar, but not identical, for the three different initial community similarities (Fig. 2.3). It is important to emphasize that even though the range of possible values of Δ_J is the same for the 3 initial community similarities, the critical upper and lower bounds differ ($J_{initial} = 0.25$: -25 to 75%; $J_{initial} = 0.50$: -50 to 50%; $J_{initial} = 0.75$: -75 to 25%). Regardless of the initial community similarity and the number of winners or losers, scenarios I1, E2, E4, IE2, and IE4 always caused an increase in community similarity (i.e., biotic homogenization), whereas scenarios I2, E1, E3, IE5 and IE7 always caused a decrease in community similarity (i.e., biotic differentiation). The remaining four scenarios (IE1, IE3, IE6, IE8) resulted in both positive and negative Δ_J for all initial community similarities, although the median Δ_J for these scenarios was consistently either positive or negative across the gradient of initial community similarities. The one exception, however, was scenario IE3, which predicted a positive median Δ_J for $J_{initial} = 0.25$, no median change in compositional similarity for $J_{initial} = 0.50$, and a negative median Δ_J for $J_{initial} = 0.75$ (Fig. 2.3). In summary, measures of central tendency and dispersion were found to vary with initial community similarities (Fig. 2.3). Median Δ_J either increased (e.g., E4), decreased (e.g., I1, I2, E3, IE1-IE8) or showed no relationship (e.g., E1, E2) with increasing initial community similarity (Fig. 2.3), and variation in Δ_J either increased (e.g., I2, E1, E3, E4, IE1, IE3, IE5-IE8), decreased (e.g., I1, IE2, IE4) or showed no relationship (e.g., E2) along the same gradient.

To gain a finer understanding of the influence of numbers of winners and losers on the homogenization process, and thus to provide insight into the sources of variation in predicted levels of Δ_J in Figure 2.3, we examined 3 different ratios of losers to winners (hereafter denoted by L:W). Increasing L:W ratios represent increasing levels of extinction pressure associated with an invasion, or proportionally greater effects of environmental alteration on rates of extinction compared to rates of invasions. The 3 levels simulated were low ($0 < L:W \leq 1$), intermediate ($1 < L:W \leq 2$) and high ($L:W > 2$). We found that variation in Δ_J to be a function of the L:W ratio (Table 2.2). Regardless of the initial community similarity, increasing L:W led to increasing Δ_J under scenarios IE6 and IE8, decreasing Δ_J under scenarios IE1, IE3, and IE4, and no effect under scenario IE5 and IE7. Interestingly, the relationship between Δ_J and L:W for scenario IE2 depends on the level of initial community similarity. The varying effects of L:W on Δ_J shown in Table 2.2 provide insight into why particular scenarios (i.e., IE1, IE3, IE6 and IE8) show both positive and negative Δ_J in Figure 2.3.

These results show that predicted patterns of Δ_J can exhibit a positive, negative or no relationship with increasing numbers of losers relative to winners and that the direction of change does not generally vary as a function of initial similarity (Table 2.2, Fig. 2.3). Consequently, we explore in greater detail the effects of varying contributions of winners and losers on predicted levels of Δ_J for $J_{initial} = 0.50$ (again, averaging across all values of species richness) because the results from these simulations were generally intermediate in magnitude. Figure 2.4 shows that scenarios I1, E2, and E4 always resulted in positive Δ_J, where as scenarios I2, E1, and E3 always resulted in negative Δ_J. Patterns of homogenization and differentiation were more complex for the remaining scenarios. For example, community similarity increased with increasing numbers of the same winners and either increasing numbers of different or unshared losers (scenarios IE2 and IE4: Fig. 2.4D and F) or decreasing numbers of the same or shared losers (scenarios IE1 and IE3: Fig. 2.4C and E). In contrast, community similarity decreased with increasing numbers of different winners and either increasing numbers of different or unshared losers (scenarios IE6 and IE8: Fig. 2.4H and J) or decreasing numbers of the same or shared losers (scenarios IE5 and IE7: Fig. 2.4G and I). The relative influence of L:W to observed patterns in Δ_J depended on the particular invasion-extinction scenario and on the numbers of winners and losers involved in the interaction. The # of winners exhibited the greatest influence on Δ_J under scenarios IE1, IE3, IE6 and IE8 when the # of losers is large, whereas the # of losers showed the greatest effects in scenarios IE2, IE4, IE5 and IE7 when the # of winners is small.

Figure 2.5 illustrates patterns of average Δ_J (averaged across all species richness and for $J_{initial} = 0.50$) for each invasion-extinction scenario under different L:W. Community similarity is predicted to increase when same species establishment is accompanied with no extinction (I1), extinction of different species (IE2), or unilateral extinction of an unshared species (IE4), or when only extinction of different (E2) or unshared species (E4) occurs. In contrast, community similarity is predicted to decrease when different species establishment is accompanied with no extinction (I2), extinction of the same species (IE7), or unilateral extinction of a shared species (scenario IE5), or when only extinction of the same (E1) or shared species (E3) occurs. For the remaining scenarios, the expected Δ_J is a function of L:W. When the number of losers is less than the number of winners, Δ_J is dependent solely on the specific taxonomic identities of the winning species, but not the identities of the losing species (Fig. 2.5B). Consequently, invasion of the same species, on average, resulted in positive Δ_J, whereas the invasion of different species produced negative Δ_J. However, when there are a greater number of losers than winners, the direction and magnitude of Δ_J depended on both the number and identity of the winning and losing species (Fig. 2.5C, D).

Discussion

We have shown that changes in community similarity are a function of the type and number of winning and losing species, the historical degree of similarity among the communities, and to a lesser degree the richness of the recipient communities. Figure 2.6 provides a unifying model for homogenization, and highlights the deterministic relationships between the invasion-extinction scenarios, the number of winners and losers, and patterns in biotic homogenization. The two-dimensional space in Figure 6 indicates the scenarios that are expected to cause homogenization given different combinations of numbers of winners and losers (i.e., L:W), which are independent of species richness and the level of initial community similarity. Scenarios I1, E2 and E4, and IE2 and IE4 will always result in homogenization, independent of the number of winners, losers, and the ratio of the two. Scenario IE1 only results in homogenization when the number of winners is greater than the number of losers, whereas the opposite is true for scenario IE6. Homogenization will occur via scenario IE3 only when the number of losers is half that of the number of winners, and via scenario IE8 only when the number of losers is two times the number of winners. The varying effects of the number of winners and losers on levels of homogenization account for the fact that scenarios IE1, IE3, IE6 and IE8 can result in both homogenization and differentiation (Fig. 2.3). Finally, scenarios I2, E1, E3, IE5, and IE7 always result in biotic differentiation, regardless of the numbers of winners and losers. For scenarios that involve both species invasions and extinctions, Figure 2.6 shows that based on the relative number of winners and losers the potential for scenarios IE2 and IE4 to drive biotic homogenization is 4 times greater than scenarios IE3 and IE8, and 2 times greater than scenarios IE1 and IE6.

Our proposed conceptual model and its predictions can be used to provide important mechanistic insight into the invasion and extinction processes that are likely responsible for current patterns in biotic homogenization. For all levels of initial community similarity, predicted levels of homogenization were highest for scenarios involving the invasion of similar species and either no extinction or the differential extinction of native species across communities. These scenarios are in agreement with current empirical evidence that supports the occurrence of widespread introductions of cosmopolitan, nonnative species and the limited extirpation of native species in fish (Rahel 2000), bird (Case 1996) and plant communities (Lonsdale 1999, Sax 2002), and therefore may represent the dominant mechanisms driving the homogenization of these groups. Future studies should involve the statistical validation of the conceptual model by comparing predicted changes in community similarity under the different invasion-extinction scenarios to empirical estimates of biotic homogenization reported in the literature. For example, the elimination of the regional distinctiveness of fish faunas across the United States is perhaps the best documented example (in terms of quantifying changes in community similarity) of biotic homogenization to date (e.g., Radomski and Goeman 1995; Rahel 2000; Duncan and Lockwood 2001a; Marchetti et al. 2001; Scott and Helfman 2001; Rahel 2002), and thus provides a good opportunity to validate the conceptual model. Furthermore, for taxonomic groups currently lacking quantitative estimates of biotic homogenization (e.g., bird, plants), the conceptual model may potentially be used to provide insight into the most likely processes operating to produce contemporary patterns in biotic homogenization. The model may also offer a framework for predicting future patterns of homogenization based on estimated invasion and extinction rates of species of known taxonomic identities. Clearly, a prerequisite to generating reliable predictions of future homogenization is validation of the conceptual model using existing empirical data, an exercise that can be done for some aquatic and terrestrial taxonomic groups (Olden and Poff 2004, Chapter 3).

Important issues relevant to the study of biotic homogenization

Understanding and predicting patterns of biotic homogenization (for example, resulting from the conceptual model presented here) may be influenced by a number of largely unrecognized constraints that warrant explicit discussion. Among these are the influence of spatial and temporal scales on the investigation of homogenization, the importance of data resolution and the various approaches to quantifying homogenization, and the potential influence of species richness on observed patterns of homogenization. Here, we briefly discuss these with the hope they will receive greater attention by researchers in the future.

Biotic homogenization is a scale-dependent phenomenon, in that the observed number of winners and losers between any two time steps will be a function of the spatial extent over which the number of species is tabulated and the length of time during which species have the opportunity to invade or go extinct. In the spatial sense, increasing the extent of an analysis will increase the probability of recording species invasions because a greater number of communities and diversity of habitats are sampled. Additionally, the probability of recording an extinction event will decline because a greater diversity of habitats in the larger sampling area will promote the continued existence of populations and increase the probability of sampling relic populations. Therefore, at the regional scale, we would expect lower L:W, leading to the apparently greater relative roles of particular invasion-extinction scenarios (i.e., IE1 and IE3) in the homogenization process. As the spatial extent decreases, we would expect an increase in the probability of observing the introduction of different species and extinction of different or unshared species because the finer sampling resolution accentuates among-site habitat differences. Accordingly, at the local scale we would expect biotic differentiation via scenarios involving the establishment of different species and differential patterns of extinctions (i.e., IE6 and IE8). The spatial dependency of the biotic interactions driving homogenization may explain why Marchetti et al. (2001) found differentiation among fish communities in individual California watersheds, but homogenization in zoogeographic provinces.

Perceived patterns of biotic homogenization can also be influenced by the length of time over which homogenization is being examined. Longer periods increase the probability of observing species invasions and extinctions, leading to higher expected rates of homogenization or differentiation (assuming no temporal trends in native species turnover). This temporal dependence complicates comparisons of homogenization rates across different regions. For example, community similarity increased by 9% in Minnesota lakes between 1940 and 1992 (Radomski and Goeman 1995) and by 20% in California zoogeographic provinces between pre-1850 and 2000 (Marchetti et al. 2001). It is difficult to exclude the possibility that California exhibits a greater degree of homogenization simply because of a longer data record. Future studies should account for the potential effects of scale-dependence when studying biotic homogenization, and additional simulations (such as the ones presented here) could assist in assessing the sensitivity of measured biotic homogenization to variable observational time frames.

Data resolution and choice of statistical analyses can also influence perceived patterns of biotic homogenization. Typically, biotic homogenization is quantified by comparing community composition based on a particular similarity index, or comparing the distance among communities in species space based on clustering or ordination techniques (see Rahel 2002). The degree to which an inference of homogenization depends on the choice of statistical approach is an important, but uninvestigated, issue. More fundamentally, the numeric resolution of species data strongly influences perceived community patterns (Rahel 1990); therefore, sole reliance on presence/absence data may constrain our understanding of critical mechanisms contributing to homogenization. For example, we might expect increased variation in the relative abundances of species or decreased species evenness to be indicative of biotic homogenization and its potential ecological consequences. Quantifying the homogenization of community evenness may be particularly fruitful given its importance for invasion and ecosystem processes (e.g., Wilsey and Potvin 2000). The potential influence of species abundance on predicted patterns of biotic homogenization could be accounted for by incorporating a stochastic component into our conceptual model that represents the influence of species abundance on the outcome of native-nonnative species interactions.

Results from the conceptual models also suggest that species richness can have some influence our perception of homogenization, in that we found homogenization rate (increase in community similarity per individual invasion or extinction event) to be greater at low species richness. Consequently, observed patterns of homogenization in relatively species-poor fish or bird communities may be inflated compared to relatively speciose plant communities. Furthermore, the contribution of the different invasion-extinction scenarios to homogenization may vary globally due to geographical differences in the size of species pools. Given that species richness increases with spatial scale, we might also expect greater measured rates of homogenization at the local versus the regional scale. In addition, although we examined the influence of species richness on biotic homogenization based solely on the mathematical properties of adding or subtracting species from the recipient communities, species richness could also influence the number of winning and losing species. For example, if invasibility increases with resident species richness (see Levine and D'Antonio 1999 for a recent review), then we might expect the observed range of L:W to be partially a function of species richness, which might therefore influence the relative contributions of the biological mechanisms driving homogenization.

Prospectus

Biotic homogenization is now considered one the most prominent forms of biotic impoverishment worldwide, and it will likely continue to increase due to anthropogenic forces associated with growing human populations. So strong is this mixing force that global biotic homogenization with commensurate loss of species is argued to be the logical endpoint of the anthropogenic spread of nonnative species (Vitousek et al. 1996). To date, we have begun to better understand patterns in biotic homogenization in both aquatic (Rahel 2002) and terrestrial (Lockwood and McKinney 2001) ecosystems; however, we still lack an understanding of the mechanisms underlying current patterns and, consequently, an ability to predict future patterns of homogenization. We believe that unless study of biotic homogenization is placed in a more mechanistic and predictive framework, empirical results of homogenization studies alone will fail to provide adequate guidance in conservation efforts to maintain regional distinctness of the global biota. Accordingly, we submit that quantifying how the processes of invasion and extinction contribute to rates of biotic homogenization, and understanding how levels of habitat disturbance and connectivity mediate these processes, should be at the forefront of future research. Obtaining this knowledge is critical to enhancing our ability to predict which areas are most susceptible to increased homogenization and to determine which mechanisms primarily contribute to this process. Our conceptual framework, in conjunction with the collection, analysis and interpretation of new empirical data, can contribute to an enhanced understanding and prediction of future losses of regional distinctiveness across a variety of taxa in both space and time.

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Table 2.1. A summary of the 14 invasion-extinction scenarios used in the conceptual model for biotic homogenization (illustrated in Fig. 2.1). The scenarios are divided into 3 groups, depending on whether changes in community similarity are driven by only species invasions (scenarios I1-I2), only species extinctions (scenarios E1-E4), or both species invasions and extinctions (scenarios IE1-IE8).

Scenario	Description
Invasion only	
I1	Same species invade, no extinction of resident species
I2	Different species invade, no extinction of resident species
Extinction Only	
E1	No species invasion, extinctions in both communities involve same species
E2	No species invasion, extinctions in both communities involve different species
E3	No species invasion, extinction in one community of a species that was originally shared by both communities
E4	No species invasion, extinction in one community of a species that was originally not shared by both communities
Invasion and Extinction	
IE1	Same species invade, extinctions in both communities involve same species
IE2	Same species invade, extinctions in both communities involve different species
IE3	Same species invade, extinction in one community of a species that was originally shared by both communities
IE4	Same species invade, extinction in one community of a species that was originally not shared by both communities
IE5	Different species invade, extinctions in both communities involve same species
IE6	Different species invade, extinctions in both communities involve different species
IE7	Different species invade, extinction in one community of a species that was originally shared by both communities
IE8	Different species invade, extinction in one community of a species that was originally not shared by both communities

Table 2.2. Patterns of biotic homogenization as a function of 3 levels of initial community similarity under the 14 invasion-extinction scenarios. Reported values are medians and ranges (in parenthesis) across all levels of species richness. Low, Inter. and High represent categories describing different relative numbers of losing to winning species (for invasion and extinction scenarios only), including low # losers: # winners (0 < L:W ≤ 1), intermediate L:W (1 < L:W ≤ 2), and high L:W (L:W > 2).

	Initial community similarity								
	$J_{initial}$ = 0.25			**$J_{initial}$ = 0.50**			**$J_{initial}$ = 0.75**		
Invasion Only									
I1		25.2			16.8			8.4	
		(0.7-37.5)			(0.5-25.0)			(0.3-12.5)	
I2		-12.6			-25.1			-37.7	
		(-16.7-(-0.5))			(-33.3-(-1.0))			(-50.0-(-1.5))	
Extinction Only									
E1		-11.7			-17.1			-15.6	
		(-25.0-(0.8))			(-50.0-(-0.5))			(-75.0-(-0.3))	
E2		9.2			18.4			12.2	
		(0.5-25.0)			(1.0-50.0)			(1.5-25.0)	
E3		-13.5			-25.6			-38.5	
		(-25.0-(-1.0))			(-50.0-(-1.0))			(-75.0-(-1.0))	
E4		3.9			7.8			11.7	
		(0.3-8.3)			(0.5-16.7)			(0.8-25.0)	
Invasion and Extinction									
	Low	**Inter.**	**High**	**Low**	**Inter.**	**High**	**Low**	**Inter.**	**High**
IE1	22.7	-3.4	-11.4	13.5	-4.3	-17.1	6.0	-3.3	-15.2
	(0.0-37.3)	(-10.7-(-0.8))	(-23.7-(-1.5))	(0.0-24.9)	(-16.7-(-0.5))	(-48.0-(-1.0))	(0.0-12.4)	(-15.0-(-0.3))	(-71.2-(-0.5))
IE2	37.6	25.0	19.2	31.0	32.8	31.7	16.6	17.8	18.3
	(1.3-58.3)	(1.8-41.2)	(2.4-34.7)	(1.5-50.0)	(2.6-50.0)	(3.7-50.0)	(1.8-25.0)	(3.4-25.0)	(5.0-25.0)
IE3	18.7	-6.8	-13.9	3.9	-17.2	-28.4	-8.0	-30.7	-43.8
	(-5.0-37.0)	(-13.9-(-1.2))	(-24.0-(-2.2))	(-16.7-24.5)	(-30.0-(-1.5))	(-49.0-(-2.5))	(-32.1-12.0)	(-47.7-(-1.7))	(-74.0-(-2.7))
IE4	31.9	15.0	9.2	24.3	16.7	13.7	16.3	18.1	17.9
	(1.0-46.4)	(1.3-24.5)	(1.5-17.5)	(1.0-35.7)	(1.5-24.7)	(2.0-21.3)	(1.0-25.0)	(1.8-25.0)	(2.6-25.0)
IE5	-18.8	-18.9	-18.2	-36.2	-38.1	-33.3	-52.4	-58.0	-45.7
	(-25.0-(-1.2))	(-25.0-(-2.0))	(-25.0-(-2.8))	(-50.0-(-1.5))	(-50.0-(-2.0))	(-50.0-(-2.5))	(-75.0-(-1.7))	(-75.0-(-2.0))	(-75.0-(-2.3))
IE6	-11.6	2.4	8.9	-23.2	4.8	17.9	-36.2	3.9	11.8
	(-16.6-0.0)	(0.5-8.3)	(1.0-23.1)	(-33.2-0.0)	(1.0-16.7)	(2.1-46.2)	(-49.8-0.0)	(1.5-10.7)	(3.1-22.3)
IE7	-19.1	-19.8	-19.4	-37.5	-40.9	-38.6	-54.9	-63.1	-58.6
	(-25.0-(-1.5))	(-25.0-(-2.5))	(-25.0-(-3.4))	(-50.0-(-2.0))	(-50.0-(-2.9))	(-50.0-(-3.9))	(-75.0-(-2.5))	(-75.0-(-3.4))	(-75.0-(-4.4))
IE8	-12.5	-1.5	2.1	-25.0	-3.1	4.1	-37.5	-4.6	6.2
	(-16.6-(-0.2))	(-4.7-0.0)	(0.3-7.5)	(-33.3-(-0.5))	(-9.3-0.0)	(0.5-14.9)	(-49.9-(-0.7))	(-14.0-0.0)	(0.8-22.4)

Figure 2.1. A conceptual model depicting 14 scenarios representing different pathways or mechanisms by which species invasions and extinctions can drive biotic homogenization (increased community similarity) and differentiation (decreased community similarity). The 14 scenarios are divided into 3 groups, depending on whether the process is driven by only species invasions (scenarios I1-I2), only species extinctions (scenarios E1-E4), or both invasions and extinctions (scenarios IE1-IE8), and are derived from the combination of answers to a series of dichotomous questions represented as splits in figure (and discussed in the text). We quantitatively illustrate patterns of community change associated with each of these scenarios using two recipient communities (sites 1 and 2) with an initial community similarity of 50% ($J_{initial} = 0.50$) based on an initial pool of 4 species (a, b, c and d); and using Jaccard's coefficient to quantify changes in community similarity. Species occurrence is coded 0 or 1, and highlighted species represent changes in community membership due to a species invasion (represented by "1") or species extinction (represented by "0"). Under scenario IE4, for example, species e becomes established in sites 1 and 2, and species c (which was originally unshared by the communities) goes extinct in site 2, causing the Jaccard's coefficient to increase from 0.50 to 0.75 (i.e., 25% homogenization). Conversely, under scenario E3, no species invade, and species b (which was originally shared by the communities) goes extinct in site 2, causing the Jaccard's coefficient to decrease from 0.50 to 0.25 (i.e., 25% differentiation).

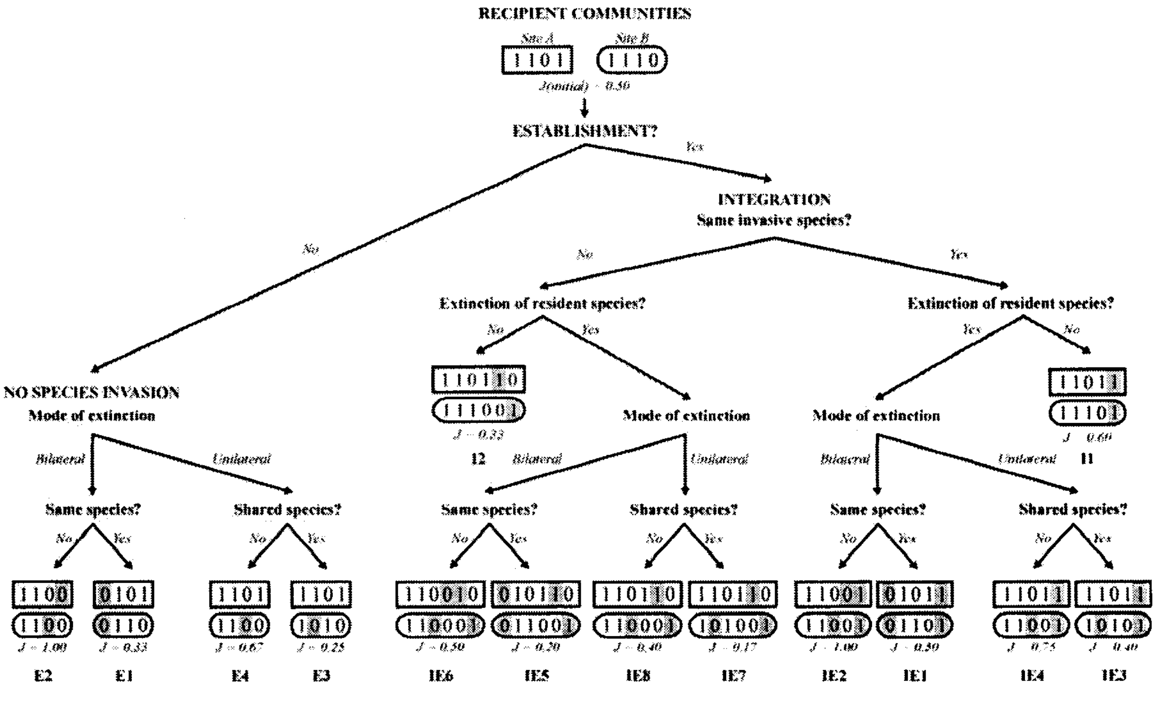


Figure 2.2. Patterns of biotic homogenization as a function of species richness for an initial community similarity of 50% ($J_{initial} = 0.50$) under the 14 invasion-extinction scenarios. Results are averaged across over all combinations of the number of winners and losers. Positive % change in community similarity indicates homogenization, whereas negative % change in community similarity indicates differentiation. Dotted lines represent scenarios I1-I2, dashed lines represent scenarios E1-E4, and solid lines represent scenarios IE1-IE8. Curves are based on simulation results from species richness values from 4 to 100 (by increments of 4) and data points were removed for clarity. Relationships were similar for $J_{initial} = 0.25$ and $J_{initial} = 0.75$, and therefore were not presented for brevity.

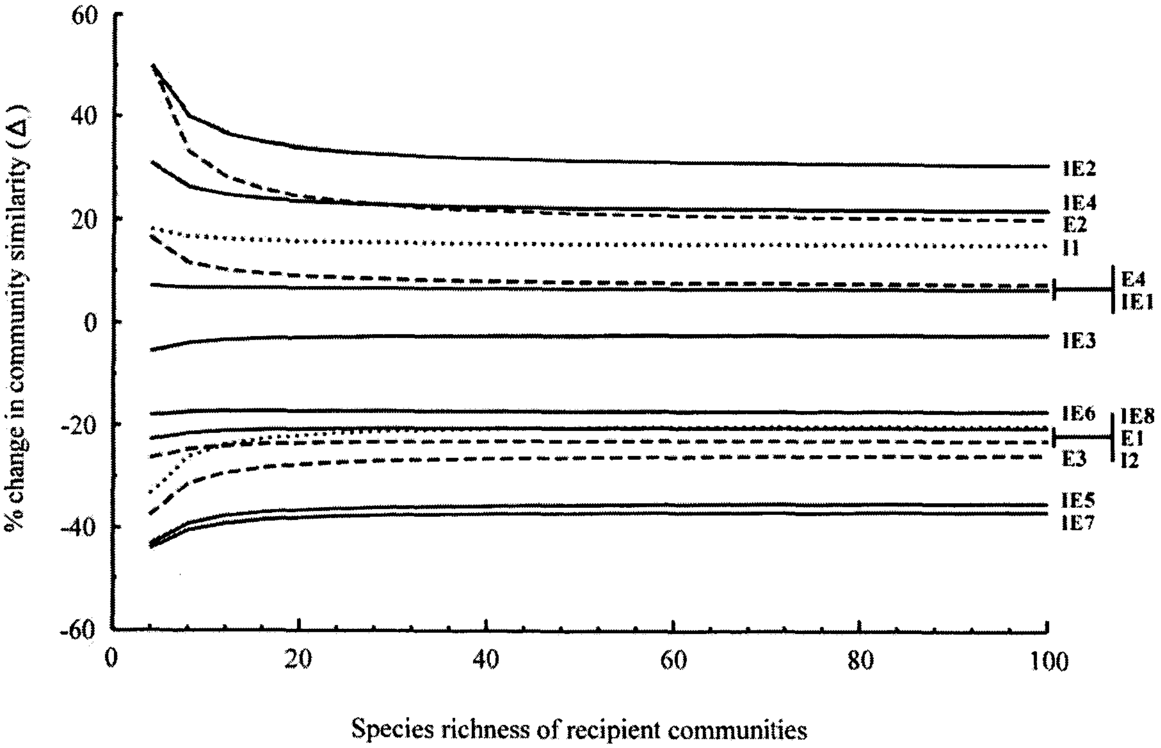


Figure 2.3. Patterns of biotic homogenization under the 14 invasion-extinction scenarios for 3 levels of initial community similarity ($J_{initial}$ = 0.25, 0.50 and 0.75). Results are averaged over all levels of species richness (see Figure 2.2) and all combinations of numbers of winners and losers. Square symbol is the median, boxes represent interquartile ranges, and whiskers represent the minimum and maximum values. Dashed line demarcates homogenization (positive community similarity) from differentiation (negative community similarity).

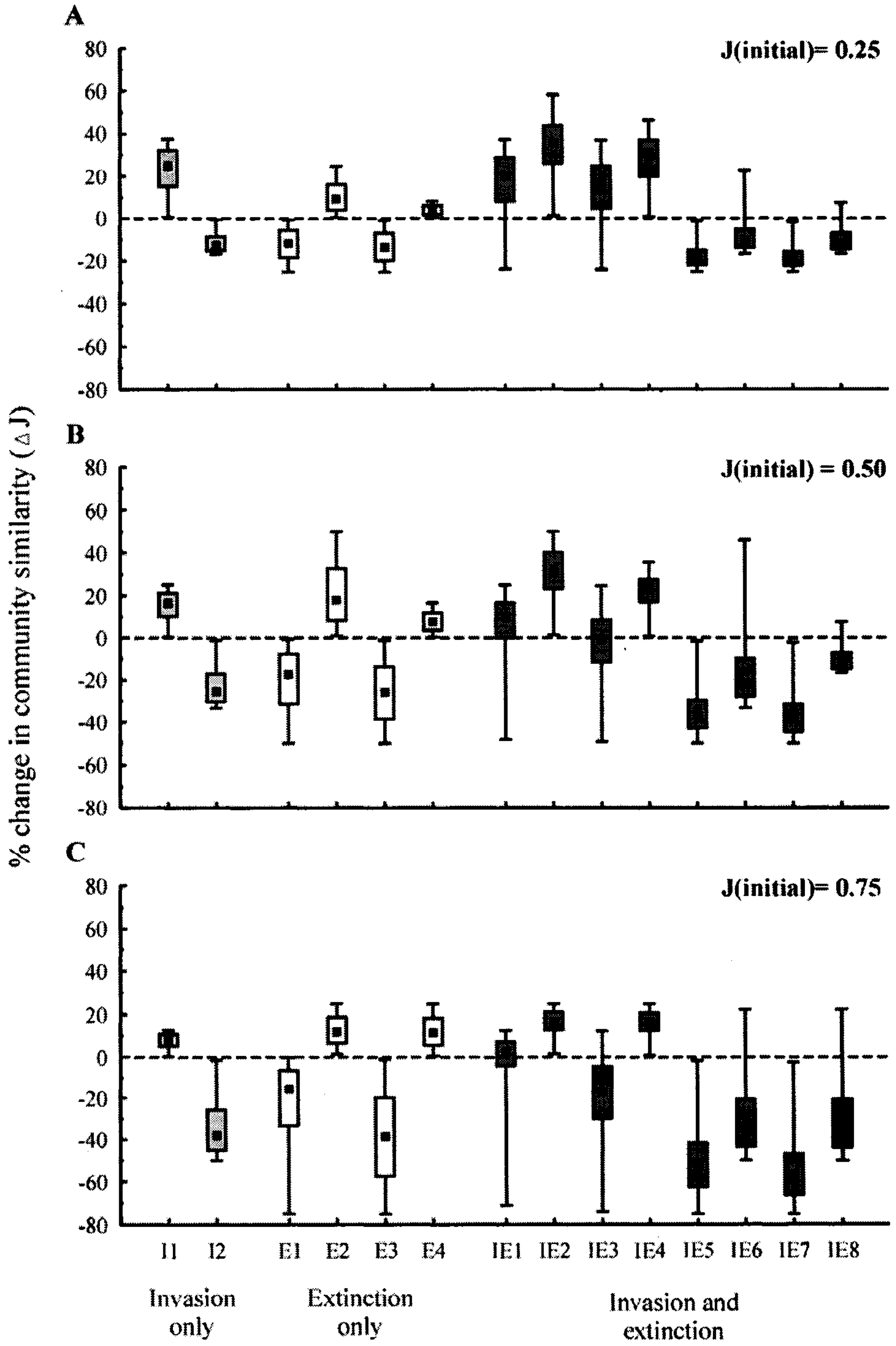


Figure 2.4. Patterns of biotic homogenization under the 14 invasion-extinction scenarios, based on $J_{initial} = 0.50$, as a function of varying numbers of winning species (i.e., number of nonnative species established in the recipient communities) and losing species (i.e., number of native species gone extinct in the recipient communities). For all simulations the number of winners ranged from 0 (i.e., scenario E1-E4) to s (i.e., all other scenarios), whereas the possible number of losers was constrained by the number of species that the communities shared or did not share and the number of species that were available to become extinct, and therefore varied depending on the initial community similarity and particular scenario. The number of losing species for scenarios IE1 – IE8 is represented by sets of curves reported in intervals of 4, from 4 to 24 for scenarios IE1, IE3, IE5 and IE7, and from 4 to 12 for scenarios IE2, IE4, IE6 and IE8. Curves in panels (C) – (J) do not originate at the y-axis because scenarios IE1 – IE8 always involve at least one winner.

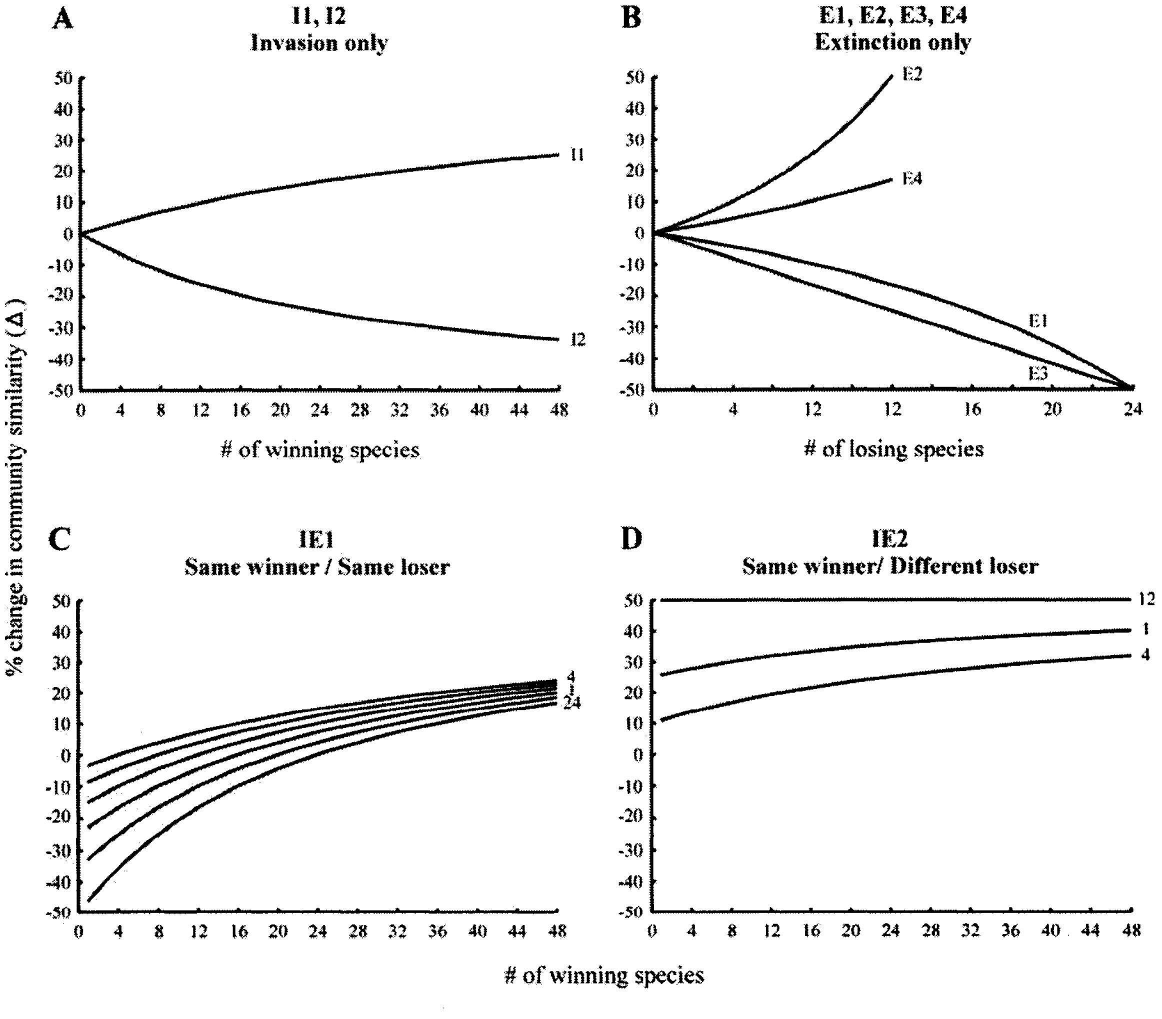


Figure 2.4. continued.

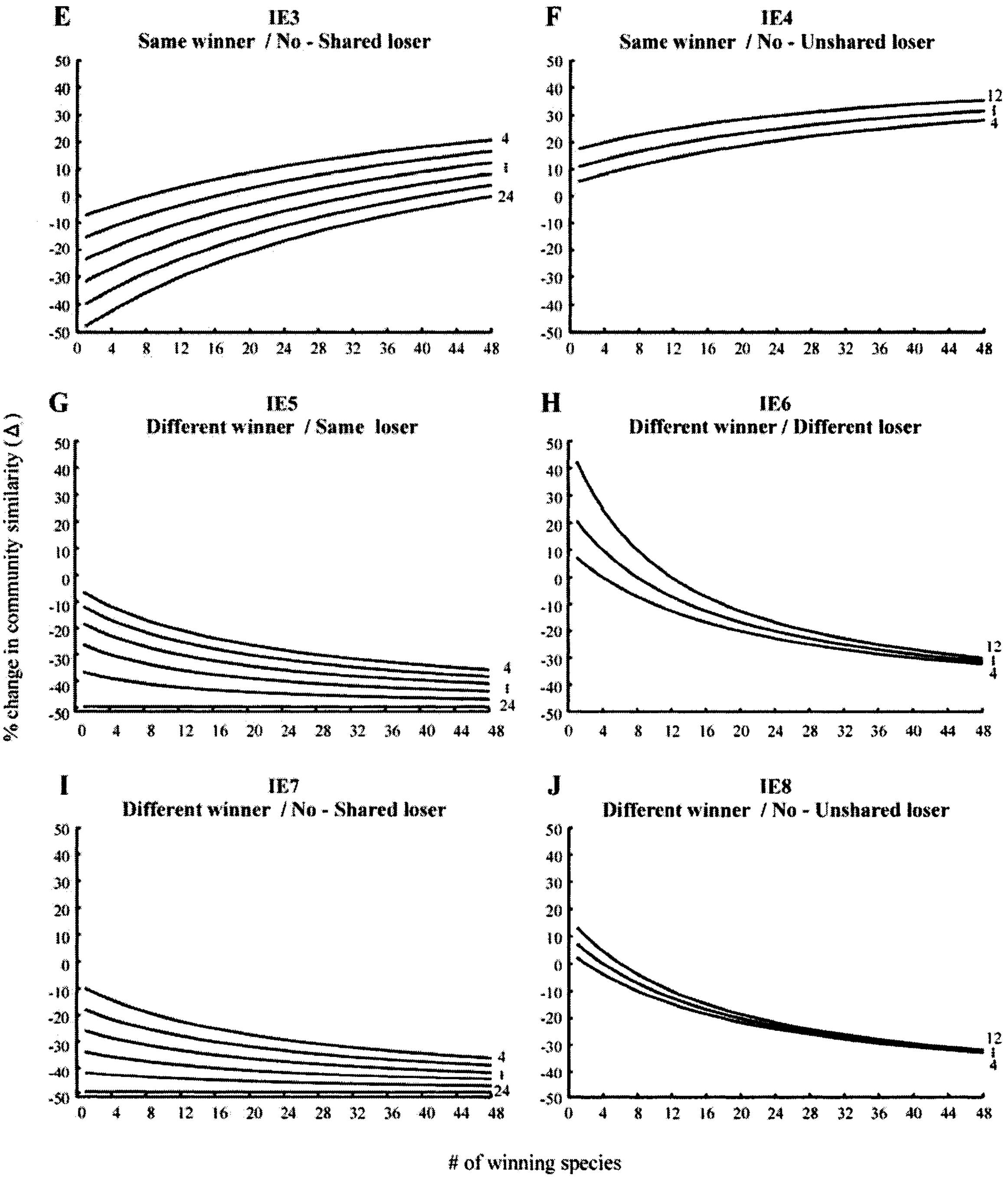


Figure 2.5. Patterns of biotic homogenization under the 14 invasion-extinction scenarios describing (A) invasion only and extinction only events, and invasion and extinction events categorized by relative number of losing to winning species (L:W): (B) low (0 < # losers: # winners ≤ 1), (C) intermediate (1 < # losers: # winners ≤ 2), and (D) high (# losers: # winners > 2). Results are averaged over all levels of species richness and represent $J_{initial} = 0.50$. Square symbol is the median, boxes represent interquartile ranges, and whiskers represent the minimum and maximum values. Dashed line demarcates homogenization (positive community similarity) from differentiation (negative community similarity).

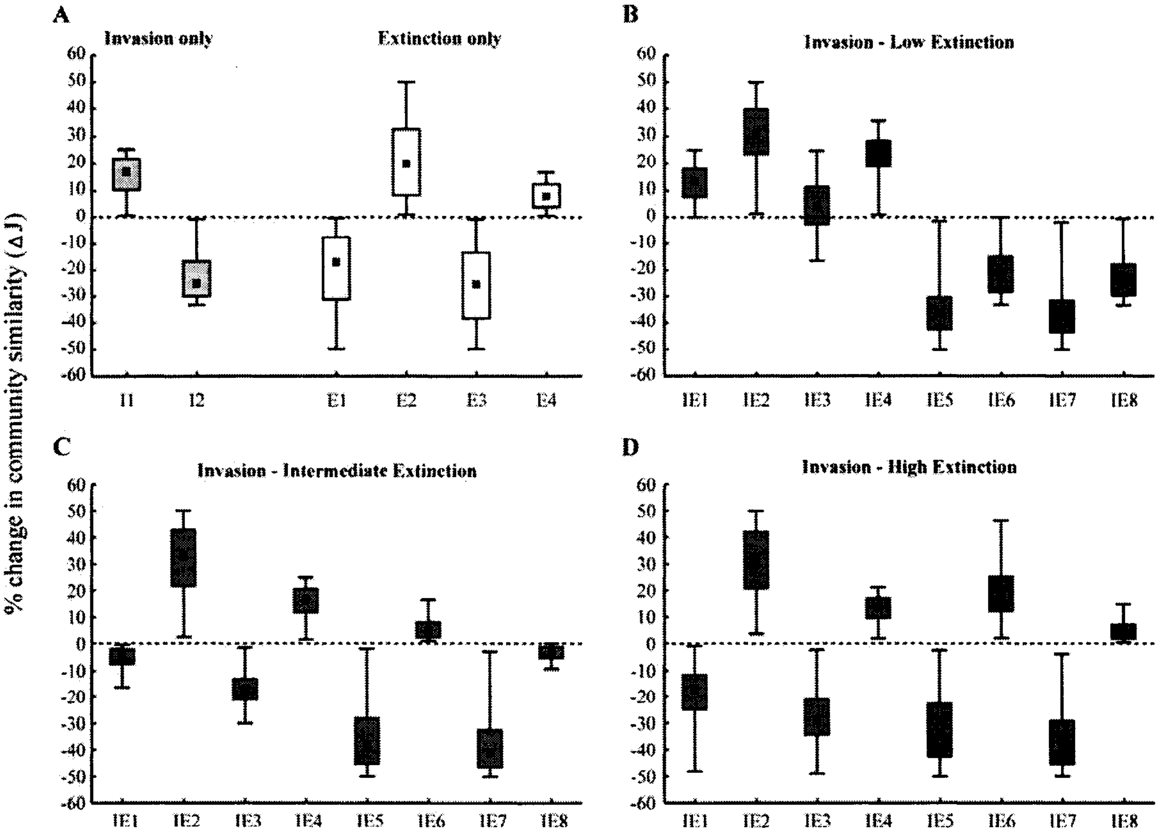
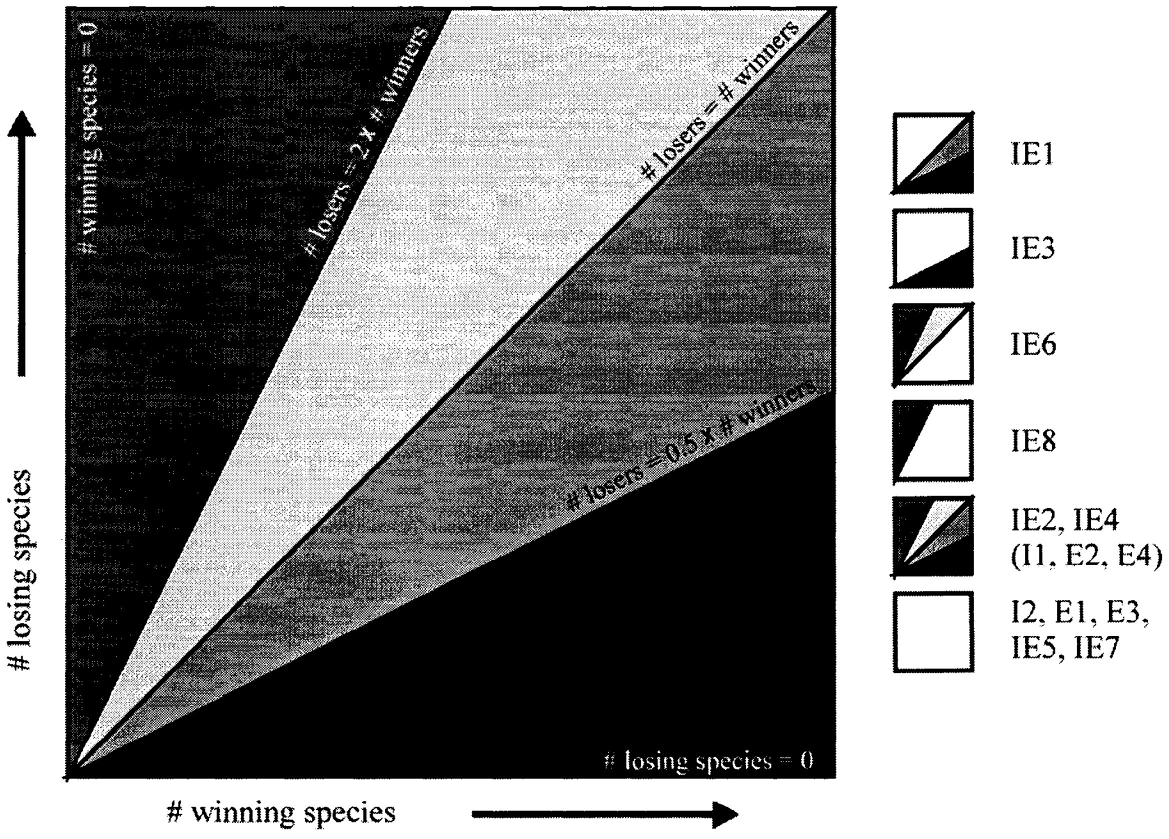


Figure 2.6. A proposed unifying model for biotic homogenization illustrating the conditions (i.e., relative number of winning and losing species) in which biotic homogenization (and not differentiation) is predicted to occur, independent of both species richness and initial community similarity. Diagonal clines represent different ratios of # winners to # losers, and the shaded portions of scenarios (panel on the left) provide conditions where homogenization is predicted to occur for each scenario. Different degrees of shading are intended only to help differentiate among the various scenarios that lead to homogenization. For example, scenario IE1 results in homogenization only when the number of winners is greater than the number of losers; scenarios IE2 always results in homogenization; and scenario I2 never results in homogenization. Note that scenarios I1, E2 and E4 always result in homogenization, but because they do not involve both winners and losers they are represented in parenthesis with IE2 and IE4.



Chapter

3

Ecological Processes Driving Biotic Homogenization: Testing a Mechanistic Model using Fish Faunas

Abstract

Biotic homogenization, the process of gradual replacement of native biotas by nonindigeous and locally expanding non-native species, is rapidly diminishing the regional distinctiveness of global terrestrial and aquatic ecosystems. Although the empirical study of biotic homogenization is substantial and growing, the mechanisms underlying its dynamics remain poorly understood. We recently developed a theoretical model that predicts levels of biotic homogenization or differentiation (i.e., decreased community similarity) according to a series of distinct mechanisms that describe the outcomes of various interactions between native species, non-native species, and the environment. Here, we test this model using empirical data for freshwater fish faunas in the United States at three spatial scales: the entire continent, zoogeographic provinces in California and watersheds within these provinces. Our analysis reveals that, in general, mechanisms depicting widespread introductions of cosmopolitan species and either no or differential spatial patterns of native species extirpations explain fish community homogenization across multiple spatial scales. Our results also highlight the potential effect of spatial grain on the perceived importance of different invasion-extinction scenarios shaping patterns of homogenization and differentiation. Next, we discuss the utility of the model for providing insight into the dominant ecological processes likely driving the homogenization of other major taxonomic groups that currently lack quantitative estimates of community change. Our study is the first to quantitatively examine the relative importance of different ecological mechanisms that can generate observed patterns of biotic homogenization. Using this model may allow advance

prediction of future patterns of homogenization by explicitly considering underlying ecological processes and mechanisms.

Introduction

The regional distinctiveness of biological communities reflects historical factors that have restricted species ranges via physical isolation, ecological interactions and evolutionary diversification (Huston 1994). In contrast to the paleontological record that reveals only episodic mixing of isolated biotas, such as during the Great American Interchange after the formation of the Panama isthmian land bridge (Vermeij 1991), global biotic exchange has been dramatically accelerated by humans in historical times. Charles Elton (1958) was perhaps the first to recognize this phenomenon when he discussed the dissipation of Wallace's Faunal Realms by global commerce during European settlement. In the past few decades humans have hastened the mixing process by dissolving natural biogeographic barriers through activities such as canal building, international commence, exotic pet trade, intentional translocations, aquaculture and horticulture (Courtenay and Stauffer 1990, Carlton and Gellar 1993, Litvak and Mandrak 1993, Naylor et al. 2001, Reichard and White 2001). The introduction of cosmopolitan, non-native species, in conjunction with the loss of native (often endemic) species is causing the breakdown of regional distinctiveness of the Earth's biota, a process termed *biotic homogenization* (Vitousek et al. 1997, McKinney and Lockwood 1999).

Patterns of biotic homogenization (or more specifically taxonomic homogenization) are defined simply as an increase in species similarity among a set of communities through time. This phenomenon has received increased attention in recent years for numerous taxonomic groups, including plants (Rooney et al. 2004), birds (Lockwood et al. 2000, Jokimäki 2003), insects (Blair 2001), reptiles and mammals (Wilson 1997), marine algae (Carlton 1996), mussels and amphibians (Duncan and Lockwood 2001a), snails (Cowie 2001), zooplankton (Beisner et al. 2003) and fish (Radomski and Goeman 1995, Rahel 2000, Marchetti et al. 2001, Scott and Helfman 2001), although only quantified for a small subset of these groups. Despite this wealth of interest, our understanding of the process remains very limited. For instance, biotic homogenization can arise from a number of ecological mechanisms representing specific, often quite distinct, interactions among native species, non-native species, and the environment. Several factors can regulate patterns and rates of homogenization, including the degree of initial differences in species similarity among the communities coming in contact (reflecting zoogeographic history), the taxonomic identities of the introduced and extirpated species, and the spatial distribution and number of species introductions and extirpations across the landscape (reflecting both natural and anthropogenic factors related to vectors of introduction and habitat modification). Our inability to distinguish among these various ecological and environmental drivers of biotic homogenization impedes our ability to explain current patterns or predict future rates of homogenization and thus intervene to minimize the potentially serious ecological and evolutionary consequences (Olden et al. 2004, Chapter 1).

The first mechanistic investigation of biotic homogenization was recently provided by Olden and Poff (2003) (Chapter 2), who developed a predictive model that forecasts trajectories of biotic homogenization or differentiation (i.e., decreased community similarity) according to a series of distinct mechanisms that describe the outcomes of various interactions between native species, non-native species, and the environment. In this paper we test this mechanistic model using freshwater fish faunas, the only taxonomic group for which quantitative estimates of homogenization are published. We analyze three data sets at three spatial scales: the continental United States (Rahel 2000), zoogeographic provinces in California (Marchetti et al. 2001), and the watersheds within these California provinces (Marchetti et al. 2001). To test the model, we hypothesized *a priori* which specific mechanisms would best describe the interactions between native fish species, non-native fish species and environmental modification at the three scales. Next, we applied the model to generate model predictions of changes in community similarity according to a suite of ecological mechanisms and compared them to the published findings of fish fauna homogenization and differentiation.

Our empirical validation of the mechanistic model provides important insight into the dominant ecological processes driving contemporary changes in fish community similarity within and across the United States. For major taxonomic groups currently lacking quantitative estimates of biotic homogenization, we discuss the utility of the model for exploring different invasion and extirpation processes likely to be dominant shapers of community change in those groups. Identifying the possible ecological processes leading to observed patterns in community similarity is the first step toward a mechanistic understanding and prediction of biotic homogenization and our paper is the first quantitative investigation of specific mechanisms responsible for patterns of biotic homogenization in a major taxonomic group. Taken together, the mechanistic model provides an important framework for interpreting the growing number of studies documenting patterns of biotic homogenization across a broad number of taxonomic groups.

An overview of the theoretical model of biotic homogenization (Olden and Poff 2003, Chapter 2)

Taxonomic homogenization (the most commonly studied form of biotic homogenization: Olden et al. 2004, Chapter 1) refers to an increase in species similarity among a set of communities and is quantified as the change in the pair-wise community similarity (based on species presence/absence) over a specified time interval (Rahel 2002). The model of Olden and Poff (2003) (Chapter 2) describes 14 ecological mechanisms by which different rates and patterns of species invasions and extinctions (or extirpations, hereafter used interchangeably) can cause changes in community similarity. These 14 scenarios, summarized in Table 3.1, represent possible outcomes resulting from unique combinations of interactions among species and the environment that are well supported in the aquatic and terrestrial literature (see Olden and Poff 2003, Chapter 2 for empirical examples for each scenario). The invasion-extinction scenarios are divided into three groups depending on whether only species invasions (scenarios I1-I2), only species extinctions (scenarios E1-E4), or both species invasions and extinctions (scenarios IE1-IE8) occur in the recipient communities.

For each invasion-extinction scenario the model systematically varies: (1) the number of introduced and extinct species; (2) the initial similarity among the communities (hereafter referred to as J_{initial}); and (3) the initial species richness of the communities; to generate predictions of change in community similarity based on Jaccard's coefficient of similarity (hereafter referred to as ΔCS). The number of introduced species ranged from 0 to initial species richness, whereas the maximum possible number of extinct species was constrained by the number of species that the communities originally shared or did not share and the number of species that were available to become extinct, and therefore varied depending on the initial community similarity and the particular scenario. A positive ΔCS represents biotic homogenization and a negative ΔCS represents biotic differentiation.

Empirical evidence for fish fauna homogenization throughout the United States

Elimination of the regional distinctiveness of fish faunas across the United States is the best quantitative documentation of biotic homogenization to date (e.g., Radomski and Goeman 1995, Rahel 2000, Duncan and Lockwood 2001a, Marchetti et al. 2001, Scott and Helfman 2001, reviewed by Rahel 2002). The estimates of fish homogenization and differentiation reported by Rahel (2000) and Marchetti et al. (2001) are among the only published in the literature (but see Radomski and Goeman 1995). These two datasets are optimal for testing the model because they were collected over a similar time period (ca. the last century), which minimizes potential bias in estimates of homogenization resulting from length of observation period (Olden and Poff 2003, Chapter 2). Using current ecological thought we generated several *a priori* hypotheses regarding the most plausible ecological mechanisms driving patterns of fish fauna homogenization or differentiation in the United States at 3 different spatial scales (see Table 3.1).

At the continental scale, Rahel (2000) compared present day to pre-European settlement fish faunas across the 48 conterminous United States. On average, pairs of states were reported to have 15.4 more species in common than before European settlement, which resulted in an average homogenization of 7.2%. Rahel (2000) attributed patterns of homogenization to the widespread introduction of cosmopolitan species and only the limited extirpation of native species, a hypothesis that is also supported for the major drainages of North America (see Gido and Brown 1999). Evidence also suggests that a common suite of species comprise most widespread introductions (Gido and Brown 1999, Rahel 2000) and that particular species are more prone to extinction (Angermeier 1995, Duncan and Lockwood 2001b). Based on this understanding, we hypothesized that continental fish fauna homogenization is driven primarily by scenarios involving introductions of the same species, accompanied by either no species extinctions (I1), extinction of the same species (IE1) or differential extinction of species that were originally shared by the communities (IE3) (Table 3.1). More precisely, we hypothesized that patterns of homogenization would most closely fit the mechanisms depicted in IE3 because species extinctions are likely to occur differentially across the landscape in response to non-random patterns of habitat degradation (Moyle 1986, Richter et al. 1997) and the large spatial grain (i.e., political states) at which homogenization is quantified will increase the diversity of habitats and communities sampled, thereby increasing the probability that pairs of states will historically share the same species.

Next, we use the data of Marchetti et al. (2001) to test the model at two finer spatial scales: zoogeographic provinces of California and watersheds within these provinces. Given the different spatial grains at which homogenization was quantified and California's unique geographic and hydrologic history (Mount 1995), we expected different invasion-extinction scenarios to vary in importance in shaping patterns of fish community composition between provinces and between watersheds.

At the provincial scale, Marchetti et al. (2001) found zoogeographic provinces to exhibit, on average, a 20.3% increase in community similarity ($n = 6$). Analogously to continental-scale homogenization, province-scale changes in fish community similarity are expected to be driven by the introduction of a common group of species and minimal extinction of native species (Moyle 2002). We therefore hypothesized that change in provincial similarity will be driven by scenarios I1, IE1 or IE3, and of these scenarios (Table 3.1), we predicted scenario I1 to be of primary importance given the minimal number of species extinctions in California (Moyle 2002).

At the watershed scale, Marchetti et al. (2001) reported that the watersheds within the 4 major zoogeographic provinces in California exhibited, on average, a 10.7% decrease in community similarity ($n = 7$, 10, 11 and 15). This smaller spatial grain implies an increased probability of observing species introductions and extinctions of different or originally unshared species in the communities, because finer sampling resolution should accentuate among-site habitat and species differences. Therefore, at this scale, in addition to the scenarios discussed above for provinces, we expected scenarios IE6 and IE8 to be potentially important for driving patterns of community change (Table 3.1).

Lastly, to further explore the model's utility, we examined the 11 watersheds within the South Coast province, the unique zoogeographic history of which suggests additional invasion-extinction scenarios may operate to drive homogenization. Historical fish communities of this province are believed to be very similar due to the presence of many anadromous species and Pleistocene connections during periods of low sea level (Moyle 2002). Indeed, Marchetti et al. (2001) reported an average historical community similarity of 63.3% among the watersheds. Further, these watersheds have likely experienced haphazard species introductions from multiple sources (e.g., aquaculture, aquarium escapees). Together, these two lines of evidence led us to hypothesize the predominance of scenario I2, in addition to the potential contributions of scenarios IE6 and IE8 (discussed above) (Table 3.1).

Generating model predictions of fish fauna homogenization and differentiation

We extended the mechanistic model of Olden and Poff (2003) (Chapter 2) to generate predictions of change in community similarity (i.e., predicted levels of homogenization and differentiation) according to each of the 14 invasion-extinction scenarios. Input parameters of the model include: (1) the initial level of community similarity ($J_{initial}$), (2) the number of introduced and extinct species, and (3) the initial species richness of the communities. First, given the wide range of initial similarities reported across the sampling units of states ($J_{initial}$=0.00 to 0.89), provinces ($J_{initial}$=0.00 to 0.58), and watersheds ($J_{initial}$=0.00 to 1.00), we generated model predictions for all levels of $J_{initial}$ from 0.00 to 1.00, increasing by increments of 0.01. These incremental predictions allow a detailed exploration of the model's utility. Second, to account for varying rates of species invasions and extinctions both within and among the sampling units, we averaged ΔCS across all possible combinations and numbers of introduced and extinct species. Third, because model predictions have been shown to be independent of species richness values exceeding 20 (Olden and Poff 2003, Chapter 2), we set initial species richness to 100, a reasonable estimate of the mean number of fish species across all datasets. All simulations were conducted using computer macros in MatLab® written by J.D. Olden.

Predicted ΔCS for each of the invasion-extinction scenarios are illustrated in Figure 1A-C, and show exhibit either linear or unimodal relationships with $J_{initial}$. Invasion only (I1 and I2), extinction only (E3), and both invasion and extinction scenarios (IE1-IE8) reduce community similarity (i.e., differentiation) with increasing $J_{initial}$, whereas the magnitude of ΔCS for the remaining scenarios (E1, E2, E4) initially increases and then decreases with $J_{initial}$. Independent of $J_{initial}$ the model predicts homogenization for scenarios I1, E2, E4, IE1, IE2, IE4 and differentiation for scenarios I2, E1, E3, IE5-8; only scenario IE3 leads to both homogenization and differentiation.

Validating the model using fish faunas of the United States at three spatial scales

We used two approaches to test the model and differentiate among the alternative ecological processes driving the homogenization of fish faunas. First, using regression analysis we qualitatively compared (i.e., visual inspection) model predictions of ΔCS (Fig. 3.1A-C) to empirical patterns of ΔCS (Fig. 3.1D-E) as they vary across the entire range of $J_{initial}$. Polynomial regression (second-degree) was used for scenarios E1, E2 and E4 because they were clearly non-linear, and simple linear regression were used for the remaining scenarios. Second, we quantitatively validated the model by seeding it with the actual values of $J_{initial}$ for each pair-wise comparison for each scale (i.e., state-state, province-province, watershed-watershed pairs) to estimate mean and variance of ΔCS for each scenario. Empirical values of ΔCS were then compared to the predicted ΔCS for each scenario using a student's t-test with significance based on a Bonferroni-corrected significance level of $\alpha_{critical} = 0.004$ (note: a non-corrected $\alpha_{critical} = 0.05$ produced similar results) (Fig. 3.2). Scenarios that showed concordance with empirical patterns of ΔCS for both approaches implicate their importance in fish fauna homogenization.

At the continental scale, model predictions of ΔCS according to the 14 invasion-extinction scenarios showed variable agreement with observed levels of ΔCS reported by Rahel (2000). The comparison of regression lines showed that predicted ΔCS model predictions for scenarios I1, IE1, IE3 and IE4 have highest concordance with observed patterns of ΔCS, thus supporting the importance of these ecological processes for driving broad-scale biotic homogenization (Fig. 3.1A,C,D). Of these scenarios, three match our *a* *priori* hypotheses (Table 3.1). However, only model predictions of ΔCS for scenario IE3 did not differ significantly from empirical values of ΔCS ($t = 1.37$, df = 1127, $P > 0.004$: Fig. 3.2A). Scenario IE3 is further supported by the fact that predictions for the other three scenarios failed to detect biotic differentiation, a phenomenon observed for 130 of the 1128 pair-wise state comparisons (Fig. 3.1D).

At the provincial scale, scenarios I1, IE1, IE3 and IE4 agree well with observed patterns of changes in fish community similarity (Fig. 3.1A,C,E). Again, 3 of these 4 scenarios match our *a priori* hypotheses (Table 3.1). The strongest correspondence was for scenario I1, in which the slope and y-intercept were very similar to empirical patterns of ΔCS (Fig. 3.1A,E) and only model predictions from this scenario did not differ significantly from empirical values (t = -2.28, df = 14, $P > 0.004$: Fig. 3.2B).

At the watershed scale, model predictions for scenarios E1, IE3 and IE6 showed strong concordance with empirical patterns of community change (Fig. 3.1B,C). Predicted ΔCS for all these scenarios did not significantly differ from observed ΔCS (t = -7.81 – 7.14, df = 225, $P > 0.004$: Fig. 3.2C). Scenarios IE3 and IE6 match our *a priori* hypotheses (Table 3.1); however, strongest evidence was for scenario IE3 because visual inspection of Fig. 3.1F shows that scenarios E1 and IE6 failed to predict biotic homogenization, a phenomenon which was observed for 44 of the 226 pair-wise watershed comparisons (Fig. 3.1F).

Within the South Coast province specifically, observed changes in fish community similarity among watersheds (Fig. 3.1F) were consistent with predictions provided by the model for scenario I2 (Fig. 3.1A) and scenario IE8 (Fig. 3.1C). Model predictions for both these scenarios were the only that did not significantly differ from actual ΔCS (t=-0.03 – 1.87, df=54, $P > 0.004$: Fig. 3.2D).

Discussion

The empirical homogenization and differentiation of fish communities at different spatial scales provides strong support of the mechanistic model of Olden and Poff (2003) (Chapter 2). The strength of this model is that it is simple enough to be tractable analytically yet realistic enough to be applicable to the study of biotic homogenization at a variety of spatial scales. Our results strongly support current scientific evidence implicating both widespread introduction of cosmopolitan species and the differential extinction of native species (likely caused by the loss or modification of critical habitat) as determinants of fish community change across the United States (e.g., Richter et al. 1997, Rahel 2000). In contrast, at the finest spatial scale (watersheds within the South Coast Province of California), we found strong evidence for the importance of different species invasions and either no extinction (I2) or differential extinction (IE8) of unshared native species for shaping patterns of biotic differentiation. This agrees with the hypothesized sporadic introduction of aquarium fishes throughout this province (Marchetti et al. 2001), as well as the fact that decreased spatial grain likely increases the probability of observing the introduction of different species and the extinction of different or unshared species, because finer sampling resolution accentuates among-site habitat and community differences (Olden and Poff 2003, Chapter 2).

The mechanistic model can also be extended to gain insight into the likely dominant invasion and extinction processes shaping community change in taxonomic groups for which adequate, quantitative estimates of homogenization are unfortunately lacking (Fig. 3.1A-C). Such an examination could be guided by current information regarding how the particular taxonomic group is being threatened by non-native introductions and human disturbance. For example, the global avifauna continue to lose their regional distinctiveness due to the widespread introduction of cosmopolitan bird species, coupled with the extinction of endemic species via habitat alteration and the effects of introduced non-avian predators (Lockwood et al. 2000). Therefore, we would predict large-scale patterns of avian homogenization to be driven primarily by mechanisms describing the invasion of the same non-native species and the differential extinction of native species (i.e., IE3 or IE4). Quantitative tests of such hypotheses will require the explicit consideration of the spatial and temporal scales at which both the data was collected and the ecological mechanisms are believed to be operating for the particular taxonomic group. Taken together, based on the robust performance of our model for fish communities we believe it offers a framework for predicting future patterns of homogenization for a variety of taxonomic groups.

We acknowledge that multiple invasion and extinction processes are likely important for driving biotic homogenization and differentiation. Indeed, rates and taxonomic identities of species invasions and extinctions (i.e., different invasion-extinction scenarios) vary nonrandomly across the landscape with respect to existing patterns of human-caused habitat degradation and species introductions (e.g., Seabloom et al. 2002), as is seen for many taxonomic groups (e.g., Case 1996, McKinney 2001a,b). Further, mechanisms of homogenization may vary even within taxonomic groups that experience different rates of invasions and extinctions in different environments (e.g., island vs. continental biota: Case 1996; Lonsdale 1999, or between island biota: Sax et al. 2002). For example, fish faunas in the eastern United States appear to have adjusted to non-native invasions without much loss of native species (i.e., invasion only scenarios), whereas for more disturbed aquatic ecosystems in the western United States, introduced species appear to have greater negative impacts on native communities (i.e., both invasion and extinction scenarios) (Moyle 1986). Therefore, given the likely existence of multiple drivers of homogenization we expect imperfect correspondence between model predictions that based on only single invasion-extinction scenarios and observed patterns of fish community change. Despite this, the model shows an excellent fit to the empirical data, strongly implicating specific invasion-extinction mechanisms in shaping patterns of homogenization and differentiation in fish faunas of the United States.

Conclusion

Biotic homogenization of communities is an emergent property of species invasion and extinction, and its quantification is sensitive to the specific ecological mechanisms operating across the landscape. Although many studies have qualitatively documented biotic homogenization in both aquatic and terrestrial ecosystems, we still lack a solid quantitative understanding of the underlying invasion and extinction processes driving patterns of community change. Consequently, our ability to predict future patterns of biotic homogenization will continue to be limited unless we begin to employ more mechanistically-based models (e.g., Olden and Poff 2003, Chapter 2) that account for differential rates of species introductions and extinctions that vary both spatially and taxonomically (Collins et al. 2002). Gaining this knowledge will define not only the manner in which this process threatens global biotas, but also the proactive management scenarios required to suppress it.

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Table 3.1. A summary of the 14 invasion-extinction scenarios of the mechanistic model of Olden and Poff (2003) (Chapter 2) representing different ecological mechanisms by which species invasions and extinctions can drive biotic homogenization (i.e., increased community similarity) and differentiation (i.e., decreased community similarity). The scenarios are divided into 3 groups, depending on whether changes in community similarity are driven by only species invasions events (scenarios I1-I2), only species extinctions events (scenarios E1-E4), or both species invasion and extinction events (scenarios IE1-IE8). **Predictions** refers to the *a priori* predictions of invasion-extinction scenarios playing dominant roles in driving fish community change at each scale: continental United States (C), California's provinces (P), California's watersheds (W), California's South Coast province watersheds (w). **Supporting Evidence** refers to those model predictions showing the strongest agreement with empirical estimates of community change at each scale based on qualitative (Fig 3.1) and quantitative (Fig. 3.2) assessments. Underlined values for quantitative support indicate those scenarios with the strongest overall agreement (see text for details).

Scenario	**Description**	**Predictions**	**Supporting Evidence**	
			Qualitative	Quantitative
Invasion only events				
I1	Same species invade, no extinction of resident species	C, P, W	C, P	P
I2	Different species invade, no extinction of resident species	W, w	w	w
Extinction only events				
E1	No species invasion, extinctions in both communities involve same species		W	W
E2	No species invasion, extinctions in both communities involve different species			
E3	No species invasion, extinction in one community of a species that was originally shared by both communities			
E4	No species invasion, extinction in one community of a species that was originally not shared by both communities			
Invasion and extinction events				
IE1	Same species invade, extinctions in both communities involve same species	C, P, W	C, P	
IE2	Same species invade, extinctions in both communities involve different species			
IE3	Same species invade, extinction in one community of a species that was originally shared by both communities	C, P, W	C, P, W	C, W

IE4	Same species invade, extinction in one community of a species that was originally not shared by both communities		C, P	
IE5	Different species invade, extinctions in both communities involve same species			
IE6	Different species invade, extinctions in both communities involve different species	W, w	W	W
IE7	Different species invade, extinction in one community of a species that was originally shared by both communities			
IE8	Different species invade, extinction in one community of a species that was originally not shared by both communities	W, w	w	w

Figure 3.1. Patterns of change in community similarity (ΔCS) as a function of the initial similarity among communities ($J_{initial}$) (both represented by Jaccard's coefficient of similarity expressed as a percentage) based on model predictions for (A) only species invasions scenarios (I1-I2), (B) only species extinctions scenarios (E1-E4), and (C) both species invasion and extinction scenarios (IE1-IE8), and based on empirical values for (D) the continental United States, (E) the zoogeographic provinces of California, and (F) the watersheds of the four major provinces of California (empty circles, solid line) and the watersheds of the South Coast province (filled circles, dotted line). Model predictions are averages for all combinations of numbers of introduced and extinct species for each $J_{initial}$ (see text for more details). Dashed line demarcates homogenization (positive ΔCS) from differentiation (negative ΔCS). Least-squares regression lines are in Appendix 3.1.

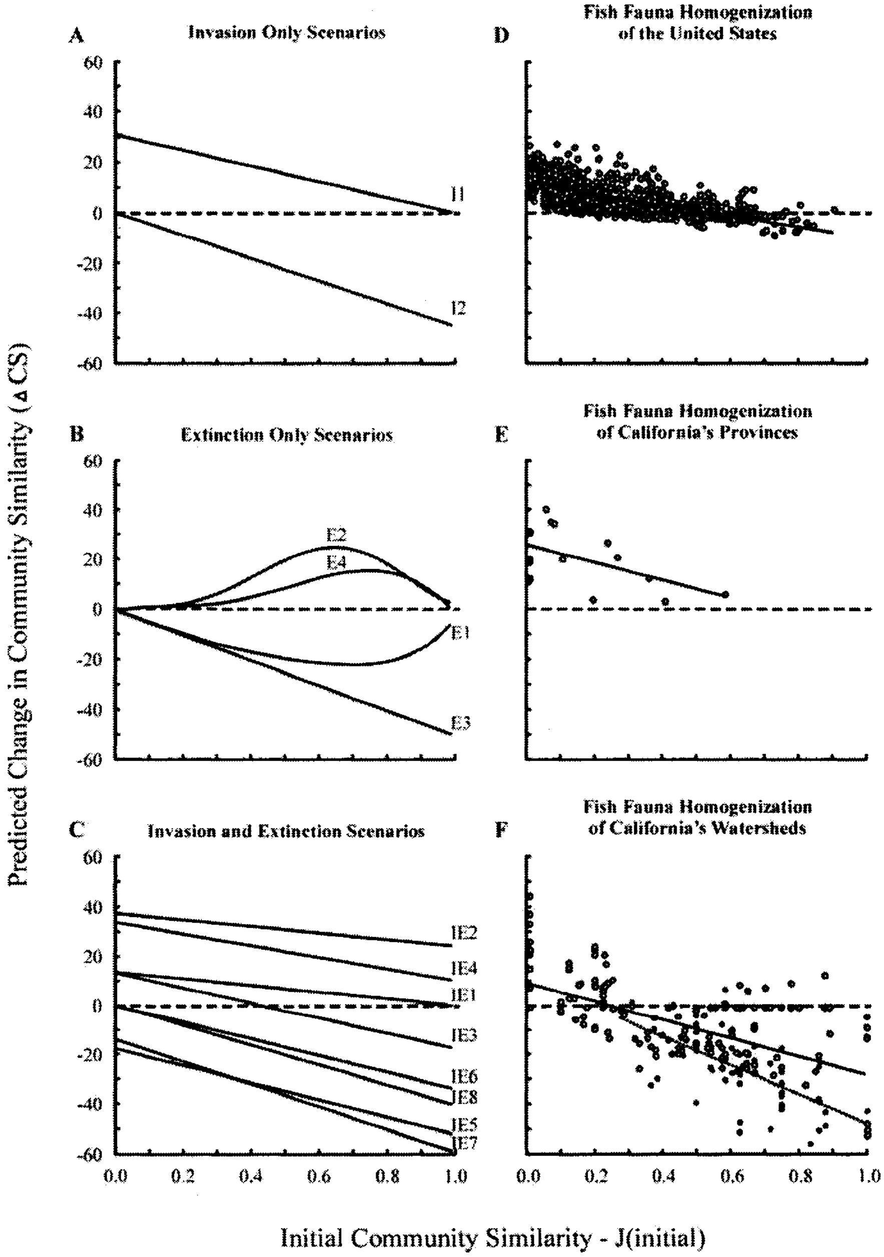
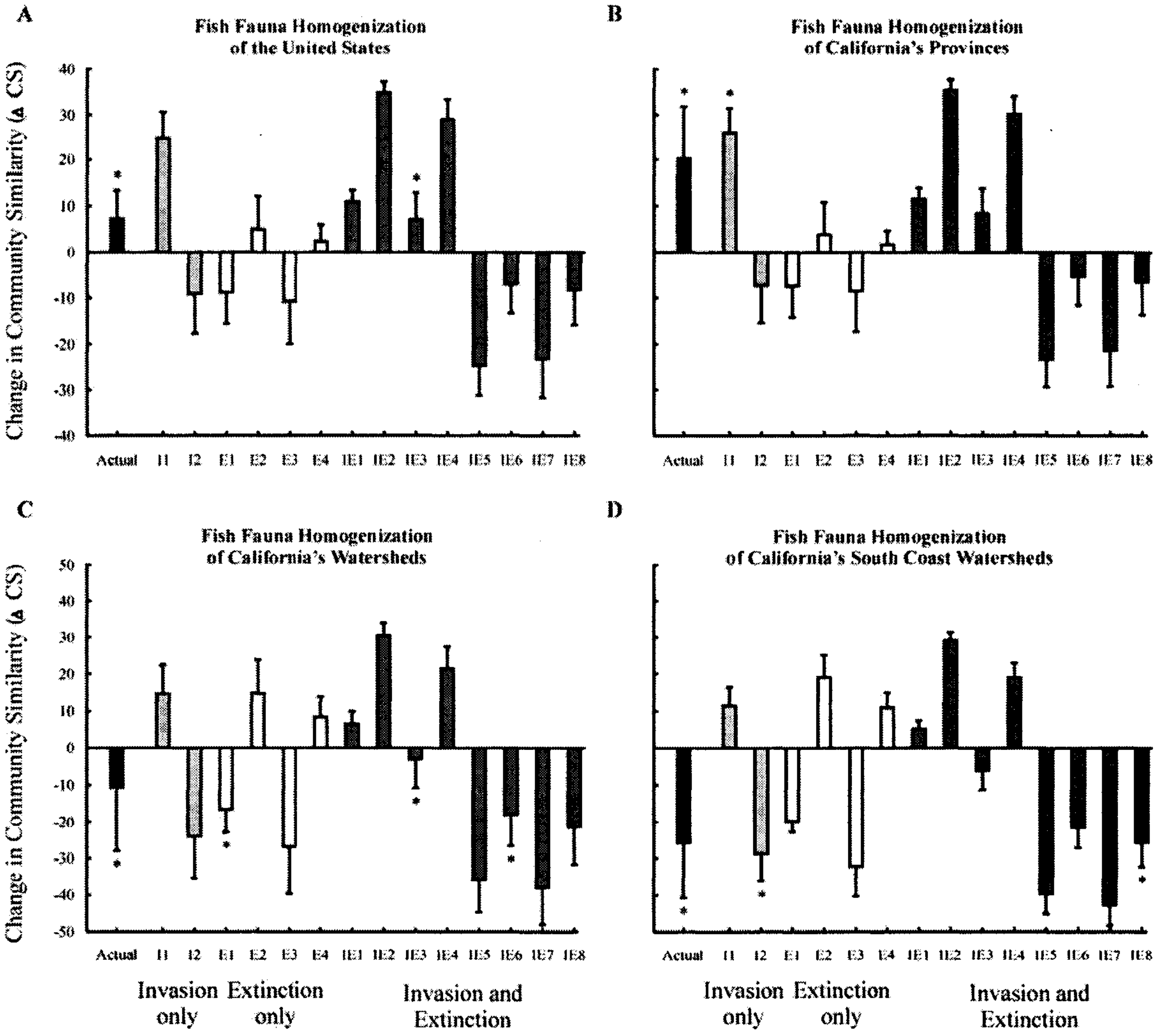


Figure 3.2. Mean (bar) and standard deviation (whiskers) of changes in community similarity (ΔCS) for model predictions based on each of the 14 invasion-extinction scenarios (generated using actual values of initial fish community similarities) and for empirical values across the continental United States (A), the zoogeographic provinces of California (B), the watersheds of the four major provinces of California (C) and the watersheds of the South Coast province (D). Asterisks represent non-significant differences between actual and predicted ΔCS based on a student's t-test, thus providing support for the importance of the particular scenario. Dashed line demarcates homogenization (positive ΔCS) from differentiation (negative ΔCS).



Appendix 3.1. Least-squares regression lines for Figure 3.1 are as follows: (I1) $y = 30.94 - 0.31\mathrm{J}_{\mathrm{initial}}$; (I2) $y = 0.0 - 0.45\mathrm{J}_{\mathrm{initial}}$; (E1) $y = 2.36 - 0.78J_{initial} + 0.006J_{initial}^{2}$; (E2) $y = -11.26 + 1.03J_{initial} - 0.009J_{initial}^{2}$; (E3) $y = 0.0 - 0.50\mathrm{J}_{\mathrm{initial}}$; (E4) $y = -5.58 + 0.46J_{initial} - 0.003J_{initial}^{2}$; (IE1) $y = 13.70 - 0.14\mathrm{J}_{\mathrm{initial}}$; (IE2) $y = 37.50 - 0.13\mathrm{J}_{\mathrm{initial}}$; (IE3) $y = 13.32 - 0.31\mathrm{J}_{\mathrm{initial}}$; (IE4) $y = 33.78 - 0.24\mathrm{J}_{\mathrm{initial}}$; (IE5) $y = -17.76 - 0.34\mathrm{J}_{\mathrm{initial}}$; (IE6) $y = 0.0 - 0.34\mathrm{J}_{\mathrm{initial}}$; (IE7) $y = -13.92 - 0.45\mathrm{J}_{\mathrm{initial}}$; (IE8) $y = 0.0 - 0.41\mathrm{J}_{\mathrm{initial}}$; (United States) $y = 11.79 - 0.23\mathrm{J}_{\mathrm{initial}}$; (California provinces) $y = 25.92 - 0.36\mathrm{J}_{\mathrm{initial}}$; (California watersheds) $y = 9.20 - 0.38\mathrm{J}_{\mathrm{initial}}$; (California South Coast province) $y = 10.49 - 0.57\mathrm{J}_{\mathrm{initial}}$.

Chapter 4

Long-term Trends of Native and Non-native Fish Faunas in the American Southwest

Abstract

Environmental degradation and the proliferation of non-native fish species threaten the endemic, and highly unique fish faunas of the American Southwest. The present study examines long-term trends (> 160 years) of fish species distributions in the lower Colorado River Basin and identifies those native species (*n*=28) exhibiting the greatest rates of decline and those non-native species (*n*=48) exhibiting the highest rates of spread. Among the fastest expanding invaders in the basin are red shiner, fathead minnow, green sunfish, largemouth bass, western mosquitofish and channel catfish, species considered to be the most invasive in terms of their negative impacts on native fish communities. Interestingly, non-native species that have been recently introduced (1950+) have generally spread at substantially lower rates as compared to species introduced prior to this time (especially from 1920 to 1950), likely reflecting reductions in human-aided spread of species. We found general agreement between patterns of species decline and extant distribution sizes and official listing status under the US Endangered Species Act. "Endangered" species have generally experienced greater declines and have smaller present-day distributions compared to "threatened" species, which in turn have shown greater declines and smaller distributions than those species not currently listed. A number of notable exceptions did exist, however, and these may provide critical information to help guide the future listing of species (i.e., identification of candidates) and the upgrading or downgrading of current listed species that are endemic to the lower Colorado River Basin. The strong correlation between probability estimates of local extirpation and patterns of native species decline and present-day

distributions suggest a possible proactive conservation strategy of implementing management actions for declining species prior to extreme rarity and imperilment.

Introduction

> "the Colorado [River], along the greater part of its lonely and majestic way, shall be forever unvisited and undisturbed." *Lieutenant Joseph C. Ives (1857)*

Undeterred by legends of earlier expeditions that had failed, in 1868 John Wesley Powell was successful in his first historic journey down the treacherous Colorado River. Shortly thereafter, he stated his strong belief that, although considerably remote, the western resources were meant to be "redeemed" from a state of idleness for societal use (deBuys 2001). During the next 130 years Powell's vision was realized, and the waters of the Colorado River played a pivotal role in the settlement, growth and economic development of the American Southwest (Carlson and Muth 1989). Efforts to tame the Colorado River began soon after the arrival of western Europeans, and today hundreds of dams and diversion structures have created one of the most controlled rivers on Earth (Fradkin 1981). The Colorado River now provides irrigation water for more than 3.7 million acres (1.5 hectares) of farmland and delivers water and electrical power to 30 million people in the United States and Mexico (Mueller and Marsh 2002).

The Colorado River ecosystem has been greatly changed during the last century both by environmental alterations and by the introduction and spread of non-native fish species. The construction of water development projects began in the early 1900s (Fradkin 1981, Carlson and Muth 1989), and by the 1960s much of the mainstem river had been converted into a system of dams and diversions. Such changes continue to compromise the efficiency of life-history adaptations that have evolved to allow native fishes to thrive in the historically harsh, fluctuating environment of the Colorado River Basin (Minckley and Deacon 1968, 1991, Miller 1961). These dramatic environmental alterations have also facilitated the widespread and human-assisted invasion of non-native fish species that prey on and compete with native fishes (Douglas et al. 1994, Minckley 1991, Marsh and Douglas 1997, Marsh and Pacey 2003).

The case for conservation for the lower Colorado River Basin is most urgent as the distributions of native fish species continue to decline at unprecedented rates and the spread of non-native fishes accelerate at an unparalleled speed (Minckley et al. 2003). Of the 31 native fish species in the lower Colorado Basin, 25 are extinct, extirpated, listed under the US Endangered Species Act (USFWS 1999), or believed to have suffered significant declines in distribution (Minckley 1991). Remnant native populations are highly fragmented, compounding the problem of recovery and further elevating the probability of extinction (Fagan et al. 2002). In contrast, the deliberate introduction of non-indigenous fishes in the lower Colorado River Basin began in the late 1800s (Minckley 1999) and today more than 90 species have been introduced, over half of which are considered established (Rinne and Janisch 1995). Long-term conservation and management strategies for the Lower Colorado River Basin require knowledge about rates of change in the distribution of native and non-native species over time. Such strategies should be based on the analysis of large-scale, long-term datasets, which when combined with small-scale experimental studies, will provide complementary approaches to better understanding distributional shifts of native and non-native species and their association with altered environmental regimes. Broad-scale studies provide the foundation for proactive conservation by identifying native species declines prior to extreme rarity so that management efforts can be implemented before imperilment (Anderson et al. 1995, Patton et al. 1998).

To date, evidence for the widespread replacement of native fish communities by non-native species in the lower Colorado River Basin has been largely anecdotal and has lacked rigourous quantification. This is not to say that species' distributions have not, and are not continuing to change. Rather the extent to which species' distributions have decreased or increased over time has only been investigated for a limited number of species (mainly mainstem "big-river" species) and therefore remains largely unknown (and not quantified) for the majority of the species pool. We address this research need by presenting a historical perspective on long-term trends of native and non-native freshwater fish species distributions in the lower Colorado River Basin using an unparalleled dataset containing tens of thousands of records collected over a century and a half. By conducting a broad, spatio-temporal assessment of changes in patterns of species' occurrences, we shed important insight into rates of native species decline and non-native species expansion for the entire, present-day species pool of lower Colorado River Basin. We address the question of whether long-term distribution trends can act as a surrogate for local extirpation risk of native species and "test" the biological component of the United States Endangered Species Act by comparing these trends to species' official status. This comparison may help address the question of whether governmental legislation is, in fact, helping identity (and conserve) those rare, endemic species that have experienced substantial declines in their distributions and are currently rare in the lower Colorado River.

Methods

The Colorado River is the primary waterway and lifeline of the American Southwest. Our study focused on the lower basin of the Colorado River (hereafter called lower CR Basin), which includes ca. 26,000 km of streams and rivers between Glen Canyon Dam (located at the border between Arizona and Utah, U.S.A.) and the Gulf of California, and drains ca. 362,750 km^2 from five states of the United States and northwestern Mexico (Fig. 4.1). To examine long-term temporal trends in native and non-native freshwater fish faunas we used the SONFISHES database (Desert Fishes Council, http://www.desertfishes.org/na/gis/index.html). This database was developed by the tireless efforts of the late ichthyologist W. L. Minckley and contains >38,000 occurrence records for 132 freshwater fish species from over 150 years of research throughout the lower CR Basin. SONFISHES contains incidence, identity, and collection data for the complete holdings of major regional museum collections, numerous smaller holdings, and records from peer-reviewed and gray literature sources. Records are geo-referenced to within 1 km of their collecting site in a Geographic Information System (see Unmack 2002 for details).

Using ArcGIS (Environmental Services Research Inc., v. 8.3) we plotted 28,755 locality records from 1840 to 2000 (excluding occurrence records resulting from artificial translocations and reintroductions) for 28 native species and 48 non-native species from the SONFISHES database onto a digital coverage of streams and rivers in the lower CR

Basin (U.S. Geological Survey Enhanced River Reach File 2.0: http://www.usgs.gov/). We summarized the dataset in several ways to address the objectives of the study. Based on the large size and high temporal frequency of locality records in the dataset (see Table 5.1) we were able to examine species patterns for 5 time periods: pre-1960; 1960-69; 1970-79; 1980-89; and 1990-1999. Following Fagan et al. (2002), historical locality records for native species were considered to be those collected prior to 1980, whereas modern (or extant) native records were collected between 1980 and 1999. For native species, historical presences and extant absences constitute true extirpation events because modern records in the dataset are almost exclusively the result of intensive efforts by federal or state agencies to determine species' complete distributions prior to listing decisions under the U.S. or Mexican Endangered Species Acts (Fagan et al. 2002).

For each time period, we calculated the total river kilometres that each species was present by summing the length of the river segments (defined as a section of river delineated by two confluences) in which the species was recorded. Importantly, if a species was collected multiple times in the same river segment in the same time period, the length of the river segment was counted only once when calculating total river kilometres. Species' distributions were estimated by dividing the total river kilometres that a species was present by the total river kilometres where all species were present during the specified time period (see Table 4.1). This approach attempts to account for the influence of differential sampling effort (assumed to be proportional to the number of records) through time. Distributions were represented as a percentage and are assumed to provide an approximation for the total size of the species distribution in the entire lower CR Basin.

For native species, distributional changes were calculated by subtracting extant range size (1980-1999) from historical range size (pre-1980) and dividing by historical range size. Regression analyses with curve estimation (SPSS, v.11) were conducted to assess relationships between extant distribution size (%), percent distributional change and the estimated probability of local extirpation (as given for 25 species in Table 1 of Fagan et al. 2002). Pairwise *t*-tests were used to compare distributional change and extant distributions between species with different official statuses under the U.S. Endangered Species Act (data obtained from the United States Fish and Wildlife Service: Threatened and Endangered Species System, http://endangered.fws.gov, as of July 2004). For non-native species, dates of introduction were estimated using both Table 6 of Mueller and Marsh (2002) and year of first occurrence in the SONFISHES database. Extant distributions were divided by the number of years since introduction (calculated from 2000) to estimate the rate of non-native species spread in the basin (km·year^{-1}). Regression analyses were conducted to assess relationships between date of introduction, extant distribution size, and rate of spread for each species.

Results

Temporal patterns of native fish distributions

Over the past century and a half, native fishes have predominantly decreased in their spatial distributions throughout the lower CR Basin. Native fish species typically showed dramatic declines in the size of their distributions, a trend, however, that varied among species from 100% range reduction to 14% range expansion (Table 4.2). In total, the distribution of 23 species decreased and 5 species slightly increased. Distribution trends over time illustrate that species have exhibited differential patterns of change. Gila trout, Virgin River spinedace and Gila topminnow, for example, have shown gradual reductions in their distribution, whereas Colorado pikeminnow, bonytail, razorback sucker, spikedace and Gila chub (among others) have shown punctuated declines. Other species appear to be occupying relatively constant ranges in the basin, including roundtail chub, bluehead sucker and Sonora sucker. Extant native fishes range from being completely absent (i.e., 0%) to occupying an estimated two-fifths of the basin (Table 4.2). According to our results using modern locality records, five species have been extirpated and 15 species currently occupy extremely small distributions in the basin (< 5%), whereas other species still exhibit relatively broad distributions (> ca. 30%), e.g., specked dace, longfin dace, desert sucker and Sonora sucker.

With respect to identifying those species that warrant special concern and targeted conservation efforts, it is necessary to examine associations between the probability of local extirpation and broad-scale temporal trends in their distributions. We obtained estimates of local extirpation for 25 native species from Table 1 of Fagan et al. (2002), who calculated these probabilities using the SONFISHES database as the proportion of historic records at a 5-km reach scale having no modern records (e.g., if an extinct species was present in 50 of 1000 pre-1980 records, its extinction probability would be 0.95). We found a significant positive and linear relationship between percent distributional decline and the probability of extirpation ($R^2 = 0.807$, $P < 0.001$), indicating that native species exhibiting greater declines in their distributions at the whole basin scale also have a greater risk of local extirpation (Fig. 4.2A). By examining deviations from this relationship we see that humpback chub (label X) and Virgin River spinedace (L), for example, have a higher estimated local extirpation risk compared to what is expected according to their basin-level decline over time (large positive residual). In contrast, desert pupfish (B), spikedace (N), loach minnow (R) and desert sucker (U) have a much lower extirpation risk as predicted from their level of distributional decline (large negative residual). Additionally, we found a significant negative and non-linear relationship between extant distribution size and the probability of local extirpation ($R^2 = 0.571$, $P < 0.001$, quadratic curve), indicating that species with smaller present-day distributions have a greater estimated risk of local extirpation (Fig. 4.2B). Species such as roundtail chub (V) and Sonora sucker (Y) have greater probability of extirpation than that expected from their present distributions in the basin, whereas the local extirpation probabilities of loach minnow (R), headwater chub (AA) and Little Colorado spinedace (BB) are much lower than is suggested from their current distributions. Visual examination of this figure suggests a threshold relationship where species with extant distributions greater than 10% are at much lower risk to local extirpation (probability < 0.5) compared to those species will extremely small distributions.

Comparisons of species distributional change and extant distribution size with categories of official status under the U.S. Endangered Species Act (provided in Table 4.2) also revealed interesting findings (Fig. 4.3). With increasing risk category (i.e., Not listed – Threatened – Endangered), we found average distributional decline to become larger and extant distribution size to become markedly smaller. Endangered species exhibit significantly greater distributional declines compared to threatened species ($T_{1,15}$

= 2.93, $P = 0.01$) and to those species not listed ($T_{1,20} = 4.33$, $P < 0.001$). Similarly, endangered species exhibit significantly smaller extant distributions compared to threatened species ($T_{1,15} = -4.78$, $P < 0.001$) and to those species not listed ($T_{1,20} = -4.30$, $P < 0.001$). Extant distributions of threatened species were marginally smaller than species not listed ($T_{1,11} = -1.90$, $P = 0.08$), although the rate of distributional decline did not differ.

For illustrative purposes Figure 4.4 shows historical and extant distributions of three native species that exhibit markedly different % decline over time and have different ESA statuses – bonytail (Endangered, 87.5% decline), spikedace (Threatened, 45.9% decline) and specked dace (Not Listed, 16.5% decline). Historical populations of bonytail in the Salt River, Gila River and mainstem Colorado River have been lost, and present-day distributions are restricted to Lake Mohave above Davis Dam. Spikedace populations were once present in the rivers Salt, Verde, Gila and San Pedro, but are now confined to only small stretches of the Gila River and Verde River. Specked dace was historically abundant and continuous throughout the basin, but its present-day distribution is greatly reduced and highly fragmented (e.g., Virgin River).

Temporal patterns of non-native fish distributions

In contrast to native fishes, the majority of non-native fishes showed substantial increases in the size of their distributions over time (Table 4.3). At the extreme, fathead minnow, green sunfish and red shiner exhibit the greatest rates of invasion, spreading at over 50 km·year^{-1} since their dates of introduction. As expected, we found a strong, positive relationship between the rate of spread and extant distribution size ($R^2 = 0.874$, $P <$

0.001), indicating that fast spreading non-native species are generally more broadly distributed in the basin (Fig. 4.5A). A number of non-native species are much more broadly distributed in the basin as what is expected based their rate of spread, e.g., channel catfish (code 8), yellow bullhead (10) and common carp (11) (all introduced prior to 1900). In contrast, the two latest invaders to the basin, blue tilapia (9) and flathead catfish (6), were found to have very fast rates of spread, although they are still limited in their distribution due to their short invasion history.

Although we expected the positive relationship in Figure 4.5A because extant distribution size was used to calculate spread, the unexplained variation in this relationship can be attributed, in part, to the lack of a significant negative relationship between the year of introduction and rate of spread ($R^2 = 0.051$, $P = 0.124$) (Fig. 4.5B). Interestingly, we found a significant negative relationship between year of introduction and extant distribution size ($R^2 = 0.243$, $P < 0.001$) (Fig. 5.5C). Visual examination of this figure suggests a threshold relationship where non-native species introduced after 1950 have limited distributions (< 10%) whereas species will longer invasion histories in the basin have a broad range of distribution sizes (10-45%). Further, a number of species deviate from this relationship, indicating that species with long invasion histories do not necessarily have large extant distributions in the basin, e.g., yellow bass (35), white crappie (36), brown bullhead (42). Of note is that the top 5 fastest spreading non-native species (species 1-5 in Table 4.3) were all introduced between 1920 and 1950 (Fig. 4.5B) and have much greater present-day distributions than expected based on their length of invasion history (Fig. 4.5C).

Discussion

Distributions of native and non-native fishes have changed dramatically over the past century (Courtenay et al. 1984, Moyle 1986, Gido and Brown 1999), resulting in the biotic homogenization of fish faunas throughout North America (Rahel 2000, Olden and Poff 2004 (Chapter 3), Taylor 2004). Biogeographic studies that explore long-term trends in species distributions can provide important insight into predicting the identity of those species declining in their distribution and under risk of extinction (e.g., Williams et al. 1989, Reinthal and Stiassny 1991, Anderson et al. 1995, Patton et al. 1998). More generally, such studies can help understand how temporal changes in native species distributions relate to patterns of non-native species distributions, thus providing correlative insight into broad-scale implications of biological invasions.

Temporal patterns of native fish distributions

The American Southwest contains among the most threatened aquatic systems in North America, and despite early warnings (Dill 1944, Miller 1946), the unique, highly endemic, native fish fauna of the lower Colorado River Basin have become increasingly imperilled over time. Our study provides quantitative estimates of distributional trends in native fishes and show significant declines of many species over both historical and recent times. These findings provide empirical support for the observational hypothesis of Mueller and Marsh (2002) who postulated that native fishes rapidly declined between 1890 and 1935 because of intensive water management practices and the introduction of common carp, bullhead and channel catfish, which was then followed by a prolonged period when remnant communities gradually disappeared after the construction of Roosevelt, Hoover, Imperial, and a number of other dams that caused remarkable hydraulic and physical change to the basin.

Our results indicate the highest rate of declines in a number of native fish species that have previously identified as imperilled in the basin, including a number of "big-river" fishes such as Colorado pikeminnow, razorback sucker, bonytail and flannelmouth sucker; and species inhabiting marginal spring and stream habitats such as the desert pupfish and Gila topminnow (Minckley and Deacon 1991, Mueller and Marsh 2002). The last wild Colorado pikeminnow was caught in 1975 in the lower Colorado River; bonytail likely persist only in Lake Mohave; and although annual spawning occurs, razorback sucker populations consist largely of old adults with no evidence of recruitment (Minckley 1991). Other, comparatively less studied, species also experienced significant declines over time, including spikedace and woundfin. Similarly, loach minnow has seen dramatic declines when compared to historical records, although there is some evidence that its distribution has remained fairly constant over the recent decades. This finding is supported by recent work showing the local stability of remnant loach minnow populations in Arizona (Marsh et al. 2003). In contrast to the many species that have exhibited significant declines in their distributions, longfin dace, desert sucker and Sonora sucker are presently abundant throughout the basin and appear to have maintained relatively stable distributions over time. Finally, temporal trends and present-day sizes of species' distributions were highly correlated to estimates of local extirpation risk for the native fishes. This suggests that long-term studies conducted at the drainage scale might provide a coarse-level surrogate for identifying those species that are most likely to extirpated at the local reach scale.

In summary, a number of explanations are possible to describe the distributional changes observed in our study. By explicitly linking patterns of environmental degradation and non-native species distributions to patterns of native species distributions, we could gain greater insight into potential mechanisms of native imperilment and thus better tease apart the synergistic manner in which these stresses are threatening native faunas in the lower Colorado River Basin. We address these questions in a subsequent study.

Temporal patterns of non-native fish distributions

The establishment of non-native fish species has substantially changed native fish community structure in southwestern rivers (Minckley and Deacon 1968, 1991, Meffe 1985, Rinne and Minckley 1991). While the total number of non-native fishes continues to increase across the U.S. (Gido and Brown 1999, Rahel 2000, Meador et al. 2003), quantitative estimates of distributional changes are lacking for most fish, and such analyses are rarely conducted at large temporal and spatial scales that are required to properly understand these processes. Our study contributes to a better understanding of the shear magnitude in which non-native species have spread throughout the lower Colorado River Basin over the past century and points to those invaders that have exhibited considerable rates of expansion since their introduction. This information provides a scientific basis for the management of fast spreading species and enhanced education targeted specifically to reducing their future introduction by humans.

Perhaps our most striking result is that red shiner, fathead minnow, green sunfish, largemouth bass, western mosquitofish and channel catfish are the among the fastest expanding invaders in the basin, and these species have also been identified by expert ichthyologists as having the greatest negative impacts on native fish communities (Hawkins and Nesler 1991, J.D. Olden unpublished survey data). Recent studies have further supported the significant ecological effects of these non-native species on native fishes (e.g., Courtenay and Meffe 1989, Douglas et al. 1994, Marsh and Douglas 1997, Dudley and Matter 2000, Marsh and Pacey 2003), in addition to their role as vectors of exotic parasites, including the Asian fish tapeworm (Clarkson et al. 1997).

Of particular interest is that non-native species introduced after 1950 have generally spread at substantially lower rates as compared to non-native introduced prior to this time (especially 1920 – 1950), and consequently occupy much smaller distributions. The most optimistic explanation for this threshold pattern is that recent decades have seen declines in U.S. government-sanctioned introductions of gamefish or forage species outside their native ranges (Courtenay and Moyle, 1996), a pattern that reflects both a saturation of gamefish species in many drainages and a heightened awareness by fisheries biologists of the problems associated with non-native species (Rahel 1997). However, inadvertent introductions (e.g., aquarium trade releases: Padilla and Smith 2004) and unauthorized introductions (Rahel 2004) by the public continue, which likely explain the notable exceptions to this general pattern – blue tilapia and flathead catfish – both species exhibiting very high faster rates of spread since its introduction in recent decades.

Results from our study show both similarities and differences to other long-term studies of fish invasions conducted in Great Plains streams of Wyoming (Patton et al.

1998) and Oklahoma and Kansas (Gido et al. 2004). Great Plains stream are similar to desert streams in the American Southwest in that they present harsh environmental conditions and disturbance regimes (Dodds et al. 2004), and they have been invaded by a relatively large number of non-native species as compared to other regions of the United States (Gido and Brown 1999), thus making it suitable to compare rates of spread between these regions. Based on species common to all three regions, our study found that red shiner, fathead minnow, green sunfish, largemouth bass, channel catfish and black bullhead exhibit relatively high rates of spread, whereas Patton et al. (1998) found that these species' distributions were declining in Wyoming. However, similar patterns were found for common carp (range expansion) and white crappie, rock bass and yellow perch (range declines or low rates of spread). In contrast to distributional changes, comparisons of extant distribution sizes showed remarkable similarity for 15 species shared by the lower Colorado River basin and plain streams in Oklahoma and Kansas (Gido et al. 2004). In summary, these comparisons suggest that a number of non-native species exhibit similar distribution sizes in these different ecoregions, yet the rate at which they have spread to obtain their distributions differs (likely a result of different rates and timing of human introductions).

Conservation and management implications for native fishes

The United States Endangered Species Act (ESA) of 1973, together with other environmental legislation, has played an important role in the effort to conserve native fishes in the lower Colorado Basin (Minckley et al. 2003). Although in principle ESA decisions are based on the best biological information, many factors other than biology, including socioeconomic and political issues, influence most plans and projects. We believe our study provides some new insight into the biological component of the listing process for the LCR by relating long-term species' distributional trends to their federal status under the ESA. This comparison may help address the question of whether the ESA is, in fact, helping identity (and conserve) those rare species experiencing substantial declines in their distributions in the lower Colorado River Basin. Our results show good agreement between patterns of species decline and extant distribution sizes and expectations based on their official status. "Endangered" species have generally experienced greater declines in their distributions compared to "threatened" species, which in turn have shown greater declines than those species not currently listed. Likewise, non-listed species have three times larger extant distributions than "threatened" species, which in turn have two time larger distributions than "endangered" species. These patterns are reassuring, in that they support the biological underpinnings of the ESA for the native species of this region.

Interestingly, although general patterns were in agreement we did find a number of notable exceptions, which we believe can provide critical information to help guide the future listing of species (i.e., identification of candidates) and the upgrading or downgrading of current listed species that are endemic to the lower Colorado River Basin. For example, based on temporal trends and extant distribution sizes alone, our results suggest that 3 non-listed species might merit consideration for listing under ESA: headwater chub could be a candidate for threatened status (on the basis of extant distribution), and flannelmouth sucker and Virgin River spinedace could be candidates for endangered status. Our results also suggest that Apache trout have experienced significant declines and exhibit extant distributions that correspond more closely with "endangered" species and therefore could be considered for upgrading from its threatened status. Other factors not evident from distributional data support these ideas, e.g., Apache trout are also at high risk to the effects of intensive hybridization with non-native trout (Dowling and Childs 1992) as well as those arising from hatchery practices. It is very interesting to note that Apache trout was formerly listed as endangered but was downlisted in 1975 to threatened status to facilitate a management program that included recreational angling (Behnke 1992). This is an excellent example where socioeconomic issues have likely outweighed species biology in the ESA listing process.

Concerning potential data limitations

When analyzing compiled data that has not been systematically collected, as is the case in this study, it is important to consider the effects of sampling bias, spatial scale and data resolution when interpreting the results. Sampling intensity (i.e., as indicated by the number of records) increased through time for both native and non-native species. Consequently, our study provides minimum estimates of native species decline because sampling intensity in recent decades always exceeded that of previous decades, whereas the opposite is true for non-native species where rates of spread may be over-estimated. Spatial scale must also be considered when using historic data to examine species declines. Patton et al. (1998) found greater changes in species distributions at the reach scale compared to the drainage scale for 37 species in Wyoming, which suggests that smaller-scale analyses of temporal trends may provide over-estimates of species declines. Lastly, although species presence data are not as informative as abundance data for assessing temporal trends, local population fluctuations may confound trend interpretations, especially in for highly variable desert streams characteristic of the American Southwest (Eby et al. 2003). While we acknowledge the above data limitations and issues of sampling and spatial scale, we believe our analyses are appropriate for this region at a scale of study relevant to broad-scale conservation and management planning. Indeed, a number of studies have already illustrated the utility of the SONFISHES database for addressing pressing fish conservation issues in the American Southwest (e.g., Fagan et al. 2002, Unmack and Fagan 2004) and our study is the first to use this powerful dataset to address broad-scale changes in fish distributions.

Conclusion

The extensive regulation of the lower Colorado River Basin threatens native fish faunas by drastically altering natural flow, temperature and sediment regimes, and promoting the establishment and spread of non-native species. Results from this study provide a reach-scale examination of distributional trends of the fishes of the lower Colorado River Basin over the past century. These trends indicate high priorities for conservation and management efforts by identifying declining species before they are lost forever. However, before management plans can be implemented we must first recognize and quantify the degree to which native species are declining and non-native species are spreading across riverine landscapes.

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Table 4.1. Diagnostic properties of the SONFISHES database used in this study. Reported fields include the number of locality records (i.e., fish observations) and total river kilometres (i.e., total river kilometres where all species were observed) during different time periods.

Time Period	Records Native	 Non-indigenous	Total River Kilometres
Pre-1960	1,463	462	6,496
1960-1969	3,106	1,671	6,875
1970-1979	2,772	1,400	7,839
1980-1989	3,033	4,125	7,918
1990-1999	5,389	5,334	6,491
Total	15,763	12,992	14,380

Table 4.2. Temporal patterns of native fish distributions in the lower Colorado River Basin expressed as a percentage of the total kilometres of rivers where all species were observed for the particular time period. Nomenclature follows Nelson et al. (2004); "Code" refers to labels in Figure 4.2; and "Status" refers to the species' official federal status under the U. S. Endangered Species Act (X=extinct, E=endangered, T=threatened, PE=proposed for listing as endangered, and no value refers to a species not listed). "Extant range" refers to species distribution based on 1981-1999 records and "Decline" refers to the percent change in species' distribution.

Species	**Code**	**Status**	*Temporal Trends*					**Extant Range (%)**	**% Decline**
			100	**100s**	**190s**	**19s**	**19s**		
Colorado pikeminnow (*Ptychocheilus lucius*)	A	E	4.4	0.0	0.0	0.0	0.0	0.0	100.0
Desert pupfish (*Cyprinodon macularius*)	B	E	3.2	0.0	0.0	0.0	0.0	0.0	100.0
Moapa dace (*Moapa coriacea*)	C	E	1.0	0.9	0.0	0.0	0.0	0.0	100.0
Pahranagat roundtail chub (*Gila robusta jordani*)	D	E	1.2	1.1	1.0	0.0	0.0	0.0	100.0
Santa Cruz pupfish (*Cyprinodon arcuatus*)	E	X	0.7	0.7	0.0	0.0	0.0	0.0	100.0
Bonytail (*Gila elegans*)	F	E	8.1	2.4	2.0	0.6	0.8	0.5	87.7
Gila trout (*Oncorhynchus gilae*)	G	E	1.9	2.0	1.7	0.4	0.0	0.3	84.0
Woundfin (*Plagopterus argentissimus*)	H	E	3.5	2.0	0.8	0.5	0.2	0.6	78.9
White River spinedace (*Lepidomeda albivallis*)	I	E	4.2	1.9	0.0	0.7	0.0	0.6	74.3
White River springfish (*Crenichthys baileyi*)	J	E	5.5	6.1	0.0	1.2	0.0	1.0	71.1
Flannelmouth sucker (*Catostomus latipinnis*)	K		5.5	7.3	11.0	4.0	1.1	4.0	62.2
Virgin River spinedace (*Lepidomeda mollispinis*)	L		4.9	5.0	5.9	2.2	1.4	2.2	55.1
Razorback sucker (*Xyrauchen texanus*)	M	E	11.9	2.4	4.0	3.5	2.9	3.7	49.7
Spikedace (*Meda fulgida*)	N	T	12.9	2.8	4.5	3.4	4.9	4.2	45.9
Virgin River roundtail chub (*Gila seminuda*)	O	E	2.6	2.8	1.0	0.7	1.6	1.4	42.5
Gila topminnow (*Poeciliopsis occidentalis*)	P	E	8.3	2.5	1.7	3.6	3.9	3.7	36.8
Apache trout (*Oncorhynchus gilae apache*)	Q	T	4.0	6.1	5.7	2.1	4.6	4.5	26.9
Loach minnow (*Rhinichthys cobitis*)	R	T	9.8	3.8	7.0	5.3	6.8	5.8	17.9
Speckled dace (*Rhinichthys osculus*)	S		52.8	50.3	42.6	32.2	40.6	40.6	16.5
Gila chub (*Gila intermedia*)	T	PE	14.0	4.0	4.6	6.2	10.4	7.7	15.9
Desert sucker (*Catostomus clarkii*)	U		45.4	43.6	39.8	40.4	37.0	38.3	13.5
Roundtail chub (*Gila robusta*)	V		18.4	16.2	12.9	16.6	15.6	17.7	6.2
Bluehead sucker (*Catostomus discobolus*)	W		5.6	7.9	13.2	6.0	13.0	11.1	3.5
Humpback chub (*Gila cypha*)	X	E	0.6	1.5	3.0	3.0	1.4	2.5	-6.1
Sonora sucker (*Catostomus insignis*)	Y		25.9	28.5	25.4	28.5	29.5	29.3	-8.2
Longfin dace (*Agosia chrysogaster*)	Z		34.9	28.1	33.5	45.4	46.2	40.9	-11.4
Headwater chub (*Gila nigra*)	AA		3.1	2.2	1.9	2.3	2.3	2.3	-12.6
Little Colorado spinedace (*Lepidomeda vittata*)	BB	T	1.5	3.0	1.4	3.0	3.9	3.6	-14.1

Table 4.3. Temporal patterns of non-native fish distributions in the lower Colorado River Basin expressed as the percentage of the total kilometres of rivers where all species were observed for the particular time period. Nomenclature follows Nelson et al. (2004). "Code" refers to labels in Figure 4.5; and "Intro" refers the year of introduction or first observed in the basin. "Extant range" refers to species distribution based on 1980-1999 records and "Spread" refers to the rate of spread.

Species	Code	Intro	Temporal Trends					Extant Range (%)	Spread (km/year)
			1900	1900s	1970s	19s	19s		
Fathead minnow (*Pimephales promelas*)	1	1950	1.9	7.7	21.8	28.7	39.2	39.3	74.1
Green sunfish (*Lepomis cyanellus*)	2	1937	11.4	16.9	19.8	30.9	44.1	42.0	62.9
Red shiner (*Cyprinella lutrensis*)	3	1950	0.9	17.4	18.7	27.4	27.9	28.9	54.6
Western mosquitofish (*Gambusia affinis*)	4	1922	15.4	16.5	19.2	28.1	27.5	31.3	37.9
Largemouth bass (*Micropterus salmoides*)	5	1935	9.2	15.3	11.6	20.6	19.9	23.6	34.2
Flathead catfish (*Pylodictis olivaris*)	6	1962	1.0	0.6	3.1	9.3	9.3	9.5	23.7
Bluegill (*Lepomis macrochirus*)	7	1937	8.0	8.2	7.2	12.8	12.7	15.6	23.4
Channel catfish (*Ictalurus punctatus*)	8	1892	11.2	15.1	14.6	27.5	15.4	25.2	22.0
Blue tilapia (*Oreochromis aureus*)	9	1978	0.0	0.0	0.3	5.9	1.0	4.8	20.7
Yellow bullhead (*Ameiurus natalis*)	10	1899	5.7	7.6	10.9	16.3	21.8	21.9	20.4
Common carp (*Cyprinus carpio*)	11	1881	14.0	16.5	15.8	21.7	21.2	25.1	19.9
Smallmouth bass (*Micropterus dolomieui*)	12	1942	2.8	3.5	5.2	10.8	10.1	11.1	18.0
Rainbow trout (*Oncorhynchus mykiss*)	13	1900	12.4	18.7	23.3	16.7	20.3	19.1	18.0
Threadfin shad (*Dorosoma petenense*)	14	1953	1.3	6.3	3.5	8.4	2.3	7.9	15.8
Golden Shiner (*Notemigonus crysoleucus*)	15	1953	0.3	2.4	2.3	4.0	7.0	6.3	12.7
Striped Bass (*Morone saxatilis*)	16	1959	0.4	0.8	1.6	5.6	1.5	5.2	11.9
Brown trout (*Salmo trutta*)	17	1924	2.4	7.3	8.6	7.1	10.3	8.9	11.0
Goldfish (*Carassius auratus*)	18	1944	0.1	6.8	1.4	5.5	2.4	6.3	10.6
Plains killifish (*Fundulus zebrinus*)	19	1950	0.0	1.3	4.6	4.3	2.2	4.8	9.0
Black crappie (*Pomoxis nigromaculatus*)	20	1936	7.5	2.5	4.4	4.7	2.9	5.6	8.3
Black bullhead (*Ameiurus melas*)	21	1904	9.3	11.2	6.8	7.7	6.7	8.2	8.1
Sailfin molly (*Poecilia latipinna*)	22	1950	1.0	2.7	1.4	5.1	0.7	4.2	7.9
Brook trout (*Salvelinus fontinalis*)	23	1920	2.6	4.2	3.9	4.3	7.6	6.3	7.4
Walleye (*Sander vitreum*)	24	1971	0.0	0.1	0.3	0.8	1.5	1.8	5.7
Rio Grande cichlid (*Herichthys cyanoguttatus*)	25	1996	0.0	0.0	0.0	0.0	0.3	0.2	5.5
Arctic grayling (*Thymallus arcticus*)	26	1965	0.0	0.9	0.8	0.8	2.2	2.0	5.3
Cutthroat trout (*Oncorhynchus clarkii*)	27	1937	1.3	1.3	0.6	2.2	3.2	3.3	5.0
Northern pike (*Esox lucius*)	28	1969	0.0	0.0	1.3	1.5	0.1	1.3	4.0
Redside shiner (*Richardsonius balteatus*)	29	1950	0.0	0.8	1.1	2.4	0.0	2.0	3.8
Redear sunfish (*Lepomis microlophus*)	30	1951	2.2	1.7	2.7	1.8	0.7	1.9	3.6

Mozambique tilapia (*Oreochromis mossambica*)	31	1965	0.0	1.0	3.4	1.5	0.0	1.2	3.2
Redbelly tilapia (*Tilapia zilli*)	32	1965	0.0	0.0	0.3	1.4	1.0	1.1	3.1
Rock bass (*Ambloplites rupestris*)	33	1962	0.0	0.0	0.0	0.4	0.5	0.7	1.8
Guppy (*Poecilia reticulata*)	34	1950	0.0	1.3	0.5	0.8	0.4	0.9	1.6
Yellow bass (*Morone mississippiensis*)	35	1931	0.4	0.4	0.3	1.2	0.1	1.1	1.5
White crappie (*Pomoxis annularis*)	36	1934	1.8	0.4	0.0	0.1	0.7	0.6	0.8
Shortfin molly (*Poecilia mexicana*)	37	1950	0.0	3.7	0.5	0.3	0.0	0.2	0.4
Rio Grande sucker (*Catostomus plebeius*)	38	1950	1.9	0.9	0.8	0.0	0.2	0.1	0.3
White bass (*Morone chrysops*)	39	1960	0.0	0.1	0.0	0.1	0.0	0.1	0.2
Bigmouth buffalo (*Ictiobus cyprinellus*)	40	1964	0.0	0.5	0.2	0.1	0.1	0.1	0.2
Smallmouth buffalo (*Ictiobus bubalus*)	41	1950	0.0	0.5	0.3	0.0	0.1	0.1	0.1
Brown bullhead (*Ameiurus nebulosus*)	42	1910	6.6	1.5	0.0	0.0	0.0	0.0	0.0
Convict cichlid (*Archocentrus nigrofasciatus*)	43	1955	0.0	1.5	0.0	0.0	0.0	0.0	0.0
Grass carp (*Ctenopharyngodon idellus*)	44	1976	0.0	0.0	1.8	0.0	0.0	0.0	0.0
Black buffalo (*Ictiobus niger*)	45	1966	0.0	0.4	0.2	0.0	0.0	0.0	0.0
Warmouth (*Lepomis gulosus*)	46	1958	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Spotted bass (*Micropterus punctulatus*)	47	1956	0.6	0.5	0.1	0.0	0.0	0.0	0.0
Yellow perch (*Perca flavescens*)	48	1951	0.6	0.2	0.0	0.0	0.0	0.0	0.0

Figure 4.1. Map of the lower Colorado River Basin and the 28,755 locality records from the SONFISHES database used in this study. Inset shows locations of major river drainages.

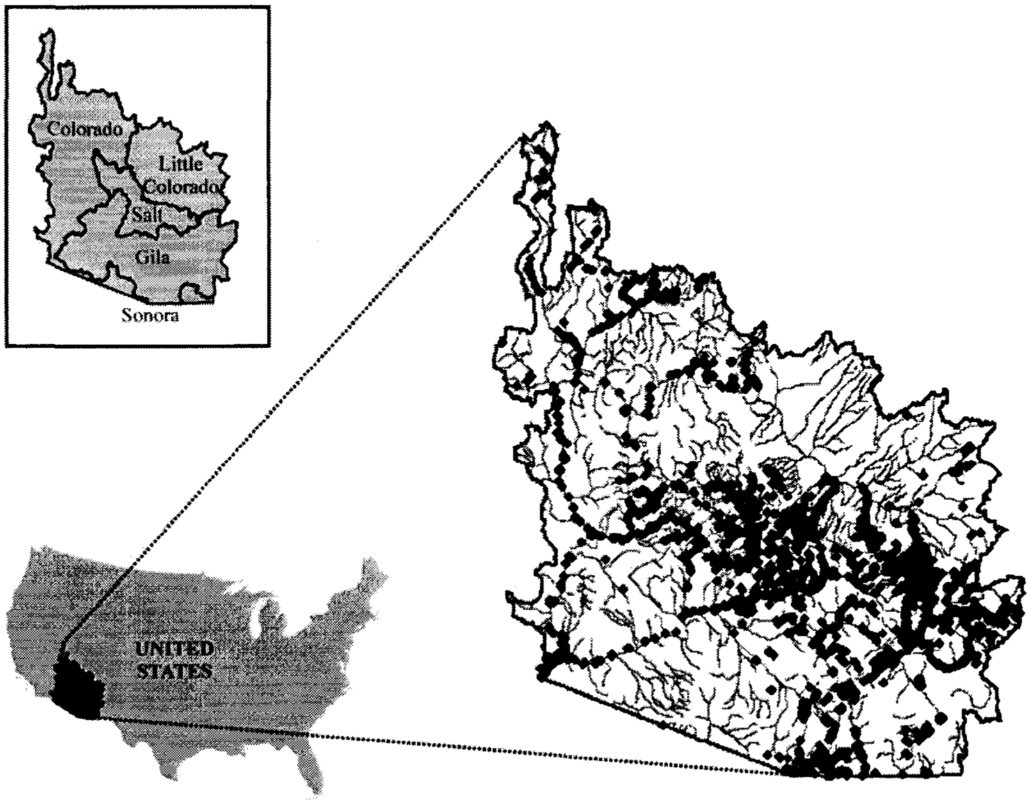


Figure 4.2. Comparisons of % distributional decline, extant distribution size (%) and probability of local extirpation of native fishes in the lower Colorado River Basin. Solid lines represent least-squares regression lines. Letter codes refer to native species in Table 4.2.

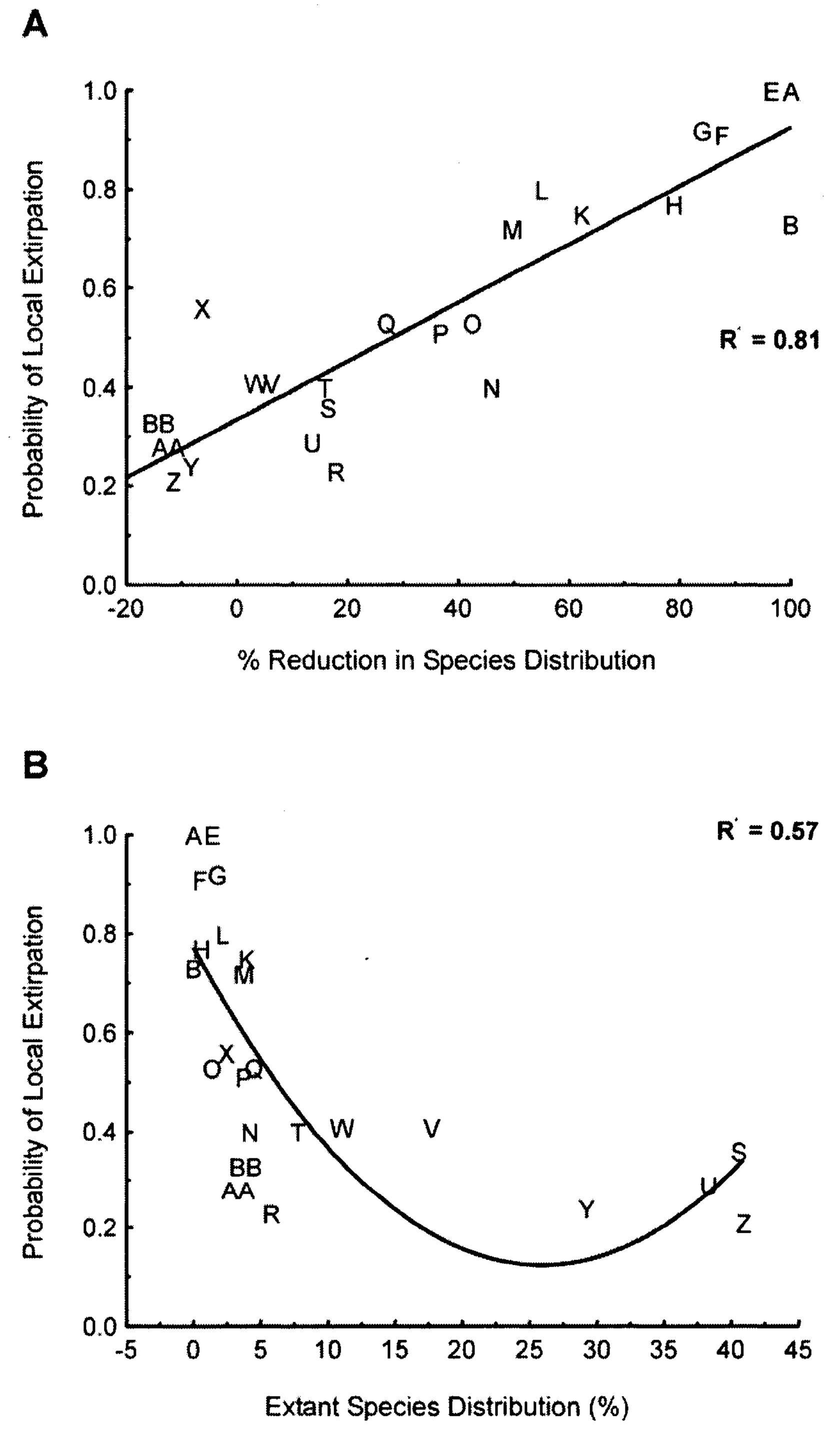


Figure 4.3. Comparisons of % distributional decline and extant distribution size (%) of native species classified as non-listed, threatened and endangered under the U.S. Endangered Species Act (see Table 4.2 for classifications). Bars represent means and whiskers represent 1 standard error.

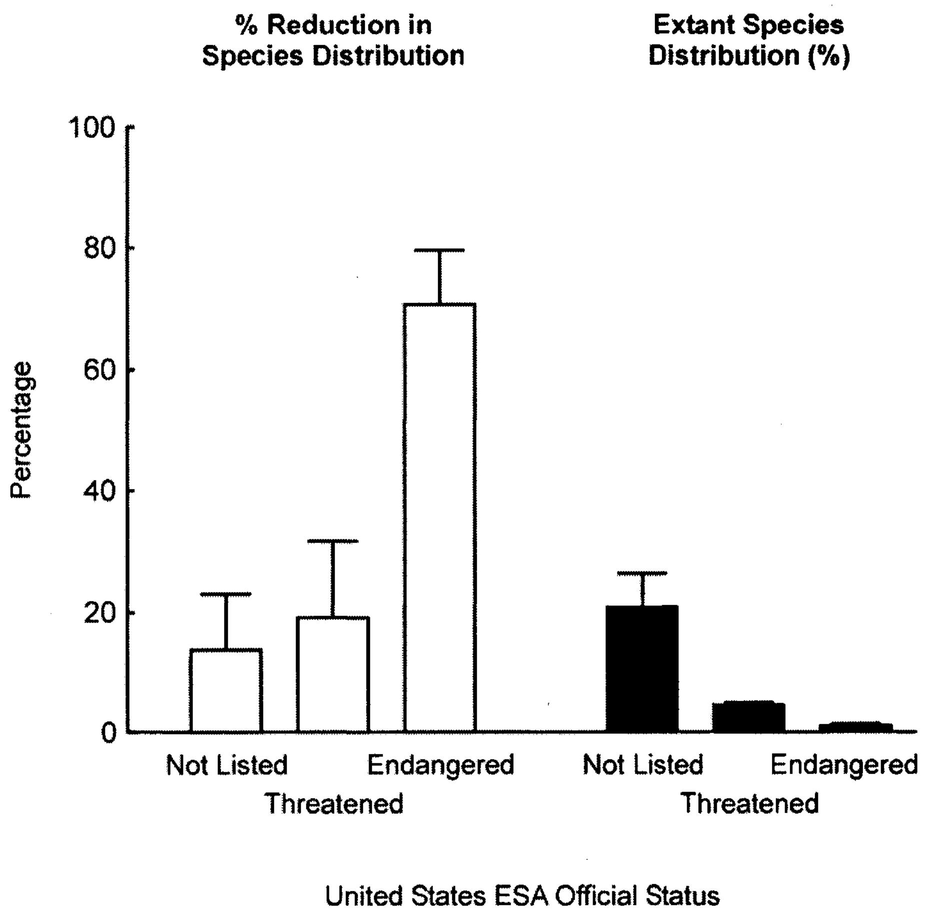


Figure 4.4. Maps of historical and extant distributions of three native fishes – (A) bonytail, (B) spikedace and (C) specked dace – exhibiting markedly different % decline over time and having different statuses under ESA. Thicker lines represent river segments where the species was recorded present during the time period. See inset of Figure 4.1 for locations of major river drainages.

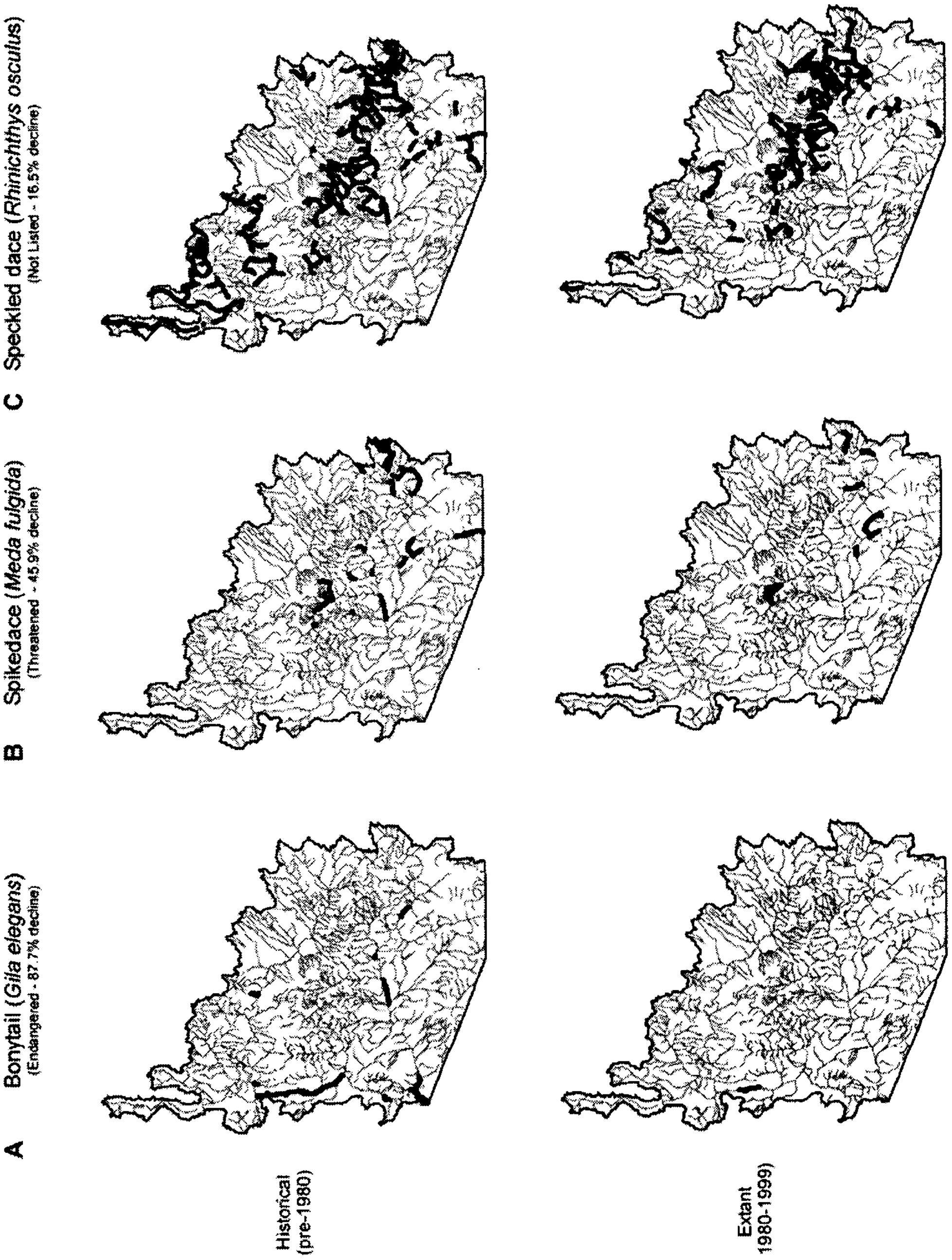
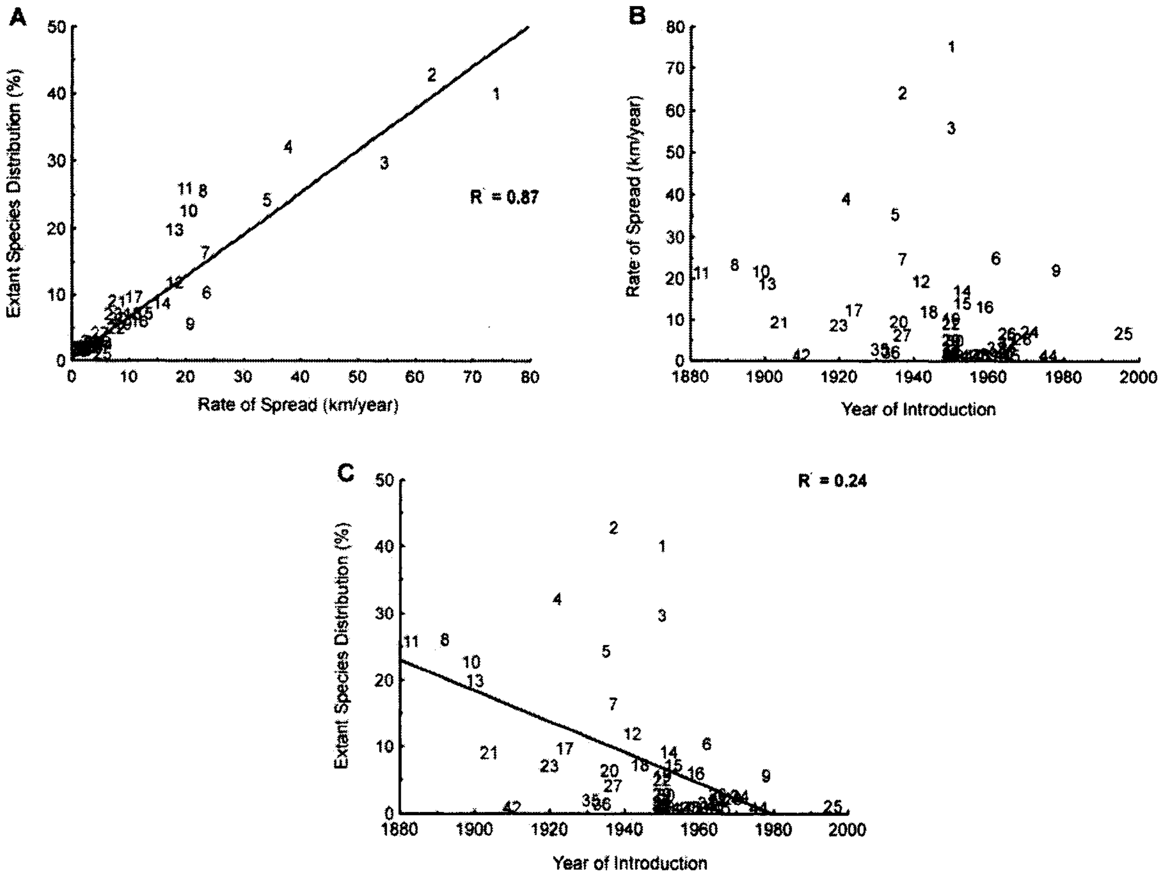


Figure 4.5. Comparisons of extant distribution size (%), rate of spread (km·year^{-1}) and year of introduction of non-native fishes in the lower Colorado River Basin. Solid lines represent least-squares regression lines. Number codes refer to non-native species in Table 4.3.



Chapter

5

Comparative Life-history Strategies of Native and Non-native Fish Faunas of the Colorado River Basin: Linking Ecological Niche Theory with Rates of Invasions and Extirpations over the Past Century

Abstract

Modern life history theory continues to provide an important conceptual framework in fisheries ecology and management. The fish life-history model of Winemiller and Rose (1992), for example, identified three primary life-history strategies that represent the endpoints of a triangular continuum arising from essential trade-offs among three basis demographic parameters (survival, fecundity, and onset and duration of reproductive life). Despite the strong implications of this model for characterizing and predicting population responses to environmental change, it has surprisingly under utilized in fish ecology and has yet to be used for studying fish invasions and extinctions. The present paper provides a functional characterization of the native (an endangered, highly endemic fish fauna in the United States) and non-native ichthyofauna of the Colorado River Basin according to a comprehensive suite of morphological, behavioural, physiological and life-history traits. Using the Winemiller-Rose model as a conceptual framework, we compare the diversity of life-history strategies employed by native and non-native species and explore a number of hypotheses regarding linkages between human-induced environmental change, the creation and modification of ecological niches, and subsequent invasion and extirpation of fish species in the Colorado River Basin. Our results revealed a number of intriguing findings: (1) non-native species were located throughout the adaptive surface defined by the life-history attributes and surround the niche volume represented by the native fish species pool; (2) native species exhibiting the highest similarity to the novel life-histories represented by non-native species have shown the greatest distributional declines; and (3) non-native fishes exhibiting among the fastest

rates of spread, in general, occupied "vacant" niche positions in life-history space that have been created by human-induced modifications to the environment. In summary, our study identifies specific life-histories strategies that are associated with the greatest loss of native species and spread of non-native species over the past 160 years, and highlights the utility of using a life-history perspective to explore patterns of fish invasions and extirpations in the American Southwest.

Introduction

Humans have a penchant for supplementing their local neighbourhoods with imported plants or animals that are perceived to have special beauty or usefulness, or are simply reminders of a pleasing environment in another geographic location (Elton 1958). Many of these exotic species have been transplanted throughout the world with the intent of benefiting their "new" ecosystem, although most introductions have had quite the opposite effect and were the bane, rather than a benefit to, the new environments (Vitousek et al. 1996, Mack et al. 2000, Simberloff 2001). The negative impacts of species invasions, together with the detrimental consequences of environmental degradation, are particularly evident in North American freshwater ecosystems (Master 1990, Richter et al. 1997, Lodge et al. 1998), whose native faunas have estimated extinction rates that greatly exceed terrestrial ecosystems and are equal that of tropical forests (Ricciardi and Rasmussen 1999). In what has broadly been called the Blue Planet crisis in freshwater fish diversity (Cambray and Bianco 1998), unprecedented rates of fish invasions coupled with significant losses of native species have resulted in the remarkable homogenization of fish faunas throughout North America (Rahel 2000, Olden and Poff 2004a (Chapter 3), Taylor 2004).

Despite the apparent idiosyncratic manner in which fish species have been lost and gained over time, recent research that has shown that life-history traits may be useful predictors of both fish invasions (e.g., Kolar and Lodge 2002, Marchetti et al. 2004a, b) and extinctions (e.g., Angermeier 1995, Parent and Schriml 1995, Johnston 1999, Duncan and Lockwood 2001). In fact, modern life history theory – which owes much of its impetus to Cole's (1954) simple question "why do animals reproduce more than once" – has provided an important conceptual framework in fisheries ecology and management (Frank and Leggett 1994), for example, in the stock assessment of marine species (e.g., King and McFarlane 2003).

Life-history theory describes how particular strategies have evolved from constraints, or simultaneous "trade-offs", among life-history traits that have consequences for reproduction and fitness in different environments (Stearns 1976, 1992). Comparative studies from a diverse array of fishes in different environments have independently identified three primary life-history strategies that represent the endpoints of a triangular continuum arising from essential trade-offs among three basic demographic parameters: survival, fecundity, and onset and duration of reproduction (Kawasaki 1980, Baltz 1984, Paine 1990, Winemiller 1989, 1992, Winemiller and Rose 1992, Vila-Gispert and Moreno-Amich 2002, Vila-Gispert et al. 2002). Winemiller and Rose (1992) examined a large and representative sample of North American freshwater and marine fish species (216 species from 57 families) and provided the following descriptions of the characteristic biological and habitat attributes associated with each strategy: (*i*) *periodic strategists* are large-bodied fishes with late maturation, high fecundity per spawning event, low juvenile survivorship (i.e., no parental care), and typically inhabit predictable, seasonal environments; (*ii*) *opportunistic strategists* are small-bodied fishes with early maturation, low fecundity per spawning event, and low juvenile survivorship, and typically inhabit highly disturbed and unpredictable environments; (*iii*) *equilibrium strategists* are small to medium-bodied fishes with moderate maturation age, low fecundity per spawning event , and high juvenile survivorship (i.e., provides parental care), and typically inhabit constant environments. The three primary strategies of North American fishes have some striking similarities with earlier models for plants and insects presented in the empirical and theoretical life-history literature (Grime 1977, Southwood 1977, 1988, Greenslade 1983), but notably the Winemiller-Rose model extends the classic *r*-*K* model by splitting the *r*-strategy into the periodic and opportunistic strategies and more narrowly defines the *K*-strategy as the equilibrium strategy.

The demographic parameters of the Winemiller-Rose life-history model are direct reflections of the ways in which fish allocate energy to reproduction and the three endpoints of the continuum can be interpreted as being adaptive with respect to relative intensity and predictability of temporal and spatial variation in abiotic environmental conditions, food availability, and predation pressure. As envisioned by the authors, the model has strong implications for predicting population responses to environmental change (e.g., see VanWinkle et al. 1993). Indeed, the fact that life-history strategies are the underlying determinants for population responses to environmental change and can be used to classify typical population responses, it is surprising that this model has yet to be used in the study of fish invasions and extinctions.

This paper provides the first functional characterization of the native (a gravely endangered, highly endemic fish fauna in the United States: Minckley and Deacon 1968, 1991) and non-native freshwater fish species pools of the Colorado River Basin (90 species in total) by conducting a comparative analysis of a comprehensive suite of 22 morphological, behavioural, physiological and life-history traits. First, we explore multivariate trait space to compare the functional diversity and composition of the native and non-native species pools and gain insight into historical changes in the Colorado

River Basin in the context of species' adaptations for alternative environmental conditions (Southwood 1977, 1988) and the creation and modification of ecological niches (Chase and Leibold 2003). This analysis provides a basis for quantifying the functional redundancy or complementary nature of fish communities in the Colorado River Basin and offers the opportunity to establish the critical linkages between native fish extinctions, non-native invasions, and ecosystem functioning (Petchey and Gaston 2002, Rosenfeld 2002). Second, we evaluate the trilateral continuum model of fish life-history strategies of Winemiller and Rose (1992) for the fishes of the Colorado River Basin to address the extent to which trade-offs among three basic demographic parameters (survival, fecundity, and onset and duration of reproductive life) can shed insight into human-induced environmental change, the creation and modification of ecological niches, and subsequent invasion by non-native fishes and extirpation of native fishes. For the fishes of the lower Colorado River Basin we develop empirical tests of the hypothesis that distributional changes for native and non-native species over the past 160 years differ across the three-dimensional life-history space identified in the Winemiller-Rose model. The success of this model in identifying those life-history strategies associated with the greatest loss of native species and expansion of non-native species is viewed as a valuable starting point for interpreting the ecological mechanisms responsible for population responses to environmental change, and for developing conceptual management scenarios for native and non-native fishes in the American Southwest. Our study strongly suggests that integrating knowledge about empirical changes in species' distributions with insights provided by life-history theory will help scientists meet the challenges of conserving native biodiversity and managing the continued invasion and spread of non-native species.

Methods

Fishes of the Colorado River Basin

The Colorado River is the primary waterway of the American Southwest, flowing from the western slope of the Rocky Mountains to the Gulf of California and draining ca. 632,000 km^2 of land from seven states in the U.S. and north-western Mexico (Fig. 5.1). It occupies one-twelfth of the land of the contiguous U.S. and is divided into the upper and lower basins at Glen Canyon Dam (located near the border between Arizona and Utah, U.S.A.) for water management purposes. The upper basin produces most of the river's discharge with spring and early summer runoff in the form of snowmelt, whereas maximum discharge in the lower basin often follows winter rainstorms and late summer monsoons. As a result of long isolation and fluctuating environmental conditions, the Colorado River Basin has a unique indigenous fish fauna that is considered one of the most distinctive ichthyofauna in North America (Smith 1981). We compiled a present-day list of the native (n=28) and non-native (n=62) freshwater fishes of the Colorado River Basin (Appendix 6.1) using species accounts from Arizona (Minckley 1973, Paul Marsh per. comm.), California (Moyle 2002), Colorado (Nesler 2004), Nevada (LaRivers 1994), New Mexico (Sublette et al. 1990), Utah (Sigler and Sigler 1996), Wyoming

(Baxter and Stone 1995) and other sources from the primary literature (e.g., Carlson and Muth 1989).

Ecological and life-history traits

We examined the scientific literature, electronic databases and the use of expertise knowledge to provide the most comprehensive functional description of the native and non-native fishes of the Colorado River Basin to date. We collated data for 22 ecological and life-history attributes (collectively referred to as biological traits) that could be justified on the basis of our current state of knowledge and information available for the entire pool of species. These traits included the following. *Body morphology*: (1) maximum total body length (cm); (2) shape factor – ratio of total body length to maximum body depth; (3) swim factor – ratio of minimum depth of the caudal peduncle to the maximum depth of the caudal fin, where small factors are indicative of strong swimmers (calculated following Webb 1984). *Behaviour*: (4) water temperature preference – cold (10-17°C), cool (18-26°C) or warm water (>26°C) based on species distributions and perceived physiological optima; (5) substrate preference – rubble (including cobble and gravel), sand, silt/mud or general; (6) fluvial dependence – reliance on flowing waters for completing life cycle, e.g., flow required for feeding or reproduction (classified as yes or no); (7) current velocity preference – slow, slow-moderate, moderate, moderate-fast or fast current velocity; (8) vertical position – benthic or non-benthic based on species morphology and behaviour. *Physiology*: (9) critical thermal tolerance – low (< 30°C), moderate (30-35°C), high (35-40°C) or very high (>40°C) critical water temperature for survival. *Life history*: (10) longevity – maximum potential life span (years); (11) age at maturation (years); (12) length at maturation (cm); (13) Fecundity – total number of eggs or offspring per breeding season (#) represented on a logarithmic (base 10) scale; (14) Egg size – mean diameter of mature (fully yolked) ovarian oocytes (mm); (15) Spawning temperature – temperature at which spawning is initiated (°C); (16) Parental care - metric representing the total energetic contribution of parents to their offspring (calculated following Winemiller 1989); (17) Reproductive guild - nonguarders (open substratum spawners, brood hiders), guarders (substratum choosers, nest spawners) or bearers (internal, external) (calculated following Balon 1975); (18) Spawning substrate – mineral substrate, vegetation, pelagic or various; (19) Time to hatch – mean time to egg hatch within the range of average post-spawning water temperatures (days); (20) Larvae length at hatching – mean total length of larvae at hatching (mm); (21) Trophic guild – adult feeding mode classified as herbivore-detritivore (ca. > 25% plant matter), omnivore (ca. < 5% plant matter), invertivore or invertivore-piscivore; (22) Diet breadth – total number of major diet items consumed at any time during lifetime (#), including inorganic material, vegetative material, plankton, aquatic/terrestrial insects, oligochaetes/crustaceans/molluscs, fish/fish eggs and amphibians/mammals/birds (range 1-7).

Trait assignments were based on a multi-tiered data collection procedure. First, trait data were collected from species accounts in the comprehensive texts of the state fish faunas (see references in previous section). Second, we used species descriptions from the primary literature, state agency reports, university reports and graduate theses (Pacey and Marsh 1998 was used as a primary source of literature). Third, we obtained data from electronic databases available on the World Wide Web, including FishBase (Froese and Pauly 2003), Arizona's Heritage Data Management System and Biota Information System of New Mexico. Fourth, expert knowledge was used to assign values to a small number of trait states that could not be obtained from the previous methods (mainly inferred from closely related congenerics). To account for inter-population variation in biological traits for both native and non-native fishes we recorded trait values based on research conducted in the Colorado River Basin or more broadly in the American Southwest. When such information was not available, we used data collected from the closest geographic proximity. Trait values were represented by ordinal, nominal or continuous data. Ordinal and nominal traits were assigned a single state based on a majority of evidence rule according to adult preferences. Our knowledge of the fishes of this region enabled us to assign species to single trait categories, and therefore eliminated the need to employ fuzzy statistical analyses. For continuous traits, when a range of values were presented we used the mid-point.

Distributional changes for native and non-native fishes in the Lower Colorado River Basin

Our objective was to compare patterns of species' distributional changes for native and non-native fishes across the life-history continuum model proposed by Winemiller and Rose (1992). The data for such an empirical analysis need to be long-term and spatially-extensive, and for our study they were provided by the newly-developed SONFISHES database (Desert Fishes Council, http://www.desertfishes.org/na/gis/index.html). This database was contains >38,000 occurrence records for 132 freshwater fish species from over 160 years of research conducted throughout the lower Colorado River Basin in the

Sonoran Desert ecoregion. Records include incidence, identity, and collection information for the complete holdings of major regional museum collections, numerous smaller holdings, and records from peer-reviewed and gray literature sources, and they are geo-referenced to within 1 km of their collection site in a Geographic Information System (see Unmack 2002 for details).

Using ArcGIS (Environmental Services Research Inc., v. 8.3) we plotted 28,755 locality records from 1840 to 2000 (excluding occurrence records resulting from artificial translocations and reintroductions) for 23 native species and 47 non-native species from the SONFISHES database onto a digital coverage of streams and rivers (U.S. Geological Survey Enhanced River Reach File 2.0: http://www.usgs.gov/). Following Fagan et al. (2002), we considered those records collected prior to 1980 to represent historical localities and those records collected between 1980 and 1999 to represent modern or extant localities. For native species, historical presences and extant absences constitute true extirpation events because modern records in the dataset are almost exclusively the result of intensive efforts by federal or state agencies to determine species' complete distributions prior to listing decisions under the U.S. or Mexican Endangered Species Acts (Fagan et al. 2002). For the historical and modern time periods we calculated the total river kilometres occupied by each species by summing the length of the river segments (defined as a section of river delineated by two confluences) in which the species was recorded. Native species' distribution ranges were estimated by dividing the total river kilometres that the species was present by the total river kilometres where all species were recorded during the time period. Percent distributional decline was then calculated for each native species by subtracting extant range size from historical range size and dividing by historical range size. For non-native species, rate of spread (km·year^{-1}) was calculated as the species' extant distribution divided by the number of years since introduction (calculated from 2000 and estimated from Table 6 of Mueller and Marsh (2002) and year of first occurrence in the SONFISHES database). We refer the reader to Olden and Poff (2004b) or Chapter 4 for more details and Appendix 5.2 for values of native distributional declines and non-native rates of spread.

Statistical Analyses

When dealing with comparative data it is important to consider whether the traits demonstrate phylogenetic effects, i.e. whether closely related species tend to be similar phenotypically (Fisher and Owens 2004). Given the broad phylogenetic diversity of the species pool examined in this study, we followed Grafen (1989) and calculated phylogenetic relatedness by ranking fish families by the degree of derived characters, from most ancient to the most derived using Nelson (1994) and Lee et al. (1980) and used this information to compute a phylogenetic distance matrix. We refer the reader to Kolar and Lodge (2002) for a biological example using this approach. Next, a matrix of trait similarities for the 90 fish species according to the 22 biological attributes was calculated using Gower's similarity coefficient – a multivariate similarity index that facilitates mixed data types, including binary and multi-state discrete traits and continuous traits (Legendre and Legendre 1998). Using a modified version of the technique presented by Diniz-Filho et al. (1998), we partitioned the total variance in the biological trait distance matrix into its phylogenetic and specific components using a Mantel test. The Mantel test is analogous to a simple correlation in that it correlates two distance matrices that have been unfolded into single column vectors (Legendre and Legendre 1998). For the purposes of our study we regressed the phylogenetic matrix against the trait matrix to derive a matrix of residuals that represent trait similarities among species after controlling for similarities expected from common phylogenies. Results from the Mantel test showed a weak and marginally significant correlation between the trait and phylogenetic distance matrices (Mantel's standardized r = 0.25, $P = 0.08$). Principal coordinate analysis was then performed on the residual similarity matrix to summarize the dominant patterns of variation among the biological traits and examine functional separation between native and non-native species in reduced ordination space. In all cases the first two principal components were retained to facilitate visual interpretation of the resulting plots.

To evaluate the fish life-history continuum model we followed Winemiller and Rose (1992) by plotting the positions of the fish species in relation to three life-history traits: (1) $\log_e$ maturation size (a surrogate of maturation age and highly correlated with maturation size in our study, r = 0.81); (2) $\log_e$ mean fecundity; and (3) investment per progeny (calculated as the sum of $\log_e$ egg diameter and $\log_e$ parental care). Visual analyses were used to examine the association between species' position in trivariate life-history space and empirical estimates of native distributional declines and non-native rates of spread in the lower Colorado River Basin.

Results

The two-dimensional PCoA ordination illustrated a number of unique functional differences between the native and non-native fish species pools of the Colorado River Basin (Fig. 5.2). The first two principal components explained 35.5% of the total variation in the 22 biological traits (both were statistically significant based on the broken-stick rule: Jackson 1993), and the addition of the third or fourth axis produced little modification in the general pattern of interpretation. The most striking result was that the non-native species pool occupied most of the ordination space and nearly encircled the more limited trait coverage represented by the native species pool. Therefore, the functional composition of the non-native species pool exhibited greater functional diversity and is considered to be unique, in part, from the native species pool. Although the majority of traits showed minimal differences between native and non-native species, a few traits were strongly and consistently associated with the non-native species pool. The first principal axis identified a dominant trait gradient that contrasted the native fishes occurring predominantly in the right-hand side of the ordination (21 out of 28 species with positive scores) from a substantial number of non-native fishes that occurred in the left-hand side of the ordination (35 out of 62 species with negative scores). Ordination space occupied only by the non-native species' pool included fishes lacking dependence on fluvial conditions to complete their life cycle, preferring slow currents, and exhibiting broad omnivorous diets. These species also typically prefer warm water, have high critical thermal maxima, spawn in vegetation at high initiation temperatures, and typically mature at an early age and smaller size, produce smaller eggs that hatch quicker, and exhibit larger swim factors.

Positions of native and non-native fishes in relation to the three demographic axes of the life-history continuum model provided strong evidence for the basic form of the triangular adaptive surface (Fig. 5.3). Importantly, the fishes of the Colorado River Basin encompassed the entire numeric range of life-history values presented by Winemiller and Rose (1992), and therefore the position of a species within the life-history continuum is considered relative to the North America freshwater fish fauna. Our results showed that native and non-native fishes of the Colorado River Basin occupy very different positions on the adaptive surface that is anchored by the periodic, opportunistic and equilibrium strategy endpoints. The native species pool was characterized by a small volume in the centre of the trivariate space, i.e. species typically occupied intermediate positions within the life-history continuum rather than occurring in the endpoint regions. In fact, the majority of native fishes were located along an axis connecting the opportunistic endpoint and the edge connecting the periodic and equilibrium endpoints. Notable exceptions included species that showed closer affiliations to the periodic (e.g., bonytail, Colorado pikeminnow and razorback sucker), opportunist (e.g., Gila topminnow) and equilibrium (e.g., cutthroat trout) endpoints, although their extreme positions were still dwarfed by a number of species in the non-native pool. Non-native species, in contrast, were represented across the entire adaptive surface, including the extreme regions representing the periodic (e.g., common carp, striped bass), opportunist (e.g., guppy, western mosquitofish) and equilibrium (e.g., bullheads, catfishes, lake trout, smallmouth bass) endpoints (scientific names provided in Appendix 5.1). Of particular interest was that non-native fishes dominated the equilibrium and opportunistic regions of the life-history space, in addition to strongly defining the edge joining the opportunist and periodic strategies (Fig. 5.3).

Within the three-dimensional life-history space we plotted species in relation to their distributional change over the past century in the lower Colorado River Basin (Fig. 5.4). Native fishes located in the most extreme endpoints of the adaptive space represented by the native species pool have exhibited the greatest declines in their distributions (Fig. 5.4a, c). Species showing the greatest proximity to periodic, opportunistic and equilibrium strategies showed 75%, 69%, and 84% distribution declines, respectively. In constrast, those species occupying immediate positions between these endpoints exhibited substantially lower declines ($\overline{X}$=8.4%, range=0.0 – 26.9%). Non-native species showed a striking pattern where equilibrium strategists exhibited the highest rates of spread in the lower Colorado River (Fig. 5.4b, d), in addition to those species positioned along the life-history axis joining the opportunistic and equilibrium endpoints, including the three fastest spreading species – fathead minnow (74.1 km·year^{-1}), green sunfish (62.9 km·year^{-1}) and red shiner (54.6 km·year^{-1}). In contrast, non-native species located in closer proximity to the periodic strategy region showed relatively lower rates of spread.

Discussion

Our study shows that present-day native and non-native fish species of the Colorado River Basin exhibit divergent life-history strategies representative of North American fishes, and it provides a functional basis for understanding the mechanisms responsible for the continued decline of native fishes and rapid spread of non-native fishes in the American Southwest. The challenges associated with conserving and managing fishes in the Colorado River Basin are perhaps best understood by considering the evolution of the native species fauna, which originated in a system that was very different than the one that exists today. Native fishes of the Colorado River had a long evolutionary history of adaptations to a habitat template characterized by extreme, seasonal variations in flow and generally turbid waters (Miller 1961, Smith 1981), conditions that are largely absent today. Altered environmental conditions now compromise efficiency of life-history adaptations that evolved to allow native fishes to thrive in the historically harsh, fluctuating environments, and at the same time may facilitate the invasion of non-native species, many of which are not adapted to the natural conditions of the basin.

In the context of adaptations for alternative environmental conditions, life-history comparisons of native and non-native species pools provide a unique opportunity to gain insight into how fish species have differentially responded to habitat change over large spatial and temporal scales. To the extent that the collection of niches of the native species pool represents the entire niche space that was historically available in the Colorado River Basin (given that most extinct species, e.g., *Cyprinodon arcuatus* (Monkey Springs pupfish), still have close relatives that are currently present, e.g.

Cyprinodon macularius (desert pupfish)) our study suggests that human-induced environmental changes to the river created a number of vacant ecological niches (*sensu* Herbold and Rahel 1986, see Chase and Leibold 2003 for review) that facilitated the establishment of non-native species. During the last century water development projects have caused significant changes in physical habitat, flow regimes, water temperature, sediment load, nutrient transport, and other facets of water quality throughout the basin (Carlson and Muth 1989). Also, the construction of dams has replaced large areas of lotic habitat with massive reservoirs of lentic habitat. Such environmental changes, in fact, are reflected in the functional trait space represented by the non-native species pool but not the native species pool. These non-native fishes exhibit requirements for slow-moving, warm waters, and are generally weaker swimmers and do not require fluvial conditions to complete their life-cycle (e.g., shads and sunfishes). Moreover, these species typically exhibit broader and more flexible diet requirements, a finding supported by reduced frequency of floods, increased fine sediment accumulation, and potentially depressed biotic production caused by river regulation (e.g. Osmundson et al. 2002).

In support of previous research for freshwater fishes in a diversity of environments (Winemiller 1989, Winemiller and Rose 1992, Vila-Gispert and Moreno-Amich 2002, Vila-Gispert et al. 2002), the fishes of the Colorado River Basin conform to the triangular continuum model that defines three primary life-history strategies (periodic, opportunistic and equilibrium) in three-dimensional adaptive space arising from the interrelationships among three basic demographic parameters of survival, fecundity, and onset and duration of reproductive life. The present study is the first to use the Winemiller-Rose model to provide a life-history perspective on patterns of distributional change for native and non-native fishes, and it produced a number of striking results. Native species were found to exhibit intermediate positions in adaptive space and were absent from the endpoints defining the periodic, opportunistic and equilibrium life-history strategies. In fact, the majority of native fishes were located along an axis connecting the opportunistic endpoint and the edge connecting the periodic and equilibrium endpoints, an axis that presumably defines a gradient of evolutionary "bet-hedging" (Cole 1954) considered adaptive in highly unpredictable environments where conditions are occasionally so bad that recruitment fails entirely (Cohen 1966, Stearns 1976). The frequency with which native species fall along this axis would seem consistent with a historical habitat template that could be broadly characterized by extreme seasonal variations in environmental conditions.

In contrast, non-native species were located throughout the adaptive surface, showing strong representation in all three endpoint strategies and mostly surrounding the niche volume represented by the native fish species pool. Interestingly, native species exhibiting the closest positions to the endpoint strategies have shown the greatest distributional declines in the lower Colorado River Basin, whereas species showing more balanced trade-offs between the periodic, opportunistic and equilibrium strategies have shown much smaller reductions. These observations strongly suggest that those native species closest to the unique life-history space occupied by non-native species (viz., the extreme periodic, opportunistic and equilibrium strategies) exhibit the most similar niches and perhaps are at greatest risk to competition from non-native fishes. This is significant in that those same native species may have similar niches to non-native species that have successfully established in the Colorado River Basin and therefore are perhaps better suited to the current habitat template of the river. Interestingly, the fastest spreading non-native species were positioned between the opportunistic and equilibrium endpoints and represent species having longer life spans than the opportunistic strategists. These species' populations can withstand periods of unfavourable environmental conditions and allow for better recruitment, but still exhibit more stable populations within constant environmental regimes due to associations with the equilibrium strategy.

The presence of non-native species and the absence of native species in the extreme endpoints of the life-history space provide further support that "vacant niches" do, or did, exist in the Colorado River Basin. For the non-extreme positions in the three-dimensional life-history space, however, the value of the concept of a vacant niche is perhaps less obvious. Our study suggests that niche separation between native and non-native species influence the likelihood of establishment or spread of a non-native species. For example, in terms of the establishment of non-native fishes, equilibrium strategists and species located midway between the opportunistic and periodic strategies were conspicuously located in vacant niche space, although many other non-native species were found to be clustered in the centre of life-history space and were not clearly distinguishable from the native species pool.

We interpret these results with caution because we do not know the identities, and therefore the life-history strategies, of those non-native species that failed to establish. Perhaps a more compelling result was that non-native fishes exhibiting among the fastest rates of spread (e.g., fathead minnow, green sunfish, catfishes, bullheads, smallmouth bass) occupied the largest void on the adaptive surface that was not represented by the native species pool (i.e., the region closest to the equilibrium strategy). The equilibrium strategy is considered to be consistent with the suite of characteristics often associated with the traditional *K*-strategy of adaptation to life in resource-limited or density-dependent environments (Pianka 1970), and it is advantageous in environments with low variation in habitat quality and strong direct and indirect biotic interactions (Winemiller and Rose 1992).

The results from our study have a number of important ramifications for interpreting fish community structure from a life-history perspective. McCann (1998) used a series of stage-structured competition models to explore patterns of dominance and coexistence of different fish life-history strategies according to varying levels of juvenile density-dependent mortality. In environments that promote low juvenile density dependence (e.g., high juvenile resource densities and low levels of predation), the models predicted that the periodic and opportunistic strategies are most competitive. Indeed, we found that native fish species were located predominantly between these two strategies, and we would expect such strategies to be favoured in historical environments that lacked heavy juvenile predation by piscivorous, non-native fishes and exhibited natural flooding regimes that inundated floodplains and provided vital resources. In contrast, McCann's model predicts that in environments promoting high juvenile density dependence (e.g., low juvenile resource densities and high levels of predation), equilibrium strategists should be competitively dominant. These predictions conform to the prevalence of non-native equilibrium strategists and the notion that current conditions of the Colorado River are generally characterized by greater predation pressure from non-native fishes and increased resource limitation resulting from reduced inundation of floodplains caused by river regulation. Finally, it is interesting to note that at intermediate levels of juvenile density dependence, the opportunist and equilibrium strategists are predicted to co-exist because opportunists are more competitive than the equilibrium strategists during the juvenile stage, while the equilibrium strategists are more competitive than the opportunists during the adult stage. Interestingly, the continuum between opportunist and equilibrium strategies was dominated by rapidly spreading non-native fishes. While this line of research is still preliminary, clearer patterns are likely to emerge when detailed attention is focused on particular species in specific habitats with comparable environmental conditions.

The trilateral life-history model of Winemiller and Rose (1992) can provide a foundation for developing conceptual management scenarios for invasive species of the Colorado River Basin based on generalized population dynamics and responses to environmental conditions assumed under the different life-history strategies. The present study is the first application of this model to the study of fish invasions and extirpations. The finding that rapidly spreading, non-native fishes are located predominantly along the opportunist-equilibrium life-history axis provides important guidance in the management of species invasions in the Colorado River Basin. For example, a number of non-native species exist only in the upper basin and that exhibit life-history strategies very similar to fast spreading species in the lower basin, including creek chub and sand shiner. These species, if provided the opportunity to establish in the lower basin, might be expected to exhibit rapid rates of spread on the basis of their life-history strategies. In conclusion, the results from our study suggest that it may be possible to examine a range of management policies for different life-history strategies in different environmental settings (e.g., reservoir vs. tailwater habitats) with the goal of minimizing the future spread of non-native fishes. Such policies could be optimized for particular strategies and then applied to those species.

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Figure 5.1. Map of the Colorado River Basin located in the American Southwest.

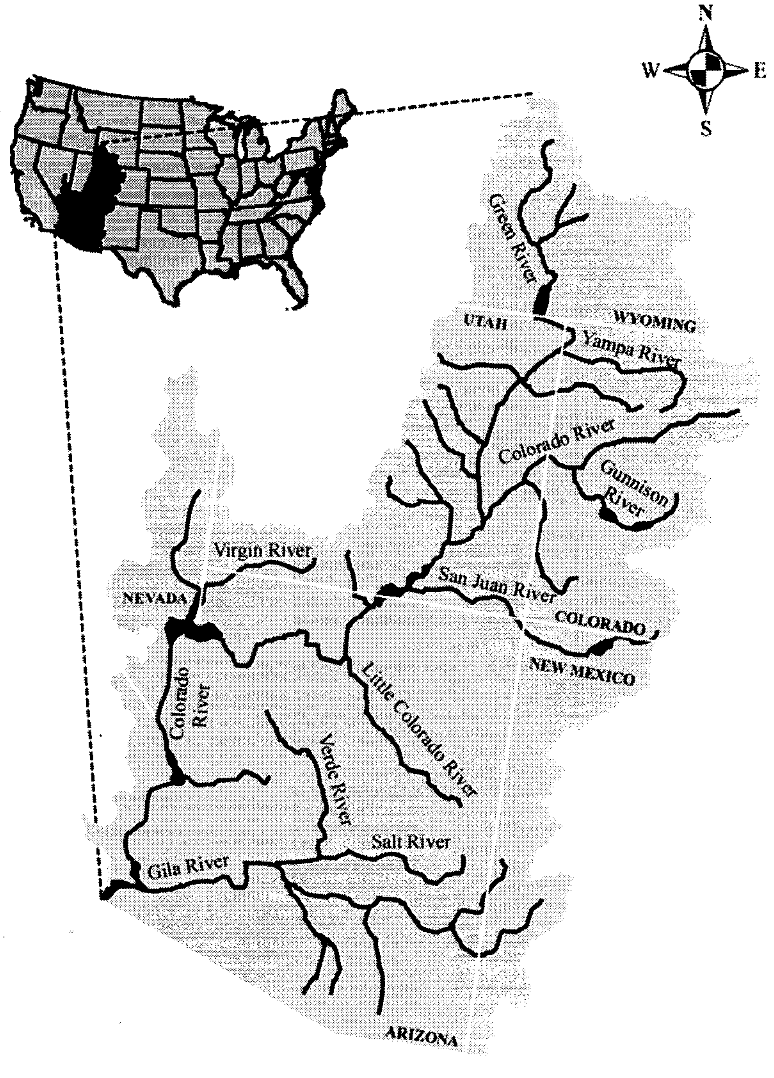


Figure 5.2. Ordination resulting from the principal coordinate analysis on the 22 biological traits of the 90 fish species comprising the native and non-native fish species pools of the Colorado River Basin. A. Fish species bi-plot where filled circles represent native species and empty circles represent non-native species. B. Plot of the traits with high loadings (> 0.50) on the first two principal components (see Methods for trait descriptions). Appendix 5.3 contains the same fish ordination bi-plot with species' labels according to Appendix 5.1.

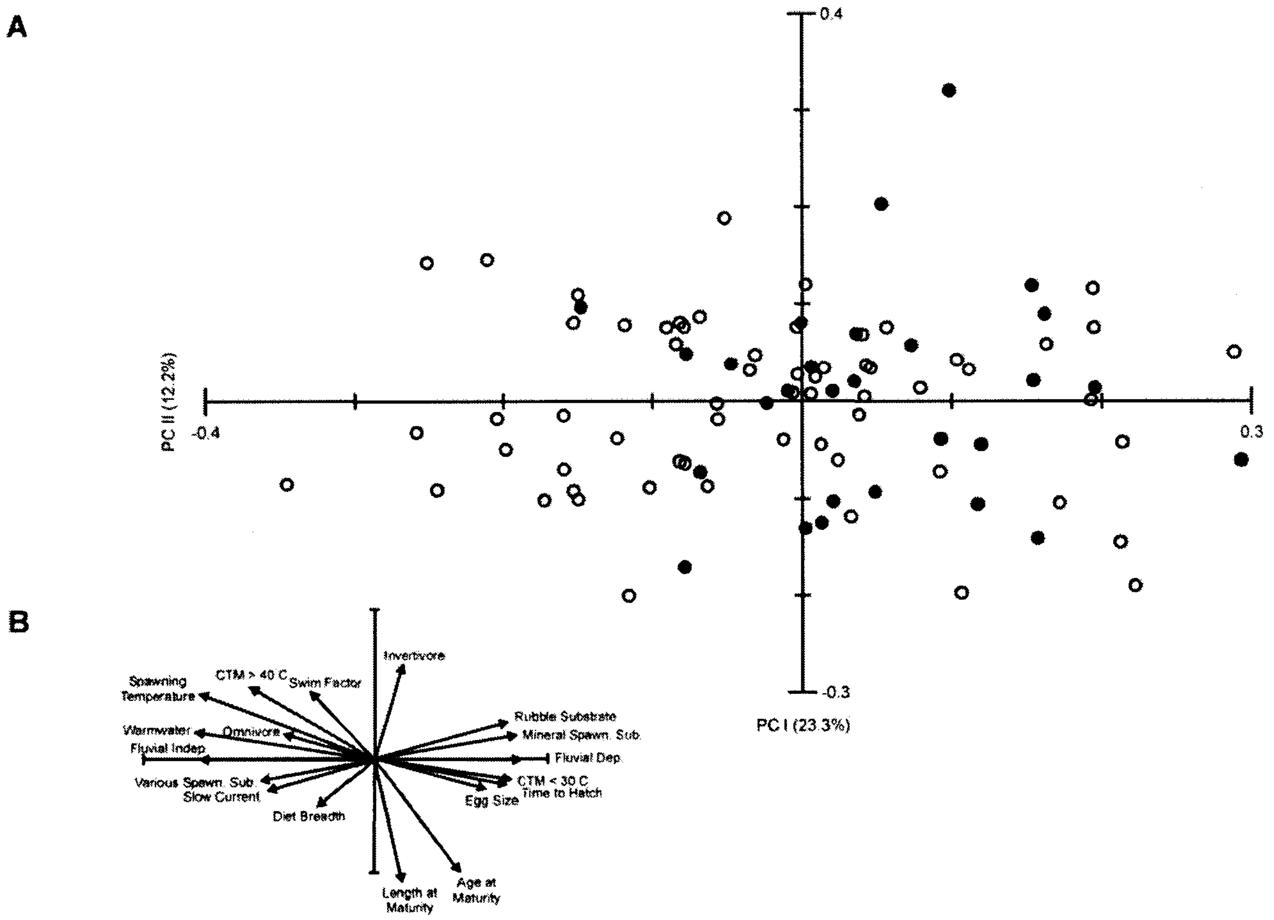


Figure 5.3. Three-dimensional plot of $\log_e$ maturation length, $\log_e$ mean fecundity, and relative investment per progeny (a surrogate of juvenile survivorship that was equal to $\log_e$ ((egg diameter + 1)(parental care +1)) for the fishes of the Colorado River Basin according to the trilateral continuum model of fish life-histories presented by Winemiller and Rose (1992). Native species are solid symbols and non-native species are empty symbols, and periodic (Period.), opportunistic (Opport.), and equilibrium (Equil.) strategies are labelled. Panels A and B are the same plots from different vertical perspectives. Inset illustrates a smoothed spline surface fitted to all the species to show the life-history adaptive surface and the positions of the three strategies. Appendix 5.4 contains the same 3-D plot with species' labels according to Appendix 5.1.

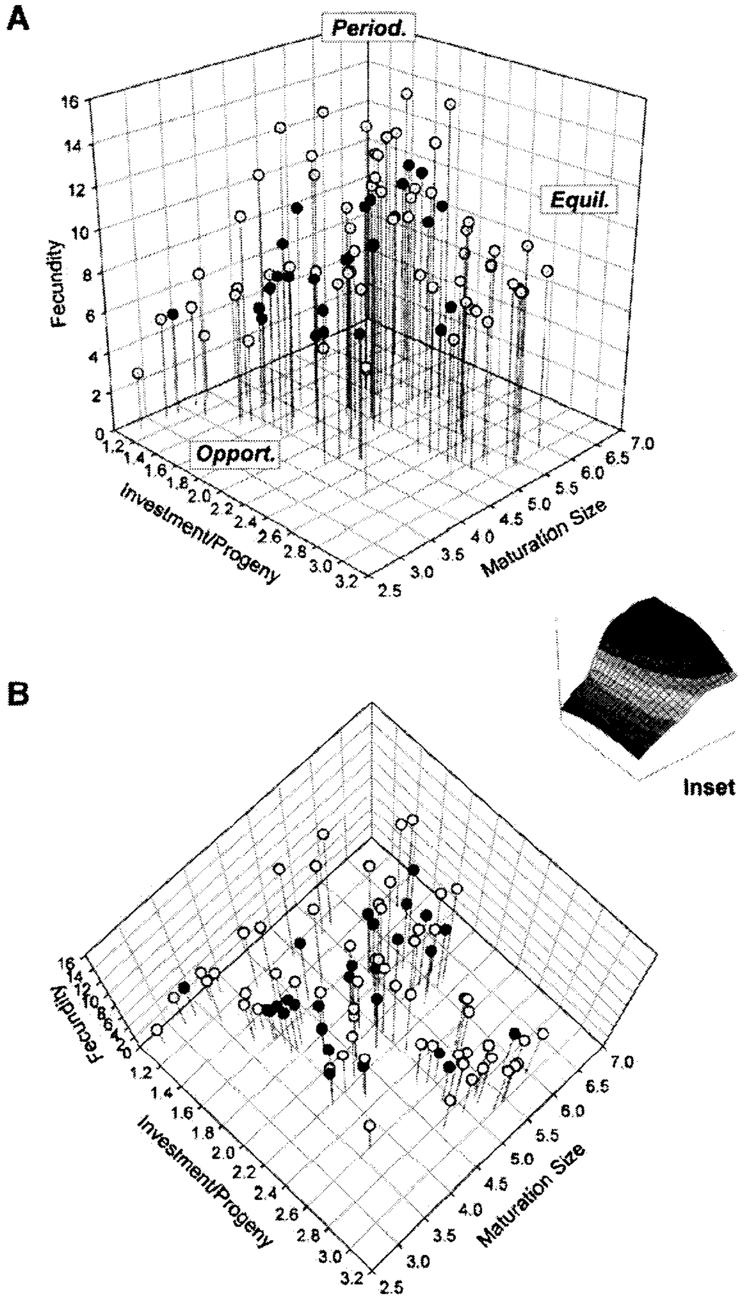
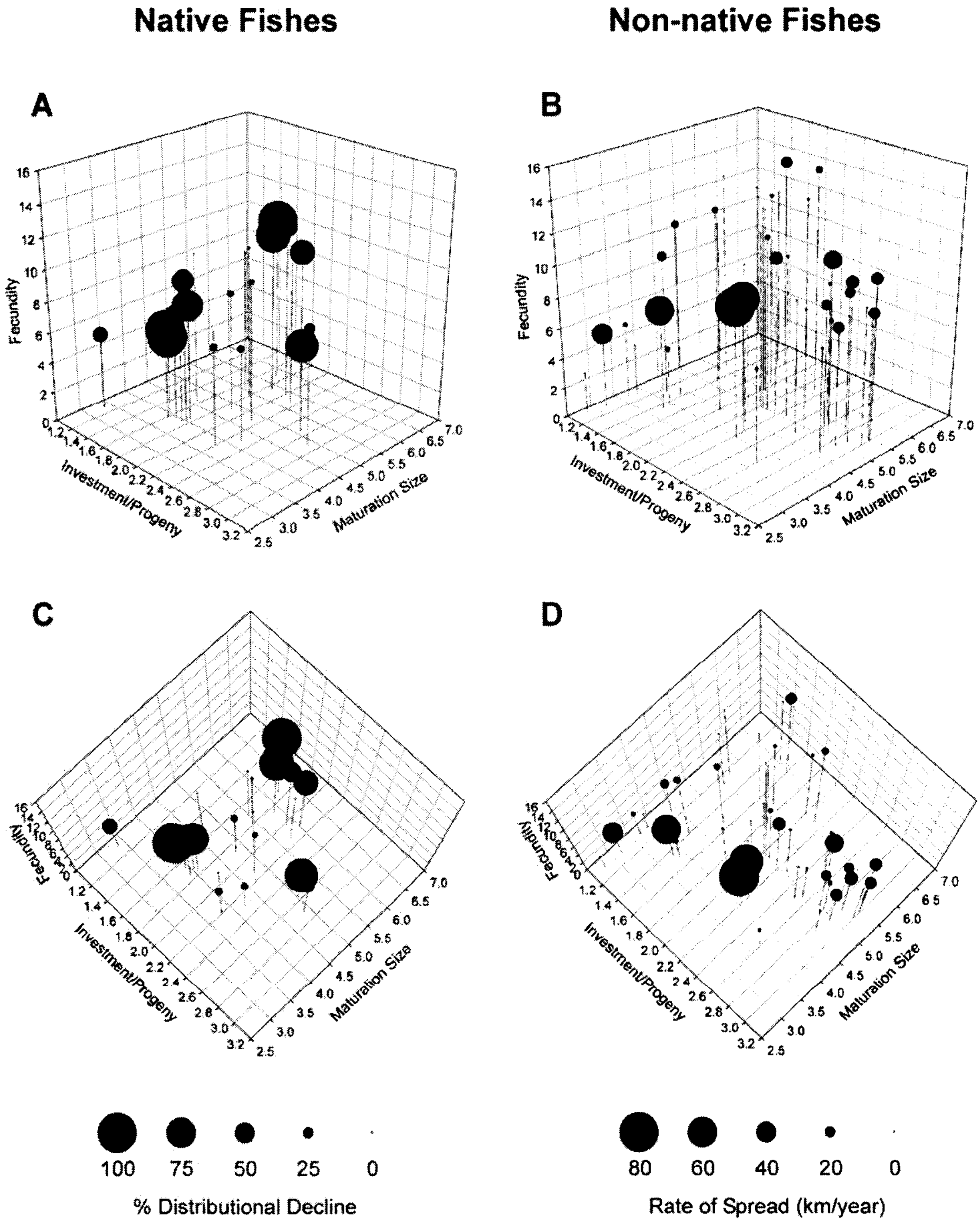


Figure 5.4. Three-dimensional plot of $\log_e$ maturation length, $\log_e$ mean fecundity, and relative investment per progeny (a surrogate of juvenile survivorship that was equal to $\log_e$ ((egg diameter + 1)(parental care +1)) for the native (panels A, C) and non-native (panels B, D) fishes of the Colorado River Basin. The size of the symbols is scaled to the percent decline for native species and rate of spread for non-native fishes (see legend). Panels A-C and B-D are the same plots from different vertical perspectives. See Figure 5.3 for the position of the periodic, opportunistic, and equilibrium strategies. Note clustering of native species in C and axis of high spread in D.



Appendix 5.1. Freshwater native (*n*=28) and non-native (*n*=62) fish species of the Colorado River Basin examined in our study. Nomenclature follows Nelson et al. (2004) and common names are the basis for species abbreviations for native species. Code couplets include species abbreviation (first element) and letter code (second element) for native species and number code (first element) for non-native species.

Native species: *Catostomus clarkii* - desert sucker (DSu, A); *Catostomus discobolus* - bluehead sucker (BSu, B); *Catostomus insignis* - Sonora sucker (SSu, C); *Catostomus latipinnis* - flannelmouth sucker (FSu, D); *Catostomus platyrhynchus* - mountain sucker (MSu, E); *Xyrauchen texanus* - razorback sucker (RSu, F); *Cottus bairdii* - mottled sculpin (MSc, G); *Cottus beldingii* - Paiute sculpin (PSc, H); *Gila cypha* - humpback chub (HCh, I); *Gila elegans* – bonytail (B, J); *Gila intermedia* - Gila chub (GCh, K); *Gila nigra* - headwater chub (WCh, L); *Gila robusta* - roundtail chub (RCh, M); *Lepidomeda mollispinis* - Virgin River spinedace (VSp, N); *Lepidomeda vittata* - Little Colorado River spinedace (CSp, O); *Meda fulgida* – spikedace (S, P); *Moapa coriacea* - Moapa dace (MDa, Q); *Plagopterus argentissimus* – woundfin (W, R); *Ptychocheilus lucius* - Colorado pikeminnow (CPi, S); *Agosia chrysogaster* - longfin dace (LDa, T); *Rhinichthys osculus* - speckled dace (SDa, U); *Rhinichthys cobitis* - loach minnow (LMi, V); *Cyprinodon macularius* - desert pupfish (DPu, W); *Poeciliopsis occidentalis* - Gila topminnow (GTo, X); *Oncorhynchus gilae apache* - Apache trout (ATr, Y); *Oncorhynchus clarkii* - cutthroat trout (CTr, Z); *Oncorhynchus gilae* - Gila trout (GTr, AA); *Prosopium williamsoni* - mountain whitefish (MWh, BB). **Non-native species:** *Catostomus ardens* - Utah sucker (1); *Catostomus catostomus* - longnose sucker (2); *Catostomus commersonii* - white sucker (3); *Catostomus plebeius* - Rio Grande sucker (4); *Ictiobus bubalus* - smallmouth buffalo (5); *Ictiobus cyprinellus* - bigmouth buffalo (6); *Ictiobus niger* - black buffalo (7); *Ambloplites rupestris* - rock bass (8); *Lepomis gulosus* – warmouth (9); *Lepomis cyanellus* - green sunfish (10); *Lepomis gibbosus* – pumpkinseed (11); *Lepomis macrochirus* – bluegill (12); *Lepomis microlophus* - redear sunfish (13); *Micropterus dolomieui* - smallmouth bass (14); *Micropterus punctulatus* - spotted bass (15); *Micropterus salmoides* - largemouth bass (16); *Pomoxis annularis* - white crappie (17); *Pomoxis nigromaculatus* - black crappie (18); *Herichthys cyanoguttatus* - Rio Grande cichlid (19); *Archocentrus nigrofasciatus* - convict cichlid (20); *Oreochromis aureus* - blue tilapia (21); *Oreochromis mossambica* - Mozambique tilapia (22); *Tilapia zilli* - redbelly tilapia (23); *Dorosoma cepedianum* - gizzard shad (24); *Dorosoma petenense* - threadfin shad (25); *Carassius auratus* – goldfish (26); *Ctenopharyngodon idellus* - grass carp (27); *Cyprinella lutrensis* - red shiner (28); *Cyprinus carpio* - common carp (29); *Gila atraria* - Utah chub (30); *Hybognathus hankinsoni* - brassy minnow (31); *Notemigonus crysoleucus* - golden shiner (32); *Notropis stromineus* - sand shiner (33); *Pimephales promelas* - fathead minnow (34); *Rhinichthys cataractae* - longnose dace (35); *Richardsonius balteatus* - redside shiner (36); *Semotilus atromaculatus* - creek chub (37); *Esox lucius* - northern pike (38); *Culaea inconstans* - brook stickleback (39); *Fundulus sciadicus* - plains topminnow (40); *Fundulus zebrinus* - plains killifish (41); *Ameiurus melas* - black bullhead (42); *Ameiurus natalis* - yellow bullhead (43); *Ameiurus nebulosus* - brown bullhead (44); *Ictalurus punctatus* - channel catfish (45); *Pylodictis olivaris* - flathead catfish (46); *Morone chrysops* - white bass (47); *Morone mississippiensis* - yellow bass (48); *Morone saxatilis*

- striped bass (49); *Perca flavescens* - yellow perch (50); *Sander vitreus* - walleye (51); *Gambusia affinis* - western mosquitofish (52); *Poecilia latipinna* - sailfin molly (53); *Poecilia mexicana* - shortfin molly (54); *Poecilia reticulate* – guppy (55); *Oncorhynchus mykiss* - rainbow trout (56); *Oncorhynchus mykiss aguabonita* - golden trout (57); *Oncorhynchus nerka* – kokanee (58); *Salmo trutta* - brown trout (59); *Salvelinus fontinalis* - brook trout (60); *Salvelinus namaycush* - lake trout (61); *Thymallus arcticus* - arctic grayling (62).

Appendix 5.2. Distributional changes for native (n=23) and non-native (n=47) fishes of the lower Colorado River Basin estimated using the SONFISHES database (see Methods for details). Values are presented as percentage declines in distribution – positive represents distribution declines and negative represents distribution expansion. Cells containing "-" refer to those species only present in the upper Colorado River Basin. Nomenclature follows Nelson et al. (2004). Note that cutthroat trout (*Oncorhynchus clarkii*) is native to the upper basin but non-native to the lower basin and was not included in the analysis.

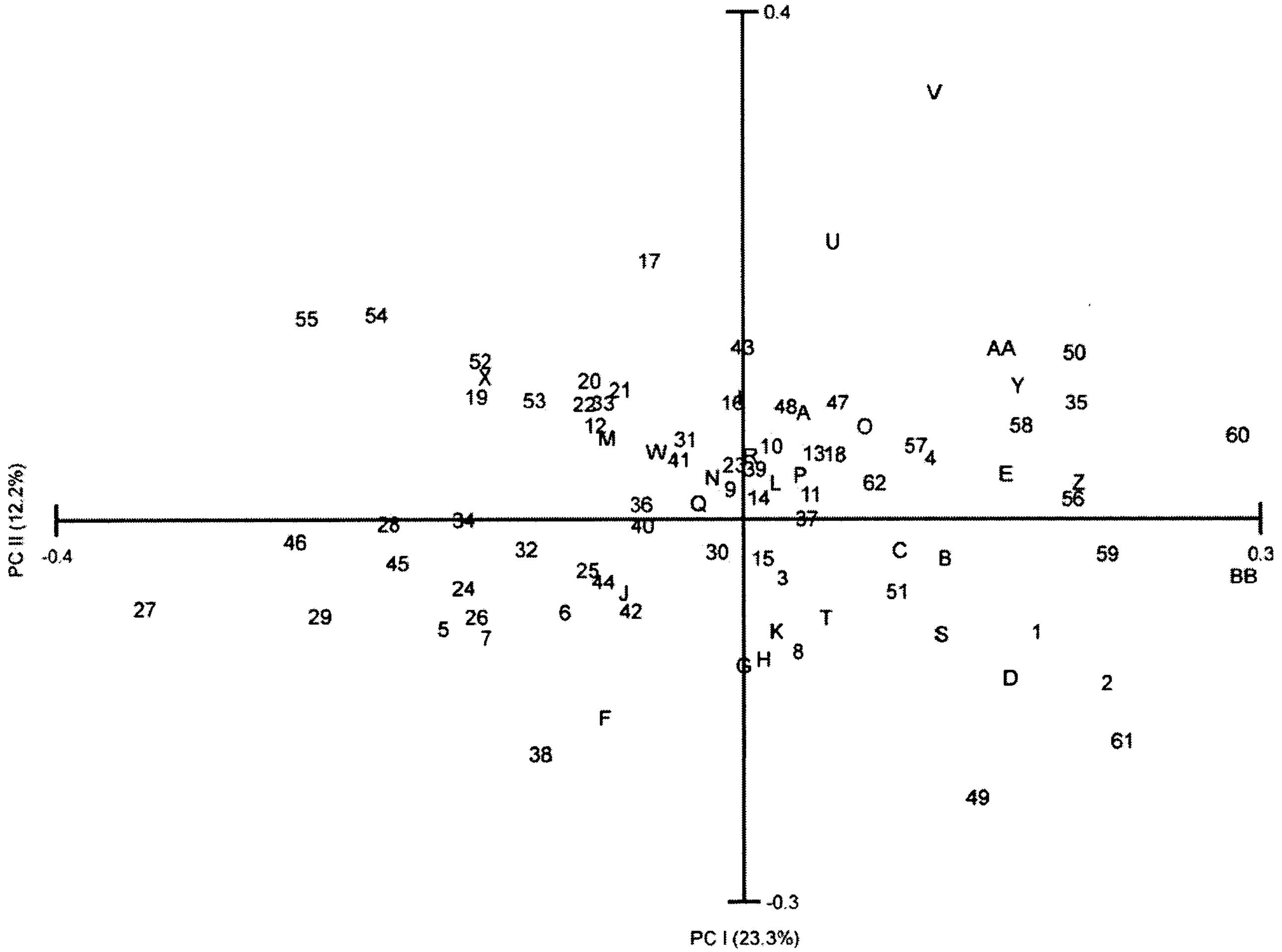
Native Species	Decline (%)
Catostomidae	
Catostomus clarkii - desert sucker	13.5
Catostomus discobolus - bluehead sucker	3.5
Catostomus insignis - Sonora sucker	-8.2
Catostomus latipinnis - flannelmouth sucker	62.2
Catostomus platyrhynchus - mountain sucker	-
Xyrauchen texanus - razorback sucker	49.7
Cottidae	
Cottus bairdii - mottled sculpin	-
Cottus beldingii - Paiute sculpin	-
Cyprinidae	
Gila cypha - humpback chub	-6.1
Gila elegans - bonytail	87.7
Gila intermedia - Gila chub	15.9
Gila nigra - headwater chub	-12.6
Gila robusta - roundtail chub	6.2
Lepidomeda mollispinis - Virgin R. spinedace	55.1
Lepidomeda vittata - Little Colorado R. spinedace	-14.1
Meda fulgida - spikedace	45.9
Moapa coriacea - Moapa dace	100.0
Plagopterus argentissimus - woundfin	78.9
Ptychocheilus lucius - Colorado pikeminnow	100.0
Agosia chrysogaster - longfin dace	-11.4
Rhinichthys osculus - speckled dace	16.5

Non-Native Species	Spread (km·year^{-1})
Catostomidae	
Catostomus ardens - Utah sucker	-
Catostomus catostomus - longnose sucker	-
Catostomus commersonii - white sucker	-
Catostomus plebeius - Rio Grande sucker	0.3
Ictiobus bubalus - smallmouth buffalo	0.1
Ictiobus cyprinellus - bigmouth buffalo	0.2
Ictiobus niger - black buffalo	0.0
Centrarchidae	
Ambloplites rupestris - rock bass	1.8
Lepomis gulosus - warmouth	0.0
Lepomis cyanellus - green sunfish	62.9
Lepomis gibbosus - pumpkinseed	-
Lepomis macrochirus - bluegill	23.4
Lepomis microlophus - redear sunfish	3.6
Micropterus dolomieui - smallmouth bass	18.0
Micropterus punctulatus - spotted bass	0.0
Micropterus salmoides - largemouth bass	34.2
Pomoxis annularis - white crappie	0.8
Pomoxis nigromaculatus- black crappie	8.3
Cichlidae	
Herichthys cyanoguttatus - Rio Grande cichlid	5.5
Archocentrus nigrofasciatus - convict cichlid	0.0
Oreochromis aureus - blue tilapia	20.7

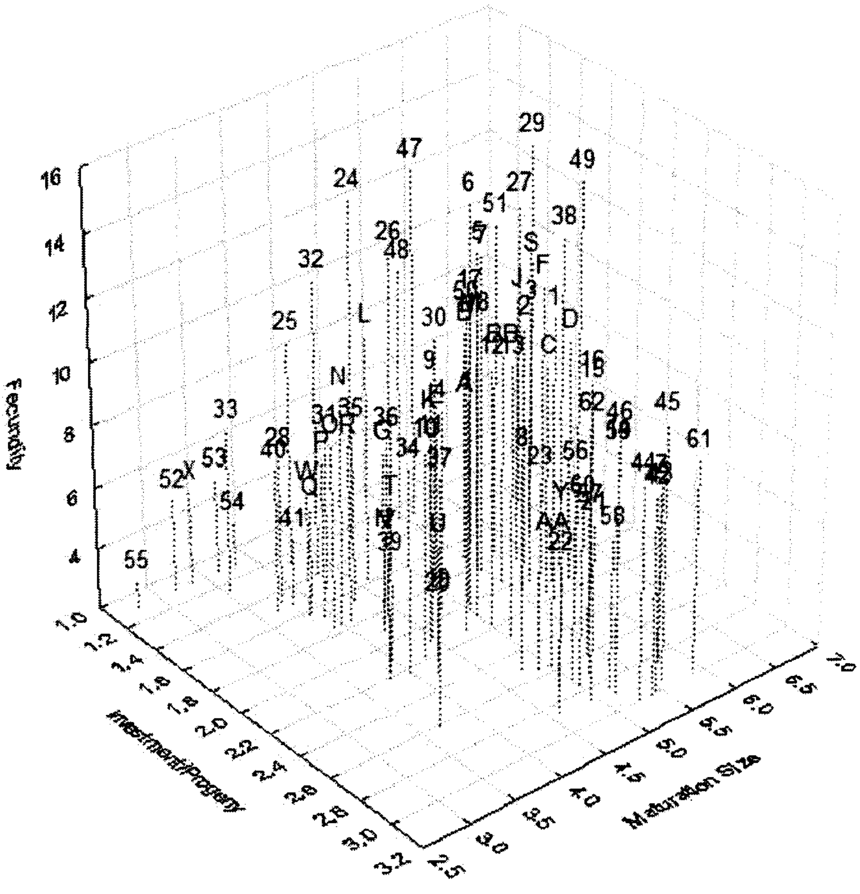
Rhinichthys cobitis - loach minnow	17.9
Cyprinodontidae	
Cyprinodon macularius - desert pupfish	100.0
Poeciliidae	
Poeciliopsis occidentalis - Gila topminnow	36.8
Salmonidae	
Oncorhynchus gilae apache - Apache trout	26.9
Oncorhynchus clarkii - cutthroat trout	-
Oncorhynchus gilae - Gila trout	84.0
Prosopium williamsoni - mountain whitefish	-
Oreochromis mossambica - Mozambique tilapia	3.2
Tilapia zilli - redbelly tilapia	3.1
Clupeidae	
Dorosoma cepedianum - gizzard shad	-
Dorosoma petenense - threadfin shad	15.8
Cyprinidae	
Carassius auratus - goldfish	10.6
Ctenopharyngodon idellus - grass carp	0.0
Cyprinella lutrensis - red shiner	54.6
Cyprinus carpio – common carp	19.9
Gila atraria - Utah chub	-
Hybognathus hankinsoni - brassy minnow	-
Notemigonus crysoleucus - golden shiner	12.7
Notropis stromineus - sand shiner	-
Pimephales promelas - fathead minnow	74.1
Rhinichthys cataractae -longnose dace	-
Richardsonius balteatus - redside shiner	3.8
Semotilus atromaculatus - creek chub	-
Esocidae	
Esox lucius - northern pike	4.0
Fundulidae	
Fundulus sciadicus - plains topminnow	-
Fundulus zebrinus - plains killifish	9.0
Gasterosteidae	
Culaea inconstans - brook stickleback	-
Ictaluridae	
Ameiurus melas - black bullhead	8.1
Ameiurus natalis - yellow bullhead	20.4
Ameiurus nebulosus - brown bullhead	0.0
Ictalurus punctatus - channel catfish	22.0
Pylodictis olivaris - flathead catfish	23.7

	Moronidae	
	Morone chrysops - white bass	*0.2*
	Morone mississippiensis – yellow bass	1.5
	Morone saxatilis - striped bass	11.9
	Percidae	
	Perca flavescens - yellow perch	*0.0*
	Sander vitreus - walleye	5.7
	Poeciliidae	
	Gambusia affinis - western mosquitofish	*37.9*
	Poecilia latipinna - sailfin molly	7.9
	Poecilia mexicana - shortfin molly	0.4
	Poecilia reticulate - guppy	1.6
	Salmonidae	
	Oncorhynchus mykiss - rainbow trout	18.0
	Oncorhynchus mykiss aguabonita. - golden trout	-
	Oncorhynchus nerka - kokanee	-
	Salmo trutta - brown trout	11.0
	Salvelinus fontinalis - brook trout	7.4
	Salvelinus namaycush - lake trout	-
	Thymallus arcticus - arctic grayling	5.3

Appendix 5.3. Ordination resulting from the principal coordinate analysis on the 22 biological traits of the 90 fish species comprising the native and non-native fish species pools of the Colorado River Basin. Letter and number codes refer to native and non-native species, respectively, and are presented in Appendix 5.1.



Appendix 5.4. Three-dimensional plot of $\log_e$ maturation length, $\log_e$ mean fecundity, and relative investment per progeny (a surrogate of juvenile survivorship that was equal to $\log_e$ ((egg diameter + 1)(parental care +1)) for the fishes of the Colorado River Basin according to the trilateral continuum model of fish life-histories presented by Winemiller and Rose (1992). Native species are solid symbols and non-native species are empty symbols. Letter and number codes refer to native and non-native species, respectively, and are presented in Appendix 5.1.



Chapter

6

Living on the Edge: Species Trait Synergisms and the Predisposition of Endemic Fishes to Rarity, Extirpation and Extinction

Abstract

The causes and consequences of species extinctions remain a central question in conservation biology and predictive suites of ecological and life-history traits have proven to provide reasonable estimates of species extinction risk across a diverse array of taxonomic groups. The literature is replete with studies linking individual traits to perceived risk of global extinction, yet the manner in which trait synergisms (i.e., non-additive interactions among traits) may differentially contribute to species rarity, local probability of extirpation and risk of global extinction has never, to our knowledge, been examined. The present study conducts this analysis for the native freshwater fishes of the Colorado River Basin, a gravely endangered, highly endemic fish fauna in the United States, by relating a comprehensive suite of morphological, behavioural, physiological and life history traits to empirical-based estimates of species rarity and probability of extirpation, and expert-based estimates of perceived extinction risk to habitat degradation and interactions with non-native fishes. Our results point strongly to the importance of trait synergisms in rendering fish species more or less vulnerable to different levels of perceived extinction risk from different sources of threat, and they provide the first empirical evidence supporting the commonly-held assumption that the attributes of species that contribute to their rarity will further predispose them to local extirpation and global extinction. Moreover, our results highlight the subtle manner by which traits may differentially influence species' risk of extirpation versus extinction, in that particular trait combinations were related to increased probability of local extirpation, but decreased risk of global extinction of native fishes. Thus, the intrinsic traits of species can enhance

predictive conservation biology, although such advances are only likely to be achieved from studying trait synergisms and partitioning the extinction process according to species' rarity, local probability of extirpation, and perceived level of global extinction from different ecological threats.

Introduction

Faced with the current biodiversity crisis, recent efforts at national, regional, and local levels across many countries have emphasized the urgent need for more rigourous and comprehensive risk-analysis frameworks for preventing the future loss of native species (Caughley 1994, Vane-Wright et al. 1991, Sala et al. 2000). Progress in this regard has come, in part, from a wealth of empirical evidence from a diverse set of taxa suggesting that a number of intrinsic biological traits can render species more vulnerable to extinction (Cole 1954, Elton 1958, Terborgh 1974, see reviews by Lande 1988, Pimm et al. 1988, McKinney 1997, Purvis et al. 2000). The identification of such 'extinction-prone traits' contributes significantly to the development of proactive, management strategies aimed at safeguarding native species with the greatest risk of extinction and provides critical guidance to managers and policymakers in their allocation of scarce conservation dollars (Angermeier 1995, Lockwood et al. 2002).

Advances in the evolving science of predicting species extinctions on the basis of their biological traits will likely come from an explicit consideration of how traits synergistically combine to predispose species to rarity, to place them at differential risk to local extirpation and global extinction, and to render them vulnerable to extinction through different ecological mechanisms. Unfortunately, we have seen only limited progress in these areas of research. First, previous studies have principally focused on establishing relationships in a trait-by-trait manner, and thus have failed to fully appreciate the multiplicity by which species traits may synergistically combine to place species at greater risk to extinction, a phenomenon supported by theory (Lawton 1994, McKinney 1997) and only recently quantified (Davies et al. 2004). Second, for the most part this research has concentrated on establishing trait linkages with perceived risk to global extinction. Therefore it has yet to consider the specific pathways that traits may operate to predispose species to this end, such as through effects on rarity and local extirpation (Duncan and Young 2000) and vulnerability to the different ecological mechanisms that underlie the extinction process (Owens and Bennett 2000). In so far as species traits have recently been shown to exhibit different associations with the different stages of the invasion sequence (Kolar and Lodge 2001), the ambiguity surrounding the manner in which traits may differentially contribute to the extinction process – from species rarity to local extirpation to global extinction – needs to be clarified.

The present study addresses the aforementioned gaps in our knowledge by providing the first examination of how biological traits act synergistically to predispose species to rarity, local probability of extirpation and global risk of extinction associated with different ecological threats. We conduct this analysis for the native freshwater fishes of the Colorado River Basin, a gravely endangered, highly endemic fish fauna in the United States (Minckley and Deacon 1968, 1991), by relating a comprehensive suite of morphological, behavioural, physiological and life history traits to empirical-based estimates of species rarity and probability of extirpation, and expert-based estimates of perceived extinction risk to habitat degradation and interactions with non-native fishes. Importantly, our study makes two novel contributions to both the theory and application of trait-based approaches in conservation biology. First, we explore how trait synergisms can render fish species more, or less, vulnerable to rarity, local extirpation and global extinction, compared to expectations according to individual traits. These findings speak to the importance of considering multiple attributes when making predictions of species' vulnerability on the basis of intrinsic traits. Second, we are first to concurrently assess the degree in which similar suites of biological traits are associated with patterns of species' rarity, probability of local extirpation and perceived extinction risk from different sources of threat for a major taxonomic group. By way of this comparison, we are afforded the unique opportunity to (*i*) test the widely held, yet rarely addressed, assumption that the attributes of species that contribute to their rarity will further predispose them to greater risk of extinction (Pimm et al. 1988, Gaston 1994, Johnson 1998), (*ii*) question conventional wisdom asserting that those traits associated with local extirpation (i.e., population vulnerability) will similarly render species to global extinction (i.e., species vulnerability) (McKinney 1997), and (*iii*) provide the first examination that simultaneously discriminates among species varying both in their level of extinction risk and the specific source of their threat on the basis of biological traits. This latter analysis enables us to test current ecological theory (Brown 1971, Diamond 1984, Pimm et al. 1988), which predicts that sources of extinction risk disrupting the balance between fecundity and longevity (e.g. species invasions) should be detrimental for species with "slow" life histories, whereas sources of extinction risk that reduce niche availability (e.g. habitat loss) should be most dangerous to species that are ecologically specialized.

Methods

Native fishes of the Colorado River Basin. The Colorado River originates on the western slope of the Rocky Mountains and flows southwest towards the Gulf of California and the Pacific Ocean through ca. 632,000 km^2 of land encompassing seven states of the United States and regions of north-western Mexico (Fig. 6.1). Using state-wide species accounts we compiled a present-day list of the freshwater native fish species pool of the Colorado River Basin from which adequate trait data could be assembled (28 species in total: see Appendix 6.1).

Biological traits. We collating data for 22 ecological and life-history attributes (collectively referred to as biological traits) that are believed to be associated with imperilled native fishes in the Colorado River Basin (and more generally the American Southwest) and that could be justified on the basis of our current state of knowledge and information available for the entire pool of species. These traits included the following. *Body morphology*: (1) maximum total body length (cm); (2) shape factor – ratio of total body length to maximum body depth; (3) swim factor – ratio of minimum depth of the caudal peduncle to the maximum depth of the caudal fin, where small factors are indicative of strong swimmers (calculated following Webb 1984). *Behaviour*: (4) water temperature preference – cold (10-17°C), cool (18-26°C) or warm water (>26°C) based on species distributions and perceived physiological optima; (5) substrate preference – rubble (including cobble and gravel), sand, silt/mud or general; (6) fluvial dependence – reliance on flowing waters for completing life cycle, e.g., flow required for feeding or reproduction (classified as yes or no); (7) current velocity preference – slow, slow-moderate, moderate, moderate-fast or fast current velocity; (8) vertical position – benthic or non-benthic based on species morphology and behaviour. *Physiology*: (9) critical thermal tolerance – low (< 30°C), moderate (30-35°C), high (35-40°C) or very high (>40°C) critical water temperature for survival. *Life history*: (10) longevity – maximum potential life span (years); (11) age at maturation (years); (12) length at maturation (cm); (13) Fecundity – total number of eggs or offspring per breeding season (#) represented on a logarithmic (base 10) scale; (14) Egg size – mean diameter of mature (fully yolked) ovarian oocytes (mm); (15) Spawning temperature – temperature at which spawning is initiated (°C); (16) Parental care - metric representing the total energetic contribution of parents to their offspring (calculated following Winemiller 1989); (17) Reproductive guild - nonguarders (open substratum spawners, brood hiders), guarders (substratum choosers, nest spawners) or bearers (external) (calculated following Balon 1975); (18) Spawning substrate – mineral substrate, vegetation or pelagic; (19) Time to hatch – mean time to egg hatch within the range of average post-spawning water temperatures (days); (20) Larvae length at hatching – mean total length of larvae at hatching (mm); (21) Trophic guild – adult feeding mode classified as herbivore-detritivore (ca. > 25% plant matter), omnivore (ca. < 5% plant matter), invertivore or invertivore-piscivore; (22) Diet breadth – total number of major diet items consumed at any time during lifetime (#), including inorganic material, vegetative material, plankton, aquatic/terrestrial insects, oligochaetes/crustaceans/molluscs, fish/fish eggs and amphibians/mammals/birds.

Trait assignments were based on a multi-tiered data collection procedure. First, trait data were collected from species accounts in the comprehensive texts of state fish faunas of the region (Everhart and Seaman 1971, Minckley 1973, La Rivers 1994, Sublette et al.

1990, Baxter and Stone 1995, Sigler and Sigler 1996, Moyle 2002). Second, species descriptions from the primary literature, state agency reports, university reports and graduate theses were used. Third, we obtained data from electronic databases available on the World Wide Web, including FishBase (Froese and Pauly 2003), Arizona's Heritage Data Management System (AZHDMS) and Biota Information System Of New Mexico (BISON). Fourth, expert knowledge was used to assign values to a small number of trait states (< 5%) that could not be obtained from the previous investigations (mainly inferred from closely related congenerics).

Species rarity, probability of extirpation, extinction risk and sources of threat. Given the high fish endemism of the Colorado River Basin, we are able to estimate native species' risk to both local extirpation and global extinction. We categorized species into their perceived level of global extirpation risk and ecological mechanism of threat by conducting a survey of 20 expert fish biologists (see Acknowledgements) who have extensive knowledge with the ichthyofauna of the Colorado River Basin. Respondents were asked to classify species according to their present-day perceived relative risk of extinction using 4 categories (none, low, moderate or high) and the primary source of threat believed to be associated with their imperilment using 6 categories (altered flow regimes, altered temperature regimes, altered physical habitat conditions, predation by non-native fishes, competition with non-native fishes or other interactions with non-native fishes, e.g., hybridization). Although we allowed respondents to identify multiple sources we specified that only primary threats should be listed. Survey results were tabulated and a majority rule was used to classify native species into 5 categories based on combinations of their level of extinction risk and primary source of threat: (1) none/low risk, (2) moderate risk- habitat degradation, (3) moderate risk-species invasions, (4) high risk- habitat degradation, (5) high risk-species invasions (see Appendix 6.1). In the rare instances when ambiguous survey results arose we used our expert judgement to conservatively assign species to categories. Notably, our survey focused on coarse-level classifications of extinction risk and threat in order to facilitate generalizations for the species and maximize respondent participation (see Kolar and Lodge 2002 for a similar survey approach). Although native fishes are threatened by both habitat degradation and non-native species to varying degrees, we classified species into a single category according to their primary source of threat.

We obtained empirical estimates of species rarity and local probability of extirpation for 22 out of the 28 native species from Fagan et al. (2002). Their study used the SONFISHES database - an extensive dataset containing > 38,000 point observations of fish occurrences in the lower Colorado River Basin collected over a 160 year period (1840-1999) throughout the Sonoran Desert ecoregion (http://www.desertfishes.org/na/gis/index.html). The authors calculated modern "scale-area" curves to obtain a scale-independent quantitative measure of spatial rarity following the methodology of Kunin (1998) and calculated extirpation probabilities at the 5-km scale based on proportional patterns of historic (1840-1980) versus modern occurrences (1981-1999).

Statistical Analyses. We used classification and regression trees (CART: Breiman et al. 1984) to model associations between the suite of biological traits and 3 responses: (1)

perceived extinction risk/source of threat (28 species classified into 5 categories) in the Colorado River Basin, (2) empirical estimate of species rarity (22 species assigned a value between 0 – abundant and 1 – rare), and (3) empirical estimate of local probability of extirpation (22 species assigned a value between 0 – zero probability and 1 – high probability) in the lower Colorado River Basin. Although CART has only recently been more widely recognized in ecology (De'ath and Fabricius 2000), this analytical technique has great promise in such studies because it provides a number of distinct advantages compared to other statistical approaches, including its ability to model non-linear, interactive relationships among mixed variable types and handle missing data (Olden and Jackson 2002). This is a particularly important advantage for trait studies that are aimed at examining the influence of synergistic combinations of both categorical and continuous attributes.

Briefly, CART is a nonparametric statistical approach that uses a recursive partitioning algorithm to repeatedly partition the data set according to the explanatory variables (biological traits) into a nested series of mutually exclusive groups each of them as homogeneous as possible with respect to the response variable (here rarity, extirpation, extinction). We used the Gini impurity criterion to determine the optimal variable splits (i.e., the primary splits that are represented in the final tree), and terminated splitting when nodes contained less than 5 observations. Optimal decision tree size was determined by constructing a series of cross-validated trees and selecting the smallest tree such that its estimated error rate is within one standard error of the minimum size (i.e., 1-SE rule: see De'ath and Fabricius 2000). By formalizing these relationships using decision trees, we generated a dichotomous key for classifying species rarity, probability of extirpation, and extinction risk and source of threat, according to unique combinations of interacting biological traits. Based on the branching architecture we interpret the primary splits that represent the defining trait conditions that were the most important in the classification process, as well as the best competitive surrogate splits (SS) that also showed high classification power and closely mimic the action of a primary split. Inspection of traits forming surrogate splits can lead to a more complete understanding of relationships within the data by facilitating the exploration of how the attributes representing primary splits may simply be surrogates for other biological attributes that are similarly correlated with species' rarity, extirpation, extinction. Because CART inherently models interactions among independent variables, the presence of multiple traits nested in a tree indicates the existence of trait synergisms. Analyses were conducted using CART 5.0 software (Salford Systems Inc.). N-fold cross validation was employed to provide an unbiased estimate of decision tree performance and Cohen's κ coefficient of agreement was used to assess the classification performance of the decision trees compared to random expectations (Fielding and Bell 1997).

Controlling for phylogenetic inertia. It is expected that species share similar life-history traits through descent from common ancestry (Brooks and McLennan 1991), and therefore it is inappropriate to treat species as equivalent units with independent functional traits in statistical analyses. Accordingly, we explored the significance of correlations between phylogenetic and trait similarities among the native fishes of the Colorado River Basin and controlled for phylogenetic inertia in the classification and regression trees.

We constructed a phylogeny of the native freshwater fishes of the Colorado River Basin by modifying the phylogenetic tree presented by Fagan et al. (2002) based on the research of Smith et al. (2002) (see Appendix 6.2). Following Webb (2000) we assembled a phylogenetic distance matrix by tabulating the total number of nodes that separate species in the reference phylogeny according to the branching topology. We performed a Mantel test to assess the degree of correlation between phylogenetic distances and trait distances based on Gower's similarity coefficient (Legendre and Legendre 1998). As expected, trait distances were highly correlated with phylogenetic distances among species (Mantel's standardized $r = 0.86$, $P < 0.001$), indicating that species with similar phylogenetic histories also share similar suites of traits.

Current approaches for controlling the effects of phylogenetic inertia are based on the method of independent contrasts, which partitions the total variation of a quantitative trait in different species into distinct phylogenetic and specific (i.e., residual) components (Felsenstein 1985). However, none of the methods available for calculating independent contrasts (e.g., Purvis and Rambaut 1995) or other eigenvector approaches (e.g., Diniz-Filho et al. 1998, Giannini 2003) can accommodate combinations of nominal, ordinal and continuous trait data that are used in the present study. Therefore, we followed Grafen (1989) and accounted for phylogeny by including a ranked phylogenetic relatedness index in the CART analyses. We calculated phylogenetic relatedness of the species pool by ranking fish families by the degree of derived characters, from most ancient to the most derived using information from Nelson (1994) and Lee et al. (1980). We refer the reader to Kolar and Lodge (2002) for a biological example using this approach. To test the explanatory power of the ranked phylogenetic relatedness index in CART we assessed the relationship between two phylogenetic distance matrices: one constructed using the phylogeny described previously and one constructed using the ranked relatedness index. Results showed a strong, significant correlation between these distance matrices (Mantel's standardized $r = 0.63$, $P < 0.001$) supporting the appropriateness of the phylogenetic relatedness index used in the analyses.

Results

Species rarity, probability of local extirpation and risk to global extinction from species invasions and habitat degradation were found be predictable according to unique, synergistic combinations of biological traits that include habitat position, reproductive strategy, diet specialization and swimming performance (as indicated by body morphology). CART represented a powerful methodology for elucidating such complex patterns by revealing the multiplicity in which biological traits may operate in an interpretable, hierarchical model.

Perceived level and source of extinction risk was correctly classified for 21 out of the 28 native species as a function of multiple biological traits (75% correct classification, $\kappa = 0.773$, $P < 0.0001$, Fig. 6.2). More specifically, the level of extinction risk was correctly classified with 75% accuracy (none/low = 80%, moderate = 80%, high =69%) and source of extinction threat was correctly classified with 72% accuracy (invasive species = 64%, environmental alteration = 100%). The most common pattern of misclassification was that species with high risk of extinction from species invasions were incorrectly categorized as either under moderate extinction risk by the same mechanism or under high risk from environmental alteration. The branching sequence of the classification tree suggested a three-tiered hierarchy to classifying species level and source of extinction risk. Species under none/low risk of extinction were identified at the root of the tree on the basis of their habitat position. Next, species threatened by different sources of extinction were discriminated in the middle branches according to their reproductive strategies. Lastly, species under moderate versus high risk of extinction from a particular source were recognized in the terminal leafs based on their degree of diet specialization.

The overall architecture of the classification tree illustrated that whether species are expected to exhibit moderate or high extinction risk from either invasive species or environmental alteration depended not on a single trait state but on combinations of multiple traits. Species under high risk of extinction from biological invasions were identified as occupying a benthic habitat position (i.e., living on or near the streambed) and exhibiting either relatively low fecundity or exhibiting higher fecundity with delayed maturity (i.e., greater sizes and age) along with a specialized diet on aquatic or terrestrial invertebrates. This contrasts those species under moderate risk from the same mechanism, which were similarly characterized as highly fecund, late-maturing species, but which exhibited more flexible diet requirements and were relatively short-lived. Species under high risk of extinction from environmental alteration were identified as generally benthic in their habitat position, reaching maturity at smaller sizes (and ages), exhibited higher fecundity, and displaying relatively specialized diets.

Modern-day species rarity of native fishes in the lower Colorado River Basin was predictable on the basis of unique trait combinations ($r = 0.76$, $P < 0.01$, Fig. 6.3). The branching sequence of the regression tree showed that very long-lived species were more likely to be rare (i.e., those species with a rarity index greater than the mean value of 0.68) compared to species with less than a 25-year life span. Moreover, rare species were also characterized as exhibiting exceptionally low fecundity or alternatively as occupying the water column (i.e., non-benthic) and displaying poor swimming ability (i.e., high swim factor). In contrast, relatively more common species (i.e., those species with a rarity index less than the mean value of 0.68) were more likely to be either benthic in their habitat position or non-benthic and with a stronger swimming ability.

Probability of local extirpation of native fishes in the lower Colorado River Basin was also predictable as a function of multiple biological traits ($r = 0.80$, $P < 0.01$, Fig. 6.4). Species with high extirpation probability (i.e., greater than the mean of 0.54) were identified as being longer-lived and displaying delayed maturity (i.e., maturing at larger size and greater age) with lower fecundity and longer times to egg hatch. In contrast, species with low probability of extirpation (i.e., less than the mean of 0.54) were found to have faster reproductive strategies and either a higher degree of parental care (by either guarding or hiding their brood), or alternatively broad diets (i.e., omnivores) or strong swimming ability.

Discussion

For the highly endemic and threatened fish fauna of the Colorado River Basin we found strong support that biological traits act synergistically to predispose native species to increased rarity, higher probability of local extirpation, and greater risk of global extinction associated with habitat degradation and biological invasions. Attributes associated with "slow" life histories (e.g., long-lived, large body size, delayed maturity, low fecundity), specialized diets and specific habitat requirements are shown to operate in concert to render fish species to even greater perceived extinction risk than expected from their individual contributions. Similarly, the synergistic effects of short longevity and low fecundity submit native fishes to the highest rarity equal only to that seen in longer-lived species. Naturally following from our results was that trait synergisms (or more technically trait antagonisms) also operated to reduce rarity and extinction risk; as was illustrated for short-lived, low fecund species that are less rare if their morphology indicated a strong swimming ability, and species with 'slow' life histories that are buffered from high extinction risk if they exhibit broad diet requirements. In short, our results point strongly to the importance of trait synergisms in rendering species more, or less, vulnerable to rarity and eventual extinction, and highlight the need to explicitly consider the complex, interactive manner in which species traits may influence the extinction process in future studies (Davies et al. 2004).

To our knowledge, the present study is the first to use a trait-based approach to simultaneously discriminate among species varying in their level of extinction risk from different ecological mechanisms. Our analysis produced a number of very intriguing results. We found that species traits were highly prognostic of native fishes under different levels of perceived vulnerability to extinction from habitat degradation and interaction with non-native species (the two primary sources of threat to freshwater ecosystems: Richter et al. 1997), and according to the decision tree operated in a systematic, three-tier manner. First, habitat occupancy distinguished between species under moderate or high risk of extinction from those under minimal risk (i.e., none/low), next, life-history traits differentiated between species threatened by species invasions versus habitat degradation, and lastly, diet specialization separated between those species under moderate versus high risk of extinction within the specific source of threat. Our results also provide the first evidence suggesting that biological attributes may differentially predispose fish species to different ecological mechanisms that underlie contemporary patterns of extinction. In support of theory (Brown 1971, Diamond 1984, Pimm et al. 1988), we found that extinction risk via introduced species is greater for native fishes with 'slow' life histories (i.e., long-lived, slow and old maturing species), whereas extinction risk via habitat loss/alteration is greater for fishes exhibiting more specialized diet requirements. These findings build significantly upon the study of Owens and Bennett (2000) who provided the first examination of trait associations with different sources of extinction threat for avian families, but importantly, whose analysis did not distinguish between multiple levels of extinction risk associated with the threats and was limited to three biological traits that were considered individually. The results from this study strongly suggest that our ability to predict species responses to future threats using intrinsic traits will be greatly enhanced by concurrently considering multiple levels of extinction risk and the specific mechanisms through which their effects are mediated. Such investigations will ensure that apparent trait associations are not confounded by separate levels or sources of extinction risk.

Our study tested the widely held, yet rarely addressed, hypothesis that the attributes of species that contribute to their rarity will further predispose them to local extirpation and global extinction (Pimm et al. 1988, Gaston 1994, Johnson 1998). Alternatively, we might expect that rare species possess attributes not because they contributed to their rarity, but because rarity in the first place favoured the adoption of those attributes (Gaston 1994). Consequently, rather than predisposing species to further rarity and eventual extinction, rare species may exhibit a variety of traits that make them more likely to persist despite the predicament of low population size in a fluctuating environment (e.g., Rabinowitz et al. 1989, but see Duncan and Young 2000). Our results showed strong concordance between those traits identified as being associated with species rarity and those related to probability of local extirpation and perceived risk of global extinction. Highly vulnerable fishes were primarily long-lived, slow-maturing, and exhibited low fecundity, weak swimming abilities and specialized diets. These results suggest that specialized species with slow life-histories may be prone to multiple jeopardies produced by a synergistic combination of fewer individuals associated with increased rarity, and increased probability to local extirpation and global extinction associated with narrow tolerances and long recovery times to environmental change (Lawton and May 1995). Indeed, the unfortunate consequence of exhibiting such traits is reflected in the imperilled status of a number of native species in the Colorado River Basin, including the Colorado pikeminnow, bonytail, razorback sucker and flannelmouth sucker (Minckley and Deacon 1991), who have exhibited significant declines over the past century (Olden and Poff 2004, Chapter 4). Furthermore, the finding that fish species with stronger swimming abilities (and as a corollary likely better dispersers) are relatively less rare and exhibit lower probabilities of extirpation lends support to the hypothesis of Fagan et al. (2002) that differential fish dispersal and riverine fragmentation are the mechanisms driving the observed positive association between rarity and extirpation for the fishes of the lower Colorado River Basin. In summary, our results provide strong evident that those attributes associated with species rarity are, in fact, also related to species' likelihood of extirpation and extinction for fish faunas of the Colorado River Basin. Therefore, the synergistic effects of slow life-history, poor dispersal ability and specialized diet may not only predispose species to greater chance of extirpation and extinction, but also promote increased rarity and its associated demographic effects on species persistence (Lande 1993).

Although widely implied in conservation texts, it is surprising that only tentative evidence exists to support the notion that population risk is positively associated with species risk (McKinney 1997). In fact, species traits provide the opportunity to test for this relationship, yet studies have focused almost exclusively on linking species traits to either perceived risk of local extirpation (e.g., Dulvy and Reynolds 2002, Brashares 2003) or global extinction (e.g., Bennett and Owens 1997, Duncan and Lockwood 2001), and have not examined both these process concurrently with respect to species' traits. Our results showed a high degree of similarity between those species traits associated with local probability of extirpation and perceived risk of global extinction, thus providing empirical evidence for a positive relationship between population vulnerability and species vulnerability. Fish species with greater longevity, slow reproduction strategies, and specialized feeding were found to be more vulnerable to both reach-scale extirpation and basin-scale extinction. Interestingly, our findings also point to subtle differences in the identities of extirpation- and extinction-prone attributes. Fish species with specialized diets consisting of mainly invertebrates are considerably more prone to both extirpation and extinction when compared to species with more generalist diets (i.e., omnivores). However, species occupying the middle of this diet gradient (i.e., herbivore/detritivores, invertivore/piscivores) were found to exhibit greater probabilities of local extirpation, but at the same time are at a lower risk of global extinction. These results provide preliminary evidence that although similar biological traits may predispose species to both processes, particular trait synergisms may, in fact, render species more prone to local extirpation but at the same time buffer them from global extinction. Given that extinction is rarely catastrophic, but occurs incrementally as local populations are loss or extirpated from portions of their geographic range, we argue that the subtle manner in which traits may differentially influence species' risk of extirpation versus extinction requires further investigation.

Conservation biology is faced with many challenges in the coming decades, perhaps the most important of which involves understanding why species vary in their risk of endangerment and predicting those species most susceptible to extinction in the future. The intrinsic traits of species can play a considerable predictive role in addressing these pressing questions, which is likely to come from the study trait synergisms and partitioning the extinction process according to species' rarity, local probability of extirpation and perceived level of global extinction from different ecological threats.

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Figure 6.1. Map of the Colorado River Basin located in the American Southwest.

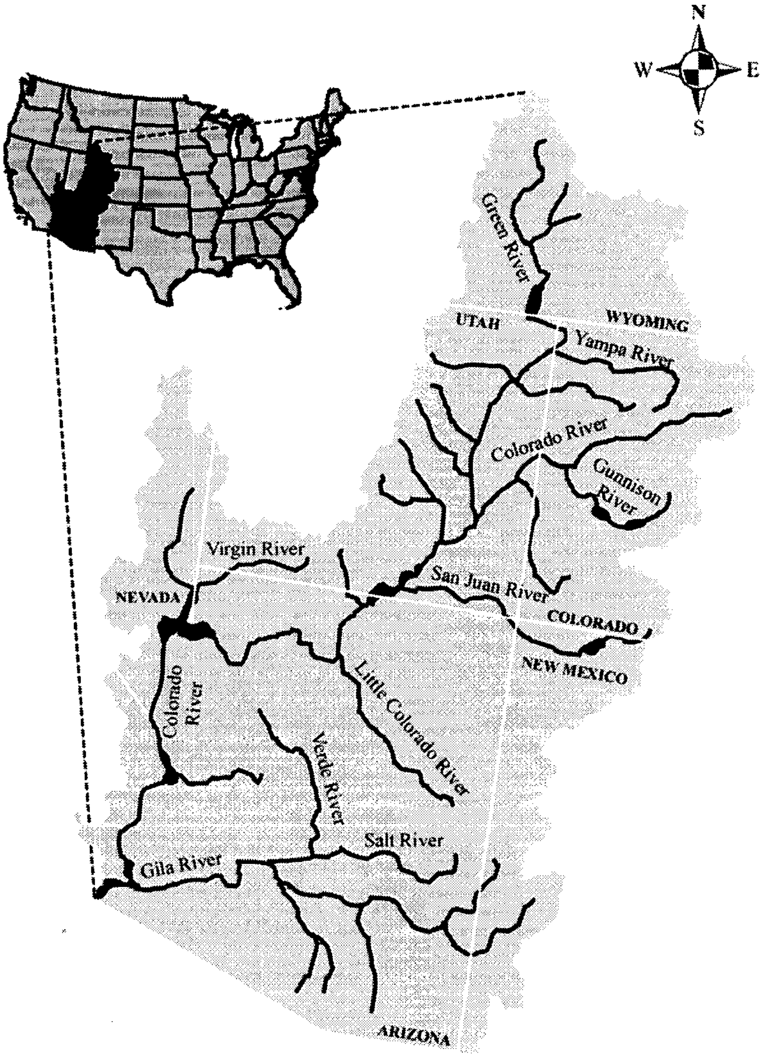


Figure 6.2. Classification tree discriminating among native species of the Colorado River Basin (*n*=28) according to perceived level of extinction risk and primary source of threat. Five categories based on risk/threat combinations are distinguished: none/low risk, moderate risk- habitat degradation, moderate risk-species invasions, high risk- habitat degradation, and high risk-species invasions (see Appendix 6.1 for results).

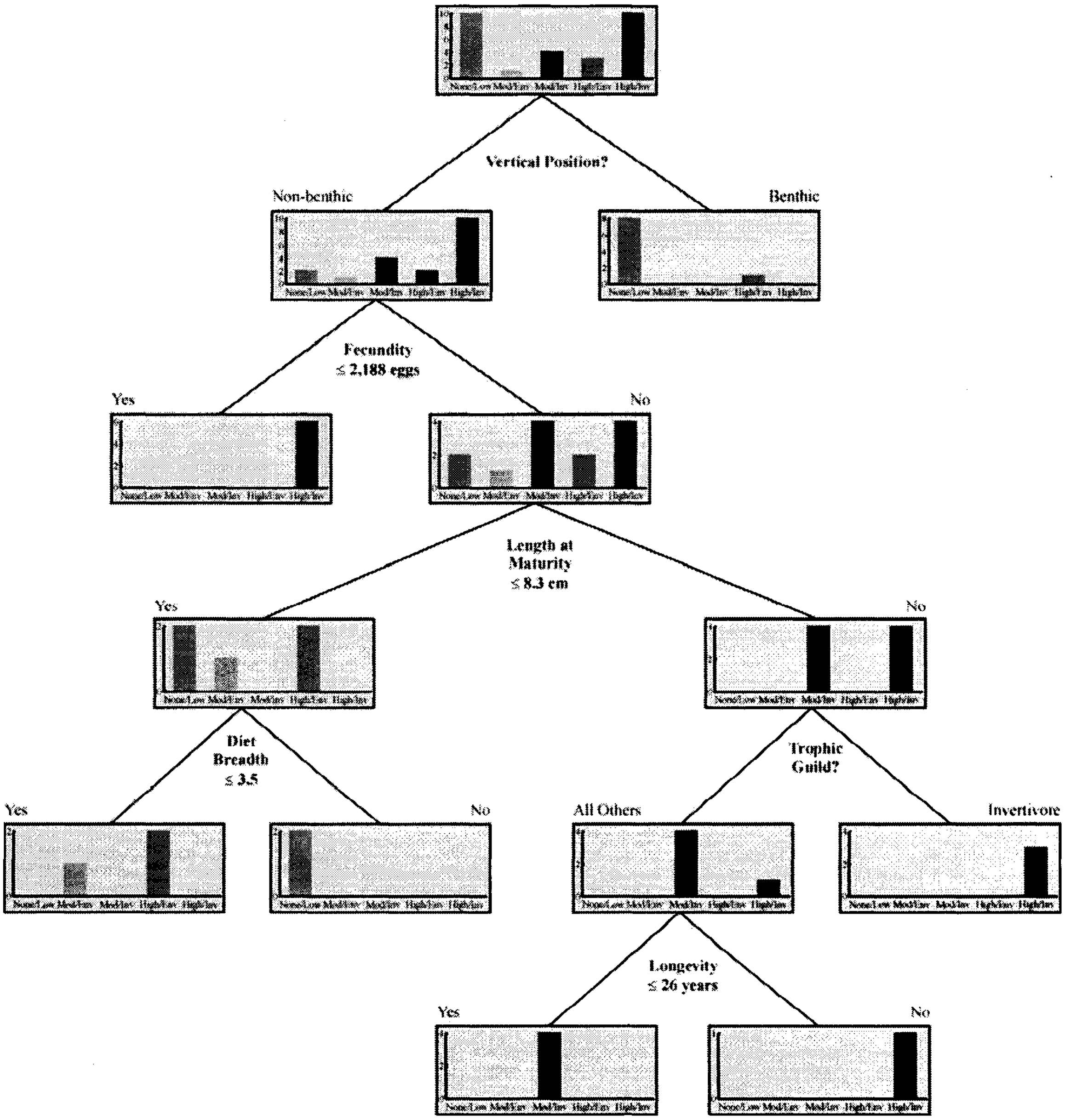


Figure 6.3. Decision tree discriminating among native species of the Lower Colorado River Basin (n=22) according to empirical estimates of species rarity. Rarity values range between 0 (i.e., abundant) and 1 (i.e., rare).

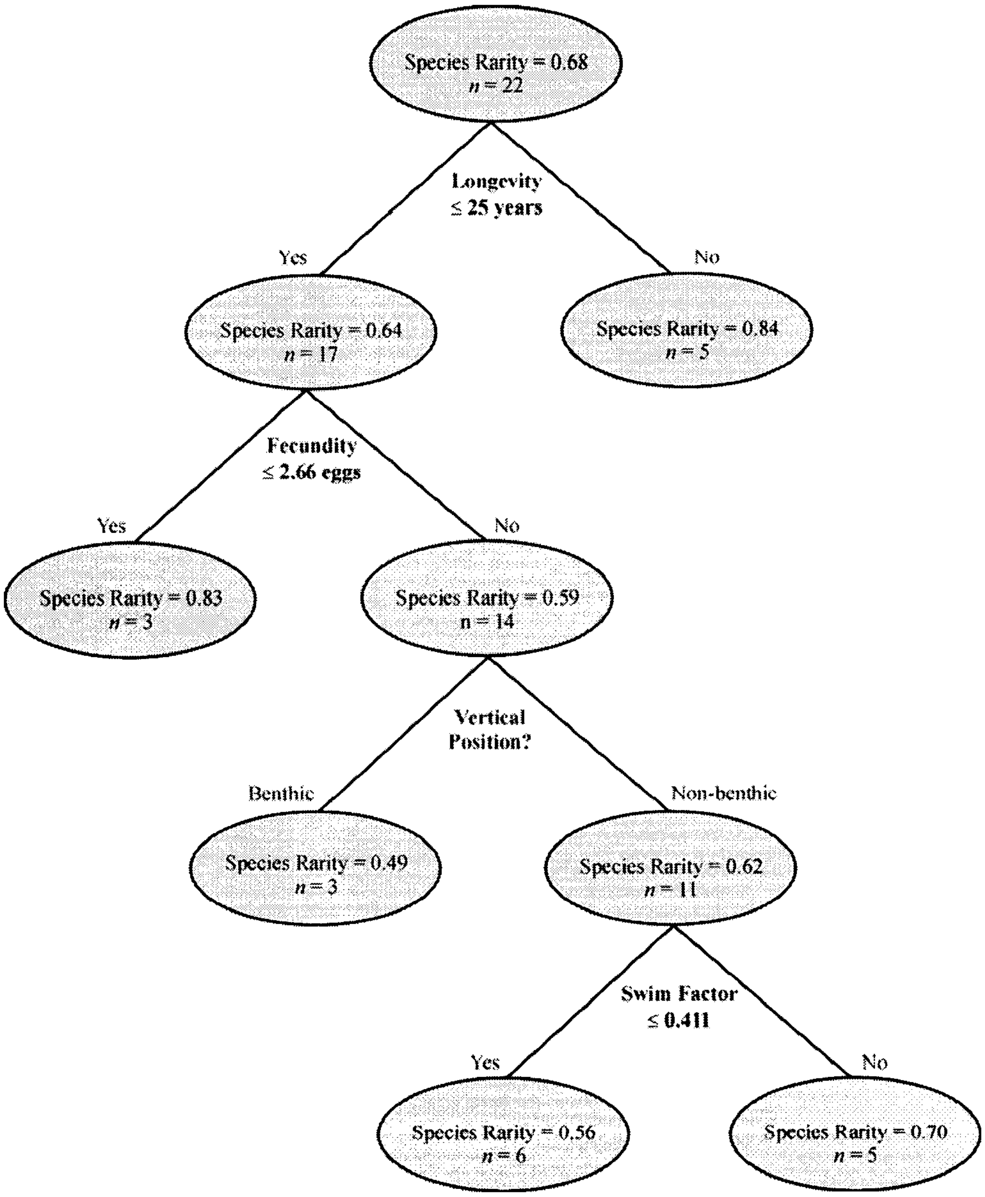
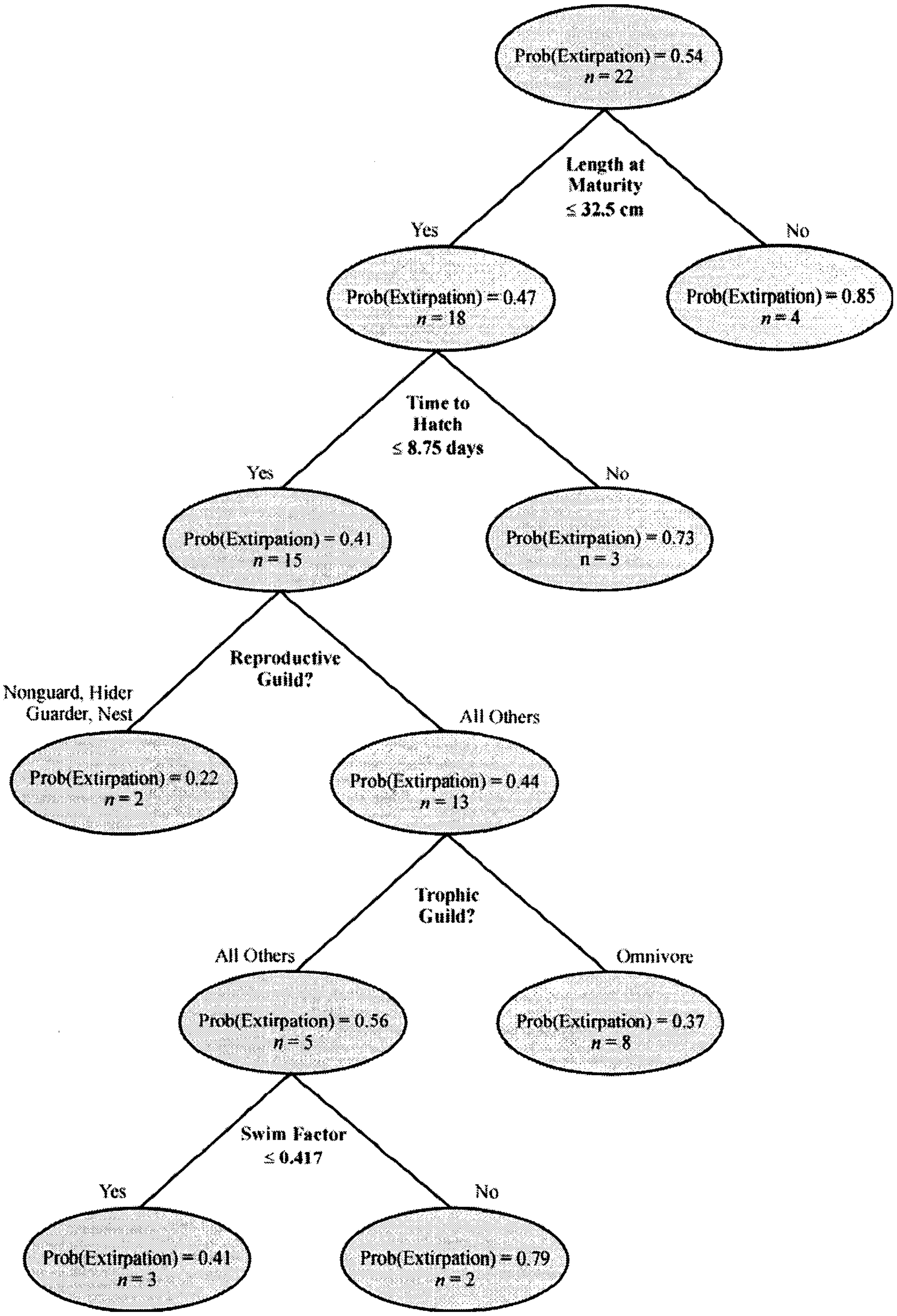


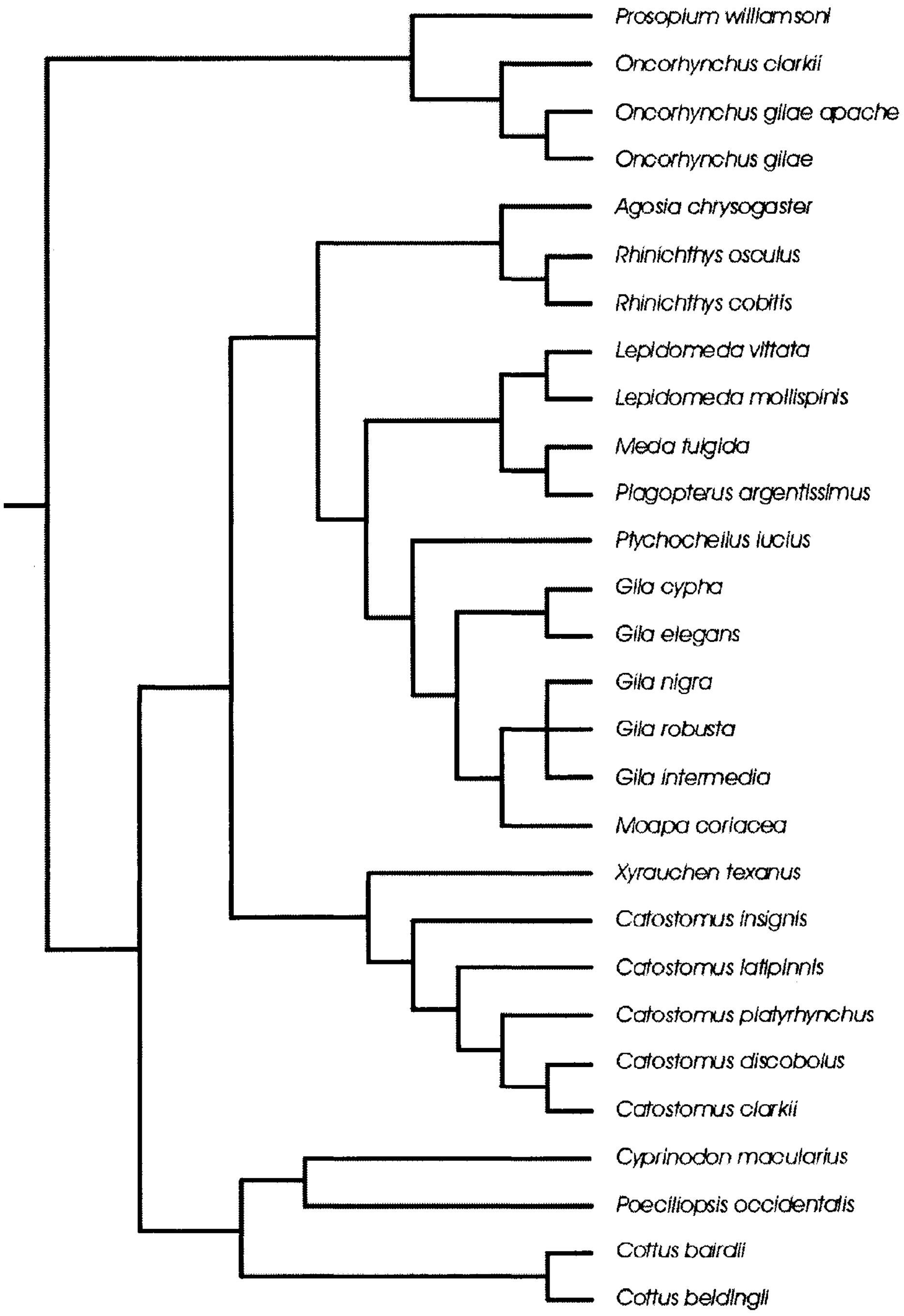
Figure 6.4. Decision tree discriminating among native species of the Lower Colorado River Basin (*n*=22) according to empirical estimates of local extirpation probability.



Appendix 6.1. Freshwater native fish species of the Colorado River Basin examined in our study according to present-day faunas of Arizona (Minckley 1973, Paul Marsh per. comm.), California (Moyle 2002), Colorado (Nesler 2004), Nevada (LaRivers 1994), New Mexico (Sublette et al. 1990), Utah (Sigler and Sigler 1996) and Wyoming (Baxter and Stone 1995). Scientific names follow Nelson et al. (2004). Also included are results from the survey (see Methods). Extinction risk refers to relative level of vulnerability to extinction (None/low, Moderate or High) and primary cause refers to the likely major cause of decline (Environment – Altered flow regime, thermal regime or physical habitat, Biotic – predation or competition by non-native fishes).

Species	**Survey Results**	
(*Scientific name* - common name)	**Extinction Risk**	**Primary Cause**
Catostomidae		
Catostomus clarkii - desert sucker	None/Low	Environment
Catostomus discobolus - bluehead sucker	None/Low	Biotic
Catostomus insignis - Sonora sucker	None/Low	Biotic
Catostomus latipinnis - flannelmouth sucker	None/Low	Environment
Catostomus platyrhynchus - mountain sucker	None/Low	Biotic
Xyrauchen texanus - razorback sucker	High	Environment
Cottidae		
Cottus bairdii - mottled sculpin	None/Low	Environment
Cottus beldingii - Paiute sculpin	None/Low	Environment
Cyprinidae		
Gila cypha - humpback chub	High	Biotic
Gila elegans – bonytail	High	Biotic
Gila intermedia - Gila chub	Moderate	Biotic
Gila nigra – headwater chub	Moderate	Biotic
Gila robusta - roundtail chub	Moderate	Biotic
Lepidomeda mollispinis - Virgin River spinedace	High	Environment
Lepidomeda vittata - Little Colorado River spinedace	High	Biotic
Meda fulgida - spikedace	High	Biotic
Moapa coriacea - Moapa dace	High	Biotic
Plagopterus argentissimus - woundfin	High	Environment
Ptychocheilus lucius - Colorado pikeminnow	Moderate	Environment
Agosia chrysogaster - longfin dace	None/Low	Biotic
Rhinichthys osculus - speckled dace	None/Low	Biotic
Rhinichthys cobitis - loach minnow	High	Biotic
Cyprinodontidae		
Cyprinodon macularius - desert pupfish	High	Biotic
Poeciliidae		
Poeciliopsis occidentalis - Gila topminnow	High	Biotic
Salmonidae		
Oncorhynchus gilae apache - Apache trout	High	Biotic
Oncorhynchus clarkiii - cutthroat trout	Moderate	Biotic
Oncorhynchus gilae - Gila trout	High	Biotic
Prosopium williamsoni - mountain whitefish	None/Low	Environment

Appendix 6.2. Qualitative phylogeny of the native freshwater fishes of the Colorado River Basin.



Chapter 7

Upstream and Downstream Recovery of Fish Faunas to Multiple Dam-Induced Disturbance Gradients

Abstract

The great societal utility of running waters has resulted in the extensive exploitation of streams and rivers throughout the world, a process greatly facilitated by the construction of hundreds of thousands of dams globally. Dams and river regulation constitute one of the primary sources of disturbance in aquatic ecosystems, yet little empirical evidence exists to support whether, and if so how, fish faunas respond spatially to multiple gradients of environmental disturbance downstream and upstream from dams.

Using paired sister rivers – the regulated Jackson River (Gathright Dam - a flood control, coldwater-release dam) and unregulated Cowpasture River situated in the mid-Atlantic highlands of southeastern U.S. – we provide the first study that documents the upstream and downstream recovery of a fish assemblage to multiple environmental disturbances caused by river regulation. Our results illustrated a strong, attenuating disturbance gradient with increased downstream distance from Gathright Dam. Flow regimes (increased summer and decreased winter flows, decreased seasonal variability, magnitude and duration of low flows and altered timing of flows), water temperatures (decreased in summer), substrate composition (increased embeddedness) and macroinvertebrate biomass (decreased) were highly altered in the tailwaters, and in large part, attenuated non-linearly in response to the punctuated contributions of downstream tributaries. Patterns of fish recovery took a number of forms, including no recovery (i.e., extirpation from the tailwaters) to complete recovery, which in many instances corresponded with expectations based on species life histories and environmental tolerances. We found that tributaries not only initiated the recovery of environmental

conditions, but also provided critical warmwater refuge from the cold, trout-managed tailwaters. Using an information theoretic model selection approach we assessed the relative importance of the different environmental drivers for explaining patterns of fish population and community recovery in the tailwaters of the Jackson River. Results from this study also provided strong evidence for the upstream impacts of Gathright Dam on fish assemblages. The abundance of small-bodied minnow species, which are highly susceptible to predation by smallmouth bass, was highly depressed above the dam and showed a strong recovery with increasing distance from the reservoir. An opposite trend was observed for smallmouth bass, suggesting that upstream reaches may be increasingly vulnerable to invasion and predation by facultative riverine species that become established in reservoirs and move upstream in large numbers.

In conclusion, our study illustrates, for the first time, the importance of multiple gradients of environmental disturbance for shaping the downstream, non-linear recovery of fish assemblages to river regulation. We provide strong evidence for the role of tributaries in promoting downstream recovery of environmental conditions and providing permanent thermal refugia for warmwater fishes in the tailwaters. The findings from this study have important implications for the design of monitoring projects and the management of native warmwater fishes in rivers regulated for tailwater trout fisheries.

Introduction

Running waters provide numerous goods and services for humankind, including a source of water for domestic, industrial and agricultural purposes, a means of power generation and waste disposal, routes for navigation, and opportunities for recreation and spiritual experiences. The great utility of running waters has resulted in the extensive exploitation of streams and rivers throughout the world (Malmqvist and Rundle 2002), a process greatly facilitated by the construction of hundreds of thousands of dams globally (Smith 1971, Gleick 2000, WCD 2000). Fragmentation and flow regulation of running waters is especially evident in the northern third of the world (Dynesius and Nilsson 1994), and the United States is a global leader in this regard, having over 76,500 "large" dams over 2 meters in height (USACE 2002) and an estimated 2,000,000 or more small dams (Graf 1999) that contribute to the fragmentation of nearly one million kilometers of riverine landscape including over 98% of medium-sized rivers (Echeverria et al. 1989, Benke 1990). As a result, one is hard pressed to find a stream or river whose natural flow regime has not been altered by human intervention.

There are numerous ecological impacts associated with the extensive fragmentation and regulation of free-flowing rivers (Zwick 1992, Pringle et al. 2000). Fragmentation promotes the isolation of fish populations by disrupting the movement and migration of individuals between freshwater and marine environments. The imperiled status of many salmon stocks in the Pacific Northwest is in part attributable to the gauntlet of dams these fish encounter in their migration to and from the ocean (Levin and Schiewe 2001). Fragmentation also threatens the persistence of inland fish species by blocking movement between habitats that are essential in the species' life history (Schlosser 1991) and preventing the exchange among isolated populations needed to maintain metapopulation dynamics (Rieman and Dunham 2000). In addition, dams have significant ecological effects on downstream riverine ecosystems by altering a number of dominant environmental drivers, including the modification of natural flow and thermal regimes, reduced sediment flux, and increasing algal growth, among others (Ward and Stanford 1979, Ligon et al. 1995, Poff et al. 1997). Some modifications have been purposely aimed at benefiting a small subset of fish species. For instance, most of the larger dams throughout the United States and the world have dramatically modified riverine thermal regimes by selectively releasing cold, hypolimnetic water from thermally stratified reservoirs aimed at establishing productive trout fisheries in the downstream, or tailwater, reaches of the dammed river (Ward 1982, 1985).

Dams and water diversions that modify environmental conditions and fragment the natural longitudinal continua of streams are considered to be a primary source of physical disturbance and now constitute an active area of research in stream ecology (Resh et al. 1988, Poff et al. 1997, Lake 2000, Poff and Hart 2002). Spawning from this research is the general consensus that river regulation has detrimental effects on downstream ecosystems by disrupting the habitat template upon which fish populations and communities are structured. Upon examining the literature, however, it is overwhelmingly apparent that, although we have made great strides in understanding the biological implications of dam-induced disturbances, there remains a number of critical gaps in our current state of knowledge with respect to how river regulation impacts fish communities. In many respects these knowledge gaps stem from the broader realization that stream ecologists have focused almost exclusively on studying temporal recovery of organisms to disturbance (reviewed by Niemi et al. 1990, Yount and Niemi 1990, Detenbeck et al. 1992, Clements and Newman 2002), but have paid considerably less attention to the spatial context of recovery in riverine ecosystems. The opportunity to substitute space for time to assess recovery appears to be an attractive alternative, yet it has been largely overlooked.

A wealth of empirical evidence has provided strong support for the effects of dams on fish assemblages by way of simple comparisons between surveys conducted upstream from the reservoir to those conducted immediately below the dam. Beyond this, however, we still have virtually no understanding of whether, and if so how, fish assemblages respond to gradients of environmental disturbance and are spatially structured in the downstream reaches below dams. In fact, of the limited number of studies that have examined the spatial recovery of fish species in dam tailwaters (i.e., Bain et al. 1988, Kinsolving and Bain 1993, Phillips and Johnston 2004), only one study was designed specifically to address such this question (Kinsolving and Bain 1993). This is strong contrast to the study of benthic macroinvertebrates, which have received much greater attention in this regard (e.g., Voelz and Ward 1989, 1990, 1991, Stevens et al. 1999, Vinson 2001). The limited focus devoted to this area of research is surprising given that the study of natural longitudinal patterns of fish community structure (Shelford 1911, Burton and Odum 1945) and the environmental factors responsible for such patterns (Sheldon 1968, Schlosser 1991) have a rich history in stream ecology. More generally, longitudinal trends in riverine ecosystems have played a central role in cornerstone conceptual frameworks such as the river continuum concept (Vannote et al.

1980) and the effects of dams on the river continuum as formulized in the serial discontinuity concept (Ward and Stanford 1983).

It is perhaps not surprising that we have a poor understanding of fish fauna recovery given that we have yet to quantify how major environmental drivers, which are ultimately responsible for fish recovery, are modified by river regulation and how these effects potentially attenuate in the downstream reaches. As a result, studies continue to make the simplifying assumption that critical environmental drivers (and consequently fish assemblages) recovery in a linear fashion downstream from dams (e.g., Kinsolving and Bain 1993, Phillips and Johnston 2004), although basic ecological knowledge and limited empirical evidence suggest that recovery gradients are likely non-linear and considerably more dynamic. For example, the most prevalent sources of environmental disturbance associated with river regulation include alterations to natural flow regimes, water temperatures, sediment transport processes and the associated availability of food resources. In the most general sense, we may expect that streamflow recovery is related to the attenuation processes associated with the dynamics of pool storage, discharge and tributary inputs (Dunne and Leopold 1978); thermal recovery is dictated by increased contact with the atmosphere and hydrologic inputs from warmwater tributaries (Stevens et al. 1997, Preece and Jones 2002); and, the recovery of sediment characteristics is influenced by increased frequency of flushing flows and the contribution of sediments from incoming tributaries (Rice et al. 2001, Osmundson et al. 2002). For these reasons it is unlikely that downstream watercourse distance from the dam will alone be an adequate surrogate for environmental recovery because of the non-linear manner in which streamflow, temperature and streambed conditions are expected to attenuate below dams.

Interestingly, despite the importance of tributaries in natural riverine ecosystems (Benda et al. 2004) and the longitudinal continuum (Bruns et al. 1984), the potential roles they play in promoting downstream recovery of environmental conditions and in providing permanent refugia for source populations that seed the recovery of fish faunas are completely unknown.

Lastly, an interesting consequence of the historical and logical emphasis on the unidirectional flow of water and energy in riverine ecosystems, the downstream effects of dams have been the traditional focus, whereas the potential upstream effects on fish faunas remain virtually unexplored (Pringle 1997). Evidence in support of such impacts has been slow to accumulate but include: habitat degradation associated with the process of headwater erosion or "headcutting" in small streams (Patrick et al. 1991), compositional changes of upstream fish assemblages due to barriers to upstream movement or riverine fishes (Reyes-Galiván et al. 1996) and increased movement of reservoir fishes (Wilde and Ostrand 1999), and the expiration of species above the dam due to reduced potential for re-colonization after disturbance (Winston 1991). Recent evidence suggests that upstream effects may be the cause of increased spatial variation observed in headwater fish assemblages in regions with many dams (Herbert and Gelwick 2003). Facultative riverine species may also increase in abundance in reservoirs and move upstream where they may compete with and prey upon obligate riverine species (Ruhr 1956, Erman 1973). For example, smallmouth bass (*Micropterus dolomieu*) is a dominant predator in aquatic systems that inhabits both lentic and lotic environments, and it has been shown to adversely impact small-bodied fish abundance and diversity, especially minnow species (Chapleau et al. 1997, Findlay et al. 2000, Jackson 2002). In short, the potential upstream effects of dams on fish faunas have only recently been recognized and have yet to be rigourously quantified.

In light of the shear magnitude of river regulation throughout the United States and the world, an understanding the spatial dynamics of stream fish recovery to dam-induced disturbances constitutes a critical research need. The present study is the first to assess the cumulative impact of multiple environmental disturbances caused by river regulation on the downstream and upstream recovery of fish assemblages. In this investigation we ask how dominant environmental drivers that structure fish assemblages in riverine ecosystems, namely flow regimes, water temperatures, sediment processes and benthic macroinvertebrate biomass, are altered by river regulation and we explore the dynamics of their recovery in the downstream tailwaters. This analysis provides important insight into longitudinal disturbance gradients in tailwater environments by assessing how environmental recovery is related to watercourse distance from the dam and the spatial arrangement and characteristics of incoming tributaries. Next, we explore spatial patterns of fish population and assemblage recovery and relate these to the aforementioned disturbance gradients, with the aim of gaining the first correlative insight into the specific mechanisms by which river regulation influence fish faunas. This examination quantitative testing of the widely-held hypothesis that environmental conditions - and by extension the riverine fish assemblages - recover linearly in the tailwaters. Lastly, we provide the first quantification of the effects of dams on the upstream recovery characteristics of fish populations and assemblages, thus addressing the potential bi-directional impacts of river regulation.

Methods

Study system and background

This study was conducted on two 4th-order rivers located in the Valley and Ridge physiographic province in the mid-Atlantic highlands of Virginia in the southeastern United States. The highly-regulated Jackson River and free-flowing Cowpasture River merge to form the James River (Fig. 7.1). The Valley and Ridge province consists of elongate parallel ridges and valleys (oriented northeast-southwest) that are underlain by folded and faulted clastic and carbonate sedimentary rocks formed during the Paleozoic Era. This area supports an oak-chestnut forest – mainly white oak, chestnut oak, and red oak – with a small number of hickory species, which at higher elevations yield dominance to northern hardwoods that more typical in the northeastern United States. The Jackson River was impounded by the construction of Gathright Dam (85 m in height) in 1981, which resulted in the creation of Lake Moomaw (storage ca. 77,700,000 m^3) – a 19 km, 10.2-km^2 reservoir with an average depth of 24.2 m (Plate 7.1). Gathright Dam is operated by the Army Corp of Engineers and is mandated for flood control, low flow augmentation for fisheries resources, and maintenance of a water base for recreation. Monthly minimum tailwater flow releases vary on a seasonal basis from 4.47 m^3/s (158 ft^3/s) in December and January to 8.01 m^3/s (283 ft^3/s) in July. The term "tailwater" as used herein applies to modified lotic reaches downstream from Gathright Dam. Beginning in October 1990, thermal regimes downstream from Gathright Dam were regulated using a blended water release strategy that selectively draws water of different temperatures from 10 portals at 9 elevations along the thermocline of Lake Moomaw to establish a tailwater trout fishery. Since this time, main channel reaches of the Jackson River below Gathright Dam exhibit substantially lower summer water temperatures compared to natural thermal regimes that existed prior to dam closure (Fig. 7.2B). Tailwater thermal regimes currently exhibit a highly predictable periodicity with low inter-annual variation, where maximum annual water temperatures are strictly controlled and do not exceed 15.3 °C, which is the upper end of the temperature range considered optimal for trout production. In contrast, water temperatures prior to the closure of the dam were highly variable and commonly reached 25-30 °C during the summer; a pattern driven primarily by seasonal climatic patterns and one typical of most unregulated rivers in southeastern United States such as the Cowpasture River. In summary, as a consequence of dam closure and operation for a tailwater trout fishery, strong downstream gradient in discharge and temperature occurs below Gathright Dam. In contrast, the sister river of the Jackson River, the Cowpasture River, is one of the last remaining large, free-flowing rivers in the eastern United States and is characterized by a natural flow and thermal regime typical of unregulated rivers of the region (Plate 7.1).

Study design

Our study was conducted during the spring and summer months of 2002. The Jackson River and Cowpasture River were each delineated into 10 mainstem segments defined as the main channel river bounded by tributary junctions. These included 7 segments over a 28-kilometer stretch of the Jackson River tailwaters (denoted J1-J7), 3 segments over a 10-kilometer stretch of the Jackson River upstream from Gathright Dam (denoted JA-JC) and 10 segments over a 55-kilometer stretch of the Cowpasture River (denoted C1-C10) (Fig. 7.1). In addition, we surveyed 3 permanent tributaries of the Jackson River (Cedar Creek, Falling Spring and Indian Draft) and 3 permanent tributaries of the Cowpasture River (Thompson Creek, Stuart Run and Mill Creek). The two study systems and the location of sampling sites were chosen to ensure that the systems were as similar as possible with the sole exception of the presence of Gathright Dam. In the statistical sense, the Jackson River can be considered the impacted system or "treatment" and the Cowpasture River is the un-impacted system or "reference". Both systems are characterized by similar climate and geology, share the same regional fish species pool (Jenkins and Burkhead 1994), and sampling sites on both rivers are located across the same range of elevations and contributing drainage areas (Appendix 7.1).

Fish collection

Fish communities were sampled using prepositioned area electrofishing (PAE: 2.0 × 4.0 m in size; Bain et al. 1985) that were powered by a 5,000-W Coleman® Powermate generator and controlled by a Coffelt pulsator unit (Coffelt Manufacturing, Flagstaff, Arizona, USA). PAEs were built by the first author following the design outlined by Temple et al. (2000). PAE have several advantages over traditional collecting methods, including reduced probability of driving fish from their original location (thus enhancing precision of fish habitat measurements: Walsh et al. 2002) and reduced differential capture efficiency related to fish size, species fright to electrofishing operation and habitats sampled (Bowen et al. 1998, Ensign et al. 2002). This sampling technique has been successfully used to estimate species richness, density and relative abundance in shallow waters of medium-sized rivers (i.e., orders 4-7) by Bain et al. (1988), Kinsolving and Bain (1993) and Freeman et al. (2001), among others. Prior to the commencement of the sampling, we mapped the electrical field surrounding the PAE and found that the voltage gradient dissipated by less than 0.1 V/cm at a distance approximately 0.5 m from the electrodes, thus providing an effective electrical field throughout the PAE that is required for accurate sampling (Fisher and Brown 1993).

We sampled by haphazardly deploying 30 PAEs throughout each of the 20 mainstem river segment (and 10 PAEs in each of the 6 tributaries) in similar habitats: riffles, runs and accessible pools less than 1.0 m in depth). Sampling locations were spaced equally as possible within each segment and typically encompassed 4-6 riffle-run sequences. Bowen and Freeman (1998) examined the relationship between species richness and different levels of sampling effort using PAEs in the 7th order Tallapoosa River, Alabama, and found that 30 PAEs effectively sampled 70-80% of the fish species. Therefore, the sampling effort employed in our study provides a good balance between an adequate level of sampling accuracy and the extensive time required to survey the large number of sites examined in this study and the processing of all fish in the field. For each sample, the PAE frame was placed on the streambed and left undisturbed for at least 15 minutes. At the conclusion of the resting period, two individuals positioned themselves ca. 10 m downstream from the frame with dip nets. The PAE was then energized with 230-V alternating current for 20 seconds and the netters rapidly approached the frame and collected stunned fish that originating inside the PAE. Immediately after the shocking period the generator operator kicked through the sampling area in an upstream to downstream direction to dislodge fishes from the substrata and the entire frame was visually searched. All the fish collected were identified, enumerated, measured for total length (mm) and biomass (g) and then released in the field.

After collection and processing of all the fish from a PAE grid we measured a series of habitat characteristics, including current velocity, depth and streambed substrate composition. Surface current velocity was measured by timing the float of an orange through the frame, repeating 5 times and calculating the average velocity (Hynes 1970). To facilitate depth and substrate measurements, we visually divided the PAE frame into eight $1m^2$ sections. At the center of each section we measure water depth to the nearest centimetre and percent substratum composition by visual estimation following the modified Wentworth scale, i.e., silt/sand, gravel, pebble, cobble and boulder (Cummins 1962). Values were tabulated across the 8 sections to obtain an average depth and percent substrata categories for each frame. Statistical analysis comparing the habitat characteristics of the PAE grids sampled in the Jackson River versus Cowpasture River revealed no significant differences (Appendix 7.1), and therefore no differences between fish communities are expected from habitat differences between the rivers.

Data description

Fish data

For the purposes of emphasizing broad longitudinal patterns in fish assemblages and ensuring a high level of abstraction, we pooled the PAE samples within each river segment or tributary to form composite estimates of species occurrence and abundance (see Gauch 1982 for rationale). Following Kinsolving and Bain (1993), the number of fish (by species) in each sample was transformed to an octave scale: <2 individuals = 1, ≥2 to <4 individuals = 2, ≥4 to <8 individuals = 3, etc. This geometric transformation is effective for reducing typically high variability in organism counts to an immediate range of abundance values (e.g., 0-10), and it is appropriate for community-level studies where the overwhelming numerical influence of dominant species needs to be balanced with the information from the occurrence of uncommon species (Gauge 1982), such as for fishes.

Streamflow regimes

We constructed daily streamflow time series for the study reaches of the Jackson River between 1960 and 2002 (i.e., 20 years before and 20 years after construction of Gathright Dam). We combined a conceptual rainfall-runoff modelling approach (see Watts 1997 for a review of different rain-runoff models) with a regionalization analysis that links model hydrologic parameters to physical descriptors of the watershed using an artificial neural network (see Maier and Dandy 2000 for a review of neural network applications in water resources). Mathematical rainfall-runoff models have the potential to be very useful in predicting relationships between watershed attributes and hydrological response characteristics as they can be formulated with the specific intention of characterizing the hydrological processes occurring in the watershed. Regionalization by describing these hydrological characteristics in terms of physical descriptors of the landscape using statistical models then allows estimation of the daily hydrograph for any watershed in the region. The estimation of hydrological behaviour using physiographic and climatological watershed attributes has been used widely in the literature (e.g., Thomas and Benson 1970, Jennings et al. 1994, Surian and Andrews 1999), and has mainly focused on using simple regression analysis or transferring model results based on spatial proximity (Post and Jackman 1996, 1999, Sefton and Howarth 1998, Kokkonen et al. 2003). In the present study, we employ a rainfall-runoff approach to characterize unregulated flow regimes of the Jackson River prior to the construction of Gathright Dam, which are then compared to post-Gathright conditions to quantify the degree of hydrologic alteration in the downstream tailwaters. Below, we detail the specific steps of this analysis.

The rainfall-runoff model (IHACRES) – We described patterns of streamflow in unregulated rivers of the Upper James River Basin using the rainfall-runoff model IHACRES (PC version 1.02) – Identification of unit Hydrographs And Component flows from Rainfall, Evaporation, and Streamflow data (Jackman et al. 1990). IHACRES is a lumped parameter, conceptual rainfall-runoff model, based on unit hydrograph principles, which relates total rainfall to total discharge. This model avoids the problems of overparameterization (and the resulting large parameter uncertainties) that typify many other physical-based models by including only those key hydrological processes that can be identified from observed data and not making *a priori* decisions regarding the model structure (Jakeman and Hornberger 1993). IHACRES makes use of the most commonly available hydrometeorological data (precipitation, streamflow and air temperature), and has been successful in estimating stream discharge in a variety of climates across the world (Post and Jackman 1996, 1999, Sefton and Howarth 1998, Schreider et al. 2002, Dye and Croke 2003), including the eastern United States (Kokkonen et al. 2003).

Specific details and equations underlying the IHACRES model are presented in Appendix 7.2, as well as Jakeman et al. (1990), Littlewood et al. (2003), and elsewhere; therefore, we provide only a brief discussion of the model. The model consists of two modules: (1) a non-linear loss module that calculates the amount of rainfall that is delivered to the stream and is not stored in the soil or lost to evapotranspiration (i.e., the conversion of total rainfall to effective or excess rainfall) and (2) a linear module that routes the effective rainfall to streamflow. The model has only six parameters, three in the non-linear module (τ_w, *c*, and *f*) and three in the linear module (τ_q, τ_s, and v_s), defined as follows:

(1) τ_w [days] is the drying time constant defining the rate of water loss from the watershed at 20°C.

(2) *f* [1/°C] is the rate of water loss from the watershed (i.e., drying time) due to a unit change in temperature.

(3) *c* [1/mm] is defined as the increase in watershed storage index per unit rainfall in the absence of evapotranspiration. It is normalized so that the total volume of modelled effective rainfall is equal to the total volume of observed streamflow.

(4) τ_q [days] is the time constant defining the rate of quickflow recession of streamflow from the watershed.

(5) τ_s [days] is the time constant defining the rate of slowflow recession of streamflow from the watershed.

(6) v_s [unitless] is the proportion of slowflow to total flow. The normalization on c constrains $v_s + v_q$ to equal 1 (where v_q equals the proportion of quickflow to total flow), and therefore the model requires estimation of only one of the two.

The set of 6 parameters is considered to characterize the dynamic hydrologic response of the watershed, and it can be related to physical descriptors of many watersheds in a regionalization analysis to predict time series of daily discharges at ungauged sites using time series of precipitation and air temperature (e.g., Post and Jackman 1999).

IHACRES model calibration and validation – IHACRES models were calibrated for 8 unregulated, gauged rivers in the Upper James River Basin, a geographic region that is considered homogenous with respect to geology, landuse and climate. These watersheds range in size from 85 to 1,186 km^2 and represent the only river systems in the Upper James River Basin that are monitored by the U.S. Geological Survey (USGS) for daily discharge and are located upstream from large dams or diversions. Data required for the IHACRES models include daily streamflow, precipitation and air temperature. For the period 1960-2002, daily streamflow was obtained from the USGS National Water Information System (http://water.usgs.gov), and daily precipitation (mm) and mean air temperature ($^{\circ}$C) (calculated as the average of daily maximum and minimum temperatures) records from the National Oceanic and Atmosphere Administration (NOAA) National Climatic Database (http://www.ncdc.noaa.gov). Data from 19 (precipitation) and 12 (temperature) climate stations throughout the Upper James River Basin were used in a Geographic Information System to create daily precipitation and temperature maps (30 x 30 m pixel size) using an interpolation procedure based on a spatial autoregressive model (using UTM northing and easting coordinates of the pixels and their two- and three-way interactions). Elevation was used as a covariate in the autoregressive model to account for adiabatic cooling and variation in rainfall associated with differences in elevation (east vs. west facing slopes). Elevation values for each pixel were obtained from Digital Elevation Models (DEMs) from the USGS National Elevation Dataset (http://edcnts12.cr.usgs.gov/ned/). We used an autoregressive model rather than co-kriging, as the former showed similar accuracy and took a fraction of the computing time. Bootstrapping was used to assess the accuracy of the estimated precipitation and temperature maps for 10 randomly selected days in each year by repeatedly building an autoregressive model with n-1 stations, predicting the precipitation and temperature values of the left-out station and comparing them to the actual values. Bootstrap results showed the autoregressive model performed very well for estimating both precipitation ($\overline{RMSE} = 12.6$) and temperature ($\overline{RMSE} = 1.64$). A similar interpolation approach to the one used here was employed by Klopfer (1997) to estimate monthly precipitation and temperature for the entire state of Virginia. For each of our 8 calibration watersheds, daily total precipitation was calculated as the sum of accumulated rainfall in the entire watershed and mean temperature was calculated by averaging temperatures across the entire watershed.

IHACRES models were constructed for each calibration watershed in each of 8 consecutive 5-year periods, starting on January 1 and ending on December 31 for the 20 years before (i.e., 1960-64, 1965-69, 1970-74, 1975-79) and after Gathright Dam construction (i.e., 1983-87, 1988-92, 1993-97, 1998-2002). We excluded a 3-year period (1980-1982) from this analysis during which Gathright Dam was being constructed and filled. We chose starting and ending dates with relatively low watershed moisture levels so that the difference between initial and final watershed storage can be considered neglected as assumed in IHACRES. The 5-year period was selected to balance problems of parameter variability due to too short a calibration period with problems of bias that could be induced over longer calibration periods by non-stationary watershed conditions and highly variable rainfall conditions (see discussion by Dye and Croke 2003). The IHACRES model package automatically determines the values of the parameters τ_q, τ_s, v_s and c during model optimization, whereas τ_w and f are determined through a trial and error procedure by systematically varying the values of the parameters and selecting the optimum value based on an evaluation of a range of model performance statistics, including the correlation coefficient (R) and model bias. The best models (based on each of the 5-year calibration periods) were selected on the basis of maximizing the correlation and minimizing the bias between predicted and actual daily discharge time series. These models were subsequently validated for the entire pre- or post-Gathright Dam record (depending on the calibration period) to provide an unbiased estimate of model performance. Results show that the models provided good estimates of streamflow for the 5-year calibration periods (resubsitution validation: $\overline{R} = 0.74$) and for the entire pre- or post-Gathright Dam record (external validation: $\overline{R} = 0.71$). IHACRES model parameters and statistics of predictive performance for each calibration watershed and time period are presented in Appendix 7.2.

Regionalization analysis and the prediction of daily discharge – Artificial neural networks (ANNs) were used to model the 6 hydrological response parameters estimated from the IHACRES models as a function of 5 physical descriptors of the watersheds for each of the 8 calibration time periods (i.e., 8 networks in total). Although a large number of watershed descriptors could be used in this analysis, we chose to select a small group of variables that are likely to drive hydrologic processes in our study system: drainage area (km^2), basin aspect (degrees), stream density (km/km^2), channel slope (m/m) and percent of the basin forested (see Appendix 7.3). These watershed descriptors have been shown to be important in a number of regionalization analyses using IHACRES (e.g., Post and Jackman 1999, Kokkonen et al. 2003). Advantages of ANNs over traditional, linear approaches include their ability to model non-linear associations, no assumptions concerning the distributional characteristics of the independent variables, and the accommodation of interactions among predictor variables without any *a priori* specification (Bishop 1995). Moreover, ANNs have been shown to exhibit substantially higher predictive power (based on empirical and simulated data) compared to traditional regression and classification approaches (Olden and Jackson 2002) and importantly can simultaneously model multiple response variables (Olden 2003). The present study used a feed-forward neural network trained by the back-propagation algorithm (Rumelhart et al. 1986). The architecture of this network consists of an input layer with 5 neurons representing the physical descriptors, a hidden layer with 3 neurons, and an output layer with 6 neurons representing the IHACRES parameters (see Appendix 7.3). Learning rate (η) and momentum (α) parameters (varying as a function of network error) were included during network training to ensure a high probability of global network convergence (Bishop, 1995), and a maximum of 1000 iterations was considered for the back-propagation algorithm to determine the optimal axon weights. We refer the reader to Olden and Jackson (2001) for a more comprehensive description of ANNs and the specifics of network optimization. ANNs were validated using *n*-fold cross validation and were found to perform very well for predicting the IHACRES parameters: τ_w ($\overline{R}$ = 0.91, range 0.83-0.96), f ($\overline{R}$ = 0.89, range 0.82-0.96), τ_q ($\overline{R}$ = 0.91, range 0.76-0.99), τ_s ($\overline{R}$ = 0.92, range 0.82-0.97), and v_s ($\overline{R}$ = 0.96, range 0.94-0.98), where values are based on the 8 calibration periods. Statistical relationships between the watershed descriptors and the hydrologic responses (see Appendix 7.3) correspond well with expectations based on physical processes (e.g., Post and Jakeman 1999).

Next, physical watershed descriptors were quantified for the mainstem segments and tributaries of the Jackson River and entered into the ANNs to predict the IHACRES hydrological response parameters for each of the time periods (see Appendix 7.3 for data). As these 6 parameters fully define the IHACRES model, their values were used in conjunction with the daily precipitation and air temperature time series to predict daily unregulated streamflow time series for the mainstem and tributary watersheds from 1960-2002. To assess the accuracy of the entire modelling process we conducted an independent validation by comparing predicted to actual streamflow for 2 gauges not used in the regionalization analysis: one gauge above Gathright Dam for the post-Gathright Dam years (USGS 02011400: 1983-2002) and one below the location of

Gathright Dam for the pre-Gathright Dam year (USGS 02012500: 1960-1979). Together, these gauges span the range of drainage areas and years used in the regionalization analysis and provide a robust validation of the entire IHACRES-ANN process. Our results showed that the modeling process was highly accurate; correlation coefficients for the comparison of predicted and actual discharge was 0.75 and 0.77 for gauges 02011400 and 02012500, respectively (see Appendix 7.3). In summary, we combined a deterministic rainfall-runoff modelling approach with a regionalization analysis linking model hydrologic parameters to physical descriptors of the watershed to reasonably predict daily streamflow time series for the study reaches of the Jackson River (JA-J7) for 20 years before (1960-1979) and 20 years after (1983-2002) the construction of Gathright Dam.

Water temperatures

Water temperature was measured directly in each river segment and tributary using a Thermochron iButton (model DS1921, Dallas Semiconductor Corporation) that recorded temperatures at 4 hr intervals from March 1 to July 31, 2002 (the months in which fish exhibit spawning behaviour). Mean daily water temperature was calculated for each river segment and tributary.

Substrate characteristics

For each river segment we selected a representative riffle/run and quantified substratum grain size and embeddedness by conducting a Wolman pebble count (Gordon et al. 1992) in areas that were not disturbed by fish sampling. Random transects across the stream channel from bank to bank were walked and measurements from 150 randomly selected particles were taken. Aided by snorkelling, we measured the exposed height of the particle (measured from the top of the particle surface to the streambed layer) and total particle height to calculate % embeddedness [total depth (total height – exposed height) divided by total height] following Murphy and Willis (1996). Next, the selected particle was removed from the streambed and the length of the intermediate (or *B*) axis was measured. Median substratum particle size (D_{50}), coefficient of variation in D_{50} and mean % embeddedness were calculated for each river segment.

Benthic macroinvertebrate biomass

Benthic macroinvertebrate sampling was conducted as a means to assess gradients of insect food availability for fishes. During the same dates of fish sampling, benthic macroinvertebrates were collected from each river segment using a Slack sampler following the USGS NAWQA protocols detailed in Cuffney et al. (1993) and updated by Moulton et al. (2002). The Slack sampler (also know as a Surber sampler on a stick) is the standard disturbance removal sampler used in the NAWQA Program for wadeable sites. The Slack sampler consists of a wooden handle that is attached to a rectangular net frame (50 by 33 cm) and fitted with a tapered, 500-µm Nitex™ collection net. The cod-end of the net, where sample material is trapped, is fitted with a detachable collection receptacle, which is removed to retrieve the sample. Macroinvertebrates were collected from a 0.25-m^2 area immediately upstream of the Slack sampler (delineated by an area template) by rubbing all substrate particles above the level of embeddedness. Five discrete samples using the Slack sampler were taken in a riffle/run habitat, which were subsequently combined into a single composite sample (total area sampled = 1.25 m^2) and preserved in 70% formalin. Three composite samples were taken in each river segment and used to characterize the macroinvertebrate community of the entire segment. In the laboratory, the samples were sorted and macroinvertebrates were identified following USGS NAWQA protocols (Moulton et al. 2000) to the lowest possible genus. This protocol involved placing each sample in a sorting sieve with numbered grids, and grids from which organisms were sorted were chosen at random until at least 270 (300 ± 10%) organisms were sorted. Detailed analyses of longitudinal patterns of macroinvertebrate community structure in the study sites will be the focus of another paper. For the purposes of this study we determined periphytic ash-free dry mass (AFDM) of each composite sample using standard methods (APHA 1995) to estimate the total macroinvertebrate biomass of organic matter available for fish consumption. AFDM of each composite sample was quantified and mean values were calculated for each river segment.

Quantifying levels of disturbance and patterns of downstream recovery

Recovery from disturbance implies that the impacted system will move toward some normal bounds within which it can persist (*sensu* Connell and Sousa 1983). This definition of a disturbance also implies that the system is returning toward a condition that existed before it was disturbed, that is, toward nominal behaviour, and that the disturbance itself is no longer acting. In assessing the impact of Gathright Dam on the biotic and abiotic characteristics of the Jackson River tailwaters, we wanted to determine whether, and to what extent, the altered conditions differ from what it would have been in the absence of river regulation. In this study, we quantified levels of alteration and tested for downstream recovery using an unreplicated pair of systems – the regulated Jackson River and unregulated Cowpasture River. We chose this approach because of the broad spatial extent of our study and the unrealistic possibility of conducting a site replication. Moreover, it is extremely difficult to develop truly replicated, large-scale river experiments because relatively few unregulated rivers remain in the United States.

We quantified disturbance gradients of streamflow regimes in the Jackson River using the 'Indicators of Hydrological Alteration' (IHA) presented by Richter et al. (1996). This approach assesses hydrologic variation through a river basin by comparing pre- and post-alteration streamflow data (in this case, generated discharge data from the IHACRES and regionalization analysis described above). The IHAs represent a comprehensive, multi-parameter suite of 66 hydrologic indices (33 measures of central tendency and 33 measures of dispersion), each of which describe different aspects of inter-annual variation in water conditions in terms of ecological relevant attributes (see Richter et al. 1996, 1997, 1998 for more details). These indices are grouped into five categories that represent the fundamental characteristics of the flow regime: magnitude, frequency, duration, timing and rate of change in flow conditions. In a recent study, we found that the set of IHAs adequately represents the majority of information provided by a comprehensive group of 171 hydrologic indices previously used in the literature (Olden and Poff 2003). We employed the methodology of Richter et al. (1996) to assess hydrologic alteration and quantify the spatial patterns of recovery in the Jackson River tailwaters. This approach involves computing the values of the hydrologic indices for each river segment in the Jackson River for each year in the pre-Gathright Dam series (1960-1979) and the post-Gathright Dam series (1983-2002). Non-parametric statistics are then calculated for each 20-year series, including median values representing the central tendency and the coefficient of dispersion (75th – 25th percentile) representing the variance of the hydrologic indices. Next, we compared the 66 inter-annual statistics between the pre- and post-dam time series for each river segment by calculating the percentage deviation of the post-dam condition relative to the pre-dam condition. All analyses were conducted using IHA software, version 5 (Smythe Scientific Software, Boulder, Colorado, USA).

Unlike previous studies examining downstream patterns of fish assemblages, we were able to quantitatively assess the degree of recovery of the other 3 environmental drivers (water temperatures, substrate characteristics, and macroinvertebrate biomass) by defining endpoints according to natural longitudinal gradients observed in the parallel, unregulated Cowpasture River. First, we examined whether these variables naturally vary along the Cowpasture River using a combination of visual assessment and linear regression analysis where watercourse distance (referenced from the confluence with the Bullpasture River that marks the upstream start of C1) was the independent variable. In cases where a significant longitudinal relationship was observed ($\alpha<0.05$) we quantified alteration as the percentage deviation of the observed values in the Jackson River relative to the predicted "unregulated" values according to the regression model developed for the Cowpasture River. When no significant longitudinal relationship existed we calculated percentage deviation by comparing observed values in the Jackson River relative to mean values observed across the 10 river segments in the Cowpasture River. Lastly, we assessed fish recovery in two ways. First, we used a population-level endpoint: recovery of species' density. Second, we used a set of assemblage-level endpoints: recovery of species richness, recovery of assemblage structure (e.g., similarity in species composition), and total fish biomass. Percent deviation in each biological endpoint was calculated based on longitudinal patterns in the Cowpasture River following the protocol discussed above.

Statistical analyses

We use the information theoretic model selection approach (Burnham and Anderson 2002) to evaluate a series of statistical models that assess the relative importance of different environmental drivers (streamflow, water temperature, substrate characteristics, macroinvertebrate biomass) for explaining patterns of fish population and community recovery in the tailwaters of the Jackson River. Prior to this analysis we were required to reduce the set of environmental variables to a number small enough that it would not exceed the d.f. in the dataset (i.e., n=7 tailwater segments minus 1). To meet this requirement we selected only those variables that empirical evidence suggests are important drivers for stream fishes; we removed variables that showed minimal variation in the tailwaters; and we derived a number of composite variables by averaging across environmental factors describing similar characteristics of the environment and showing similar patterns of recovery. We accomplished this by calculating 5 variables describing the major environmental recovery gradients: (1) *mean streamflow conditions* – average values of percent alteration across the 33 IHAs of central tendency to derive a single composite variable of hydrologic alteration; (2) *variance in streamflow conditions* – average values of percent alteration across the 33 IHAs of coefficients of variance to derive a single composite variable of hydrologic alteration; (3) *water temperature* – average percent alteration of daily water temperatures during the fish spawning season (March-July); (4) *substrate* – percent alteration of substrate embeddedness; and (5) *food availability* – percent alteration of AFDM.

Next, we analyzed the fish population and community endpoints as a function of the 5 environmental variables using generalized linear models (GLM) with Gaussian errors and an identity link function (McCullagh and Nelder 1989). Given that our study is the first to model the relation between fish recovery and environmental disturbance gradients below dams, we derived a set of 31 candidate models based on all possible combinations of the 5 environmental variables. Model comparisons were then performed using modified Akaike's Information Criterion for small samples (AIC_c) with maximum likelihood values from the GLMs, a model selection technique based on the trade-off between description model accuracy and parsimony (Burnham and Anderson 2002). Akaike weights were calculated using the AIC_c values to determine the conditional probabilities that each model is the best model, given the data and set of candidate models. The "evidence ratios" of Akaike weights (i.e., a ratio of the Akaike weights for a given model vs. the AIC_c-best model) were derived to quantify the strength of evidence in favour of the best model over all other candidate models. All statistical analyses were performed using S-Plus with built-in routines (Venables and Ripley 1999). We qualitatively assessed fish population and community patterns upstream from Gathright Dam (above Lake Moomaw) using visual assessment because formal analyses were not possible because of the small sample size (n=3). We examined upstream patterns of smallmouth bass (*Micropterus dolomieu*) and 15 minnow species because of the well-documented prediation effect of the former on the latter (Chapleau et al. 1997, Findlay et al. 2000, Jackson 2002).

Results

Dam impacts and downstream environmental recovery

Flow regimes

River regulation by Gathright Dam has resulted in altered downstream flow regimes, including elevated summer flows, reduced winter flows, and truncated high flow events that historically occurred during the late winter and spring months (Fig 7.3). Indicators of Hydrologic Alteration (IHA) analysis provided strong evidence that the dam has differentially influenced components of the tailwater flow regime, and that downstream patterns of recovery vary substantially and are influenced by location of incoming tributaries (Table 7.1, Fig. 7.4). Importantly, hydrologic alteration was gauged with respect to comparisons of the IHAs based on pre- and post-Gathright Dam flow records (1960-1979 and 1983-2002, respectively), and levels of alteration for segments above Gathright Dam (JA-JC) provided an estimate of natural flow variation in time. We found that after dam construction monthly discharge during the summer to early fall season (May-Sept) are substantially higher and the magnitude of flows during winter (Nov-Jan) are lower compared to pre-Gathright years. Overall, average monthly flows showed little recovery in the tailwaters (Fig. 7.4), although the deviation of winter flow magnitudes did exhibit a moderate decreasing trend. For example, November discharge recovered from 28% altered below Gathright Dam (J1) to 0% altered in the farthest downstream reach (J7). Moreover, patterns of decreased alteration in winter months were punctuated in those segments located immediately downstream from tributaries, especially Cedar Creek, the first tributary below Gathright Dam. The magnitude of short-duration low and high flow events (1-, 3- and 7-day) and baseflow were much larger in post-Gathright years (especially low flow events), whereas longer-duration events (< 30 days) have been altered by a smaller degree. These flow characteristics exhibited tailwater recovery, but importantly low flow conditions remained highly altered in all the downstream segments. Segments below tributaries exhibited punctuated decreases in percent alteration, where recoveries in low flows were equal below the 3 tributaries but were much greater for high flows downstream of Cedar Creek. Similarly, the frequency and duration of extreme flow events were altered: low events were less frequent and have shorter duration, whereas high events were less frequent but exhibit longer duration. High flow events showed slight spatial recovery in the tailwaters and appeared un-affected by the location of tributaries. Julian dates of annual minimum and maximum discharge have both been delayed in post-Gathright years (e.g., the timing of maximum flows now occurs in late March compared to late February before the construction of the dam) and did not exhibit downstream recovery. Rates of rising flows, falling flows and daily flow reversal decreased in post-Gathright years (indicating flow stabilization) and showed strong patterns of recovery in the tailwaters. For example, over a 20-kilometer stretch the number of reversals recovered completely from -50% altered (J1) to 0% altered (J6), and exhibited a punctuated recovery below Cedar Creek. For the sake of brevity, we refrain from discussing the IHA measures of dispersion (i.e., variance), and instead present these raw results in Appendix 7.4.

Water temperature

The blended water release strategy of Gathright Dam has significantly reduced tailwater temperatures of the Jackson River during the fish spawning season of March to July (Fig. 7.5A). Natural seasonal dynamics in water temperatures such as increased spring temperatures that plateau in late summer occurred in reaches above the dam (JA-JC) and in the unregulated Cowpasture River (Fig. 7.5B) but they have been completely eliminated in the tailwaters, now characterized with stable thermal conditions that exhibit minimal daily variation. The degree of thermal alteration increased as the season progressed, with the greatest effects of the dam evident in the summer months. Water temperatures recorded in the downstream river segments, however, suggest that thermal conditions did recover, but at varying degrees. Rates of recovery were the highest in the summer (May – July) compared to the spring (March – April), but in all instances, unregulated or "normal" water temperatures were not achieved in the tailwaters. At the lowest downstream reaches (J6-J7) water temperatures were still markedly lower, although some seasonal signature became more evident. Varying patterns of thermal recovery at different distances from the dam and times of year were influenced, in part, by the addition of warm water from the tributaries.

Tributaries of the Jackson River exhibited higher water temperatures than the mainstem segments throughout the season (Fig. 7.6A), while the opposite was true for the Cowpasture River, where mainstem segments were slightly warmer compared to cooler, spring-fed tributaries typical of the region (Fig. 7.6B). Importantly, Jackson River tributaries were characterized by different thermal regimes – Cedar Creek had the highest water temperatures while Indian Draft was only slightly warmer than the cool mainstem. The minimal thermal recovery in the Jackson River during the spring (Fig. 7.5A) corresponded with minimal temperature differences compared to the tributaries during this time of season, whereas higher rates of recovery in the summer matched well with greater mainstem-tributary temperature differences (Fig. 7.6A). In summary, average water temperatures over the entire spawning season illustrated a gradual, non-linear recovery downstream from the dam, with punctuated temperature spikes in segments immediately downstream from tributaries (Fig. 7.7). As expected, water temperatures showed a longitudinal increasing trend along the Cowpasture River ($R=0.92$, $F_{1,8}=43.8$, $P<0.001$), although tributary effects were not evident (results not shown).

Substrate characteristics

Results from the Wolman pebble counts showed that Gathright Dam had varying effects on the substrate characteristics of the Jackson River. Median substrate particle size (D_{50}) was much larger directly below the dam (J1), but recovered very quickly in subsequent tailwater segments (Fig. 7.8A). Coefficient of variation in D_{50} was within the natural range of values observed in the Cowpasture River, and notably the greatest substrate heterogeneity was found in the three mainstem segments located immediately downstream from tributaries (Fig. 7.8B). Mean % embeddedness was substantial higher in the tailwaters, exhibited a sharp, step-shaped recovery below Cedar Creek, and reached normative values in the lowest reaches of the Jackson River (Fig. 7.8C). Negative longitudinal trends for the Cowpasture River were only detected for D_{50} (R=-0.69, $F_{1,8}$=7.1, P=0.029).

Benthic macroinvertebrate biomass

Macroinvertebrate prey biomass as measured by Ash-Free Dry Mass (AFDM) was heavily affected by Gathright Dam and exhibited a gradual, non-linear recovery with increasing downstream distance (Fig. 7.9). AFDM recovery was relatively rapid and obtained levels equal to the Cowpasture River approximately 10 kilometers below the dam (J4), although it is interesting that AFDM levels were much higher in the upstream reaches of the Jackson River. Compared to these reaches, the tailwaters did not achieve normative levels until approximately 15-20 kilometers (J5-J6) downstream. These results also provided strong evidence for punctuated increases in AFDM below tributary confluences, a pattern that was not evidence for the Cowpasture River (*results not shown*). Positive longitudinal trends for the Cowpasture River were detected for AFDM (R=0.87, $F_{1,8}$=24.0, P=0.001).

Downstream fish recovery and its association with environmental disturbance

Patterns of fish population recovery

A total of 18,601 fish comprising 43 species in 5 families were collected. Tailwater reaches of the Jackson River contained, on average, 11 species (range 4 to 15 species), whereas upstream reaches of the Jackson River and the entire Cowpasture River contained 20 species (17 to 25) and 24 species (20 to 28), respectively. To account for any potential differences in the composition of the regional species pools of the two rivers we restricted all subsequent analyses to those fish species that occurred in both the Cowpasture River and the Jackson River above Gathright Dam (26 out of the 43 species sampled: Table 7.2). Notably, these 26 species were all spring-spawners and do not include the two salmonid species present (and managed for) in the tailwaters: rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*). Overall fish densities were > 2.5 times lower in the tailwaters of the Jackson River (1.4 fish·m^{-2}) compared to the Cowpasture River (3.5 fish·m^{-2}). However, a more realistic comparison excludes the highly abundant coldwater species, mottled sculpin (1.0 fish·m^{-2}) from the analysis, after which we found that fish densities were ≈ 9 times lower in the tailwaters of the Jackson River (0.4 fish·m^{-2}). Greater differences were observed for tributaries where fish densities were > 26 times higher than the tailwaters (0.4 fish·m^{-2} vs. 10.6 fish·m^{-2}), whereas fish densities of the mainstem and tributaries of the Cowpasture River were similar (3.5 fish·m^{-2} vs. 4.5 fish·m^{-2}).

Gathright Dam had substantial effects on the occurrence and density of fishes in the tailwaters of the Jackson River (Fig. 7.10). In total, 10 species were absent (i.e., 2 sunfishes, 6 minnows (shiners), 1 darter and 1 madtom) and the remaining 16 species showed varying responses to river regulation. A number of species were severely impacted and were rare in the tailwaters (e.g., rockbass, central stoneroller, fallfish); others were less impacted (e.g., rosyside dace, bluntnose minnow) or not impacted (e.g., torrent sucker), and some obtained higher densities (e.g., mottled sculpin, blacknose dace), compared to levels in the Cowpasture River. Patterns of downstream recovery were highly dynamic and varied greatly among the fish species. Importantly, in all cases spatial patterns were highly non-linear with respect to watercourse distance from Gathright Dam and were influenced, in large part, by the location of tributaries.

Recovery gradients were compared to natural longitudinal patterns in the Cowpasture River, which for no species showed evidence of variation with watercourse distance and therefore were presented as mean values across all river segments. Five species of the Jackson River were considered to completely recover in the tailwaters (i.e., northern hogsucker, blacknose dace, longnose dace, fantail darter and longfin darter), and these species all did so at similar downstream distances from the dam (≈ 10-15 kilometres and immediately below Falling Spring). Other species showed gradual recoveries that were punctuated immediately below tributary confluences, but failed to achieve levels observed in the Cowpasture River (e.g., central stoneroller, cutlips minnow, bluehead chub (Plate 7.1)). Finally, as mentioned above, our results showed that Gathright Dam has completely eliminated 10 species, representing almost 50% of the expected species richness. Downstream patterns of fish densities suggested that tributaries play an important role in the spatial recovery of many species. In fact, for almost all species, tributaries exhibited substantially higher densities compared to the Jackson River mainstem. For example, blacknose dace, longfin darter and longnose dace were 14, 9 and 5 times denser, respectively, in the tributaries compared to the tailwaters (Fig. 7.10). Furthermore, in some instances fish species were absent from the mainstem and only occurred in the adjoining tributaries (e.g., smallmouth bass).

Lastly, we found strong evidence for a negative relationship between fish densities and increasing distance to Gathright Dam, i.e., increasing fish densities were associated with increasing upstream distance from Gathright Dam (Fig. 7.10). This pattern was evident for 12 of the 15 minnow species, whereas the opposite pattern was observed for the piscivorous smallmouth bass, which exhibited higher-than-average (compared to the Cowpasture River) densities in the upstream segments and showed a decreasing trend with increasing distance from the reservoir.

Patterns of fish assemblage recovery

Fish communities downstream from Gathright Dam were considerably more depauperate compared to the Cowpasture River, on average containing only half the species richness (Fig. 7.11A). Recovery in species richness plateaued at 11-12 species approximately 15 kms downstream from Gathright Dam, and was punctuated below the tributaries, in particular below Cedar Creek where richness jumped from 3 to 10 species. Interestingly, species gained in J2 (downstream from Cedar Creek) were subsequently lost in J3 and J4, but then regained in J4 (downstream from Falling Spring), again indicating the importance of proximity to tributary populations. In fact, species richness of the tributaries was, in general, much higher than the tailwaters and similar to the richness of Cowpasture River tributaries (13, 15 and 18 species). Differences in species richness were mirrored by differences in community similarity (Fig. 7.11B). Communities immediately below Gathright Dam (J1) were only 10% as similar with the communities of the Cowpasture River, which slowly recovered to 35-40% after 15 kilometers below Gathright Dam, and interestingly changed little beyond this point. Community similarity also showed strong punctuated increases below tributaries. Community similarity between the tributaries of the Jackson River and Cowpasture River (34%) was much lower that the similarity among Cowpasture River tributaries (64%). Overall fish density (summed across all species, excluding mottled sculpin) showed an interesting trend where recovery was minimal for the first 10 kilometers below the dam, after which it exhibited a step-shaped increase below the confluence with Falling Spring (Fig. 7.11C). In general, recovery in fish density was minimal in the Jackson River tailwaters, and was consistently approximately 3 times lower than the Cowpasture River. Fish densities of the Jackson River tributaries, however, were extremely high and far exceeded densities observed in the Cowpasture River tributaries (0.78 – 1.92 fish·m^{-2}). Species richness and total fish density above the dam showed strong increasing trends with increasing distance upstream from the reservoir, in both cases exhibiting lower levels than the Cowpasture River for JA and JB and achieving higher levels in JC (Fig. 7.11A,C).

Associations between fish and environmental recovery

Based on the GLMs and AIC$_c$ model selection our results indicate that fishes exhibit species-specific responses to downstream alterations in flow regimes, water temperatures, substrate conditions and insect prey availability, and they point to the importance of particular environmental drivers for shaping patterns of assemblage recovery in the tailwaters. For the 15 fish species present in the tailwaters (excluding 10 species that were absent and mottled sculpin that was more abundant), results from the GLMs and AIC_c model selection showed that downstream recovery was related to both individual and additive patterns of environmental recovery (Table 7.3). AFDM, water temperature, flow regimes and embeddedness were the most important predictors of fish recovery for 5, 4, 1 and 1 species, whereas the remaining 4 species showed the strongest association with multiple environmental drivers. The best models explained between 20 and 95% of the variation in the downstream recovery of fish densities, with the exception of rosyside dace that showed a very weak association with environmental recovery (9%). The relative importance of each environmental gradients in explaining fish density recovery was estimated using a weighted sum of the Akaike weights across all candidate models (Table 7.4). In support of the best candidate models, spatial recovery in AFDM, flow regimes and water temperatures showed the greatest overall importance across all species.

Downstream recovery in flow regimes was consistently the most important factor related to the spatial recovery of fish diversity and community composition (Table 7.5). Species richness was best predicted by mean flow recovery, and the evidence ratio suggests that models using recovery in embeddedness and recovery in AFDM are also reasonable competitors. Downstream recovery of community similarity was best predicted by the recoveries of mean and variance in flow regimes and substrate embeddedness; this model is over two times more likely than the second-best model that contains only mean flow recovery. Total fish density was best predicted by recoveries in both mean and variation of flow regimes, although the evidence ratio suggests that a model with just mean flow recovery is equally powerful. Relative importance of the environmental variables in described patterns of assemblage recovery across all candidate models supports the above findings (Table 7.6). Mean flow recovery was the most important for all models, followed by either substrate embeddedness or variance in flow regimes.

Discussion

Dams and river regulation constitutes one of the primary sources of disturbance in aquatic ecosystems, yet little empirical evidence exists to indicate to what degree fish populations and communities respond spatially to downstream gradients of environmental disturbance. In fact, it was over a decade ago when Kinsolving and Bain (1993) first appealed to the scientific community that "quantitative information on spatial recovery gradients is needed quickly to maintain much of the world's declining riverine fish faunas," but this call-to-action has gone largely unheeded. Qualitatively, studies have responded with broad overarching statements that the effects of stream regulation "may extend tens or even hundreds of kilometers downstream," yet there remains a paucity of quantitative data addressing the expected attenuation of environmental disturbances below dams. As a result, studies continue to make the simplifying assumption that fish recover linearly below dams in response to linear attenuation of environmental disturbance (e.g., Kinsolving and Bain 1993, Phillips and Johnston 2004), although such studies also recognize that non-linear recovery gradients may be a more appropriate hypothesis. Until now, such hypotheses have remained largely untested, yet we argue they must be assessed to gain a more predictive understanding of the impacts of dams on riverine ecosystems and to fully appreciate the spatial dimension of disturbance gradients in stream ecology.

Environmental disturbance gradients and the non-linear recovery of fish assemblages

Previous to this study, stream fish ecologists had generally limited their investigations of disturbance to single events or sources, thus providing limited insight into how communities will respond to multiple environmental disturbances. Our study is the first to document the recovery of a fish assemblage to multiple environmental disturbance gradients that are caused by river regulation and that are hypothesized to attenuate with increased downstream distance from the dam. The disturbance gradient downstream from Gathright Dam largely attenuates non-linearly in response to the punctuated contributions of tailwater tributaries.

In this study we apply a novel approach that links a conceptual rain-runoff model to physical watershed descriptors of unregulated, gauged streams in the Upper James River to reconstruct pre- and post-dam discharge records for a series of tailwater river segments in the Jackson River. This approach was successful, in that the modeling process was highly accurate and allowed us to quantify the downstream recovery of specific components of the flow regime according to a comprehensive suite of hydrologic indices.

The most striking result from this analysis was that the magnitude, duration, frequency, timing and rates of change in flow conditions showed markedly different patterns of recovery below the dam, with some components completely recovering while others showed minimal recovery. River regulation has substantially increased the magnitude of flows during the summer and early fall when normally low flows in unregulated rivers would favour post-spawning recruitment of spring-spawning fishes (Humphries and Lake 2000). In fact, high flow events subsequent to spawning have been shown to cause substantial mortality to small young-of-the-year fish (Harvey 1987), whereas stable low-flow conditions have been correlated with increased juvenile abundances (Schlosser 1985, Freeman et al. 1988). Such negative effects of high flow conditions in post-spawning months have been observed in rivers regulated by hydroelectric dams (Freeman et al. 2001), and our results suggest that such impacts may also be evident in rivers regulated by flood control dams. In contrast, the magnitude of flows during winter months was lower in post-dam years, the time at which rainbow and brown trout spawn in the Jackson River. Notably, both summer and winter flows showed only moderate recovery in the tailwaters. The magnitude of short-duration, low flow events and baseflow were much larger in post-dam years due to augmented summer releases from the reservoir, and although these conditions persisted throughout the tailwaters they did show strong punctuated recovery downstream from the tributaries. Prolonged and elevated low-flow discharges have received relatively little attention, especially for fish, although impacts on macroinvertebrates (e.g., Pardo et al. 1998) and riparian communities (e.g., Maingia and Marsh 2002) have been documented. The timing of annual minimum and maximum discharge were also delayed in post-Gathright years and showed no recovery downstream. This finding is particularly concerning given the importance of the timing of flows for synchronizing environmental cycles and the reproductive cycles of riverine fishes (Gehrke et al. 1995). A positive result was that, although Gathright Dam has stabilized flows immediately below the dam, temporal variability in terms of rising and falling rates and daily flow reversals showed strong patterns of recovery in the tailwaters that were punctuated below tributaries. Regaining any level of temporal variability in flow conditions is considered essential for fish recovery given its importance in structuring the taxonomic (Horowitz 1978, Schlosser 1985) and functional (Poff and Allan 1995) composition of fish assemblages.

Not surprisingly, thermal regimes below Gathright Dam reflect strict management practices aimed at maintaining a productive tailwater fishery of rainbow and brown trout. Water temperatures released from the dam did not exceed 15.3°C during the spring-summer period, when normal temperatures would approach 25.0 – 30.0°C much more favourable for native warmwater species. The degree of thermal modification varied over the spring-summer period, reaching the greatest levels during the beginning of summer, and did not recover even after 25 kms below the dam. Downstream patterns of thermal recovery support the notion that warmwater inputs from tributaries play an importance role (Ward 1985). We found that water temperatures of reaches between tributaries appeared to recover linearly with distance downstream, whereas punctuated spikes in mainstem water temperatures were evident immediately below tributary confluences.

We found that the influence of tributaries on tailwater thermal recovery depended not only on the temperature of the receiving water, but also on the position of the tributary in relation to the dam. In terms of thermal recovery in the Jackson River, our results suggest that tributary position is the most important factor dictating a tributary's contribution to mainstem water temperatures. Tributaries located at increasing distances from Gathright Dam had increasing influence on tailwater temperatures, even though tributary size and water temperatures decreased along this same gradient. For example, Cedar Creek is located immediately below Gathright Dam (1 km) and although it is the largest tributary (twice the drainage area compared to the other tributaries) and contributed the warmest waters, its impact on mainstem water temperatures was much smaller compared to Falling Spring and Indian Draft. Given that the rate of thermal recovery will depend, in large part, on the number and spatial arrangement of warmwater tributaries, it is not surprising that recovery distances vary greatly among river systems. For example, thermal recovery of the River Svratka, former Czechoslovakia, required over 40 km (Ward 1982), in the Murray River, Australia, altered thermal regime were still apparent after 200 km (Walker 1979), and using rates of maximum summer warming rates, Stevens et al. (1997) estimated that for water temperatures to fully recover in the Colorado River, United States, a mainstem distance of 930 km would be required (a distance that is currently prevented by other downstream dams).

The presence of Gathright Dam and the regulation of flow regimes resulted in the modification of substrate characteristics in the tailwaters of the Jackson River. Streambeds were highly embedded immediately below Gathright Dam and characterized by large particle sizes with low substrate heterogeneity, a pattern consistent with reduced scouring flows associated with the observed stabilization of flow regimes and decline in frequency of high flow events in post-dam years. With increasing downstream distance streambed embeddedness decreased and substrate size increased, producing a recovery pattern that was strongly influenced by the location of tributaries in the tailwaters. This was particularly evident below the first downstream tributary, Cedar Creek, where substrate size and heterogeneity rebounded to within a natural range and embeddedness showed a sharp decrease toward unregulated conditions. These patterns suggest that Cedar Creek contributes fine sediments, and correspond to our previous finding of punctuated increases in the frequency of high flow events in the main channel below Cedar Creek, thereby mobilizing fine substrata and decreasing streambed embeddedness.

In contrast to the recovery of physical characteristics, total benthic macroinvertebrate biomass recovered relatively rapidly downstream from Gathright Dam and exceeded higher than normal levels in the farthest downstream reaches. We found strong evidence for punctuated increases in total biomass immediately below tributaries, supporting the notion that macroinvertebrates are likely responding to abrupt positive changes in environmental conditions (e.g., increased water temperature) and that tributaries may be providing an important source of colonists for the main channel (cf. Vinson 2001). However, it is important to note that total abundance and/or biomass of macroinvertebrates may recovery quickly, but species density and community richness and composition often show much more gradual patterns of recovery (Ward and Stanford 1979, Voelz and Ward 1989, 1990, 1991). Detailed investigation of downstream patterns of macroinvertebrate recovery is the focus of a subsequent paper, but notably, preliminary analyses have shown similar patterns for the Jackson River (*unpublished data*).

In summary, we found that environmental recovery gradients were highly non-linear due to the punctuated inputs of unregulated tributaries entering the regulated mainstem. The impacts of tributaries on mainstem environments are potentially numerous and certainly complex, not least because effects will vary between tributaries and in time as a function of the volume and character of the water and sediment that is delivered (Rice et al. 2001) relative to mainstem. Therefore, the degree to which tributaries lessen the influence of dams on mainstem rivers is expected to vary across and within regulated systems. Our results provide strong evidence for role of tributaries in shaping environmental and macroinvertebrate recovery gradients downstream from Gathright Dam, although not all tributaries contributed equally to patterns of recovery. Recent conceptual models have been advanced that stress natural discontinuities in riverine networks and address the importance of tributaries in unregulated systems, such as the link discontinuity concept (Rice et al. 2001) and the network dynamics hypothesis (Benda et al. 2004), and here we provide the first empirical evidence supporting the importance of these concepts in understanding the spatial recovery of fish assemblages in regulated rivers.

Effects of river regulation on disturbance regimes and their subsequent effects on fish species are expected to vary greatly. Populations will respond differently to disturbance depending upon the type of disturbance and the resilience of the species to that disturbance (Holling 1973). Understanding this variability is key to the better management and successful conservation of fish inhabiting regulated rivers. Patterns of fish recovery below Gathright Dam took a number of forms, including no recovery (i.e., extirpation from the tailwaters), little recovery, erratic and punctuated recovery below tributaries, threshold recovery, gradual recovery, and complete recovery. In many instances, recovery trajectories followed expectations based on species life histories or response requirements. Fluvial specialists (i.e., species requiring flowing-water habitats throughout life), including white sucker, torrent sucker, fantail darter and longfin darter (scientific names in Table 7.2), showed the strongest associations with recovery in flow regimes, warmwater species showed the strongest relationships with water temperature recovery (e.g., rockbass), species requiring specific spawning substrates were strongly associated with recovery in substrate embeddedness (e.g., bluehead chub), and insectivore specialists showed the strongest relationships with recovery in AFDM (e.g., blacknose dace, longnose dace). These results are corroborated by previous studies showing that those species dependent on flow conditions (i.e., obligate riverine species) are particularly prone to dam disturbances (Penczak and Kruk 2000) and show strong downstream recovery in regulated rivers (Kinsolving and Bain 1993, Travnichek et al. 1995).

One of the most important contributions of this study is the illustration of the potential effects of Gathright Dam on upstream riverine fish assemblages. The abundance of small-bodied minnow species, which are highly susceptible to predation by smallmouth bass (Chapleau et al. 1997, Findlay et al. 2000, Jackson 2002), was highly depressed above the dam and showed a strong recovery with increasing distance from the reservoir. An opposite trend was observed for smallmouth bass, suggesting that upstream reaches may be increasingly vulnerable to invasion and predation by facultative riverine species that become established in reservoirs and move upstream in large numbers. Indeed, previous studies have implicated this phenomenon as a major factor leading to the extirpation of fishes above dams (Ruhr 1956, Erman 1973, Winston et al. 1991). Importantly, although small sample sizes limited our ability to statistically test these patterns, our results clearly illustrate the importance of examining upstream effects of dams and impoundments and highlights how little we know about possible mechanisms by which these effects are transmitted (Pringle 1997).

Tributaries as critical thermal refugia for warmwater fishes in trout-managed tailwaters

Tributaries play an important physical role in natural riverine systems by contributing water and sediment that shape the morphology of the receiving rivers (Benda et al. 2004), and as illustrated in this study, initiating the recovery of environmental conditions downstream from dams. More directly, tributaries are critical components of the riverine landscape for fishes (Schlosser 1991), serving as dispersal corridors that support high fish diversity (Osborne and Wiley 1992) and providing thermal refugia during periods of temperature stress (Magnuson 1979). In natural systems tributaries may have higher summer temperatures than the main channel if they are smaller or more exposed to solar radiation, whereas heavily-canopied or spring-fed tributaries tend to be cooler in the summer and slightly warmer in the winter than the main channel (Ward 1985). The latter case is true of our study region and was illustrated in the Cowpasture River where spring-fed tributaries were slightly cooler than the mainstem during the spring-summer period. In contrast, river regulation and the establishment of a tailwater trout fishery in the

Jackson River has resulted in the opposite pattern, in which tailwater tributaries exhibited substantially warmer temperatures than the regulated river channel. Temperature differences are amplified during the fish-spawning season when water temperatures should be naturally rising with air temperatures (as seen in the Cowpasture River), but remain low because of dam operations that strictly release unseasonally cold water for the tailwater trout fishery.

Fish actively seek out thermal refugia when stream temperatures are outside their preferred range, although until now the majority of studies have focused on documenting coldwater dependent fish species (mainly salmonids) persisting in warm rivers during the summer months by seeking groundwater-cooled areas (e.g., Ebersole et al. 2003). Stark thermal differences between tributaries and the mainstem of the Jackson River suggest that tributaries may serve as critical sources of thermal refugia for warmwater fishes. For example, fish densities were, on average, 26 times greater in the tributaries compared to the mainstem (range from 9 to 45 times greater), whereas the same comparison for the Cowpasture River revealed minimal differences. Moreover, differences between tributary and mainstem fish densities decreased with declining differences in water temperatures as distance downstream from Gathright Dam increased. No such patterns was seen in the Cowpasture River.

In times when the mainstem cools to stressful temperatures due to management for the trout fishery, many of the unregulated tributaries remain within a suitable temperature range for development and life history events. For example, the natural temperature regime of a river provides thermal cues that stimulate fish spawning behaviour (Magnuson et al. 1979), and the disruption of these cues by the release of unseasonably cold water from deep-release reservoirs during the spring and summer have been associated with the decline of native fish species (Preece and Jones 2002). The mechanism behind such observations is likely the interruption of spawning and resorption of maturing eggs. By comparing the temperature requirements for spawning (both minimum threshold temperatures and timing) with water temperature data in the Jackson River tailwaters and tributaries, it is possible to assess the potential mechanisms by which river regulation for trout production affects spawning opportunities for warmwater fishes. This analysis will be the focus of a subsequent study, but suffice to say that tailwater temperatures failed to reach the minimum spawning temperature requirement for 50% of the species pool (13 out of 26 species), whereas spawning temperatures were met for all species in the tributaries (*unpublished data*). In fact, snorkeling surveys conducted during the study found that the mainstem of the Jackson River was almost completely devoid of gravel nests built by mound-building cyprinids (e.g., bluehead chub, central stoneroller), whereas tributaries contained high nest densities. Such effects are likely much more far-reaching given the dependence of many nest associates (mainly shiner species) that rely on these nests for spawning, a finding that supports the complete absence of shiner species in the Jackson River tailwaters but presence in the tributaries. In short, if not for tributaries a number of species would likely be completely eliminated from the tailwaters.

In summary, refugia are recognized as critical for the recovery of fishes from disturbance (Sedell et al. 1990), and our results suggest that fish colonists are derived from thermal refugia in unregulated tributaries downstream from Gathright Dam, rather than from refugia in the regulated river channel. These refugia may provide opportunities for fish to compensate for reduced growth, maturation and reproduction that would be experienced in the cold tailwaters, although the extreme species packing that occurs in the tributaries is likely to have a number of detrimental consequences. For example, the limited habitat available in tributaries will intensify competition for space and resources among individuals and may lead to decreased health. Preliminary evidence suggests that this might be the case. Comparisons of individual body condition (based on a relative condition index, K_n) indicate that tributary fishes of the Jackson River are often of lower condition compared to tributary fishes of the Cowpasture River (*unpublished data*). Furthermore, given the correlation of fish movement with stream temperature, our study suggests that Gathright Dam may have a fragmenting effect by restricting fish species to thermally-desirable tributaries and limiting movement among these thermal refugia at least during spring-summer. Such "thermal barriers" to movement may lead to restricted gene flow among isolated tributaries and cause patterns of genetic differentiation that are directly related to fish species thermal tolerances and intrinsic mobility. These questions are currently being explored.

Management Implications

The findings from this study have important implications for the design of monitoring projects and the management of flood control dams. A new paradigm in watershed management focuses on the role of natural flow regimes in maintaining the ecological integrity and function of riverine ecosystems (Poff et al. 1997). According to this perspective, restoration of natural or normative (given that complete restoration is generally not an option) hydrology is considered the key to recovering biodiversity and ecosystem processes in degraded watersheds (Stanford et al. 1996). Managing dams to maintain or improve riverine fish populations, however, first requires a sound understanding of fish responses to downstream gradients of environmental disturbance. This includes knowledge of not only abiotic gradients, such as flow and thermal regimes, but also the specifics of the macroinvertebrate assemblage structure and food base responses. Our study contributes significantly to this understanding by demonstrating the specific aspects of the downstream disturbance regimes that the recovery of fish populations and assemblages are most tightly linked. This information can help guide management strategies by identifying restoration goals aimed at improving environmental conditions for the benefit of multiple species or even entire assemblages.

We must also realize that the benefits of reducing several disturbances are likely to be multiplicative, so that the cumulative benefits of improved management of multiple disturbances are likely to be greater than the benefits resulting from reducing any single disturbance. Moreover, reducing only one source of disturbance may have no biological effect because other limiting disturbances are still present in the tailwaters. For example, cueing to the natural hydrographic and thermal regimes in riverine systems may trigger congregation of fish at spawning sites and increase spawning success in regulated rivers (Jonsson 1991), although it has been shown that spawning for some species may only be initiated if small pulses of high flow events (i.e., normative flows) are synchronized with periods where minimum spawning temperature thresholds are exceeded (e.g., King et al. 1998). Thermal restoration of tailwaters must also be extended in time because fish may start spawning when minimum water temperatures exceed a threshold but then suspend or abort spawning if temperatures fall below the threshold. Moreover, successful spawning will not necessarily lead to high recruitment if water temperatures are not then maintained at appropriate levels for some time for development of the embryos and larvae. Explicit consideration of species' spawning requirements (i.e., timing, length and temperature of spawning) and larval development schedule are particularly important to develop best management scenarios and ensure the successful restoration of tailwater fish assemblages. Dams that are outfitted with multi-level withdrawal structures (such as Gathright Dam) provide the greatest flexibility to meet such demands because dam operators can control both the volume and temperature of water released (Vinson 2001).

It is important to note that dam management need not be considered in opposition to species of direct societal importance in either the tailwaters or the reservoir. For example, Johnson et al. (2004) found that reservoir managers may actually have considerable latitude for new operations of large dams (including increased spring releases) without negative consequences to the reservoir. Furthermore, it must be recognized that management practices can have a number of unanticipated consequences if current physical and biological constraints (e.g., invasive species) are not taken into account (Frissell and Bayles 1996). This is not an issue for our study system given the low number of non-native species, but it could be extremely important in other systems (e.g., Marchetti and Moyle 2001).

In summary, knowledge of the relative importance of environmental drivers shaping downstream fish recovery will play an important role in recognizing complex interactions shaping fish recovery and incorporating them into management plans. Our study suggests that in the same way that short-term studies are often inappropriate for long-term management of regulated rivers (Petts 1980), it is likely to be equally inappropriate to only consider small spatial scales (Fausch et al. 2002). Furthermore, no matter what specific management actions are taken, it is very apparent that warmwater tributaries will play a critical role for assisting the rehabilitation process by providing a source of fishes for the recolonization the main channel.

Toward an unifying understanding of dam disturbances in regulated rivers

Understanding and predicting how dam-induced disturbances affect riverine fish faunas requires us to understand the processes involved. Bender et al. (1984) distinguished between pulse perturbations, defined as short-term alterations in the abundance of species within a community followed by relatively rapid biological recovery, and press perturbations, defined as sustained alterations to the community often resulting in the elimination of species and establishment of a new community (called biological accommodation). In an important conceptual refinement, Glasby and Underwood (1996) discriminated between discrete and protracted press and pulse perturbations to reflect the idea that the effects from a particular disturbance can have either short-term or long-term effects on the system. Although such distinctions could be chalked up to simple semantics, they are required to avoid ambiguity surrounding the definition of an ecological disturbance (Rykiel 1985), and we argue are necessary to differentiate how different environmental disturbances stemming from river regulation and dams operated for different purposes may have specific, and possibly divergent, effects on riverine ecosystems. We explore this topic in greater detail below.

River regulation modifies long-term flow and thermal regimes, and therefore should be considered a discrete or protracted press perturbation, depending on whether fish assemblages exhibit short-term recovery or continued accommodation to the disturbance, respectively. Our results suggest that dams may represent both a discrete and protracted press perturbation depending on the component of the fish fauna is being examined (species vs. assemblage) and what direction impacts are being investigated (upstream vs. downstream). For the species pool, river regulation appeared to represent both discrete and protracted disturbances depending on the particular species. This result is not surprisingly given that we expect different species to show different capacities for resilience and recovery as a function of life history and evolutionary history (Poff and Ward 1990). An interesting finding was that the upstream recovery of fish assemblages was relatively rapid and natural conditions were reached ca. 10 kms above the reservoir, indicating that Gathright Dam may represent a discrete press disturbance on upstream fish assemblages. In contrast, species richness and community composition exhibited only moderate recovery and established new levels and composition in the tailwaters, suggesting a downstream accommodation of fish assemblages to a protracted press disturbance.

By comparing fish assemblages below dams with different operation strategies we can gain important insight into how different types of press disturbances differentially influence spatial gradients of fish recovery. For example, we might expect that the ecological implications of a flood control impoundment (such as the Jackson River) are distinctly different from those of a hydroelectric facility, and similarly, a deep-release dam may have quite different effects than a surface-release reservoir. We can qualitatively assess such questions by comparing our results (flood-control dam with temperature modification) with those of three regulated systems in south-eastern US and that examined the downstream recovery of fish assemblages below a flood-control dam without thermal modification (Phillips and Johnston 2004), and below a hydrologic dam with thermal modification (Hunter 2003), and below a hydrologic dam without thermal modification (Kinsolving and Bain 1993). Species richness and community composition exhibit gradual downstream recovery below flood control dams both with (our study) and without modifications to the thermal regimes (Phillips and Johnston 2004, Fig. 2, 3), with some evidence of accommodation after 30 kms downstream. Similarly, fluvial species exhibited strong downstream recovery in our study, as well as downstream of rivers regulated by hydroelectric facilities (Kinsolving and Bain 1993, Fig. 5,6; Hunter 2003, Fig. 1.10). Finally, a particularly interesting result was that the recovery of total fish density and species richness for dams with different flow operations but both managed for tailwater trout fisheries (i.e., coldwater releases) were remarkably similar (Hunter 2003). Conclusions from this qualitative comparison of studies suggest that fish recovery at the community-level may be similar among regulated rivers despite different flow and thermal disturbance regimes. More formal investigations of such comparisons are required in the future to better elucidate the potential universality by which river regulation may influence fish assemblages.

Conclusion

Our results illustrate, for the first time, the importance of multiple gradients of environmental disturbance for shaping the downstream, non-linear recovery of fish assemblages to river regulation. We provide strong evidence for the value of tributaries for promoting downstream recovery of environmental conditions and providing permanent thermal refugia for native warmwater fishes in the tailwaters. To date, the importance of tributaries for warmwater fishes has not been recognized and we argue that a better understanding of their role is needed to protect remnant warmwater fish assemblages from the adverse effects of coldwater releases established for trout fisheries.

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Table 7.1. Results of the Indicators of Hydrologic Alteration analysis for the Jackson River. Values represent pre-Gathright Dam (1960-1979) and post-Gathright Dam (1983-2002) hydrologic indices (monthly magnitudes presented in cubic meters per second) and percent deviation (Alter) according to the comparison of pre- vs. post-Gathright Dam indices (see Methods). The 33 hydrologic indices are divided into 5 groups representing different components of the flow regime. Group means are computed as the mean of all deviations (in absolute values) within the group. Methodology and calculations follows Richter et al. (1996). Indicators of Hydrologic Alteration for measures of dispersion are presented in Appendix 7.4.

Indicator of Hydrologic Alteration	**River Segment**														
	JC			**JB**			**JA**			**J1**			**J2**		
	Pre	**Post**	**Alter**	**Pre**	**Post**	**Alter**	**Pre**	**Post**	**Alter**	**Pre**	**Post**	**Alter**	**Pre**	**Post**	**Alter**
Monthly magnitude															
October	2.6	1.3	52	2.7	1.4	47	2.6	1.7	-36	7.2	5.4	-25	7.6	5.7	-25
November	2.7	2.5	8	2.9	2.9	2	3.1	3.2	-4	6.7	4.8	-28	6.5	5.6	-14
December	4.1	4.1	0	4.6	4.6	0	5.4	5.3	-2	10.3	4.8	-54	11.4	6.3	-45
January	5.4	4.4	18	5.5	5	9	5.6	5.7	-2	13.5	8.3	-39	14.8	9.8	-34
February	6.5	5.5	15	6.7	6.3	6	7.4	6.9	-7	16.8	13.3	-21	17.4	15.1	-13
March	7.7	6.8	11	8.1	7.8	4	9	8.9	1	18.9	22.7	20	20.4	24.4	20
April	5.9	4.7	20	6.2	5.3	15	6.6	5.7	14	16.8	18.7	12	19	20.1	6
May	3.4	4.2	23	3.7	4.6	24	3.6	4.9	35	9.4	16.2	73	9.8	17.1	74
June	2.1	2.1	1	2.3	2.4	1	2.6	2.5	1	4.8	8.1	69	5	8.3	66
July	1.5	1.6	5	1.7	1.8	7	1.8	2.1	14	3.7	8.2	119	3.7	8.6	130
August	1.4	1.6	17	1.5	1.8	15	1.6	1.9	17	3.1	8	163	3.2	8.5	164
September	1.8	1.1	38	1.8	1.3	27	1.7	1.5	14	3.6	7.2	96	3.8	7.5	99
MEAN			**17**			**13**			**12**			**60**			**58**
Magnitude and duration of annual extremes															
1-day minimum	0.1	0.1	55	0.1	0.1	70	0.1	0.2	92	0.3	4.2	1207	0.4	4.5	1124
3-day minimum	0.1	0.1	25	0.1	0.2	38	0.1	0.2	62	0.4	4.2	1049	0.4	4.5	1016
7-day minimum	0.2	0.2	3	0.2	0.2	24	0.2	0.2	49	0.4	4.3	879	0.5	4.6	859
30-day minimum	0.6	0.4	34	0.6	0.4	29	0.6	0.5	14	1.4	4.4	216	1.4	5	248
90-day minimum	1	0.9	12	1.1	1.1	4	1.3	1.3	1	2.6	4.7	78	2.7	5.6	106
1-day maximum	38.5	34.8	10	41.5	37.5	10	47.5	41.9	12	85.6	128.4	50	96.7	134.3	39
3-day maximum	28.3	25.2	11	29.6	27.9	6	34.5	29.9	13	68.5	112.4	64	79.2	116.4	47
7-day maximum	20.1	17.1	15	21.6	19.4	10	22.9	21.5	6	51.4	71.5	39	59.2	76.1	28
30-day maximum	12.8	10.9	15	12.5	12.1	3	12.4	13.5	9	30.3	38.8	28	33.5	42.4	27

90-day maximum	9.3	8.1	12	9.6	9.8	2	10.2	11.8	15	22.7	28.5	26	25	31.2	25
# of zero-flow days	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baseflow	0	0	6	0	0	11	0	0	8	0	0.3	676	0	0.3	667
MEAN			**17**			**17**			**23**			**359**			**349**
Timing of annual extremes															
Julian date of minimum	264	276	7	265	276	6	263	276	7	265	324	32	265	331	36
Julian date of maximum	46	57	6	46	64	10	48	64	9	54	87	18	54	83	16
MEAN			**7**			**8**			**8**			**25**			**26**
Frequency and duration of high and low pulses															
Low pulse count	17	14	-18	17	13	-24	16	12	-25	16	0	-100	16	0	-100
Low pulse duration	5.1	6.3	-24	5.1	6.7	-31	5.3	7.5	-42	5.8	0	-100	6.1	0	-100
High pulse count	25	23.5	-6	23.5	25	-6	23.5	24.5	-4	21	8	-62	20.5	7.5	-63
High pulse duration	3.1	3.1	0	3.1	3.1	2	3.2	3.5	11	4.3	9.1	111	4.4	9.8	123
MEAN			**12**			**16**			**21**			**93**			**97**
Rate and frequency of change in conditions															
Rise rate	3.5	2.9	-20	3.7	3.1	-14	3.7	3.5	-6	7	5.8	-18	6.9	3.9	-44
Fall rate	-1.5	-1.3	-17	-1.7	-1.4	-17	-1.6	-1.5	-3	-2.8	-4.8	71	-3	-2.3	-23
# of reversals	143	134.5	-6	141	133.5	-5	139	130.5	-6	130.5	65	-50	129.5	125.5	-3
MEAN			**14**			**12**			**5**			**46**			**23**

Table 7.1 continued.

Indicator of Hydrologic Alteration	River Segment														
		J3			J4			J5			J6			J7	
	Pre	Post	Alter	Pre	Post	Alter	Pre	Post	Alter	Pre	Post	Alter	Pre	Post	Alter
Monthly magnitude															
October	7.7	5.7	-25	7.7	5.8	-26	7.9	5.8	-26	8.1	6	-26	8.3	6.1	-26
November	6.5	5.8	-11	6.6	5.9	-9	6.7	6.2	-7	6.8	6.7	-2	7	7	0
December	11.6	6.8	-41	11.7	7	-40	12.3	7.7	-37	12.8	8.2	-35	12.9	8.6	-34
January	15.1	10.2	-32	15.2	10.4	-32	15.6	10.9	-30	16.2	11.7	-28	16.5	12.1	-27
February	17.6	15.7	-11	17.7	15.9	-10	18.2	16.9	-8	18.5	17.7	-4	18.9	18.2	-4
March	20.3	24.9	22	20.3	25.1	23	21.1	26.1	24	21.7	27	24	22.1	27.4	24
April	19.5	20.2	4	19.5	20.4	5	20	21.2	6	20.3	22	9	20.4	22.3	9
May	9.9	17.3	75	9.9	17.4	76	10.1	17.9	77	10.4	18.4	76	10.5	18.7	77
June	5.1	8.4	64	5.2	8.4	63	5.4	8.6	61	5.5	8.9	61	5.6	9	61
July	3.8	8.7	130	3.8	8.7	130	4	9	125	4.2	9.2	119	4.3	9.3	117
August	3.3	8.6	163	3.3	8.7	161	3.5	8.8	152	3.7	9	144	3.8	9.1	140
September	3.8	7.6	99	3.8	7.6	99	3.9	7.7	95	4	7.8	94	4.1	7.9	94
MEAN			**56**			**56**			**54**			**52**			**51**
Magnitude and duration of annual extremes															
1-day minimum	0.4	4.6	1094	0.4	4.6	1081	0.4	4.6	1016	0.4	4.7	967	0.4	4.7	959
3-day minimum	0.4	4.6	988	0.4	4.6	978	0.5	4.6	921	0.5	4.7	897	0.5	4.7	896
7-day minimum	0.5	4.6	843	0.5	4.6	844	0.5	4.7	823	0.5	4.8	817	0.5	4.8	807
30-day minimum	1.5	5.2	255	1.5	5.2	256	1.5	5.4	253	1.6	5.5	252	1.6	5.6	255
90-day minimum	2.8	5.8	109	2.8	5.9	109	3	6.2	109	3.1	6.4	108	3.1	6.5	109
1-day maximum	98	135.5	38	98.5	136	38	102.2	137.9	35	106.3	140.1	32	108.1	141.4	31
3-day maximum	81.6	117.3	44	82.7	117.8	42	87.7	119.3	36	91.3	121.3	33	92.1	122.4	33
7-day maximum	60.2	77.2	28	60.6	77.6	28	61.6	79.5	29	62.2	81.4	31	62.5	82.6	32
30-day maximum	34.5	43.5	26	34.9	44	26	37	46.2	25	38.5	47.8	24	39.1	48.8	25
90-day maximum	25.5	31.8	25	25.8	32.1	24	27	33.1	22	27.9	34.4	23	28.4	35	23
# of zero-flow days	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baseflow	0	0.3	666	0	0.3	666	0	0.3	626	0	0.3	597	0	0.3	584
MEAN			**343**			**341**			**325**			**315**			**313**

Timing of annual extremes															
Julian date of minimum	265	331	36	265	335	38	265	335	38	265	329	35	265	325	33
Julian date of maximum	65	83	10	65	83	10	65	83	10	54	83	16	54	83	16
MEAN			**23**			**24**			**24**			**26**			**25**
Frequency and duration of high and low pulses															
Low pulse count	16	0	-100	16	0	-100	15	0	-100	14.5	0	-100	14	0	-100
Low pulse duration	6.2	0	-100	6.2	0	-100	6.5	0	-100	6.5	0	-100	6.6	0	-100
High pulse count	20.5	8	-61	20	8	-60	20	8	-60	19	8.5	-55	19	9	-53
High pulse duration	4.4	9.3	111	4.4	8.9	103	4.3	8.6	102	4.3	8.4	93	4.4	7.9	80
MEAN			**93**			**91**			**91**			**87**			**83**
Rate and frequency of change in conditions															
Rise rate	6.9	4	-42	6.9	4.1	-41	7	4.4	-38	7.1	4.7	-33	7.1	4.9	-30
Fall rate	-3	-2.3	-23	-3	-2.3	-22	-3.1	-2.5	-20	-3.1	-2.6	-16	-3.1	-2.7	-14
# of reversals	129	124.5	-3	129	125	-3	128.5	125.5	-2	126	126	0	127	125.5	-1
MEAN			**23**			**22**			**20**			**16**			**15**

Table 7.2. List of fish species examined in this study. Scientific names follow Jenkins and Burkhead (1994). Other fish species present in the study sites but not included in the analysis include *Cottus girardi* (Potomac sculpin)^{C}, *Cyprinella analostana* (Satinfin shiner)^{C}, *Lepomis macrochirus* (Bluegill)^{JU}, *Nocomis raneyi* (Bull chub)^{C}, *Notropis amoenus* (Comely shiner)^{C}, *Notropis procne* (Swallowtail shiner)^{C}, *Notropis semperasper* (Roughhead shiner)^{C}, *Noturus gilberti* (Orangefin madtom)^{C}, *Oncorhynchus mykiss* (Rainbow trout)^{JD}, *Percina notogramma* (Stripeback darter)^{C}, *Percina peltata* (Shield darter)^{C,JD}, *Percina roanoka* (Roanoke darter)^{C}, *Phoxinus oreas* (Mountain redbelly dace)^{JU,JD}, *Scartomyzon cervinus* (Black jumprock)^{C}, Salmo trutta (Brown trout)^{JU,JD}, *Semotilus atromaculatus* (Creek chub)^{C}. Superscripts denote locations of species occurrence: Cowpasture River (C) and the Jackson River upstream (JU) and downstream (JD) of Gathright Dam.

Scientific Name	Common Name
Catostomidae - Suckers	
Catostomus commersoni	White sucker
Hypentelium nigricans	Northern hogsucker
Thoburnia rhothoeca	Torrent sucker
Centrarchidae - Sunfishes	
Ambloplites rupestris	Rock bass
Lepomis auritus	Redbreast sunfish
Micropterus dolomieu	Smallmouth bass
Cottidae - Sculpins	
Cottus bairdi	Mottled sculpin
Cyprinidae - Minnows	
Campostoma anomalum	Central stoneroller
Clinostomus funduloides	Rosyside dace
Exoglossum maxillingua	Cutlips minnow
Luxilus cornutus	Common shiner
Lythrurus ardens	Rosefin shiner
Nocomis leptocephalus	Bluehead chub
Nocomis micropogon	River chub
Notropis hudsonius	Spottail shiner
Notropis rubellus	Rosyface shiner
Notropis telescopus	Telescope shiner
Notropis volucellus	Mimic shiner
Pimephales notatus	Bluntnose minnow
Rhinichthys atratulus	Blacknose dace
Rhinichthys cataractae	Longnose dace
Semotilus corporalis	Fallfish
Ictaluridae – Bullhead Catfishes	
Noturus insignis	Margined madtom
Percidae - Perches	
Etheostoma flabellare	Fantail darter
Etheostoma longimanum	Longfin darter
Etheostoma nigrum	Johnny darter

Table 7.3. Summary of top General Linear Models for the 15 fish species exhibiting downstream variation in the Jackson River (exhibiting great than 10% of the weight of evidence). For completeness I have included all 26 species examined in this study. Models are sorted from best to worst according to AIC_c values, and the number of parameters does not include the model intercept. Akaike weights are interpreted as the probability that the particular model is the best model given the data and the set of candidate models. Evidence ratio provides the strength of evidence in favour of the best model over all other candidate models. R-squared values are presented for the best GLM candidate models.

Species **Model**	**AIC_c**	**Akaike weights**	**Evidence ratio**	**R^2**
White sucker				
$Flow_{Mean}$ – $Flow_{Variance}$	58.72	0.14	1.00	0.50
AFDM	59.03	0.12	1.17	
$Flow_{Variance}$	59.11	0.12	1.22	
$Flow_{Variance}$ – AFDM	59.27	0.11	1.32	
Embeddedness	59.30	0.11	1.34	
Temperature	59.40	0.10	1.40	
$Flow_{Mean}$	59.42	0.10	1.42	
Northern hogsucker				
AFDM	55.87	0.24	1.00	0.28
Temperature	57.17	0.12	1.92	
$Flow_{Variance}$	57.35	0.11	2.10	
$Flow_{Mean}$	57.58	0.10	2.35	
Torrent sucker				
$Flow_{Mean}$ – $Flow_{Variance}$ – AFDM	41.64	0.87	1.00	0.95
Rock bass				
Temperature	29.03	0.24	1.00	0.36
$Flow_{Mean}$	29.53	0.18	1.28	
$Flow_{Variance}$	30.26	0.13	1.85	
Embeddedness	30.49	0.11	2.07	
Redbreast sunfish		No downstream recovery		
Smallmouth bass		No downstream recovery		
Mottled sculpin		Greater downstream abundance		
Central stoneroller				
AFDM	33.48	0.20	1.00	0.31
$Flow_{Mean}$	33.65	0.19	1.09	
Embeddedness	34.87	0.10	2.01	
$Flow_{Variance}$	34.96	0.10	2.10	
Rosyside dace				
AFDM	58.32	0.17	1.00	0.09
$Flow_{Mean}$	58.38	0.17	1.03	
Embeddedness	58.44	0.16	1.06	
$Flow_{Variance}$	58.65	0.14	1.18	
Temperature	58.78	0.14	1.26	

Cutlips minnow				
Temperature	45.84	0.40	1.00	0.69
Flow$_{\text{Mean}}$	47.67	0.16	2.49	
Common shiner		No downstream recovery		
Rosefin shiner		No downstream recovery		
Bluehead chub				
Embeddedness	40.19	0.22	1.00	0.20
Flow$_{\text{Mean}}$	41.36	0.12	1.79	
Temperature	41.58	0.11	2.01	
Flow$_{\text{Variance}}$	41.60	0.11	2.03	
AFDM	41.64	0.11	2.06	
River chub				
Temperature	51.42	0.24	1.00	0.36
Flow$_{\text{Mean}}$	51.91	0.18	1.28	
Flow$_{\text{Variance}}$	52.64	0.13	1.84	
Embeddedness	52.88	0.11	2.08	
Spottail shiner		No downstream recovery		
Rosyface shiner		No downstream recovery		
Telescope shiner		No downstream recovery		
Mimic shiner		No downstream recovery		
Bluntnose minnow				
Flow$_{\text{Mean}}$ – Temperature – AFDM	34.25	0.87	1.00	0.69
Blacknose dace				
AFDM	49.85	0.40	1.00	0.69
Embeddedness	51.92	0.14	2.82	
Longnose dace				
AFDM	39.44	0.55	1.00	0.91
Flow$_{\text{Variance}}$ – AFDM	42.22	0.14	4.02	
Flow$_{\text{Mean}}$ – AFDM	42.92	0.10	5.69	
Fallfish				
Temperature	40.24	0.26	1.00	0.40
Flow$_{\text{Variance}}$	41.94	0.11	2.34	
Flow$_{\text{Mean}}$	41.95	0.11	2.35	
Margined madtom		No downstream recovery		
Fantail darter				
Flow$_{\text{Variance}}$	50.65	0.29	1.00	0.65
Flow$_{\text{Mean}}$	51.93	0.15	1.90	
AFDM	51.94	0.15	1.91	
Longfin darter				
Flow$_{\text{Mean}}$ – Flow$_{\text{Variance}}$	49.75	0.33	1.00	0.81
Flow$_{\text{Mean}}$	50.65	0.21	1.57	
Johnny darter		No downstream recovery		

Table 7.4. Relative importance of the environmental factors for predicting patterns of fish populations recovery based on the weight of evidence support across all candidate models. Importance is calculated by summing the Akaike weights across all models in which the variable occurs (Burnham and Anderson 2002). The larger the weight, the greater the variable contribution toward predicting fish recovery (largest values are underlined).

Species	$\text{Flow}_{\text{Mean}}$	$\text{Flow}_{\text{Variance}}$	**Temperature**	**Embeddedness**	**AFDM**
White sucker	0.21	0.29	0.13	0.14	0.23
Northern hogsucker	0.18	0.14	0.19	0.18	0.31
Torrent sucker	0.33	0.32	0.02	0.01	0.32
Rock bass	0.24	0.17	0.29	0.16	0.14
Central stoneroller	0.29	0.16	0.18	0.13	0.23
Rosyside dace	0.21	0.19	0.18	0.20	0.21
Cutlips minnow	0.22	0.13	0.46	0.10	0.09
Bluehead chub	0.17	0.19	0.15	0.33	0.16
River chub	0.24	0.18	0.29	0.16	0.14
Bluntnose minnow	0.33	0.02	0.33	0.01	0.31
Blacknose dace	0.10	0.10	0.09	0.22	0.49
Longnose dace	0.09	0.11	0.07	0.07	0.66
Fallfish	0.17	0.19	0.34	0.18	0.11
Fantail darter	0.20	0.36	0.12	0.10	0.21
Longfin darter	0.45	0.29	0.12	0.08	0.07
MEAN	**0.23**	**0.19**	**0.21**	**0.14**	**0.25**

Table 7.5. Summary of top General Linear Models for community recovery in the Jackson River (exhibiting great than 10% of the weight of evidence). Models are sorted from best to worst according to AIC_c values, and the number of parameters does not include the model intercept. Akaike weights are interpreted as the probability that the particular model is best given the data and the set of candidate models. Evidence ratio provides the strength of evidence in favour of the best model over all other candidate models. R-squared values are presented for the best candidate models.

Community metric **Model**	**AIC_c**	**Akaike weights**	**Evidence ratio**	**R^2**
Species richness				
$Flow_{Mean}$	37.10	0.23	1.00	0.67
Embeddedness	37.91	0.15	1.50	
AFDM	38.41	0.12	1.93	
Community Similarity (Jaccards)				
$Flow_{Mean}$ – $Flow_{Variance}$ – Embeddedness	29.43	0.41	1.00	0.96
$Flow_{Mean}$	31.02	0.18	2.21	
Fish density (#/m^2)				
$Flow_{Mean}$ – $Flow_{Variance}$	29.66	0.26	1.00	0.78
$Flow_{Mean}$	29.71	0.25	1.02	
AFDM	31.62	0.10	2.67	

Table 7.6. Relative importance of the environmental factors for predicting patterns of fish community recovery based on the weight of evidence support across all candidate models. Importance is calculated by summing the Akaike weights across all models in which the variable occurs (Burnham and Anderson 2002). The larger the weight, the greater the variable contribution toward predicting fish recovery (largest values are underlined).

Species	**Flow$_{Mean}$**	**Flow$_{Variance}$**	**Temperature**	**Embeddedness**	**AFDM**
Species richness	<u>0.30</u>	0.14	0.14	0.25	0.18
Community similarity	<u>0.37</u>	0.26	0.05	0.26	0.06
Fish density	<u>0.44</u>	0.24	0.12	0.07	0.12

Plate 7.1. Gathright Dam on the Jackson River (top left) and the unregulated Cowpasture River (top right). Pictured (bottom) is the bluehead chub in the Cowpasture River, a common component of warmwater fish assemblages in eastern United States, but almost completely eliminated from the tailwaters of the Jackson River. The photo shows a spawning nest with two male chubs illustrating vibrant spawning colours and tubercles and a group of females each waiting for a mating opportunity. Top photos by Julian D. Olden and bottom photo by Jeremy B. Monroe.

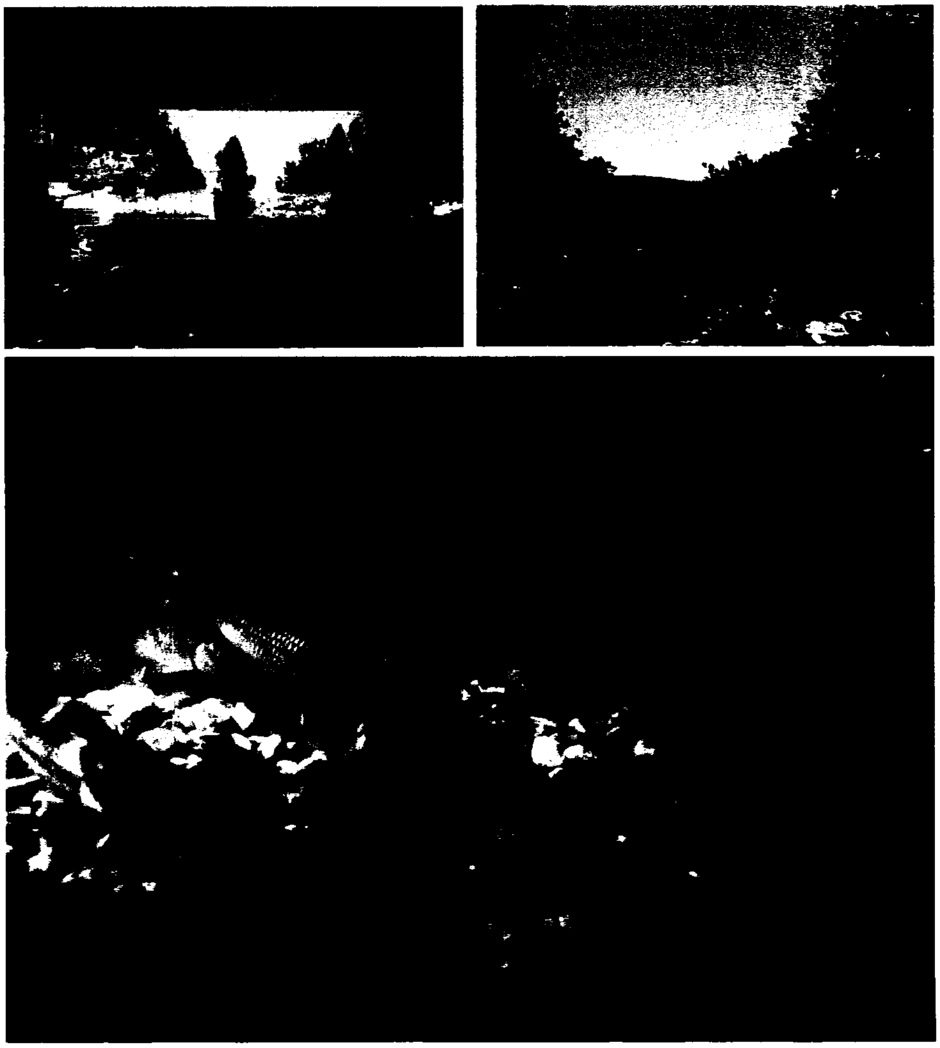


Figure 7.1. Map of the paired study systems located in the Upper James River Basin, Virginia, USA, including the regulated Jackson River (Gathright Dam) and the unregulated Cowpasture River. Mainstem sample reaches are denoted by C1-C10 for the Cowpasture River, and JA-JC and J1-J7 for the upstream and downstream segments of Jackson River (with respect to Gathright Dam), respectively. Permanent tributaries sampled include (listed in downstream order): Cedar Creek, Falling Spring and Indian Draft (Jackson River), and Thompson Creek, Stuart Run and Mill Creek (Cowpasture River).

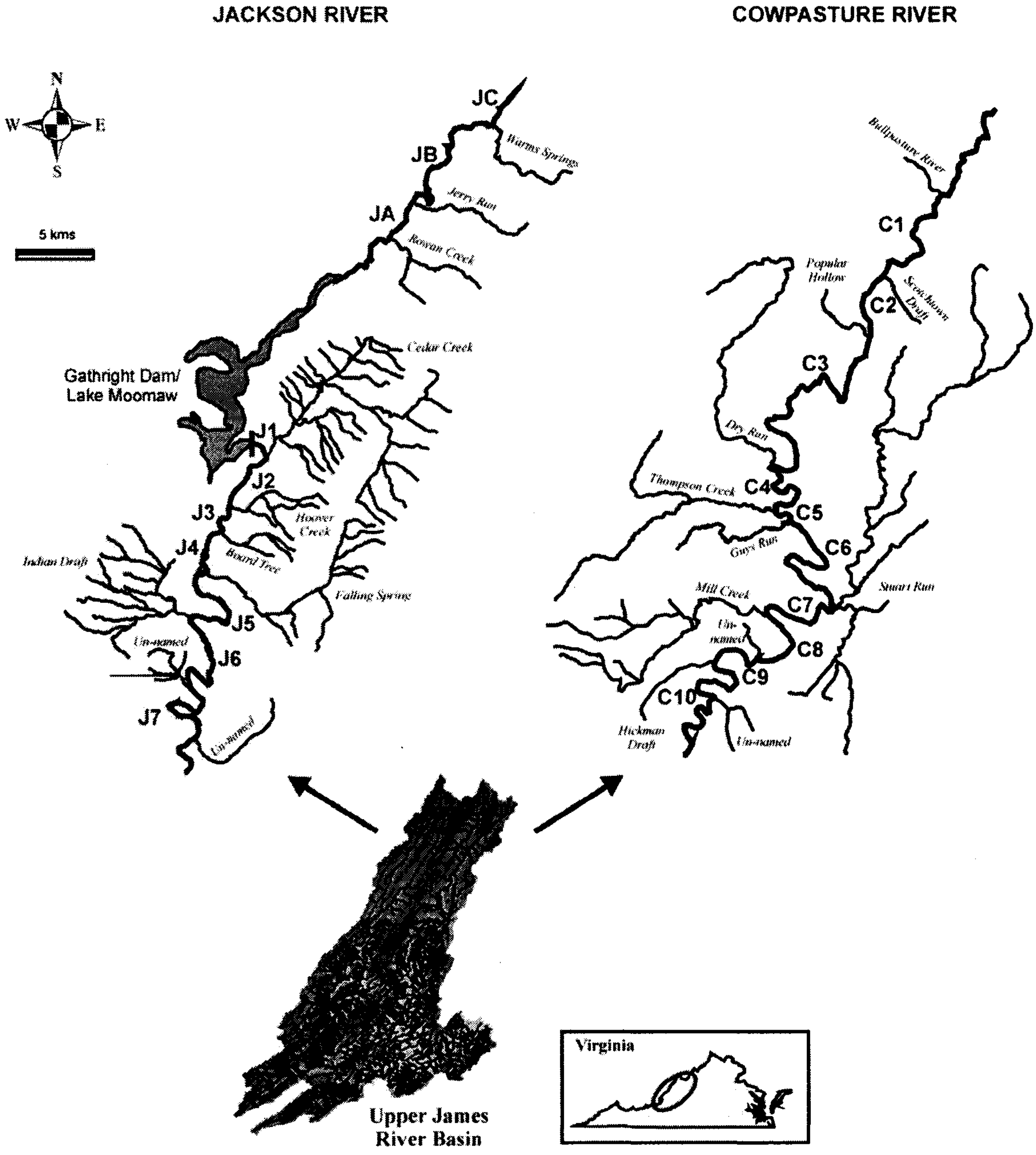


Figure 7.2. Comparisons of flow and thermal characteristics of the Jackson River before and after the construction of Gathright Dam in 1981. Panels (A) Annual hydrographs based on daily discharge (m^3/s) for pre-Gathright years (1974-1978) represented by a dotted-line and post-Gathright years (1983-2004) represented by a solid-line, and (B) Monthly water temperature (°C) for a 18-year pre-Gathright period recorded at Falling Spring (USGS Gauge 02012500, located 11 km downstream from Gathright Dam) and a 8-year post-Gathright period recorded at Gathright Dam (USGS Gauge 02011800). Tailwater thermal regimes were first regulated in 1990 and therefore this year was used to divide pre- and post-Gathright periods in panel B.

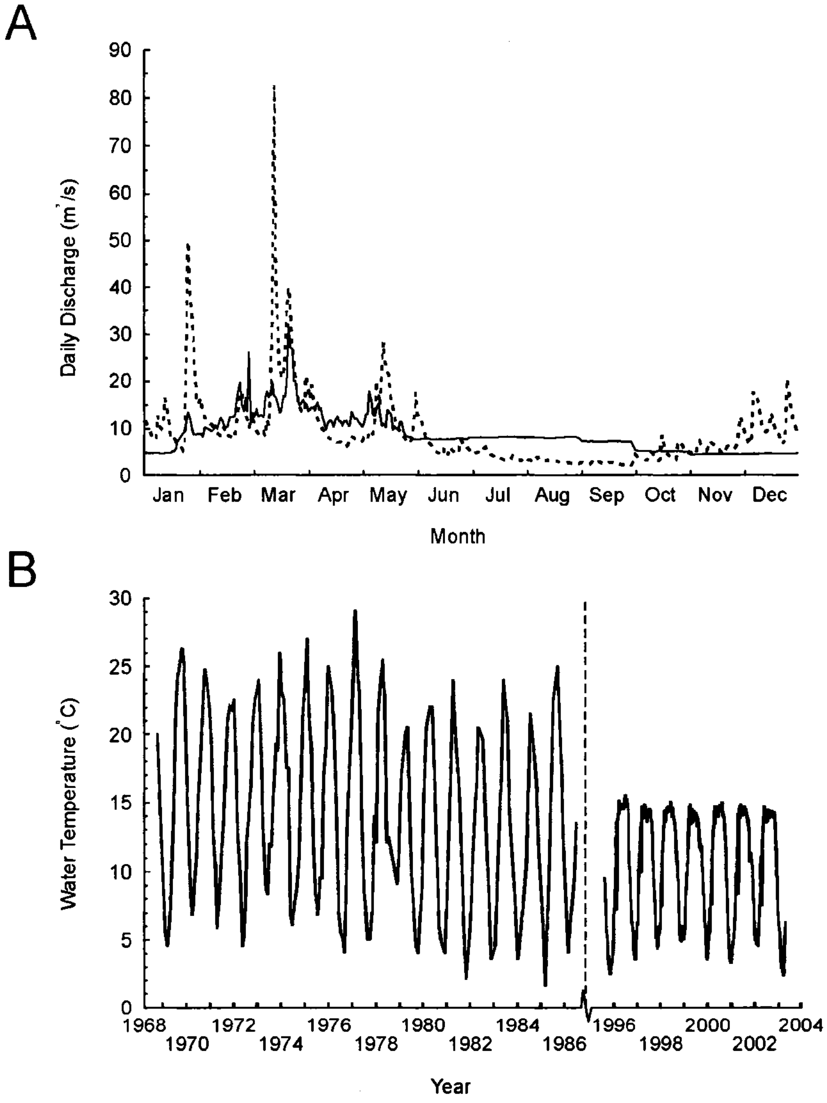


Figure 7.3. Estimated annual hydrograph for Jackson River below Gathright Dam (J1) for 20 years pre- (1960-1979) and post-construction (1983-2002).

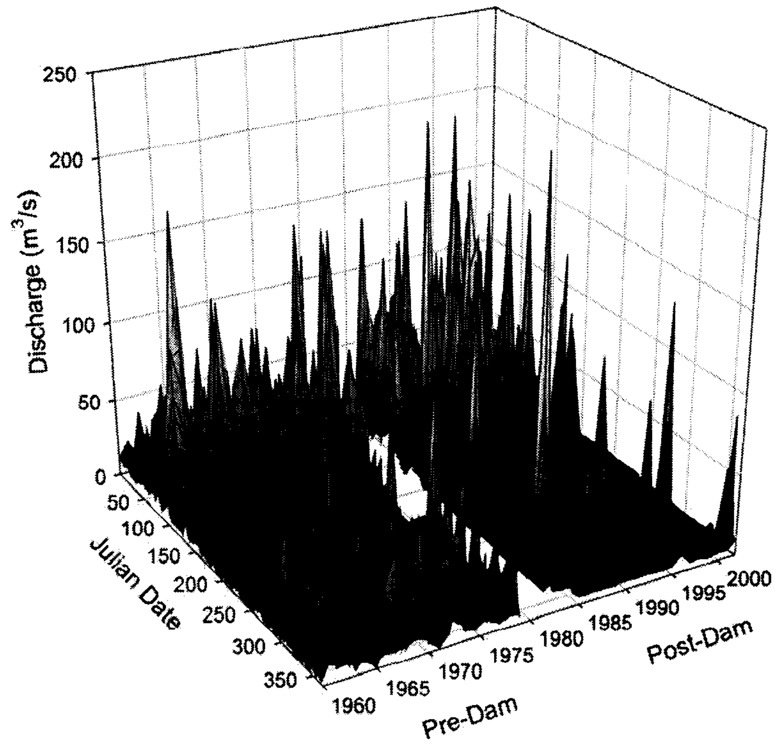


Figure 7.4. Hydrologic alteration (%) of river segments in the Jackson River according to distance upstream (negative watercourse distance) and downstream (positive watercourse distance) from Gathright Dam (demarcated by a solid vertical line at distance zero). Components of the flow regime are divided into 5 major groups and the data points represent average values for the hydrologic indices in the particular group. Panels (A) magnitude of monthly flows and magnitude/duration of maximum flows, (B) magnitude/duration of minimum flows and baseflow, (C) frequency and duration of low and high flow pulse events, (D) timing of minimum and maximum annual flow events, and (E) rate of change in flow conditions. Dotted lines demarcate the downstream tributary locations of Cedar Creek, Falling Spring and Indian Draft.

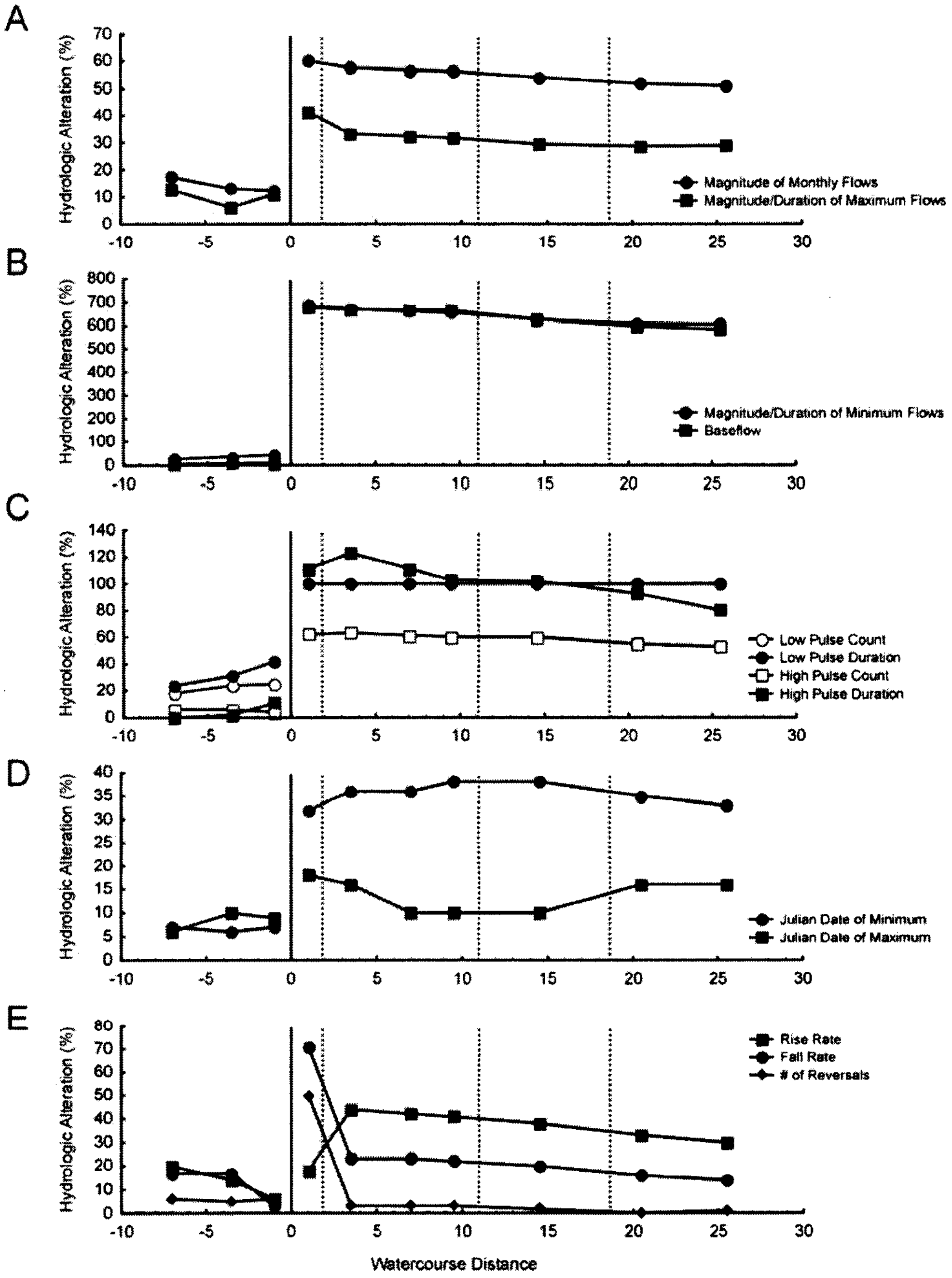


Figure 7.5. Thermographs for the Jackson River (A) and Cowpasture River (B) illustrating water temperatures (°C) for the fall-summer months during which fish spawning behaviour occurs (March-July, 2002), as it relates to watercourse distance. For the Jackson River watercourse distance refers to distance upstream (negative watercourse distance) and downstream (positive watercourse distance) from Gathright Dam (located at distance zero), whereas watercourse distances for the Cowpasture are referenced to the Bullpasture River confluence marking the upstream edge of C1 (see Figure 7.1).

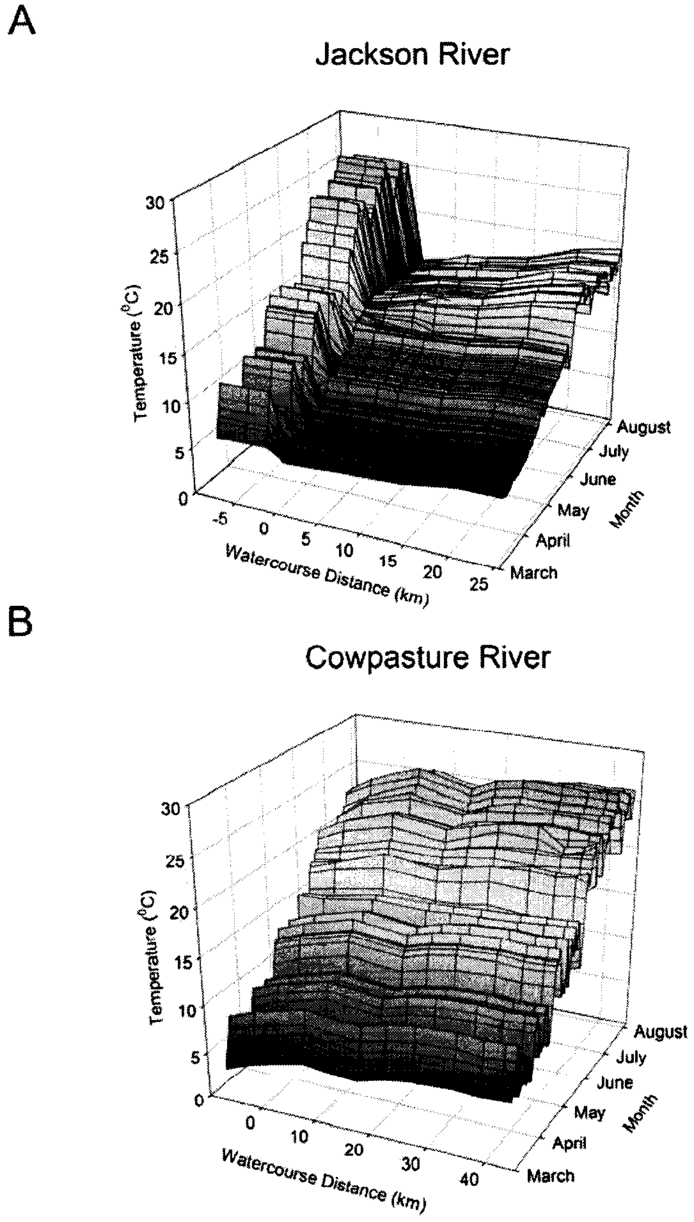


Figure 7.6. Thermographs for the Jackson River (A) and Cowpasture River (B) illustrating water temperatures (°C) for the spring-summer months during which fish spawning behaviour occurs (March-July, 2002), as it relates to mainstem segments (demarcated by solid lines) and tributaries (demarcated by dashed lines). Mainstem values represent average values across all river segments.

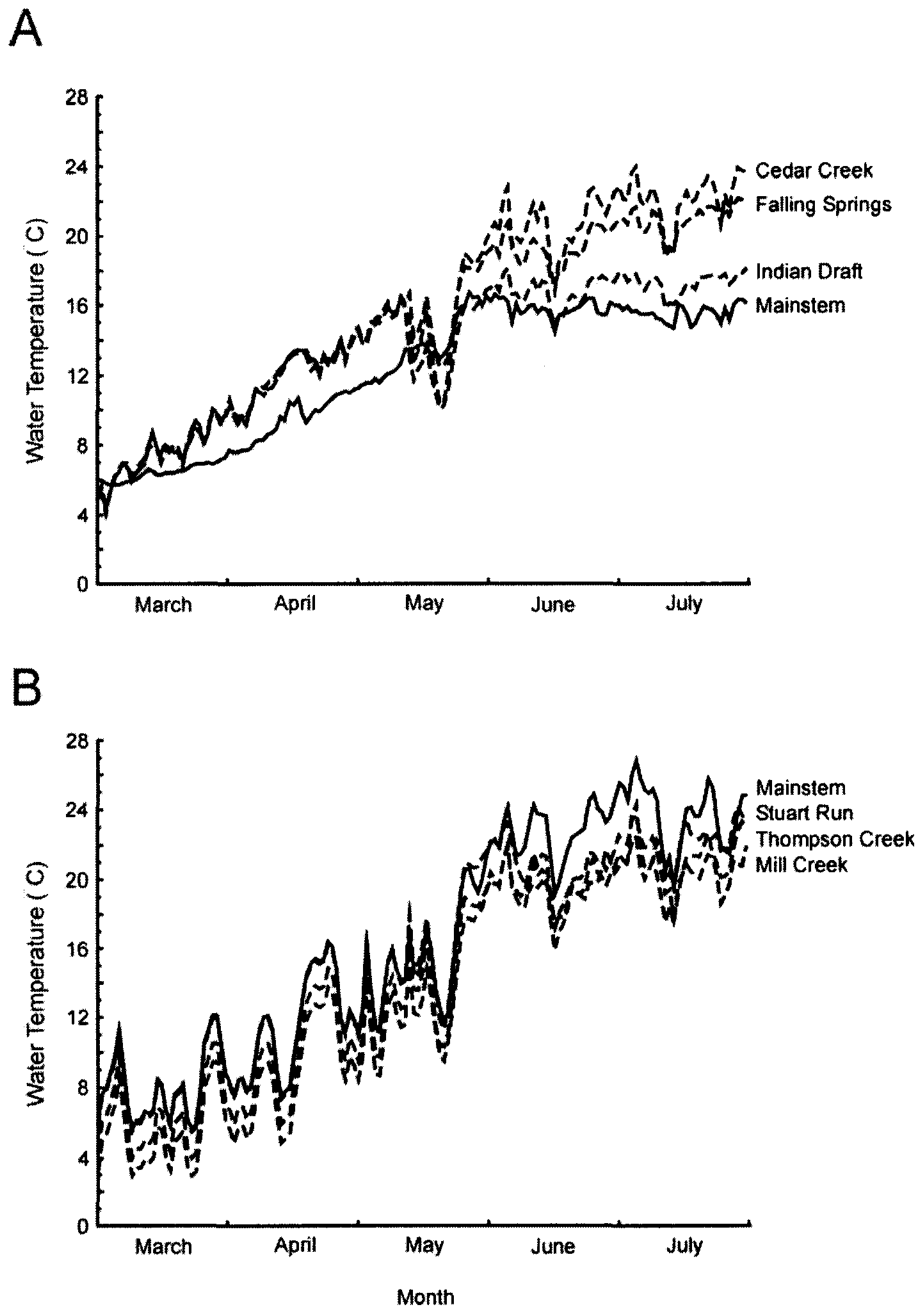


Figure 7.7. Water temperatures (°C) of river segments in the Jackson River according to distance upstream (negative watercourse distance) and downstream (positive watercourse distance) from Gathright Dam (demarcated by a solid vertical line at distance zero). Mean values for each river segment are presented. Dotted lines demarcate the downstream tributary locations of Cedar Creek, Falling Spring and Indian Draft. Dashed line represents unregulated patterns of water temperatures according to the Temperature-Distance relationship (based on linear regression) for the Cowpasture River and shaded area delimits the 95% confidence interval.

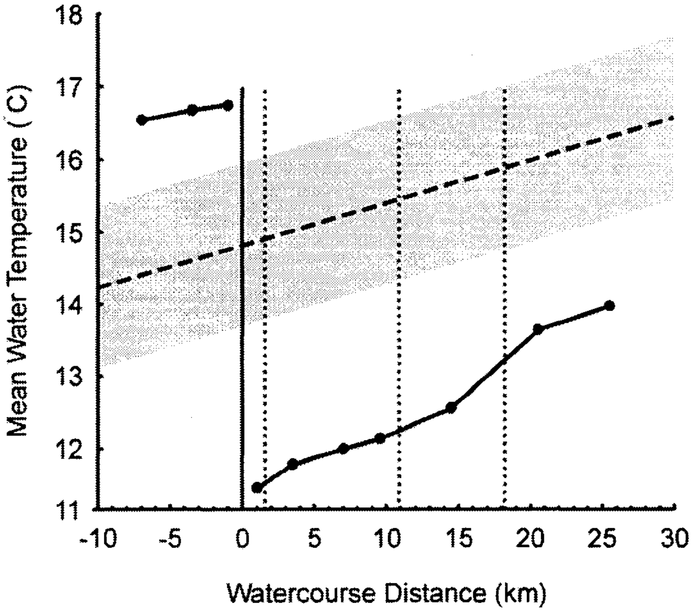


Figure 7.8. Substrate characteristics of river segments in the Jackson River according to distance upstream (negative watercourse distance) and downstream (positive watercourse distance) from Gathright Dam (demarcated by a solid vertical line at distance zero). Panels (A) median (D_{50}) particle size (mm), (B) coefficient of variation in D_{50}, and (C) percent embeddedness. Mean values for each river segment are presented. Dotted lines demarcate the downstream tributary locations of Cedar Creek, Falling Spring and Indian Draft. Dashed line represents unregulated patterns of substrate characteristics according to the D_{50}-Distance relationship (based on linear regression) for the Cowpasture River and shaded area delimits the 95% confidence interval. No significant longitudinal gradients were found for CV in D_{50} and % Embeddedness in the Cowpasture River, and therefore dashed lines represent mean values across all segments (C1-C10).

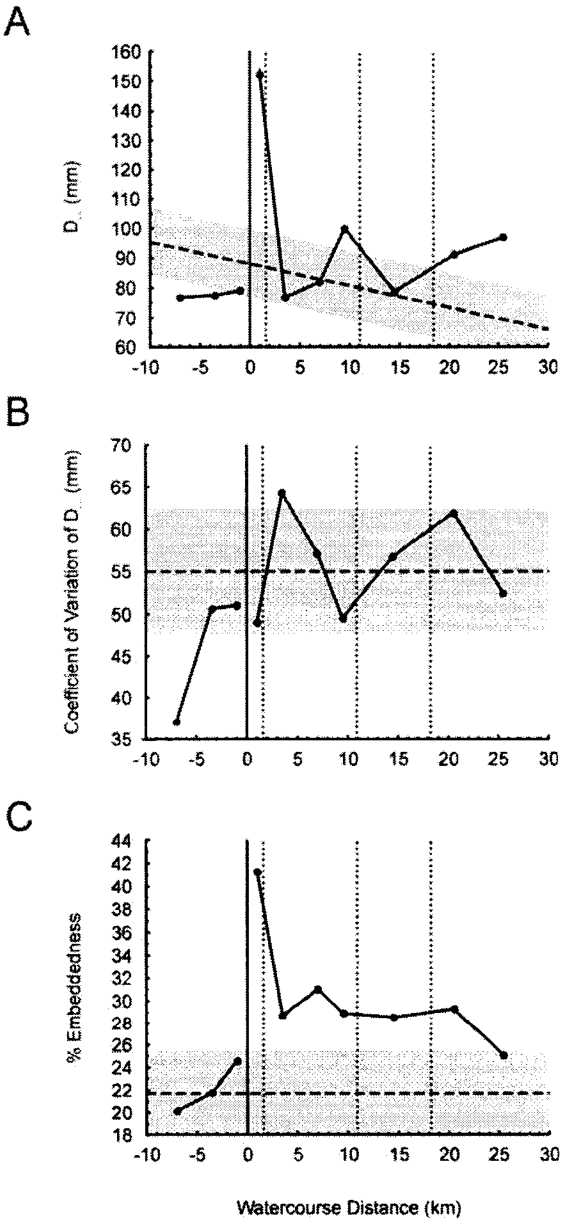


Figure 7.9. Ash-Free Dry Mass (AFDM) of river segments in the Jackson River according to distance upstream (negative watercourse distance) and downstream (positive watercourse distance) from Gathright Dam (demarcated by a solid vertical line at distance zero). Mean values for each river segment are presented. Dotted lines demarcate the downstream tributary locations of Cedar Creek, Falling Spring and Indian Draft. Dashed line represents unregulated patterns of AFDM according to the AFDM-Distance relationship (based on linear regression) for the Cowpasture River and shaded area delimits the 95% confidence interval.

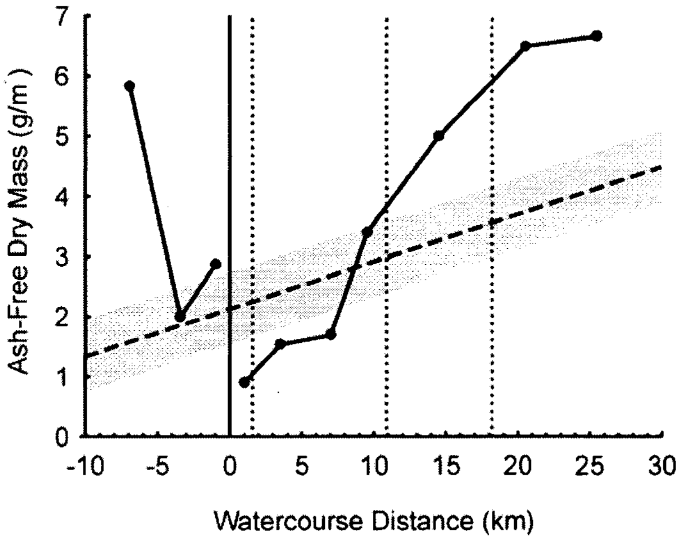


Figure 7.10. Fish species density (# octaves/m^2) of river segments in the Jackson River according to distance upstream (negative watercourse distance) and downstream (positive watercourse distance) from Gathright Dam (demarcated by a solid vertical line at distance zero). Mean values for each river segment are presented. Dotted lines demarcate the downstream tributary locations of Cedar Creek, Falling Spring and Indian Draft and values adjacent to these lines represent fish density for the tributary. Dashed line represents mean density for the Cowpasture River and shaded area delimits the 95% confidence interval.

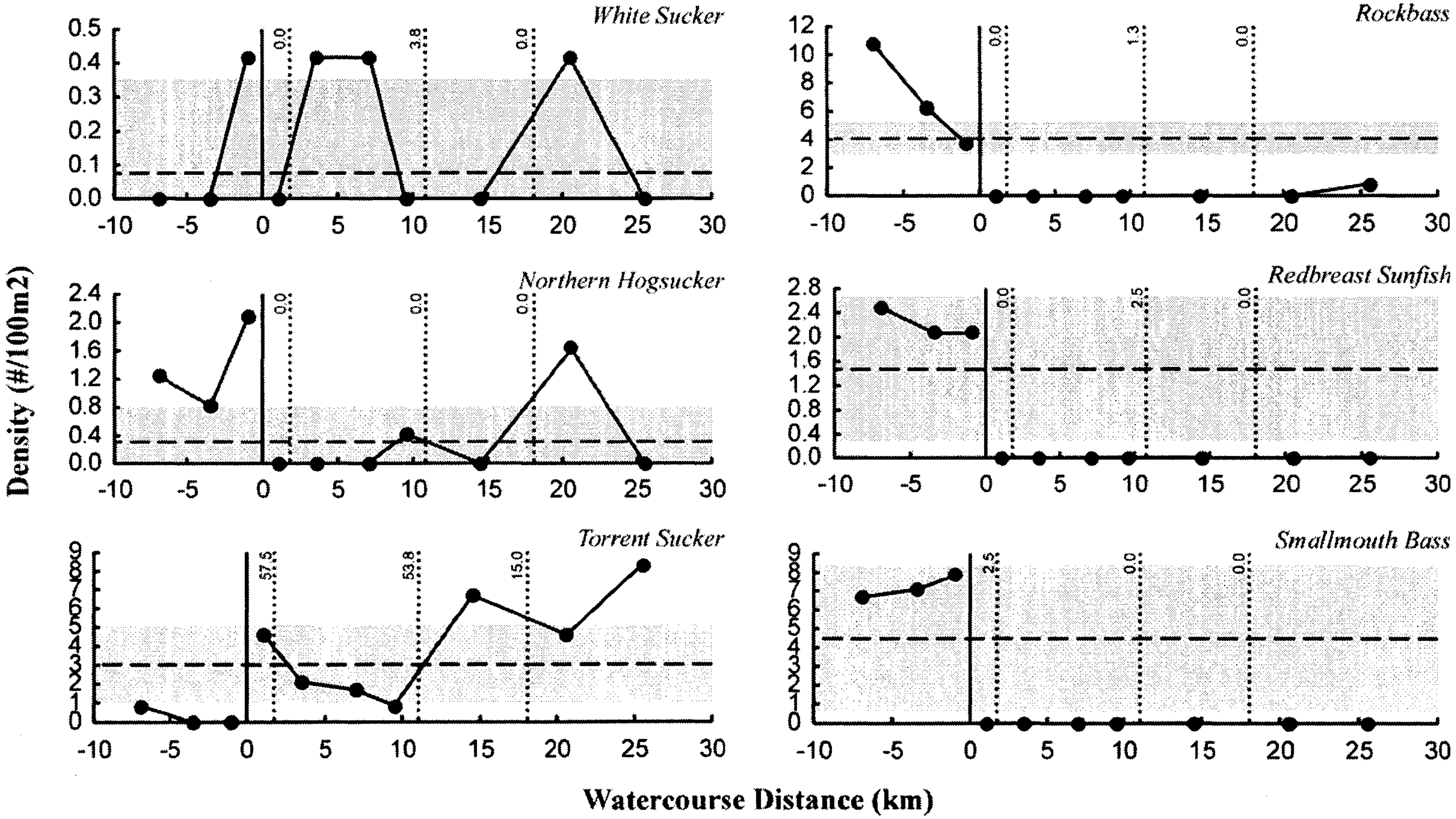


Figure 7.10. continued.

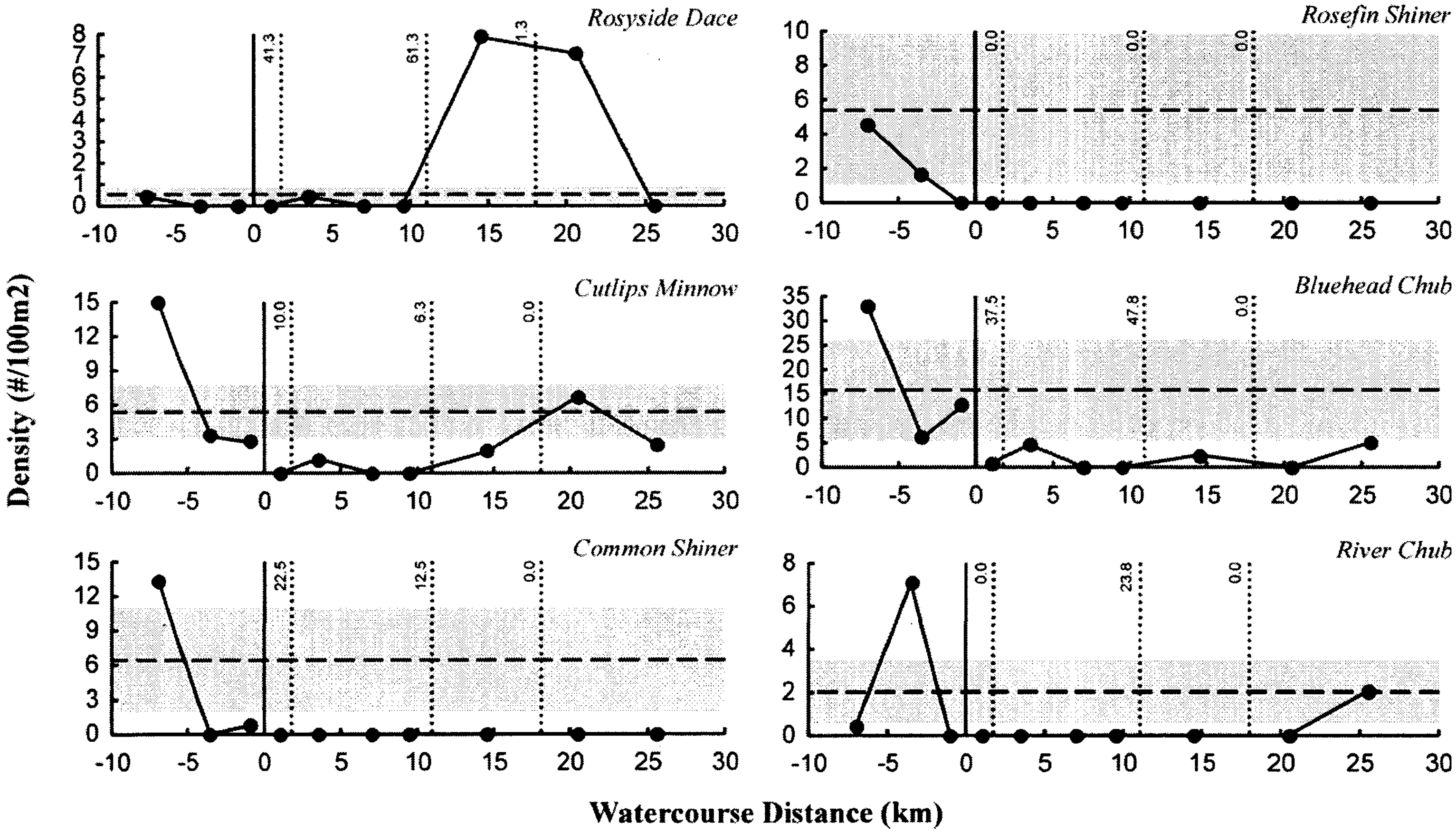


Figure 7.10. continued.

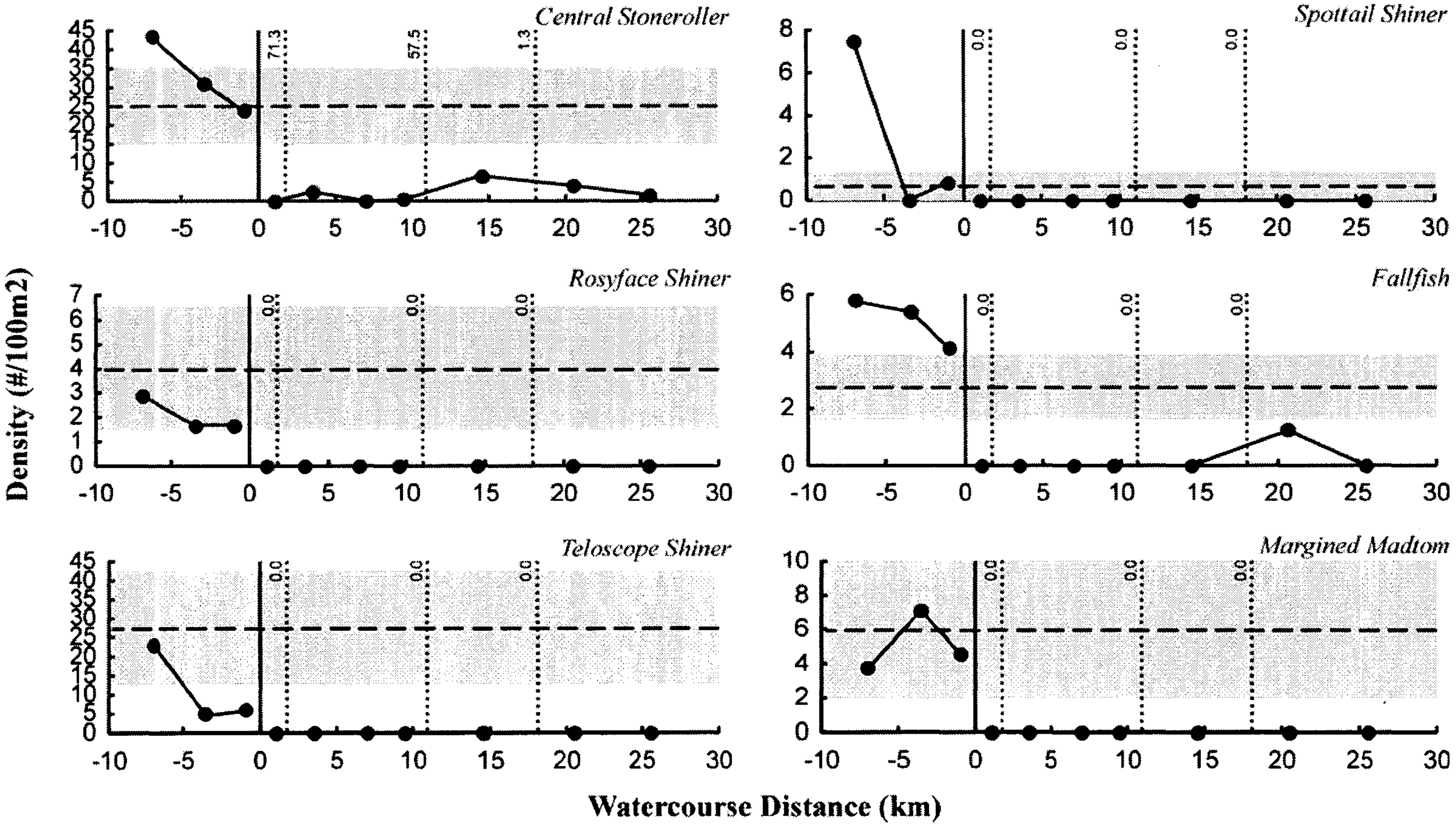


Figure 7.10. continued.

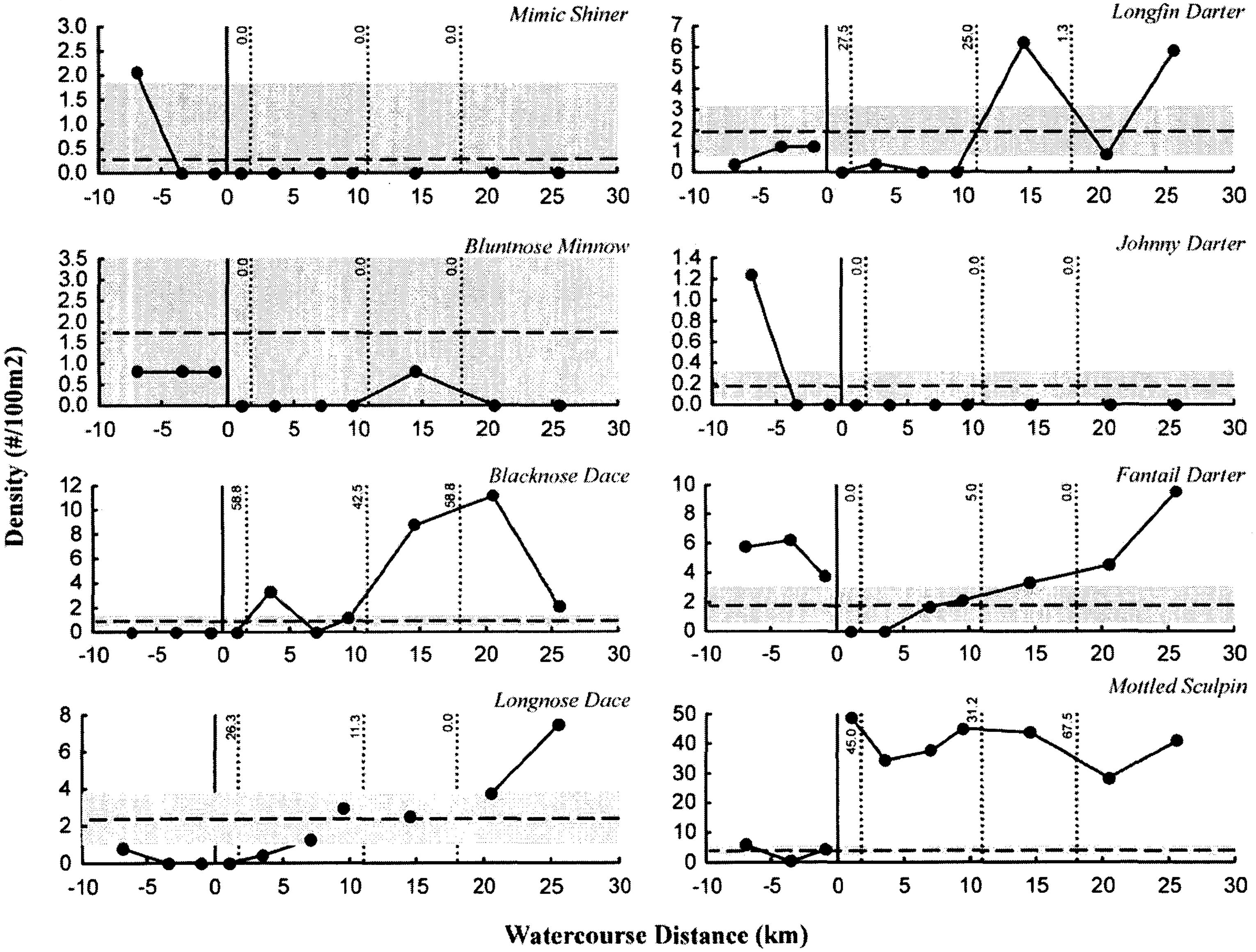
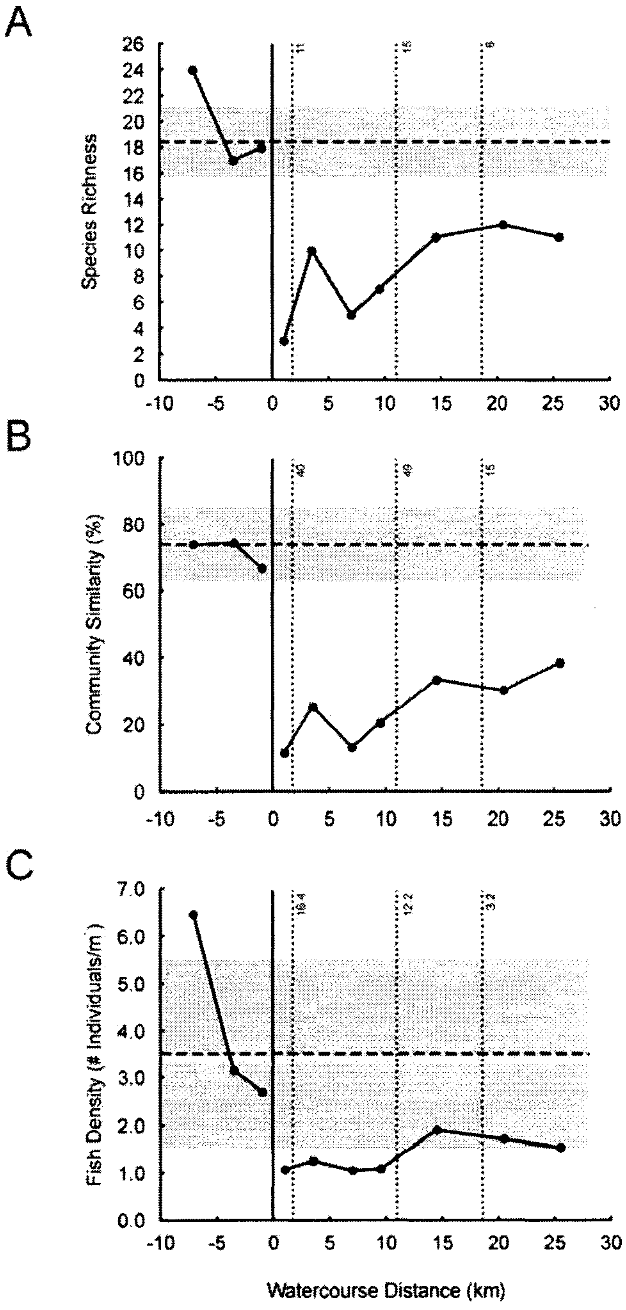


Figure 7.11. Fish community metrics of river segments in the Jackson River according to distance upstream (negative watercourse distance) and downstream (positive watercourse distance) from Gathright Dam (demarcated by a solid vertical line at distance zero). Panels (A) species richness, (B) species similarity based on species presence/absence and Jaccard's similarity index (%), and (C) fish density based on all species (#/m^2). Mean values for each river segment are presented. Dotted lines demarcate the downstream tributary locations of Cedar Creek, Falling Spring and Indian Draft and values adjacent to these lines represent metric values for the tributary. Dashed line represents mean density for the Cowpasture River and shaded area delimits the 95% confidence interval.



Appendix 7.1., Table 1. General diagnostics and habitat characteristics of the river segments sampled on the Jackson River and Cowpasture River. Prepositioned area electofishing (PAE) microhabitat characteristics (and fish surveys) were based on 30 grids for the mainstem segments and 10 grids for the tributaries. Mean values are presented. Elevation of upstream and downstream ends of the study rivers were 501 and 392 metres for the Jackson River and 495 and 386 metres for the Cowpasture River.

River Segment	Sample Date (2002)	Length (km)	Drainage Area (km^2)	PAE Micro-habitat characteristics						
				Velocity (m/s)	Depth (cm)	Boulder (%)	Cobble (%)	Pebble (%)	Gravel (%)	Other (%)
Jackson River										
Mainstem JC	June 19 – 23	4.0	325	4.7	32.3	14	43	30	11	2
Mainstem JB	May 19 – 21	3.0	360	5.0	42.7	15	37	29	16	3
Mainstem JA	May 25 – 27	2.0	401	5.0	35.0	11	39	37	11	2
Mainstem J1	July 1 – 2	1.5	904	6.8	43.9	22	39	21	18	0
Mainstem J2	June 17 – 18	4.5	990	5.2	46.2	18	33	24	24	1
Mainstem J3	June 4 – 5	1.5	1010	5.4	45.9	20	34	23	23	0
Mainstem J4	June 6 – 7	3.5	1020	6.7	40.7	8	36	34	22	0
Mainstem J5	July 22 – 24	7.0	1063	5.3	40.8	31	31	18	20	0
Mainstem J6	June 11 – 13	5.0	1106	5.0	45.2	21	36	24	19	0
Mainstem J7	July 13 – 15	5.0	1128	5.9	34.5	17	45	22	15	1
Cedar Creek	July 31	1.5	87	4.4	18.9	24	34	20	22	0
Falling Springs	July 25	1.5	43	4.4	30.5	37	19	8	31	5
Indian Draft	July 26	1.5	42	3.7	20.8	26	29	20	24	1
Cowpasture River										
Mainstem C1	June 24 – 26	6.5	483	5.1	34.2	29	37	23	11	0
Mainstem C2	May 16 – 17	3.5	522	4.9	42.4	22	42	25	9	2
Mainstem C3	July 3 – 6	15.5	540	5.0	32.1	18	43	23	14	2
Mainstem C4	June 2 – 3	5.5	642	4.1	44.3	12	43	32	13	0
Mainstem C5	June 27 – 29	1.5	696	4.7	37.6	15	38	24	16	7
Mainstem C6	June 14 – 16	9.0	713	4.4	33.1	15	39	29	15	2
Mainstem C7	May 22 – 24	5.0	851	4.8	46.0	14	38	26	21	1
Mainstem C8	July 6 – 9	4.0	913	5.1	30.0	22	35	21	15	7
Mainstem C9	June 8 – 9	2.5	922	4.6	36.1	10	36	35	18	1
Mainstem C10	July 9 – 12	2.0	933	5.2	29.4	17	44	22	17	0
Thompson Creek	July 30	1.5	54	3.9	13.8	12	35	29	24	0

Stuart Run	July 27	1.5	138	3.4	23.6	4	47	23	22	4
Mill Creek	July 29	1.5	61	4.2	26.5	19	33	20	18	10

Appendix 7.1.,Table 2. Results from an analysis of variance assessing differences between Jackson River and Cowpasture River study reaches in terms of their PAE micro-habitat characteristics.

Micro-habitat Characteristic	**Source of Variance**	**Sum of Squares**	**df**	**Mean Square**	**F**	**P**
Velocity (m/s)	Between Groups	2.52	1	2.52	7.67	.013
	Within Groups	5.90	18	0.32		
	Total	8.42	19			
Depth (cm)	Between Groups	88.20	1	88.20	2.89	.106
	Within Groups	549.41	18	30.52		
	Total	637.61	19			
Boulder (%)	Between Groups	0.45	1	0.45	.01	.913
	Within Groups	656.50	18	36.47		
	Total	656.95	19			
Cobble (%)	Between Groups	24.20	1	24.20	1.64	.216
	Within Groups	264.60	18	14.70		
	Total	288.80	19			
Pebble (%)	Between Groups	0.20	1	0.20	.01	.935
	Within Groups	521.60	18	28.97		
	Total	521.80	19			
Gravel (%)	Between Groups	45.00	1	45.00	2.70	.118
	Within Groups	299.80	18	16.65		
	Total	344.80	19			
Other (%)	Between Groups	8.45	1	8.45	2.04	.170
	Within Groups	74.50	18	4.13		
	Total	82.95	19			

Appendix 7.2. Characterizing natural streamflow regimes using the IHACRES rainfall-runoff model.

In our study, we link physical descriptors of the Upper James River Basin to patterns of watershed runoff as simulated by the rainfall-runoff model IHACRES (PC version 1.02) – Identification of unit Hydrographs And Component flows from Rainfall, Evaporation, and Streamflow data (Jackman et al. 1990). The model consists of two modules: (1) a non-linear loss module that calculates the amount of rainfall that is delivered to the stream and is not stored in the soil or lost to evapotranspiration (i.e., the conversion of total rainfall to effective or excess rainfall) and (2) a linear module that routes the effective rainfall to streamflow.

The non-linear loss module calculates the effective rainfall that contributes directly to streamflow, given time series of precipitation and air temperature. To account for the fact that runoff depends on antecedent soil moisture conditions (i.e., a watershed that is already wet will usually generate more streamflow from a given amount of rainfall than it does from the same amount of rainfall when it is initially dry), the module defines an index of soil moisture storage s_k at time step k as

$$s_k = c \cdot r_k + \left[1 - \frac{1}{\tau_w(t_k)}\right] s_{k-1} \tag{1}$$

to indicate the potential of the watershed to produce streamflow from precipitation r_k. This index varies from 0 to 1 depending on the antecedent rainfall and the rates of water loss to evapotranspiration and streamflow. A value of 0 indicates that the watershed is relatively dry and present-day rainfall will produce no effective rainfall, whereas a value of 1 indicates that the watershed is relatively saturated and present-day rainfall will become effective rainfall. In this study we set $k = 1$ day. The parameter c [1/mm] is the increase in watershed storage index per unit rainfall in the absence of evapotranspiration. In IHACRES, it is used as a normalizing parameter because it is chosen so that the volume of effective rainfall is equal to the volume of observed streamflow over the calibration period. The parameter $\tau_w(t_k)$ is the time constant [days] of watershed losses at daily mean temperature t_k and controls the timing of soil wetness decline according to

$$\tau_w(t_k) = \tau_w \exp[(20 - t_k)f], \tag{2}$$

where τ_w [days] is the drying time constant at 20°C and f [1/°C] is a factor determining the impact of a change in temperature on drying time. The reference temperature of 20°C is considered appropriate for climatic conditions in Virginia (Kokkonen et al. 2003). Lastly, effective rainfall u_k (i.e., the part of the rainfall that leaves as streamflow) is calculated as

$$u_k = r_k s_k \tag{3}$$

In summary, the non-linear module contains 3 parameters that require estimation during the modeling process (τ_w, c, and f).

Second, a linear routing module describes the travel of effective rainfall to streamflow x_k on the basis of a total unit hydrograph approximation. The module invokes a recursive relation at time step k for modeled streamflow, computed as a linear combination of its past values and current and past effective rainfall. The model's conceptual structure implies that the effective rainfall is considered to travel through two parallel stores, and therefore, the recession of streamflow is a superposition of two exponential decay functions: (1) baseflow that represent long (slow) recessions during periods of zero effective rainfall, and (2) rapid (quick) runoff responses caused by effective rainfall events. Therefore, although the hydrograph separation into quick and slow response components is purely mathematical, it is not unreasonable to link the quick component to surface and subsurface flow and the slow component to deeper soil and groundwater flows. This module model defines the quick and slow response time constants τ_q and τ_s and the quick and slow volumetric throughput parameters v_q and v_s as

$$\tau_q = \frac{\Delta}{-\ln(\alpha^{(q)})} \tag{4}$$

$$\tau_s = \frac{\Delta}{-\ln(\alpha^{(s)})} \tag{5}$$

$$v_q = \frac{\beta^{(q)}}{1-\alpha^{(q)}} \tag{6}$$

$$v_s = \frac{\beta^{(s)}}{1-\alpha^{(s)}} \tag{7}$$

where Δ is the sampling interval for the time series of observed rainfall and streamflow (i.e., 1 day in our analysis). The normalization on c constrains $v_q + v_s$ to equal 1 (and therefore the two parallel-component linear model requires estimation of only one of the two). The α and β parameters are determined by equating coefficients z^{-1} and z^{-2} in the following equation. This equation relates the second order general linear polynomial transfer function (left-hand side) to first order quick and slow flow transfer functions (right-hand side) in which the backward shift operator (e.g., $z^{-1}x_k = x_{k-1}$) is typically used for convenience of expression:

$$\frac{b_0 + b_1 z^{-1}}{1 + a_1 z^{-1} + a_2 z^{-2}} = \frac{\beta^{(q)}}{1+\alpha^{(q)} z^{-1}} + \frac{\beta^{(s)}}{1+\alpha^{(s)} z^{-1}} \tag{8}$$

The modeled streamflow x_k is represented as the superposition of quick $x_k^{(q)}$ and slow $x_k^{(s)}$ components of streamflow, given by

$$x_k^{(q)} = a^{(q)} x_{k-1}^{(q)} + b^{(q)} u_k \tag{9}$$

$$x_k^{(s)} = a^{(s)} x_{k-1}^{(s)} + b^{(s)} u_k \tag{10}$$

$$x_k = x_k^{(q)} + x_k^{(s)} \tag{11}$$

In summary, the entire IHACRES model is defined by just six parameters – three related to the non-linear module (τ_w, c, and f) and three related to the linear module (τ_q, τ_s, and v_s) – thus making it relatively simple in structure compared with many other conceptual rainfall-runoff models. The set of 6 parameters is considered to characterize the dynamic hydrologic response of the watershed, which can be related to physical descriptors in a regionalization analysis to predict time series of daily discharges from times series of daily rainfall and temperature.

Appendix 7.2., Table 1. Calibrated IHACRES parameter estimates of the 6 dynamic response characteristics for the 8 calibration watersheds located in the Upper James River Basin. Gauge refers to the United States Geological Survey Streamflow Gauge Number (www.usgs.gov).

Watershed (Gauge)	Calibration Period	Validation Period	Calibration R	Validation R	f [1/°C]	c [1/mm]	τ_w [days]	τ_q [days]	τ_s [days]	v_s
Back Creek (02011500)	1960-1964	1960-1979	0.69	0.73	3.0	378.7	14.0	1.5	5.8	0.34
	1965-1969	1960-1979	0.73	0.74	2.5	218.9	8.0	0.8	4.4	0.57
	1970-1974	1960-1979	0.73	0.73	2.0	157.0	7.0	0.8	6.8	0.54
	1975-1979	1960-1979	0.81	0.73	3.0	275.6	9.0	0.8	4.9	0.40
	1983-1987	1983-2002	0.79	0.73	2.0	228.0	8.0	1.2	18.4	0.24
	1988-1992	1983-2002	0.79	0.72	2.2	252.4	10.0	2.1	17.3	0.11
	1993-1997	1983-2002	0.67	0.71	1.8	105.3	3.0	0.9	30.0	0.47
	1998-2002	1983-2002	0.82	0.70	2.5	224.7	7.0	2.1	9.8	0.29
Dunlap Creek (02013000)	1960-1964	1960-1979	0.74	0.72	2.8	281.0	5.0	1.2	25.2	0.29
	1965-1969	1960-1979	0.64	0.72	2.0	218.3	7.0	0.7	7.7	0.56
	1970-1974	1960-1979	0.74	0.69	1.5	135.2	6.0	0.6	2.9	0.58
	1975-1979	1960-1979	0.80	0.73	2.8	312.1	8.0	0.8	4.1	0.46
	1983-1987	1983-2002	0.77	0.73	2.0	279.5	10.0	1.1	8.5	0.24
	1988-1992	1983-2002	0.72	0.69	1.3	149.8	7.0	0.8	4.7	0.61
	1993-1997	1983-2002	0.64	0.68	1.6	112.9	3.0	0.6	10.6	0.61
	1998-2002	1983-2002	0.80	0.72	2.8	269.0	6.0	1.9	18.0	0.19
Potts Creek (02014000)	1960-1964	1960-1979	0.69	0.73	2.4	288.7	9.0	1.4	12.6	0.66
	1966-1969	1960-1979	0.67	0.71	2.4	288.7	9.0	1.4	12.6	0.66
	1970-1974	1960-1979	0.74	0.69	2.1	124.0	4.0	1.3	5.3	0.39
	1975-1979	1960-1979	0.80	0.75	2.1	267.1	11.0	1.1	5.2	0.62
	1983-1987	1983-2002	0.81	0.73	2.0	255.9	10.0	1.3	7.5	0.34
	1988-1992	1983-2002	0.73	0.74	3.6	405.8	11.0	1.1	4.4	0.76
	1993-1997	1983-2002	0.69	0.73	1.7	131.1	4.0	1.0	14.5	0.60
	1998-2002	1983-2002	0.82	0.74	2.1	265.2	8.0	2.3	15.7	0.42
Bullpasture	1960-1964	1960-1979	0.72	0.71	2.9	190.8	3.0	1.6	34.4	0.49

River (02015700)	1965-1969	1960-1979	0.72	0.73	2.3	194.2	6.0	0.9	9.0	0.62
	1970-1974	1960-1979	0.73	0.72	1.9	147.2	6.0	0.8	13.9	0.64
	1975-1979	1960-1979	0.79	0.73	2.7	291.8	9.0	0.8	6.8	0.49
	1983-1987	1983-2002	0.74	0.70	2.3	138.4	4.0	1.0	60.3	0.36
	1988-1992	1983-2002	0.77	0.69	2.4	235.6	10.0	0.5	4.2	0.77
	1993-1997	1983-2002	0.68	0.71	1.9	103.0	3.0	0.6	26.6	0.53
	1998-2002	1983-2002	0.77	0.68	2.4	237.2	8.0	2.2	57.9	0.31
Cowpasture River (02016000)	1960-1964	1960-1979	0.79	0.76	2.9	2391.2	5.0	2.3	55.2	0.19
	1965-1969	1960-1979	0.67	0.77	2.0	2496.3	10.0	1.7	8.5	0.39
	1970-1974	1960-1979	0.79	0.74	2.4	1554.2	5.0	1.9	8.6	0.24
	1975-1979	1960-1979	0.82	0.76	3.2	3120.9	10.0	2.2	26.0	0.08
	1983-1987	1983-2002	0.86	0.73	2.4	1826.3	5.0	1.4	56.4	0.15
	1988-1992	1983-2002	0.75	0.74	2.0	1275.1	5.0	1.9	48.6	0.14
	1993-1997	1983-2002	0.73	0.77	1.7	1153.3	5.0	1.7	32.7	0.27
	1998-2002	1983-2002	0.76	0.73	2.1	2182.5	7.0	3.3	8.8	0.09
Johns Creek (02017500)	1960-1964	1960-1979	0.71	0.74	2.1	195.1	6.0	1.2	21.2	0.52
	1965-1969	1960-1979	0.69	0.72	2.8	208.8	5.0	1.1	15.4	0.68
	1970-1974	1960-1979	0.77	0.70	1.5	146.9	8.0	0.5	4.8	0.75
	1975-1979	1960-1979	0.81	0.76	2.4	258.3	10.0	0.6	4.4	0.78
	1983-1987	1983-2002	0.84	0.80	2.1	255.9	10.0	0.9	6.6	0.66
	1988-1992	1983-2002	0.83	0.78	2.0	232.2	12.0	0.6	5.1	0.85
	1993-1997	1983-2002	0.75	0.73	1.3	92.7	4.0	0.6	8.9	0.74
	1998-2002	1983-2002	0.84	0.78	1.9	190.7	6.0	0.4	4.9	0.90
Craig Creek (02018000)	1960-1964	1960-1979	0.74	0.77	2.5	962.8	7.0	2.5	26.9	0.35
	1965-1969	1960-1979	0.69	0.75	2.7	865.3	6.0	2.4	18.9	0.52
	1970-1974	1960-1979	0.81	0.76	1.9	711.4	8.0	2.9	38.9	0.12
	1975-1979	1960-1979	0.79	0.77	2.0	835.5	9.0	2.3	21.5	0.18
	1983-1987	1983-2002	0.78	0.73	1.9	571.4	5.0	1.2	16.4	0.38
	1988-1992	1983-2002	0.78	0.72	2.1	874.7	10.0	1.8	5.1	0.51
	1993-1997	1983-2002	0.73	0.74	1.5	357.3	3.0	1.5	15.0	0.51
	1998-2002	1983-2002	0.85	0.73	2.4	697.1	4.0	2.8	34.0	0.31
Catawba Creek	1960-1964	1960-1979	0.68	0.65	3.0	296.7	7.0	1.2	46.8	0.33
	1965-1969	1960-1979	0.66	0.66	2.9	219.9	5.0	0.4	12.3	0.61

(02018500)	1970-1974	1960-1979	0.80	0.62	1.9	95.3	3.0	0.3	24.4	0.47
	1975-1979	1960-1979	0.69	0.69	1.7	236.0	9.0	0.7	12.4	0.41
	1983-1987	1983-2002	0.49	0.47	1.7	139.0	6.0	0.7	9.6	0.43
	1988-1992	1983-2002	0.49	0.47	1.7	139.0	6.0	0.7	9.6	0.43
	1993-1997	1983-2002	0.55	0.51	2.0	251.4	9.0	1.2	22.7	0.34
	1998-2002	1983-2002	0.72	0.47	2.5	352.8	5.0	1.1	13.9	0.45

Appendix 7.3. Regionalization analysis for predicting daily, unregulated streamflow using multi-response artificial neural networks.

Table 1. Physical descriptors of the 8 calibration watersheds used in the artificial neural networks to predict the 6 dynamic response characteristics (i.e., IHACRES parameters). Gauge refers to the United States Geological Survey Streamflow Gauge Number (www.usgs.gov).

Watershed – Gauge (Latitude, Longitude)	Physical Descriptors Drainage Area (km^2)	Basin Aspect (degrees)	Stream Density (km/km^2)	Channel Slope (m/m)	Basin Percent Forested
Back Creek – 02011500 (38.0694, 79.8972)	365.95	183.04	0.34	20.27	89.69
Dunlap Creek – 02013000 (37.8028, 80.0472)	431.76	186.35	0.91	19.11	92.44
Potts Creek – 02014000 (37.7289, 80.0425)	396.27	191.46	1.07	15.62	92.20
Bullpasture River – 02015700 (38.1953, 79.5706)	277.50	168.53	0.32	13.74	81.23
Cowpasture River – 02016000 (37.7917, 79.7597)	1186.09	180.68	0.59	15.78	88.74
Johns Creek – 02017500 (37.5061, 80.1069)	285.90	176.89	1.02	13.63	91.47
Craig Creek – 02018000 (37.6658, 79.9117)	856.43	178.54	1.03	14.67	91.52
Catawba Creek – 02018500 (37.4681, 80.0056)	85.10	183.01	1.00	14.82	70.38

Appendix 7.3., Table 2. Model accuracy of the artificial neural networks. For each calibration period a single ANN was constructed that related the 5 physical watershed descriptors to the 6 dynamic response characteristics from the IHACRES model. Values reported include Pearson-moment correlation coefficients between actual and predicted IHACRES parameters based on *n*-fold cross validation.

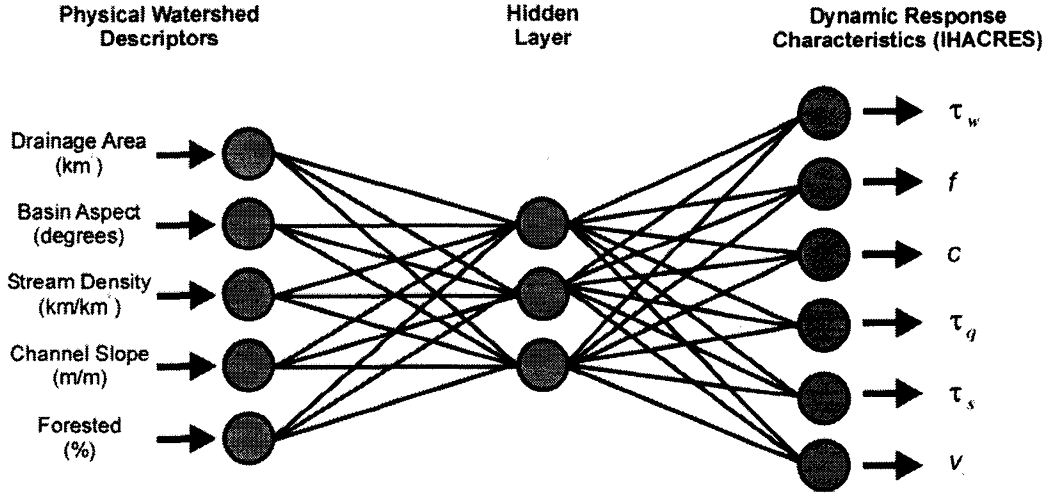
Calibration Period	**IHACRES Dynamic Response Characteristics**					
	τ_w	f	c	τ_q	τ_s	v_s
1960-1964	0.85	0.82	0.98	0.90	0.97	0.95
1965-1969	0.84	0.87	0.94	0.91	0.97	0.98
1970-1974	0.93	0.95	0.90	0.92	0.82	0.98
1975-1979	0.95	0.95	0.96	0.99	0.91	0.96
1983-1987	0.96	0.96	0.99	0.83	0.90	0.97
1988-1992	0.83	0.80	0.89	0.98	0.94	0.95
1993-1997	0.96	0.96	0.84	0.94	0.87	0.95
1998-2002	0.96	0.84	0.95	0.76	0.97	0.94
Mean R	0.91	0.89	0.93	0.91	0.92	0.96
Mean R^2	0.83	0.80	0.87	0.83	0.85	0.92

Appendix 7.3., Table 3. Relative importance (%) of the 5 physical watershed descriptors in the artificial neural networks (one network for each calibration period). Values underlined represent descriptors with a positive influence on the dynamic response characteristic in the neural network (except for mean values). The explanatory importance of the physical descriptors for predicting the IHACRES parameters was quantified using a connection weight approach (see Olden and Jackson 2002b, Olden et al. 2004 for more details). This approach calculates the product of the input-hidden and hidden-output connection weights between each input neuron and output neuron and then sums the products across all hidden neurons. The relative contributions of the variables were calculated by dividing the absolute value of each variable contribution by the grand mean (sum of all absolute variable contributions).

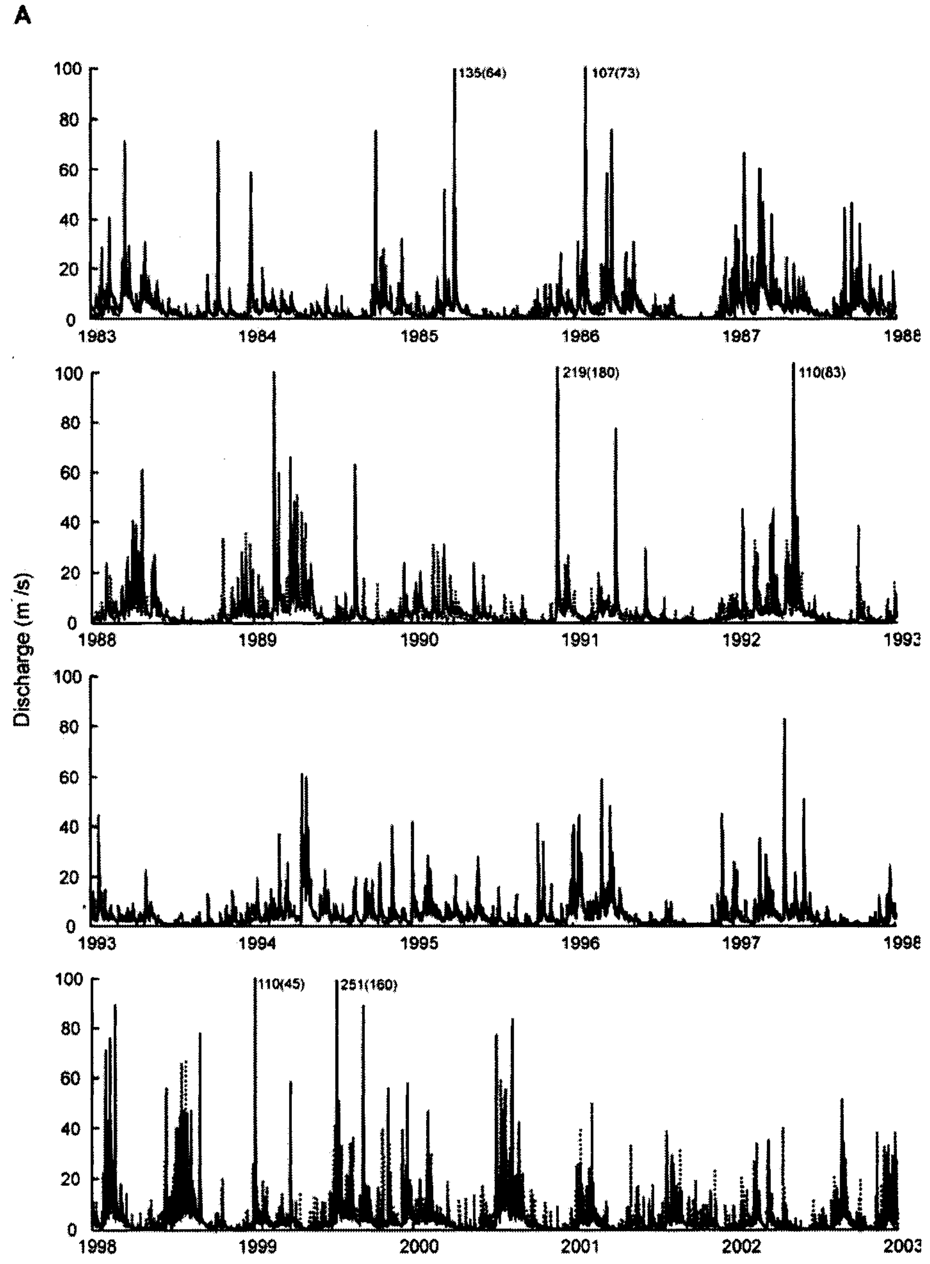
		Physical Descriptors				
Calibration Period	**Dynamic Response Characteristics**	**Drainage Area**	**Basin Aspect**	**Stream Density**	**Channel Slope**	**Basin Percent Forested**
1960-1964	τ_w	19	4	17	32	29
	f	17	18	13	48	4
	c	69	10	13	1	8
	τ_q	65	12	8	9	5
	τ_s	43	13	6	12	25
	v_s	41	1	16	21	21
1965-1969	τ_w	15	25	43	15	1
	f	27	26	38	5	3
	c	45	18	20	13	4
	τ_q	46	1	16	32	4
	τ_s	9	20	42	28	2
	v_s	41	22	29	4	3
1970-1974	τ_w	36	25	11	8	19
	f	6	38	6	9	42
	c	62	14	13	8	3
	τ_q	69	4	12	6	9
	τ_s	53	15	6	0	26
	v_s	49	19	12	8	11
1975-1979	τ_w	25	14	23	32	5
	f	12	18	24	44	1
	c	76	1	2	8	13
	τ_q	78	0	3	6	13
	τ_s	76	1	2	6	15
	v_s	55	6	11	13	15

1983-1987	τ_w	37	12	34	6	11
	f	27	18	24	15	17
	c	35	15	28	10	13
	τ_q	34	9	29	17	11
	τ_s	30	16	27	12	15
	v_s	34	8	30	17	10
1983-1987	τ_w	24	6	14	30	26
	f	32	8	14	23	24
	c	70	8	20	2	1
	τ_q	50	7	18	14	11
	τ_s	50	7	17	13	13
	v_s	37	7	15	21	20
1993-1997	τ_w	25	6	23	2	45
	f	27	13	9	11	40
	c	45	9	8	5	33
	τ_q	41	12	4	9	34
	τ_s	33	4	26	4	34
	v_s	35	9	13	3	41
1998-2002	τ_w	21	1	27	36	15
	f	3	28	39	25	4
	c	59	2	21	16	3
	τ_q	49	12	37	1	1
	τ_s	27	41	1	4	27
	v_s	25	12	40	18	5
Mean		39	12	19	14	15

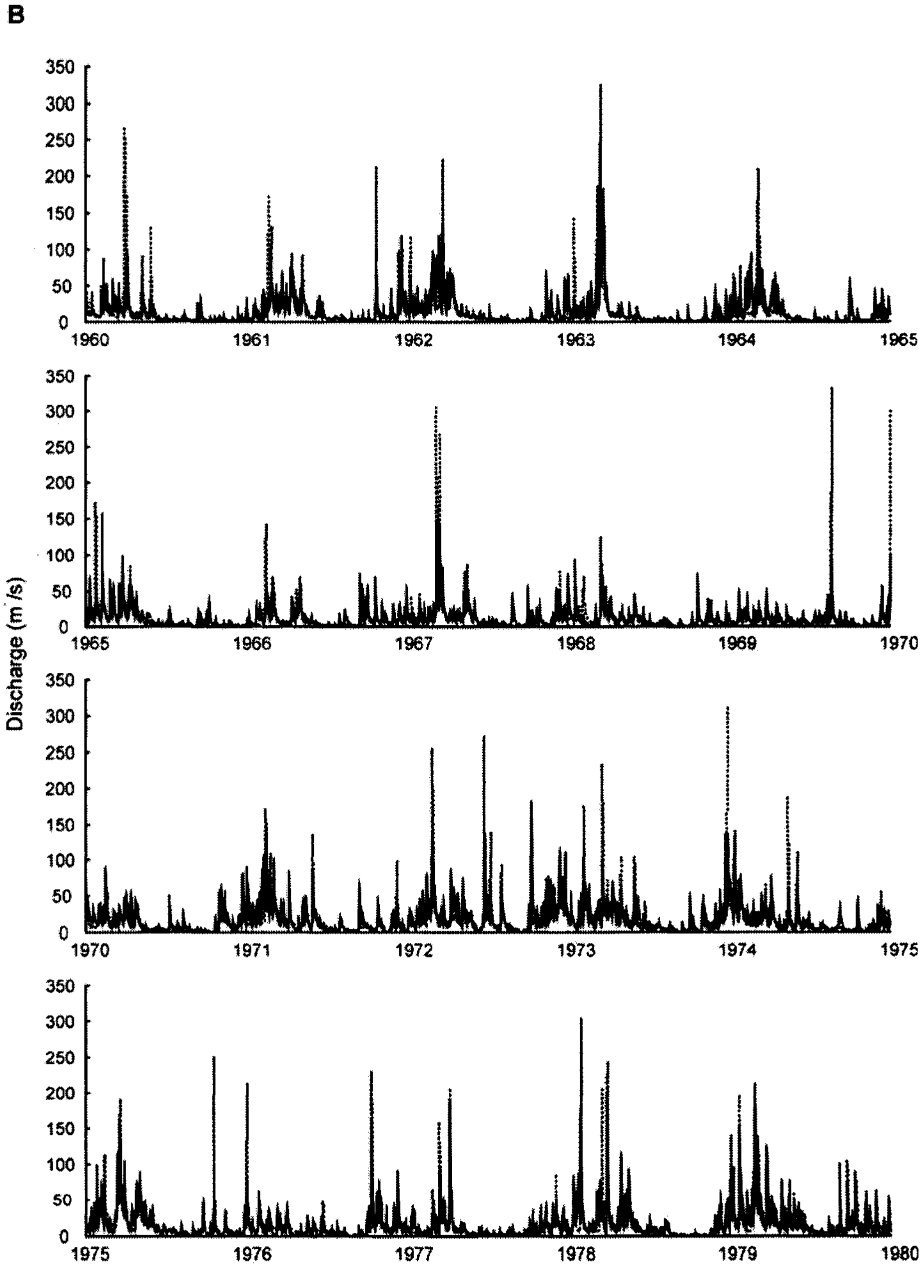
Appendix 7.3., Figure 1. Architecture of the multi-response artificial neural network for modelling the 6 dynamic response characteristics estimated from the IHACRES model as a function of 5 physical watershed descriptions.



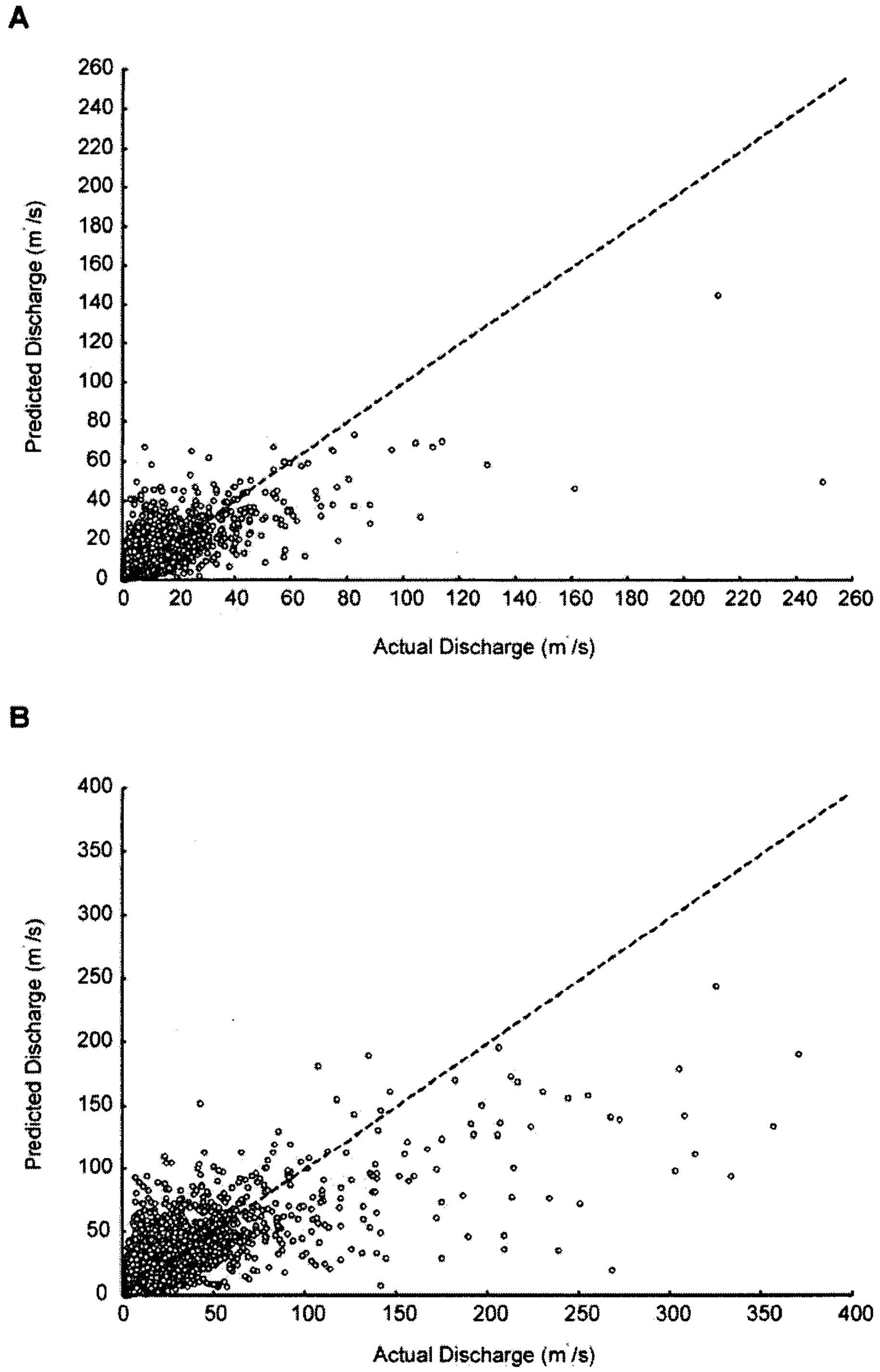
Appendix 7.3., Figure 2. Predicted daily discharge based on the IHACRES model and regionalization analysis (i.e., prediction of the 6 dynamic response characteristics as a function of 5 physical watershed descriptions using artificial neural networks) for two validation gauges in the Jackson River Basin not used in the regionalization analysis. Gauges include: (A) USGS 02011400 – Jackson River at Bacova, located above Gathright Dam (1983-2002) and (B) USGS 02012500 – Jackson River at Falling Spring, located below the current location of Gathright Dam but prior to its construction (1960-1979). Solid lines represent actual daily discharge and dotted lines represent predicted daily discharge. Outliers are labelled numerically with actual values followed by predicted values in parenthesis.



Appendix 7.3., Figure 2. continued.



Appendix 7.3., Figure 3. Predicted versus actual daily discharge for two validation gauges in the Jackson River Basin not used in the regionalization analysis: (A) USGS 02011400 – Jackson River at Bacova, located above Gathright Dam (1983-2002) and (B) USGS 02012500 – Jackson River at Falling Spring, located below the current location of Gathright Dam but prior to its construction (1960-1979).



Appendix 7.4. Results of the Indicators of Hydrologic Alteration analysis for the Jackson River.

Table 1. Percent deviation according to the comparison of pre- vs. post-Gathright Dam flow regimes for *coefficient of dispersion* of 33 hydrologic indices divided into 5 groups representing different components of the flow regime. Group means are computed as the mean of all deviations (in absolute values) within the group. Methodology and calculations follows Richter et al. (1996).

Indicator of Hydrologic Alteration					**River Segment**					
	JC	**JB**	**JA**	**J1**	**J2**	**J3**	**J4**	**J5**	**J6**	**J7**
Monthly magnitude										
October	60	41	4	-84	-81	-81	-80	-76	-73	-72
November	-42	-50	-42	-87	-80	-78	-76	-67	-59	-57
December	1	-6	1	34	18	15	13	9	5	4
January	34	14	-11	80	68	74	78	92	103	109
February	-14	-6	20	43	34	30	28	20	16	14
March	-52	-57	-60	-21	-13	-12	-11	-7	-9	-9
April	84	52	42	12	25	24	22	21	27	28
May	-48	-39	-35	-45	-42	-42	-42	-45	-47	-47
June	-43	-31	-20	-9	-8	-7	-6	-8	-9	-9
July	12	20	7	-83	-88	-89	-89	-91	-90	-90
August	61	77	108	-86	-87	-86	-86	-84	-81	-79
September	57	32	42	-91	-92	-91	-90	-88	-85	-84
GROUP MEAN	42	35	33	56	53	52	52	51	50	50
Magnitude and duration of annual extremes										
1-day minimum	-41	-59	-70	-88	-90	-89	-89	-88	-87	-87
3-day minimum	-37	-54	-65	-93	-89	-89	-89	-88	-87	-86
7-day minimum	-26	-49	-61	-94	-86	-84	-83	-80	-78	-77
30-day minimum	-5	-24	-41	-91	-81	-80	-80	-78	-74	-72
90-day minimum	115	62	18	22	-41	-41	-40	-42	-44	-45
1-day maximum	-33	-21	-8	-19	-21	-21	-22	-23	-23	-22
3-day maximum	-31	-20	-17	-10	-14	-15	-15	-15	-16	-18
7-day maximum	-40	-39	-39	25	27	24	23	14	6	3
30-day maximum	-46	-44	-47	24	5	-2	-4	-13	-15	-16
90-day maximum	-46	-51	-47	74	96	91	92	87	92	91
# of zero-flow days	0	0	0	0	0	0	0	0	0	0
Baseflow	66	41	36	-59	-62	-61	-61	-55	-51	-49
GROUP MEAN	41	39	37	50	51	50	50	49	48	47
Timing of annual extremes										
Julian date of annual minimum	38	47	47	22	18	18	18	18	18	25
Julian date of annual maximum	24	-5	-8	8	11	6	6	6	6	6
GROUP MEAN	31	26	28	15	15	12	12	12	12	16
Frequency and duration of high and low pulses										
Low pulse count	-49	-33	-44	-100	-100	-100	-100	-100	-100	-100
Low pulse duration	3	-11	-5	-100	-100	-100	-100	-100	-100	-100
High pulse count	48	75	68	184	269	259	288	237	230	212
High pulse duration	-12	2	-16	62	109	55	56	97	113	146
GROUP MEAN	28	30	33	112	145	129	136	134	136	140
Rate and frequency of change in conditions										
Rise rate	34	4	-36	347	164	165	165	163	124	105

Fall rate	-5	4	18	-143	-180	-188	-174	-126	-91	-84
# of reversals	70	81	73	137	56	66	85	147	132	142
GROUP MEAN	36	30	42	209	133	140	141	145	116	110