

Defining rarity and determining the mechanisms of rarity for North American freshwater fishes

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Abstract

Conserving rare species and protecting biodiversity depends on sound information on the nature of rarity. Rarity is multidimensional, presenting the need for a quantitative classification scheme by which to label species as rare or common. I defined rarity for freshwater fishes based on the range extents, habitat breadths, and site abundance and examined the relationship between these dimensions of rarity and imperilment. Imperiled fishes were most often rare by all three dimensions, whereas undesigned species were most often common by all three dimensions. Next, I examined the effect of sampling intensity on observed rarity of stream fish using different numerical and proportional rarity criteria and found that increasing sampling intensity increased the number of species labelled as rare with proportional criteria but did not affect the number of species labelled as rare with numerical criteria. Additional electrofishing passes within a fixed reach increases the likelihood of detecting rare and endemic species. A tradeoff between information collected and sampling resources should be carefully considered in the context of objectives when sampling for rare species. Finally, I examined the effect of regional and watershed habitat variables, biotic interaction variables, and instream habitat variables, on the rare or common status on 23 North American freshwater fishes. I also compared biological and reproductive traits among species classified into the rarity framework. Rarity was successfully explained in 19 of the 23 species and I found that regional and watershed habitat variables were the most important predictors of rarity. I also found that species large body size, high fecundity, and long age at maturity were generally more common by range extent and site abundance while those species that did not guard nests were more frequently rare by site abundance.

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Attribution

Emmanuel Frimpong co-authored Chapter 1 and Chapter 2. The manuscript for Chapter 1 is currently in press for *Conservation Biology*, and was submitted on August 9, 2008. The manuscript for Chapter 2 is currently in prep to be submitted to the *Canadian Journal of Fisheries and Aquatic Sciences* and Chapter 3 is in prep to be submitted to *Ecography*.

Emmanuel's contributions to the papers include assistance in developing the conceptual framework, evaluation of the statistical analysis, and editing the manuscripts for publication.

General Introduction

The current loss of biodiversity, both globally and in freshwater ecosystems, is staggering. Mckee et al. (2003) predict that the number of threatened species will increase by an average of 14% per nation by 2050. In freshwater ecosystems, as much of 20% of the world's freshwater fishes are already extinct (Moyle and Leidy 1992), and Ricciardi and Rasmussen (1999) predicted a future extinction rate of 4% per decade of fishes, mollusks, crayfish, and amphibians. Furthermore, Jelks et al. (2008) evaluated the imperilment of North American freshwater fishes and found that almost 40% of North American fishes are currently imperiled and almost twice as many species were considered imperiled currently in comparison to a similar list in 1989. The loss of biodiversity in freshwater ecosystems has been attributed to anthropogenic disturbances such as changes in land use, climate change, nitrogen deposition (Sala et al. 2000) introduction of non-indigenous species, habitat degradation, over exploitation, and introduction of diseases and parasites (Jelks et al. 2008).

Rarity is an important component of biodiversity and virtually all of the world's species can be considered rare in some way or another (Kunin and Gaston 1993). Rarity is also correlated with extinction risk (Mace and Kershaw 1997) and hence is an important aspect of species imperilment. Clearly, rarity is crucial to conservation biology, and understanding what rarity is and the mechanisms that lead to rarity is vital to making sound conservation decisions (Mace and Kershaw 1997).

Little is known about many of the world's rare species as a function of the inherent difficulty to find rare species (Gaston 1997) and the view by many ecologists that these species are of decreased value to ecological functioning (Kunin and Gaston 1993). Rare species may actually provide important and potentially valuable ecosystem functions, although the ecological

functions of most rare species have not yet been determined (Lyons et al. 2005). For example, the presence of one large predator has been shown to change the behavior of pool-dwelling fish in streams (Schlosser 1987; others). Also, the feeding by the northern hog sucker, a species that is frequently rare in smaller streams, dislodges materials from the benthos that then serve as a food source for other fish (Baker and Foster 1994). Fagan and Stephens (2006) hypothesized that losing rare fish species changes the nature of interspecific competition, altering the assemblage structure and damaging opportunities for long-term, biotic-driven forces such as coevolution.

Defining rarity and understanding exactly what rarity means are difficult tasks to accomplish. The rarity versus commonness dichotomy transcends the study of communities and populations. For example, rarity can be thought of as an attribute of a species, that is, a given species is rare in some way or another and this description is often casually awarded to many species (personal observation). However, to label a species as rare implies that at least one similar species, that occupies the same temporal and spatial dimensions, is common and therefore rarity cannot be divorced from community ecology. Similarly, rarity can be attributed to an assemblage based on the number of rare species in assemblage A versus assemblage B, to make community-level comparisons (Santoul et al. 2005). Unlike many measurements of species attribute, such as abundance and demographics, or measurements of assemblages such as richness or evenness, rarity does not have a single dimension by which it can be easily measured. Rarity has been defined on abundance, range size, habitat breadth, temporal persistence, threat of imperilment, genetics, enemism, taxonomic distinctness (Gaston 1997), and frequency occurrence at some spatial scale (Prendergast et al. 1993). Each of these definitions comes with different meanings and different implications to conservation. For example, a species may be

considered common based on abundance but rare based on range size or endemism. Without considering multiple rarity criteria, the rarity of any given species cannot be fully understood.

Considering spatial scale is crucial to understanding rarity. For example, Hartley and Kunin (2003) examined the effect of differing spatial scales on defining a species as rare and found that British plants were considered rare at small scales but an increased spatial extent of the study scale resulted in these species no longer being considered as rare. Additionally, they recommended conducting analyses at multiple spatial scales and carefully selecting an appropriate scale based on the research question being asked.

There is strong evidence that rare species have specific characteristics that differ from common species. This includes differences in life history traits (Murray et al. 2002), reproductive strategy, parental investment, dispersal ability, genetics, competitive ability, and patterns of resource usage (Gaston and Kunin 1997) between rare and common species. There also appears to be geographic patterns between the rare or common status of populations within species that can be attributed to environmental conditions rather than random chance (Schoener 1987). These findings suggest that rarity can indeed be predicted; some species are more likely to be rare than others and individual species are more likely to be rare in some locations than in others.

We must also consider that rarity could be an artifact of our sampling methodologies. Ineffective or incomplete sampling may lead to observed rarity when a species is actually common. In species-rich, terrestrial spider communities, Sharaff et al. (2003) determined that one species was rare as an artifact of methodology while several more were likely rare as a result of undersampling. Deciphering artifactual rarity from actual rarity is crucial to understanding rarity and for making conservation decisions about species observed to be rare.

The goal of this study is to define and describe rarity and explore possible mechanisms driving observed patterns of rarity in stream fish community samples. Three potential mechanisms will be examined: sampling intensity, spatial and temporal factors of species distributions and environmental conditions, and species traits. My research questions are: 1) what is the nature of rarity in fishes and how is rarity associated with species imperilment, 2) what is the effect of sampling intensity on observed rarity, and 3) what species traits are associated with rarity across species and what environmental factors drive rarity within species? I will examine these potential mechanisms at multiple spatial scales and determine the effect of different rarity criteria on the outcome of my results. This study should provide managers and researchers with an understanding of the forces that drive richness and rarity, and provide insight into future stream fish community sampling efforts, management, and conservation.

Chapter 1

A quantitative classification of rarity for freshwater fishes of the United States and implications for imperiled species designations

Abstract

Rare species are a vital component of biodiversity and many rare species are listed as endangered, threatened, or vulnerable. Conserving rare species and protecting biodiversity and ecosystem functioning depends on sound information on the nature of rarity. Rarity is multidimensional and has been defined a number of ways by many different researchers, presenting the need for a quantitative classification scheme by which to label species as rare or common. I constructed such a classification for North American freshwater fishes in order to better describe rarity in fishes and provide researchers and managers with a tool to streamline conservation efforts. I used (1) the range extents, (2) habitat breadths, and (3) local abundance of North American freshwater fishes and employed a variety of quantitative methods and statistical decision criteria to determine appropriate cutoffs to label a species as rare or common along each of these dimensions. The resulting classification of species into eight groups conforms to a well established framework for rarity. Fishes that were listed as endangered, threatened, or vulnerable were most often rare by local site abundance, range extent, and habitat breadths in that order, whereas unlisted species were most often common by these criteria. Species with large range extents generally had wide habitat breadths while those with small range extents tended to have narrow habitat breadths. I identified 30 species not designated as imperiled by the American Fisheries Society that were rare along all dimensions of rarity and may warrant further study or protection, while three designated species were found to be common along all dimensions and may require a review of their protection status. My approach

could be applied to other taxa to aid conservation decisions whilst also serving as a useful tool for future revisions of fish species listings.

Introduction

Protection of rare species is central to many conservation efforts and the ability to make prudent management decisions relies upon sound information about these species (Schoener 1987; Fagan & Stephens 2006). By contrast, other rare species may represent the early stages of undesirable invasions (Colautti & MacIssac 2004) and may require action to prevent potential harmful effects. Rare species may provide important and potentially valuable ecosystem functions (Moyle & Moyle 1995; Lyons & Schwartz 2001), although the ecological functions of most rare species have not yet been determined (Lyons et al. 2005). Also, losing rare species could change the nature of interspecific competition, altering assemblage structure and damaging opportunities for long-term, biotic-driven evolutionary forces such as coevolution (Fagan & Stephens 2006).

Species rarity plays an important role in the creation of federal, state, and non-governmental imperiled species lists and rarity is a strong correlate of extinction risk (Mace & Kershaw 1997). Information about species rarity is combined with assessment of threats to populate most imperiled species lists (USFWS 2009; H.W. Jelks, pers. com.). Many reasons exist for listing species as endangered, threatened, or vulnerable, including small range size, over-exploitation, habitat destruction, disease or parasitism, competition, hybridization, or predation resulting from introduced species, or an inadequacy of current regulations (Jelks et al. 2008; USFWS 2009).

Many imperiled species lists are currently in existence and the exact process used to create these lists are often varied. For the creation of the most well-known imperiled species list, the United States Endangered Species List (USFWS 2009), the process begins through United States Fish and Wildlife Service (USFWS) publication of notices of review of candidate species identified by the USFWS or through a petition. They then rank the magnitude of the threat, the immediacy of the threat, and the taxonomic distinctiveness of the candidate species to create an order of priority among candidates and propose listing status as threatened or endangered. The USFWS then seeks biological information and public comments regarding a proposed species and finally decides to list the species, withdraw the proposal, or extend the proposal (USFWS 2009).

The current process of creating the United States Endangered Species List (USFWS 2009) has several weaknesses that likely result in inconsistencies and shortcomings in designating species as imperiled. For example, the species by species approach is slow and attention is generally skewed towards high-profile species (Rohlf 1991). A quantitative system for describing species rarity would help abate these problems by objectively identifying species that are possibly deserving of imperiled status, pending assessment of threats, but have been overlooked, and by providing a tool to describe the biology of rarity for a large number of species. Such a system could also facilitate a more prompt listing of newly imperiled species, thus improving their odds for recovery (Taylor et al. 2005).

Several non-governmental agencies have also created endangered species lists. Recently, the American Fisheries Society (AFS) created an imperiled species list for North American freshwater fishes (Jelks et al. 2008). In contrast to the process employed by the USFWS, the AFS list was created by a committee of experts. The committee began with a previous list

(Williams et al. 1989) and then each member added a list of species that he or she believed to deserve further attention. Each species was then evaluated by a committee member with knowledge of the species. The evaluation process for each species included a literature review and external opinion from local experts. The committee member then suggested a designation of endangered, threatened, or vulnerable. The resulting list was then evaluated by the committee as a whole until a consensus was reached (Jelks et al. 2008).

The non-governmental AFS list has several advantages over the federal list including a more rapid listing of species and fewer political constraints that often accompany agency listing protocols. However, because species on this list are independently evaluated by different committee members and experts, there is a possibility that the evaluation process lacks consistency. A quantitative system for describing rarity may provide a means for comparing species and aid a committee in the evaluation phase of the list creation (H.W. Jelks, pers. com.).

Any discussion of rare species must begin by defining a rare species, and the criteria for rarity have taken on many forms in many disciplines (Kunin & Gaston 1993). Rarity has been defined at the site level based on total numerical abundance (total abundance in a sample) (Novotny & Basset 2000; Scharff et al. 2003; Kanno et al. 2009), on proportional abundance (abundance proportional to other members of the community) (Stevens & Willig 2002; Murray & Lepschi 2003; Kanno et al. 2009), or on community level indices (Camargo 1993; Stevens & Willig 2002). Each criterion has its own set of advantages and disadvantages. Numerical abundance is likely a good measure of population size but can be heavily influenced by sampling effort and effectiveness. Proportional abundance may not be as easily influenced by sampling effort but is affected by the total abundance of individuals across all species. Community-level indices, such as Camargo's index (Camargo 1993), can normalize proportional abundance

information with species richness, potentially rendering these indices more useful for comparing rarity across sites with differing species richness. However, this imposes differing criteria of rarity for the same species among sites.

Rarity is not restricted to the site level and has been defined with many other criteria. For example, rare species have often been defined based on their proportion of occurrence in samples confined by some spatial extent (Prendergast et al. 1993; Santoul et al. 2005; Cucherousset et al. 2008) while others have labeled species as rare based on the extent of geographic range (Fagan & Stephens 2006) or on a prior federal or state agency listing of a species as endangered, threatened, or a species of concern (Hayer et al. 2008; Petersen et al. 2008).

Although it is reasonable to assume that some species will be considered rare over converging criteria, the variation in the criteria used to label species as “rare” or “common” may result in misleading and inconsistent results within the literature. This problem, in conjunction with the lack of a quantitative methodology for listing species for protection, presents a need for a quantitative classification system that can be applied to create a common language surrounding rarity and help managers make sound conservation decisions. A hierarchical rarity classification has been developed for plants by Rabinowitz (1981) that has since been applied to mammals (Yu & Dobson 2000). In this framework, species are considered common or rare first by geographic extent, then by habitat breadth (the number of habitat types in which a species is known to exist), and finally by local population size, resulting in eight permutations, seven of which display rarity in at least one dimension of the framework and one classification group that displays commonness across all three dimensions (Table 1).

Applying the Rabinowitz (1981) model is difficult and requires a large amount of detailed data (Gaston and Lawton 1990). Since the Clean Water Act in 1972, monitoring of

biota in United States streams has become more prevalent. Recently, the United States Geological Survey (USGS) and the United States Environmental Protection Agency (USEPA) have made available large databases of stream fish samples that cover a significant proportion of the conterminous United States. Additionally, decades of detailed autecology studies of hundreds of species have provided a great amount of species-specific habitat breadth information (Lee et al. 1980; Hocutt & Wiley 1986; Page & Burr 1991). By utilizing these advancements in fish ecology, United States freshwater fishes present an excellent study taxon to quantitatively apply the Rabinowitz (1981) model. In addition, fish represent one of the most imperiled taxa on the planet and North America has a particularly diverse fish fauna (Helfman 2007; Jelks et al. 2008). Also, great numbers of rare fish species are often positively associated with areas of high biodiversity that should be protected (Lawler et al. 2003). Finally, Jelks et al. (2008) have developed a current, comprehensive imperiled species list that allows us to examine the relationship between rarity and species imperilment.

The goal of the current study is to provide an example of a quantitative classification scheme for rarity of freshwater fish species that will allow researchers to interpret rarity in their data and provide managers with a tool for making conservation decisions regarding rare species. My objectives are to: (1) establish criteria for rarity based on species range extents, habitat breadths, and local site abundances for native fishes in the conterminous United States, (2) explore patterns of rarity in fishes, and (3) apply my classification scheme to investigate the relationship between rarity and the Jelks et al. (2008) designations of fish imperilment.

Methods

Data Sources

Data were gathered from two national databases to develop the rarity classification. I used 1,040 stream sites, representing 44 states, from the USGS National Water Quality Assessment program (NAWQA) (USGS 2008) sampled between 1993 and 2004. These national databases are ideal for studying rarity at a nation-wide scale because they are distributed over a large geographic area and incorporate a large number of species. The NAWQA sample reach lengths were between 150m and 300m in wadeable streams, and 500m to 1000m for non-wadeable streams. I also used data from 308 stream sites from the USEPA Regional Environmental Monitoring and Assessment Program (REMAP) database from the mid-Atlantic US (USEPA 2008). The REMAP sites were sampled between 1993 and 1998 with electrofishing and the sample stream length was approximately 40 times the mean stream width and at least 150m, making this dataset comparable to the NAWQA protocol. Both the NAWQA and REMAP samples sought to characterize entire fish assemblages in terms of species present in a site and their proportional abundances. Because some sites in these datasets had multiple reaches and some were sampled multiple times, only the first reaches at the first sampling times were used to avoid over-representation of some sites.

Species ranges and trait information were obtained from the FishTraits database (Frimpong & Angermeier 2009). This database includes ecological trait data for over 800 species of freshwater and anadromous fishes found in the conterminous United States. The ecological traits include habitat breadth information from accounts of species associations with specific habitat descriptors such as substrate, lentic versus lotic systems, stream size, current speed, elevation, and salinity tolerance.

Data Analysis

To create my rarity classification scheme, I created distribution histograms for range extent, habitat breadth, and site abundance and placed species into appropriate bins (described below). I first visually analyzed the histograms for natural breaks in the data at which species to one side could be considered rare while those to the other side could be considered common. When a natural break was not apparent, I applied a cost-function algorithm in which cost was defined by the residual error that resulted from splitting species into two groups at any point along the range of values. The cost function was found by adding the sums of squared deviations of species values from their respective group means (Faraway 2006). I iteratively searched for the break along the histogram that gave the minimum total sum of squares. The result was the creation of two groups each for range extent, habitat breadth, and site abundance that had the maximum possible within-group similarity and between-group difference. After cutoffs for all three rarity dimensions were determined, I assigned species as “rare” or “common” for each dimension. Finally, I organized species into the Rabinowitz (1981) hierarchy based on available data.

To establish a range extent criterion, I adjusted species ranges based on size of overall range, latitudinal range, and longitudinal range using the formula: $R_{adj} = 0.5[\ln(\sqrt{R_{total}})] + 0.25[\ln(R_{lat})] + 0.25[\ln(R_{long})]$, where R_{adj} is the adjusted range of a species, R_{total} is the species' range area (km²), R_{lat} is the species' latitudinal range (km), and R_{long} is the species' longitudinal range (km). This adjustment was made because fishes are generally distributed along physical and climatic gradients that often lead to oddly shaped distributions. I plotted a histogram of species scores on the range extent criterion and then applied the cost

function algorithm to locate the break in the data at which species with a greater adjusted range could be considered common and those with a smaller adjusted range could be considered rare.

To develop a measure of habitat breadth, I first identified two broad categories of habitat breadths at the macrohabitat level (fluvial, landscape, and salinity breadths), and four categories at the microhabitat level (substrate, current, and water column breadths). Within these broad habitat categories, a total of 19 possible habitat selections were identified (Table 2). To create an Index of Habitat Breadth (IHB), each species was binary-scored on each of the 19 habitat types as “1” if the species associates with the given habitat type and “0” if it does not associate with the given habitat type, following Frimpong and Angermeier (2009). Species with more scores of “1” would tend to be habitat generalists while those with more scores of “0” would tend to be more habitat-specific or specialists. A score of “-1” was assigned in lieu of “1” for species that are migratory (potadromous or anadromous) because although these species are found in a variety of habitats, they need each habitat to complete a different phase of their life cycle and therefore cannot be considered habitat generalists. The binary habitat scores were added to create the IHB as an inverse measure of habitat breadth. The cost function algorithm, described above, was again applied to the calculated IHB values to determine an appropriate cutoff between species with narrow habitat breadths and those with wide habitat breadths.

I used “site abundance” as a surrogate for “local population size” (as in the Rabinowitz (1981) framework) because the stream samples in the two national databases do not represent spatially confined populations and were not intended to provide population estimates. Before setting a cutoff to determine which species have “consistently small” site abundances, I had to first define small site abundance. I used multiple criteria to protect against the shortcomings of arbitrary numerical and proportional cutoffs and community indices. I used fish assemblage data

for the 1,348 sites in the NAWQA and REMAP databases to establish stable cutoffs of numerical and proportional criteria and combined the result with the Camargo (1993) community criterion to develop a single classification of small versus large site abundance. To understand the statistical behavior of rarity, I plotted the number of rare species in each sample against numerical abundance criteria ranging from 1 to 100 individuals and proportional abundance criteria ranging from 0.5% to 50%. I then used visual analysis and parametric, non-linear regression to establish that both plots reached an asymptote within the range of criteria selected. Because of a large amount of variance in my data, I performed a nonlinear quantile regression using cubic splines (Chen 2009) at the 50th, 75th, 90th, and 95th quantiles that allowed me to understand the patterns and sensitivity of rarity at different quantiles. Based on the regressions, I set a small site abundance as the respective numerical and proportional abundances that satisfied approximately 80% or higher of the asymptotic rarity for at least three of the four quantiles (Fig. 1.1).

After establishing both numerical and proportional abundance cutoffs to define a small site abundance, I included the Camargo community index that defines a subordinate species as: $p_i \leq 1/S$, where p_i is the proportional abundance of species i and S is the species richness (Camargo 1993), as a third criterion for local rarity. In each of the 1,348 I classified a species as rare in the sample if it was rare by two or all the three (i.e., numerical, proportional, and Camargo) criteria (Fig. 1.1). Next, I calculated the proportion of occurrences at which each species was rare. I plotted these proportions in a histogram and visually analyzed this histogram to find at what proportion of sites a species must have a small site abundance for it to be considered “consistently rare” (Fig 1.1).

After determining thresholds between common and rare species at range extent, habitat breadth, and site abundance, I classified all species on which I had sufficient information based on the Rabinowitz (1981) framework (Table 1). I analyzed the species designated as vulnerable, threatened, or endangered by Jelks et al. (2008) (designated species) to explore where these species fall out in my classification. Some of the Jelks et al. (2008) species designations were for subspecies. I did not include those species as designated species in my analysis, as most of the available data represent the species at large and not the imperiled subspecies. A chi-squared test of homogeneity was used to test for a difference in proportions of species in rarity groups between designated species and non-designated species. To examine discrepancies between my rarity classification system and the imperiled species designations of Jelks et al. (2008), I used the Explorer tool available from NatureServe (NatureServe 2009) to evaluate species on a case by case basis. Finally, I tested for correlations among range extent, habitat breadth, and site abundance to establish how these three dimensions of rarity are related in fishes.

Results

Species range information was found for 722 native species and ranged from 440 km² to > 14 million km² while the adjusted ranges ranged from 3.2 to 8.5 (Fig. 1.2a). The cost function showed that the minimum cost of break in the adjusted range was at 6.17 (Fig. 1.2b; Table 3); hence 334 species were considered common under the range extent rarity criteria while 388 species were considered rare (Appendix A).

Information was available to calculate an IHB score for 678 native species and values ranged from 5 to 15 (Fig. 1.2c). The cost function showed the global minimum of the sums of squares to be 8.0. Therefore all species with a score ≤ 8 were considered to have narrow habitat

preferences while those with a score ≥ 9 were considered to have wide habitat preferences (Table 3). Overall 369 species had wide habitat preferences while 309 had narrow habitat preferences (Appendix A).

Site abundance data for 410 native species were found from the 1,348 NAWQA and REMAP fish datasets. The quantile regressions revealed that the number of rare species approached 80% of the asymptotic level at approximately ≤ 20 individuals for the numerical abundance criterion and $\leq 5\%$ for the proportional abundance criterion (Fig. 1.3). With the inclusion of the Camargo index, these three criteria were used to define a “consistently small” site abundance.

Over 30% of all species were categorized as rare by two or three of the numerical, proportional, and Carmargo criteria in every sample that they occurred and these species were considered to have consistently small site abundances (Fig. 1.2d). I reasoned that the sharp break in the histogram between species rare in 100% of the sites they occupy and those that were common in at least one site presents an appropriate cutoff for the site abundance criterion. I elected to place the cutoff for a consistently rare site abundance as species rare at $\geq 95\%$ of sites to ensure that I capture all rare species within a margin of 5% of error in my observations (Table 3).

Range extent and habitat breadth data were available for 399 of the 410 species that also had local abundance data, and 47 of these species were designated as imperiled by Jelks et al. (2008). The species with a full set of data were placed into the eight categories of the Rabinowitz (1981) framework (Appendix A). The most frequent category for non-designated species was group A (common by all three criteria), followed by group E (rare by extent, common by habitat and site abundance), group C (common by extent, rare by habitat, and

common by site abundance), and then group B (common by extent, common by habitat, rare by site abundance). Species designated as imperiled were most frequently found in group H (rare by all three criteria), followed by group F (rare by extent, common by habitat, and rare by site abundance) and then group B (common by extent and habitat, rare by site abundance) (Fig. 1.4). The chi-squared test showed the above differences between the grouping of designated and non-designates species to be significantly different ($p < 0.001$).

My classification identified 30 species that were rare along all three dimensions but were not designated as imperiled by Jelks et al. (2008) (Table 4). According to the Nature Serve Explorer tool, 25 of these species were classified as vulnerable, imperiled, critically imperiled, or extirpated in at least one state they occupied (Table 4). In addition, three species, the Rio Grande chub, Plains minnow, and snail bullhead, designated as imperiled by Jelks et al. (2008) were found to be common along all three dimensions of rarity.

Correlations between rarity dimensions showed that adjusted range was moderately correlated with habitat breadth (IHB score) ($r = 0.44$, $p < 0.001$). This indicates that species with larger range sizes tended to have wide habitat breadths (Fig 1.5a). However, adjusted range had almost no relationship with rarity in site abundance ($r = -0.001$, $p = 0.87$) (Fig 1.5b). Site abundance and IHB score were weakly correlated ($r = -0.13$, $p = 0.009$), indicating that species with low IHB scores (habitat specialists) tended to have slightly smaller site abundance; however, there is a great deal of variation in this relationship (Fig. 1.5c).

Discussion

Patterns of rarity in freshwater fishes

Several patterns are apparent in the final eight groupings. For non-designated fish species, groups that represented large site abundances (A, C, E, and G) had more species than those that represented small site abundances (B, D, F, and H). The opposite pattern was true for designated species as more species fell into the groups with small site abundances than the groups with large site abundances. This pattern is not surprising as small population size is correlated with high extinction risk (Mace and Kershaw 1997). As expected, few designated species fell into group A and the most populated group was group H, the most extremely rare group. The largest difference in a single group between non-designated and designated species occurred in group F which contained 20% of designated species but only 5% of non-designated species. The F grouping represents species with a wide habitat preference but small range extents and small site abundances; species in this group that are imperiled are likely facing threats other than habitat modification. In fact, of the nine designated species in this group, three are designated as imperiled because of “other” natural or anthropogenic factors including impacts of nonnative species (Jelks et al. 2008) while none of the 13 species in groups H or G are designated for this reason. The striking differences in groupings between designated species and non-designated species indicates that there are biological and ecological differences that make some species more vulnerable than others, as hypothesized by Kunin and Gaston (1997).

The patterns of rarity in freshwater fishes can also be used to guide further research in evolutionary and biogeographic mechanisms of rarity in fishes. For example, the correlations between rarity dimensions indicate that species with small ranges also have small habitat preferences and the mechanism for this phenomenon could have two possible explanations.

First, smaller habitat preferences could lead to some species occupying smaller ranges because they are not able to take advantage of open niches and therefore cannot disperse into new areas. By contrast, species with greater range extents resulting from biogeographic history may have adapted to a greater number of habitat types that are prevalent throughout parts of their larger ranges (Pyron 1999). I hypothesize that the latter explanation is a more common cause in North American fishes because many of the species with narrow habitat preferences and small range extents are darters that are thought to have allopatric speciation (e.g. Near and Bernard 2004).

Importance to conservation

My classification scheme highlights many species that could be in need of protection. Most of the 30 species that meet the rarity criteria on all dimensions (group H) but are not designated as imperiled by Jelks et al. (2008) were considered imperiled at a local level by Nature Serve. Although rarity without detailed analysis of threats is not sufficient for listing species as imperiled (Mace and Kershaw 1997; H.L. Jelks, pers. com.), rarity does correlate with extinction risk (Mace and Kershaw 1997), and as a result, these species may warrant further evaluation of their imperiled status at the national level. It is possible that these species are common at the local population level in locations that were not captured by the NAWQA and REMAP datasets; however, this list presents an opportunity to direct future research into these possibly imperiled species and expedite their protection if necessary. For example, researchers may wish to conduct more intensive sampling for these species to gain more information on their local abundances and examine possible threats that these species may face. The fact that most of these species are considered imperiled at the local level but do not appear on any national lists highlights the importance of utilizing local expertise in determining species imperilment.

I also identified several species that are designated as imperiled but whose status may merit review with regional and more up-to-date data. Three designated species that had abundance data, the plains minnow (*Hybognathus placitus*), snail bullhead (*Ameiurus brunneus*), and Rio Grande chub (*Gila pandora*) were considered common at all three levels of the hierarchy. The plains minnow is designated because of habitat destruction, the snail bullhead is designated because of habitat destruction and other natural and anthropogenic factors, and the Rio Grande chub is designated because of habitat destruction, disease and parasitism, and other natural or anthropogenic factors (Jelks et al. 2008). All three species are designated as vulnerable (the lowest level of imperilment) and the bullhead and plains minnow have a rank of G4 (on a scale of G1 as critically imperiled to G5 as secure) while the Rio Grande chub has a rank of G3. The plains minnow has an IHB score of 9, just outside of the 8 score representing the cutoff between wide and narrow habitat breadths. The snail bullhead has an IHB score of 11, and the Rio Grande chub has an IHB score of 10, both well outside of my cutoff. In addition, the snail bullhead occurred in 26 sites and was common in four of these sites, and the Rio Grande chub occurred in three sites and was common in two sites while the plains minnow was only found in one site (at which it was common). The threats that these species face may outweigh their apparent commonness in my classification, however, further investigation may be needed to rectify these differences between the Jelks et al. (2008) designation and my classification.

A large number of species, including many of those designated by Jelks et al. (2008), were not present in any of the 1,300+ sites from my databases. In this situation species can still be classified based on range extent or habitat breadth for which data are mostly available. Because small range size and habitat destruction are commonly cited as reasons for listing a species as imperiled (Jelks et al. 2008), these levels of the rarity framework may still be useful

for evaluating species designations for these reasons. In addition, abundance data is likely available for many of these species and through further collaboration, more species can be added to the framework to a more detailed comparison of rarity in fishes.

The rarity groups created in this study could aid in developing management strategies for rare species. For example, areas containing species with small range extents can be identified and protected while species with large range extents that face imperilment may require cooperative efforts between countries, states, and counties for effective management. Additionally, specific habitats can be identified, protected, or created for species with narrow habitat breadths while special attention can be given to existing populations of those species that have consistently small local populations. Knowledge of rarity can be used to guide conservation actions. For example, species that are rare by range extent and often endemic to a particular, well defined area can be monitored and protected in this area. One extreme example of such rarity is the Devil's Hole pupfish, found in one spring in Arizona. This species is under close watch and the stringent management to protect the only population known in existence (Baugh & Deacon 1988). Also, knowledge of habitat breadths can be managed based on this particular habitat. For instance, successful propagation and reintroduction of rare species depends on explicit knowledge of habitat requirements (Rakes et al. 1999).

My methodology could be easily applied to many other taxa as much information exists in the form of species range maps, habitat breadths, and abundance data from previous surveys such as aquatic insects and mussels. There may be some difficulty in applying this scheme to species that are not easily sampled, such as terrestrial invertebrates (Novotny and Basset 2000) or whose habitat requirements are not well understood such as the wintering habitat of many migratory birds. Quantitatively defining rarity for other taxa should facilitate consistency of

comparative evaluations within the literature and improve the general understanding of rarity as an ecological phenomenon with conservation implications. For example, freshwater fishes show a remarkably similar pattern of rarity compared to mammals described by Yu and Dobson (2000). Both taxa have a significant proportion of species in the most common group (A), the rarest group (H) and the group with large range extent and site abundances but narrow habitat (C). Similarly, fishes and mammals do not have many species in the groups with large range extent, wide habitat preferences, and site abundances (B), large range extent, narrow habitat, and site abundances (D), and small range extent, wide habitat preferences, and small site abundances (F). The major difference between fishes and mammals was that mammals had a large number of species in the group with small range extent, narrow habitat, and large site abundance (G) while fish had few species in this category (note that my organization follows that of Rabinowitz (1981), and the letters match the groups in Table 1 and not the letters used by Yu and Dobson (2000)). The overall similarities between fishes and mammals indicate that the biological and ecological mechanisms of rarity could also be similar.

Caution is needed when distinguishing between rare and common species. For example, range area of fishes is not a sufficient measure of extent because species dispersals are constrained by drainage basins, coast lines, temperature gradients, elevation gradients, or precipitation gradients that can lead to oddly shaped distributions (Lee et al. 1980; Hocutt & Wiley 1986). I included latitudinal range and longitudinal range to account for these factors. Besides geographic range, I selected macrohabitat and microhabitat features to capture a wider range of habitat needs of a species. Including specific habitat variables also provides managers with greater insight into how to protect species singled out by the classification scheme. For example, the guardian darter (*Etheostoma oophlax*) has an IHB score of 6, and is a benthic

species found in slow current in lowland creeks with fine sediment or vegetation. This detailed habitat requirement provides researchers and managers with preliminary information to streamline possible habitat conservation efforts for this species. At the local population level, using multiple rarity criteria is important to safeguard against the downfalls of common numerical and proportional criteria. I argue that a species that is common at the local level should be identified as such through the use of multiple criteria for rarity.

The dichotomous rare versus common classification could possibly overestimate or underestimate actual rarity and I recognize the possible utility of creating intermediate rarity groups. However, the addition of even one intermediate group on each dimension of rarity forms a 3x3x3 classification that results in 27 rarity groups. This increase in data dimensionality would certainly lead to a great deal of difficulty in the interpretation of results and the identification of patterns. The use of an intermediate rarity group should perhaps be conducted on a case by case basis in the evaluation of rarity for conservation. For example, developing intermediate groups and integrating these groups with threat assessments may help managers decide on appropriate levels of imperilment (vulnerable, threatened, or endangered) whereas the current scope of this paper focuses on imperiled versus non-imperiled status. The cost-function algorithm described in this study generalizes to the creation of any number of classes and would be useful in defining an optimal number of groups with finer resolution on each rarity dimension when desired.

Several limitations on the local abundance data used in this study should be considered in the interpretation of my final classification. The available abundance data are likely skewed towards common fish species and these species may be overrepresented in the final classification. Additionally, fishes from eastern North America were better represented than those from western North America. This problem is a result of a paucity of publicly available

data from the West. Also, many of the available data are old, dating as far back as 1993. It is likely that patterns of local abundance for some species have changed since collections have been made and this highlights yet another problem with publicly available data. Finally, as with any publically available data, there are possible errors of omission and commission in my dataset (Hitt and Angermeier 2008). It is more likely that a rare species was omitted or mistaken for a similar common species than a common species to be misidentified as a rare species, as most fish biologists are most familiar with common species. Therefore, site abundance rarity may be slightly underestimated in some of the data used for this study.

Future research could improve my classification of freshwater fishes as well as the methodologies used in this study. More thorough species accounts and more complete abundance data would likely change the placement of some species from their proposed rarity groups. As more information surfaces and species are moved into more appropriate classification groups, my classification should become more complete and more accurate. Also, the current study provides only a snapshot of rarity in fishes. Continued monitoring and analysis of freshwater fishes are needed to capture trends in diversity for future conservation.

Acknowledgements

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Table 1.1. Eight permutations of the rarity classification framework of Rabinowitz (1982) broken down by three dimensions of rarity: extent, habitat breadth, and local population size. Seven of the eight groups display rarity on at least one dimension while one group (A) is common across all three dimensions.

Range Extent		Large		Small	
Habitat breadth		Wide	Narrow	Wide	Narrow
Local population size	Large	A	C	E	G
	Small	B	D	F	H

Table 1.2. The 19 habitat types representing six broad categories used to determine index of habitat breadth (IHB) scores for 678 species in the FishTraits database (Firmpong and Angermeier 2009). Fine substrate preference indicates an association with materials such as clay, silt, and sand while coarse substrate preference indicates an association with gravel, cobble, boulder, or bedrock.

	Categories	Habitat types					
Macrohabitat	Fluvial breadth	1)Lakes	2)Large River	3)Small River	4)Creeks	5)Caves	6)Migratory
	Landscape breadth	7)Lowland	8)Upland	9)Montane			
Microhabitat	Substrate breadth	10)Fine	11)Coarse	12)Vegetation	13)Pelagic		
	Current breadth	14)Slow	15)Moderate	16)Fast			
	Position breadth	17)Benthic	18)Water column or surface				
	Salinity breadth	19)Euryhaline					

Table 1.3. The eight groups in the rarity classification scheme and the criteria cutoffs for each group.

Range Extent		Large (adj. range > 6.17)		Small (adj. range ≤ 6.17)	
Habitat breadth		Wide (IHB > 8)	Narrow (IHB ≤ 8)	Wide (IHB > 8)	Narrow (IHB ≤ 8)
Site abundance	Large	A (rare < 95% sites found)	C (rare < 95% sites found)	E (rare < 95% sites found)	G (rare < 95% sites found)
	Small	B (rare ≥ 95% sites found)	D (rare ≥ 95% sites found)	F (rare ≥ 95% sites found)	H (rare ≥ 95% sites found)

Table 1.4. Species that were rare along all three dimensions of rarity (group H) but were not designated as imperiled by Jelks et al. (2008). State occupancy and imperilment information was obtained from NatureServe Explorer.

Species	States found	State Designations
<i>Cottus baileyi</i>	VA	Imperiled (VA)
<i>Erimystax insignis</i>	AL, GA, KY, TN, VA	Vulnerable (TN, VA), imperiled (AL, GA) critically imperiled (KY)
<i>Etheostoma barrenense</i>	KY, TN	Vulnerable (TN)
<i>Etheostoma edwini</i>	AL, FL, GA	Vulnerable (GA)
<i>Etheostoma euzonum</i>	AR, MO	Vulnerable (AR)
<i>Etheostoma hopkinsi</i>	GA, SC	None
<i>Etheostoma jordani</i>	AL, GA, TN	Vulnerable (TN), imperiled (GA)
<i>Etheostoma juliae</i>	AR, MO	Vulnerable (AR)
<i>Etheostoma kennicotti</i>	AL, IL, KY, MS, TN	Imperiled (IL, MS), vulnerable (AL)
<i>Etheostoma longimanum</i>	VA, WV	Vulnerable (VA), critically imperiled (WV)
<i>Etheostoma nigripinne</i>	AL, MS, TN	Imperiled (MS)
<i>Etheostoma oophylax</i>	KY, TN	None
<i>Etheostoma punctulatum</i>	AR, KS, MO, OK	Critically imperiled (KS), vulnerable (MO)
<i>Etheostoma rupestre</i>	AL, GA, MS, TN	Vulnerable (MS, TN), imperiled (GA),
<i>Exoglossum laurae</i>	NY, NC, OH, PA, VA, WV	Vulnerable (PA, WV), imperiled (NC, NY, OH)
<i>Fundulus escambiae</i>	AL, FL, GA	Vulnerable (AL)
<i>Lythrurus atrapiculus</i>	AL, FL, GA	Imperiled (FL, GA)
<i>Moxostoma pappillosum</i>	NC, SC, VA	None
<i>Notropis asperifrons</i>	AL, GA, TN	Imperiled (GA, TN)
<i>Notropis greenei</i>	AR, MO, OK	Imperiled (OK)
<i>Notropis uranoscopus</i>	AL	Imperiled (AL)
<i>Noturus albater</i>	AR, MO	None
<i>Noturus elegans</i>	AL, KY, TN	Vulnerable (TN), extirpated (AL)
<i>Percina carbonaria</i>	TX	None
<i>Percina gymnocephala</i>	NC, VA, WV	Vulnerable (NC, VA, WV)
<i>Percina crassa</i>	NC, SC, VA	Critically imperiled (VA)
<i>Percopsis transmontana</i>	ID, OR, WA	Vulnerable (WA), critically imperiled (ID)
<i>Phenacobius crassilabrum</i>	GA, NC, TN, VA	Vulnerable (NC, TN), imperiled (VA), critically imperiled (GA)
<i>Phenacobius teretulus</i>	NC, VA, WV	Imperiled (VA, NC), critically imperiled (WV)
<i>Phenacobius uranops</i>	AL, GA, KY, TN, VA	Vulnerable (VA), imperiled (KY), critically imperiled (AL, GA)

Figures

Figure 1.1. Steps for distinguishing between rare and common species based on site abundance.

The first step of the process is to define a small site abundance while the second is to define a consistently small site abundance.

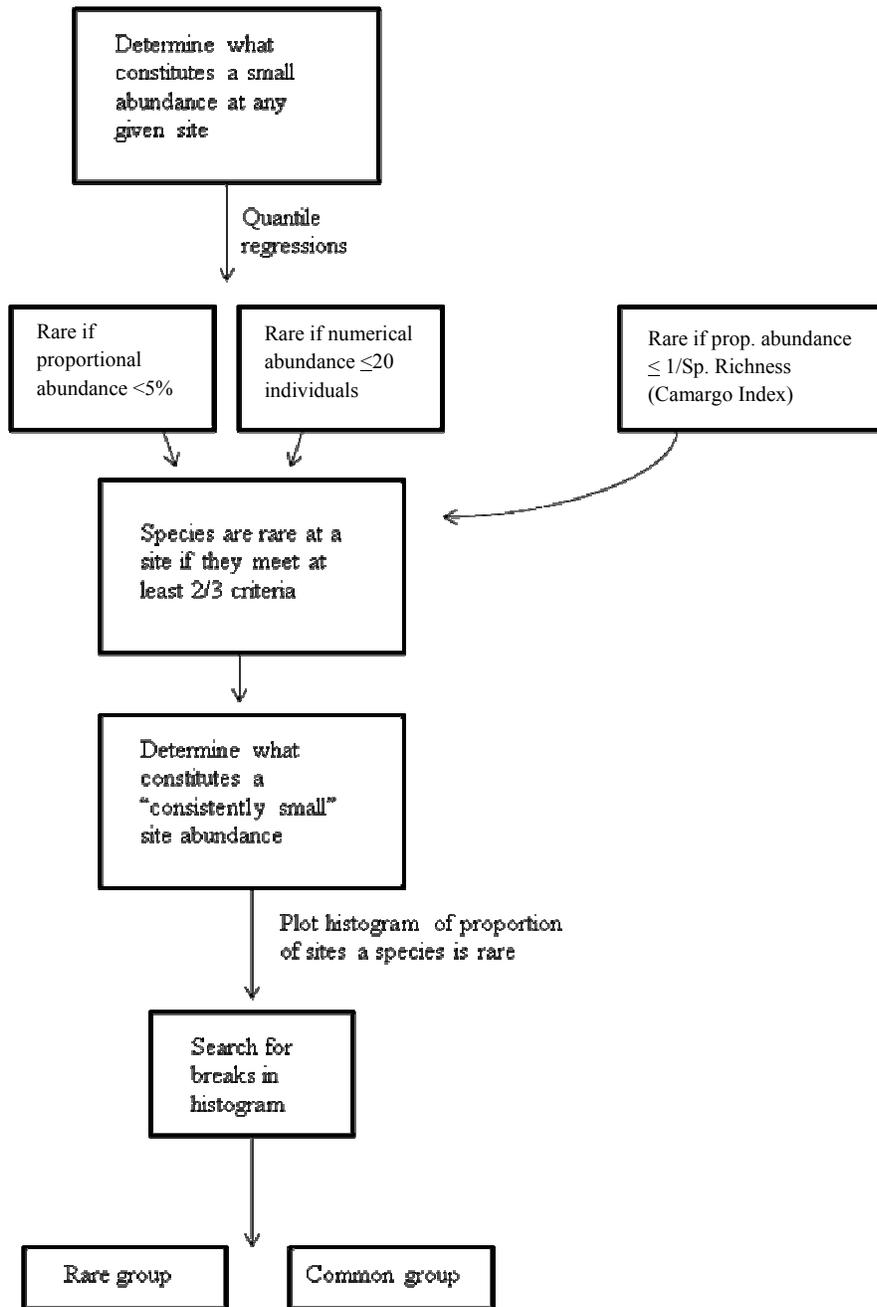


Figure 1.2. a) Histogram of adjusted species range areas, b) cost function for breaking adjusted range into two classes (where cost is defined as the total sums of squared deviations of species values from their respective group means), c) histogram of IHB scores, and d) histogram of species at proportions of sites that they occupy and meet at least two out of three local rarity criteria. Vertical lines represent the cutoff between rare (left of line) and common (right of line) for each dimension.

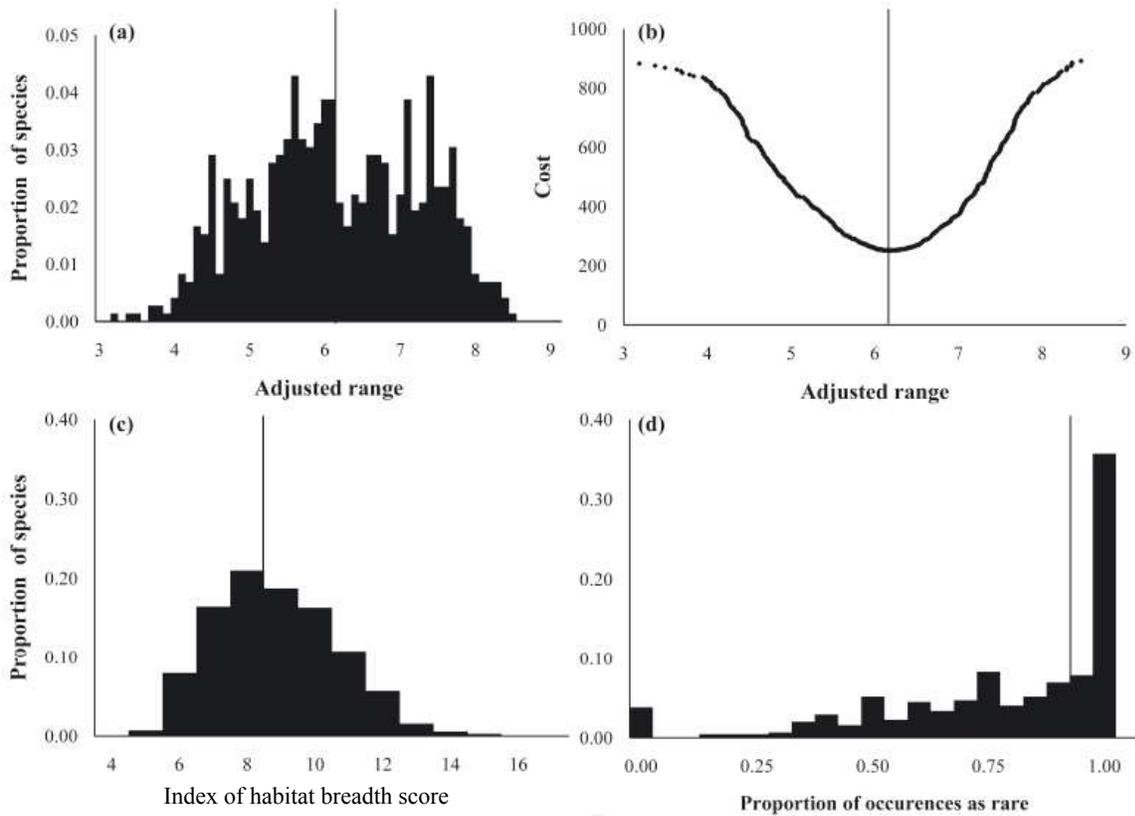


Figure 1.3. The number of species labeled as rare (y-axis) by increasing rarity criteria (x-axis) for the NAWQA and REMAP sites. Nonlinear regressions for the 50th, 75th, 90th, and 95th quantiles provide the average number of rare species for each given quantile at increasing criteria for a) numerical criteria and b) proportional abundance criteria for sites. Vertical lines represent the criterion for which the number of species classified as rare is approximately 80% of the asymptotic (stable) rarity.

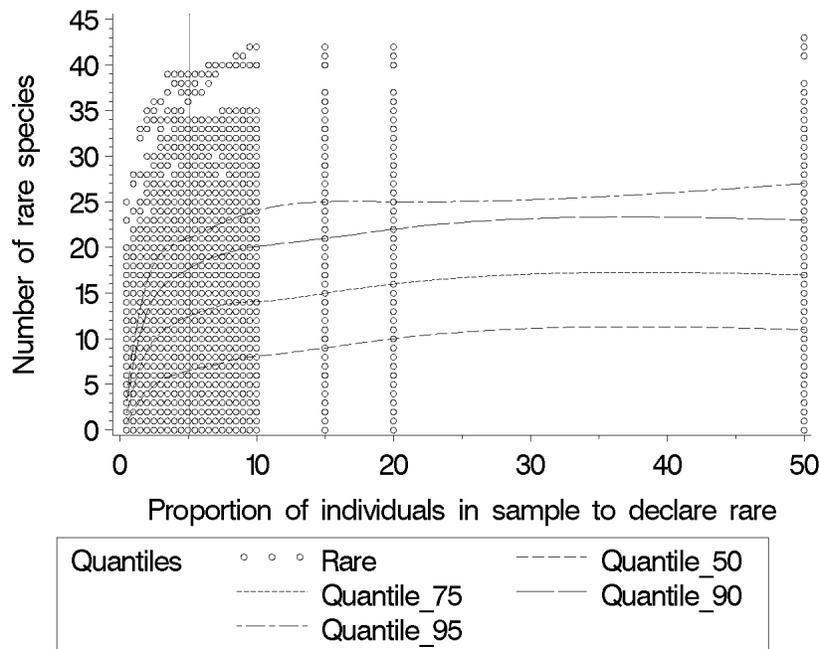
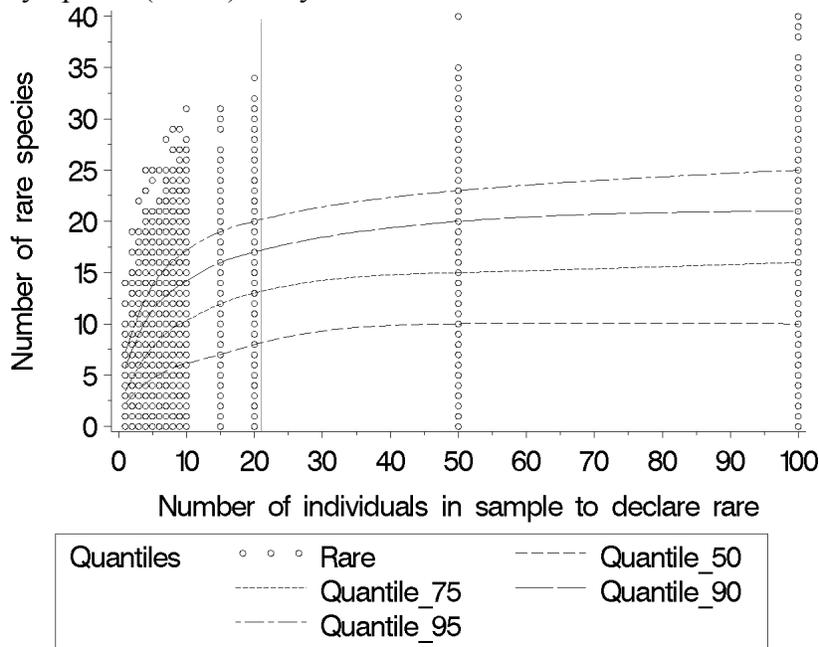


Figure 1.4. Number of total species and listed species in each of the eight final rarity classification groups. Groups are defined as: A) large range extent, wide habitat preferences, and large site abundance, B) large extent, wide habitat, small site abundance, C) large extent, narrow habitat, small site abundance, D) large extent, narrow habitat, small site abundance, E) small extent, wide habitat, large site abundance, F) small extent, wide habitat, small site abundance, G) small extent, narrow habitat, large site abundance, and H) small extent, narrow habitat, and small site abundance. Designated species (dark bars) are those species that are listed as imperiled by Jelks et al. (2008) while no-designated species (light bars) have no imperiled status.

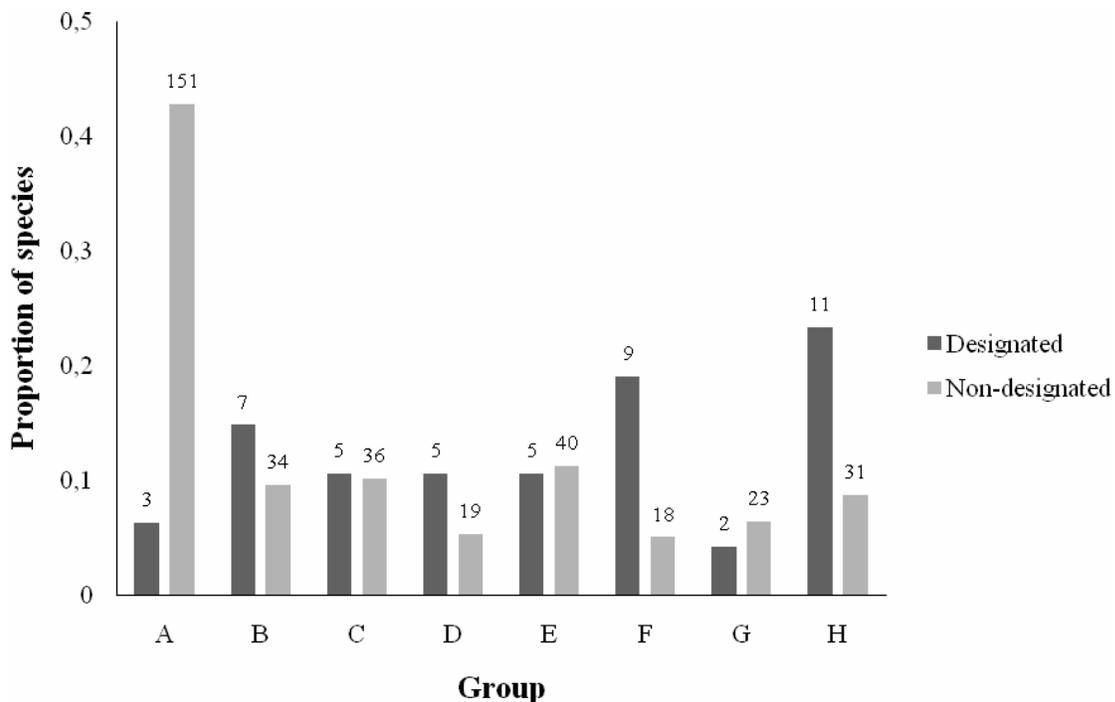
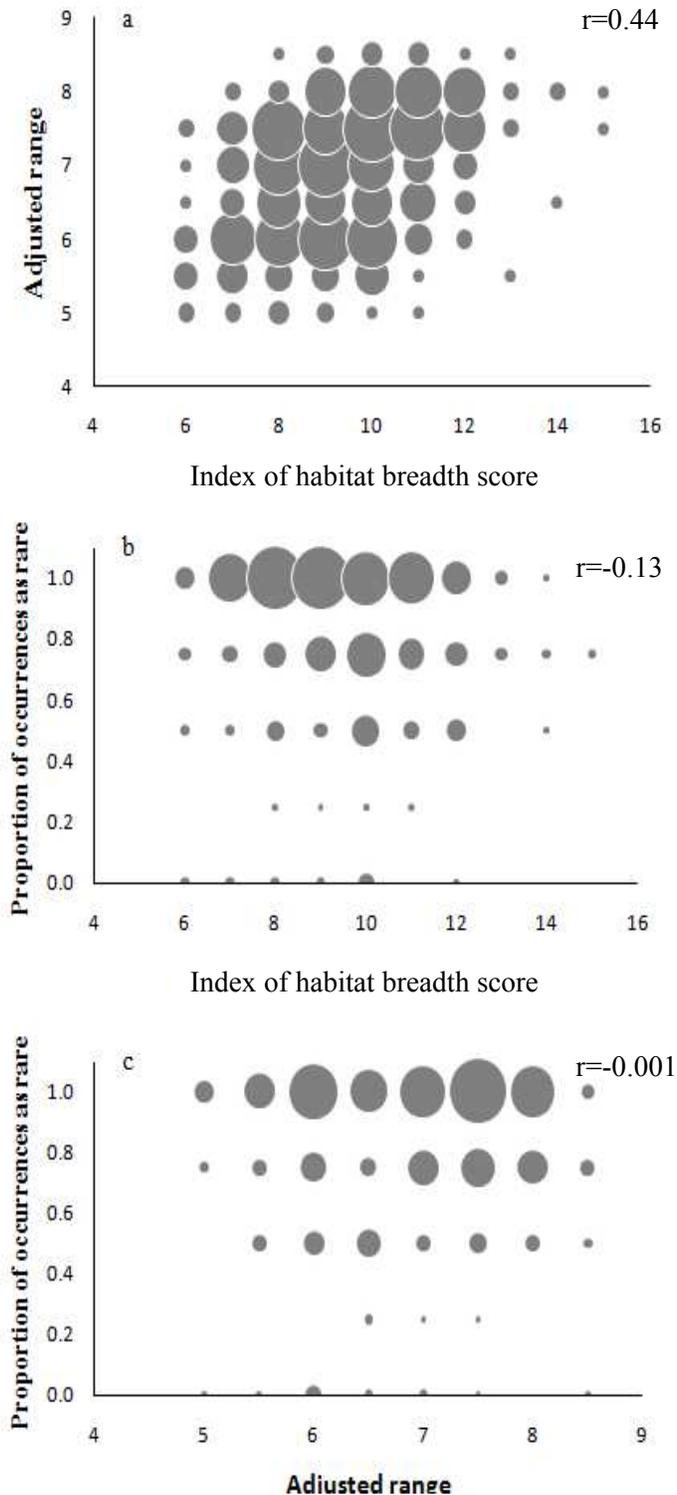


Figure 1.5. Pairwise bubbleplot matrices of 399 species classified in the rarity framework by a) Index of habitat breadth (IHB) scores and adjusted range sizes, b) IHB scores and proportions of occurrences as rare, and c) adjusted range sizes and proportions of occurrences as rare. Bubbles size represent the number of species at a given point on the plot (i.e. large bubbles indicate large numbers of species)



Chapter 2

The effect of sampling intensity on the occurrence of rare species and community assessment metrics

Abstract

Rare stream fish species are important to both conservation and bioassessment; however the effect of sampling intensity on rare stream fishes has not been documented. I examined the effect of sampling intensity on observed rarity of stream fish using different numerical and proportional abundance rarity criteria as well as effects on the assessment of stream fish communities. I compared a one-backpack electrofishing unit protocol to a two-backpack unit electrofishing protocol, a single-pass electrofishing protocol to multiple-pass protocols at a fixed sample-reach length, and increasing reach length as means to increase sampling intensity. Linear mixed models showed that increasing sampling intensity increased the number of species labelled as rare with proportional abundance criteria but did not affect the number of species labelled as rare with numerical criteria. I found no significant difference in the assessment of stream fish communities between the one-backpack and two-backpack protocols but found a significant difference in the assessment of stream fish communities among one-, two-, and three-pass electrofishing; however the difference between two- and three-pass electrofishing was minimal. These results show that a numerical rarity criterion is independent of sampling intensity and may be preferable to a proportional abundance criterion when excluding rare species in community assessments. In addition, a one-backpack electrofishing protocol may be able to characterize structural and functional composition in wadeable streams, but a two-pass protocol provides a significant improvement for many metrics. Additional electrofishing passes within a fixed reach increases the likelihood of detecting rare and endemic species. A tradeoff

between information collected and sampling resources should be carefully considered in the context of objectives when sampling for rare species.

Introduction

Rare species are critical to two facets of stream fish research and management: conservation of stream fishes and statistical analyses associated with bioassessment. To conservation biologists, rarity is often associated with imperiled species (Jelks et al. 2008) that require conservation efforts such as protection or habitat improvement. Rare species can also serve as indicators of areas of great biodiversity (Lawler et al. 2003) that are candidates for protection. To other researchers, rare species represent statistical anomalies in data that can profoundly influence the interpretation of fish community data. Some researchers have concluded that rare species increase the sensitivity of bioassessment and multivariate community analysis methods by providing valuable information (Cao et al. 1998; Cao et al. 2001), but others believe these species create noise and redundancy in data (Merchant 1999). At the site level, rarity can be defined using some cutoff of numerical abundance (Novotny and Bassett 2000; Kanno et al. 2009), proportional abundance (Reynolds et al. 2003; Stephens and Willig 2003; Kanno et al. 2009), or based on some community structural index (Camargo 1993; Stephens and Willig 2003). More recently, Pritt and Frimpong (2010) used multiple local rarity criteria to derive an ecologically meaningful definition of rarity in stream fish surveys through an analysis of nationwide site abundance data. Understanding how sampling intensity influences observed rarity at a site is important for making conservation decisions involving rarity information, such as creating imperiled species lists (Jelks et al. 2008), and for interpreting bioassessment data.

Many community attributes or metrics are also important to assessment and conservation of stream fishes and can be influenced by the presence of rare species and sampling intensity. For example, diversity indices such as Shannon Diversity Index (Weaver and Garman 1994) and Simpson Diversity Index (Magurran and Phillip 2001) can be used to identify locations with exceptional species diversity and can be sensitive to high numbers of rare species (Magurran 1988). In addition, community structural and functional metrics such as those in the index of biotic integrity (IBI) (Karr 1981) are used to identify impairment in streams at large scales (Pont et al. 2006; Pont et al. 2009). The IBI metrics that involve taxonomic richness estimates could be sensitive to the number of rare species. For example, the presence of rare species can greatly influence observed species richness which can in turn affect the outcome of bioassessment studies (Cao et al. 1998).

Stream electrofishing sampling intensity can be manipulated in a variety of ways, including change in gear type or configuration, number of electrofishing passes, or increasing sample-reach length. The effect of increasing sampling intensity can be illustrated theoretically through detection probability. Presence and abundance of a species in a sample is a function of the actual abundance of the species and the probability of capturing any individual of the species (Bayley and Peterson 2001). Different methods of increasing sampling intensity can change either or both of abundance and probability of capture. For example, increasing the reach length will increase the actual abundance of the species while increasing the number of electrofishing passes in a fixed reach length will increase the probability of any individual being captured. In both cases the detection probability of each species will be increased with increasing sampling intensity, and observed presence, absence, and abundance could be influenced depending on spatial distribution of the species.

The effect of sampling intensity on rarity has not been examined for stream fishes but has been examined for other taxa. Terrestrial entomologists have found that increasing sampling intensity increases the number of numerically rare species (Novotny and Basset 2000; Scharff et al. 2003); however, terrestrial invertebrate communities have many more species than fish communities. The theoretical effect of sampling intensity on a numerically rare species has several possible outcomes. First, a species with a truly low numerical abundance may be detected at an intermediate level of sampling but no additional individuals are found with increasing intensity (Figure 2.1a) or not detected at the start of sampling but discovered through an increase in sampling intensity (Figure 2.1b). In these cases, a species is properly classified as rare but at low sampling intensities, this species may not be found at all, which could lead to erroneous inferences about a species' site-occupancy, distribution, or frequency of occurrences. Next, a species could be numerically rare at the start of sampling, but as intensity increases the species may no longer meet the numerical criteria (Figure 2.1c), or a species that is actually common, but difficult to detect due to sampling ineffectiveness, may be numerically rare in a sample even after an increase in intensity (Figure 2.1d). In the last two cases, a species may be erroneously classified as rare when it actually does not meet the rarity criteria.

Other rarity criteria may not respond to sampling intensity in the same manner as the numerical criteria. For example, when more individuals are sampled, most are likely to represent common species or those species more susceptible to capture, thus driving down the proportion of less abundant species (Kanno et al. 2009). It is therefore unlikely that a species would be considered rare by proportional abundance at an intermediate level of sampling but not at a higher level of sampling, keeping the cutoff fixed. However, as new species are added as a result of increased sampling intensity, these additions would likely meet the proportional abundance

rarity criteria. In this way, sampling intensity would have a neutral or positive effect on the number of rare species by a proportional abundance criterion while the number of numerically rare species could be neutrally, positively, or negatively affected as individuals are added.

Sampling intensity could also play an important role in influencing observed patterns of rarity determined by proportion of sites it occurs in and geographic extent, but the effect of sampling intensity on these dimensions of rarity have not yet been determined. Because increasing sampling intensity increases detection probability, a species is likely to be observed in more sites under a high-intensity protocol than a low-intensity protocol, increasing its site occurrence and possibly increasing its observed geographic extent. The possible difference in observed extent, site-occurrence, and local abundance could have ramifications in the assessment and management of imperiled species at a watershed level (Smith and Jones 2008). Sampling intensity could also be important to characterizing species and communities at the watershed level when species are distributed patchily (Angermeier and Smogor 1995).

The effect of sampling intensity on stream fish community assessment has been examined by many researchers. For example, species richness increases with stream length sampled, eventually reaching an asymptotic level assumed to represent an exhaustive level of sampling intensity (Lyons 1992; Angermeier and Smogor 1995; Hughes et al. 2002; Dauwalter and Pert 2003a; Reynolds et al. 2003; Meador 2005; dos Anjos and Zuanon 2007). Increasing the stream length has also been shown to increase other richness/taxonomic metrics used in the indices of biotic integrity (Dauwalter and Pert 2003b).

Apparent assemblage structure has also been shown to change with electrofishing pass. Increasing the number of electrofishing passes over a fixed sampling reach has been shown to increase species richness, (Pusey et al. 1998; Meador et al. 2003; Kennard et al. 2006; Kimmel

and Argent 2006) and change the total abundance and proportional abundance of individuals in the assemblage (Pusey et al. 1998). However, some researchers have found that single-pass electrofishing provides accurate measurements of species richness and other community metrics (Simonson and Lyons 1994; Paller 1995; Reid et al. 2009). Meador et al. (2003) found that adding a second electrofishing pass resulted in the capture of additional species in half of all sites sampled and noted that multiple-pass electrofishing may be of increased importance for estimating species richness in larger streams. Increasing sampling intensity through multiple passes rather than extending the stream length could have some advantages. Pusey et al. (1998) and Kennard et al. (2006) suggested that multiple electrofishing passes could replace or reduce increasing the sample stream length as a means for increasing sampling intensity without increasing the potential confounding effects of spatial variability; however this method would likely underestimate species richness extrapolated to a larger stream reach, segment, or watershed (Smith and Jones 2005).

The type and configuration of electrofishing gear used, in terms of the number of electrofishing units deployed and field crew member responsibilities, could also have an effect on observed species richness and the number of rare species. Kimmel and Argent (2006) suggested that the addition of backpack electrofishing units with increasing stream size could improve sampling efficiency; however, the configuration of the electrofishing gear and crew has not been examined in much detail. Similarly, multiple boat electrofishing units are sometimes deployed on larger rivers by management agencies in order to increase sampling intensity and improve capture of game species (Odenkirk and Smith 2005).

In the current study I examined the effects of increased sampling intensity on observed rarity and community assessment in stream backpack electrofishing samples by comparing a

one-backpack electrofishing configuration to a two-backpack configuration, single-pass electrofishing to multiple-pass electrofishing, and a fixed reach length to incrementally increasing stream length. My objectives were to 1) examine how sampling intensity influences observed rarity using a number of rarity criteria, 2) examine how sampling intensity affects other metrics commonly employed in the assessment of stream fish communities, and 3) examine the influence of sampling intensity on the characterization of endemic species of the New River, Virginia in terms of site abundance, observed rarity, and frequency of occurrences.

Methods

Study Area

The study streams are second- to fourth-order streams in the New River basin in southwest Virginia. Multiple sites were sampled on all of these streams to capture fish assemblages across a longitudinal gradient. Sites were selected to include a variety of land use conditions and provide a representation of wadeable streams in the basin. The New River basin is characterized by high to moderate gradient streams and relatively steep topography. Land cover is primarily forest but also includes agriculture as well as low- and high-density urban areas. Although forest is currently the dominant land cover in the study area, historical deforestation and poor agricultural practices between 60-100 years ago in the Appalachian Mountains (Harding 1998; Burcher et al. 2008) have left a lasting impact in many of my study streams in the form of siltation, bank incision, and decreased bank stability. The study section of the New River is relatively species-rich, with six endemic species and several introduced species (>10).

Wadeable streams in the New River basin provide a good study system for several reasons. The New River has a high diversity of habitat types, relatively high diversity of cyprinids (34 species), centrarchids (12 species), and percids (14 species) (Jenkins and Burkhead 1993). Of the six endemic species in the New River basin, four are considered species of special concern by the Virginia Department of Game and Inland Fisheries (VDGIF) (VDGIF 2009). This moderate diversity is representative of many other systems in the eastern United States. The New River also has moderate conductivity and low turbidity, allowing for optimal electrofishing conditions and evaluation of electrofishing methods (Pritt and Frimpong unpublished data).

To capture inter-regional variability, I incorporated data from second- to fourth-order streams in the upper Wabash River basin, Indiana, collected in the summer of 2003 (Frimpong et al. 2005). Although there are differences between the upper Wabash River basin and the New River basin, such as gradient and land use, the upper Wabash has comparable species diversity to the New and was sampled with similar methods. As a result the upper Wabash basin serves as a useful regional comparison to the data from the New basin. The upper Wabash River is characterized by lower gradient streams, and more prevalent agricultural land uses. This basin complements the New River in regards to land use and stream type.

Sampling Methods

Sampling in the New River basin was conducted on approximately 50 sites during June, July, August, and September, 2008 with some additional sampling in the summer of 2009. I compared a one-backpack versus a two-backpack electrofishing configuration on a total of 23 sites on two streams, Toms Creek and Reed Creek. All electrofishing was conducted using Smith Root L-24 electrofishing units with settings adjusted based on ambient conditions. The summer

of 2008 was characterized by unusually dry weather conditions, and as a result all of the sampling occurred during low-flow conditions accompanied by relatively high temperatures (>15 C), and low turbidity (<10 national turbidity units). Conductivity ranged from 2.3 to 51.4 microsiemens per liter and as a result electrofishing voltage ranged from 200 to 500 volts. The one-backpack samples were conducted with one electrofishing unit and two netters, one on either side of the unit while the two-backpack samples were conducted with two electrofishing units and two netters, one with each electrofishing unit. On Toms Creek (sampled 2008 and 2009), two consecutive reaches 130m long were sampled, one with a single backpack unit and the other with two units; the order was randomly decided. On Reed Creek (sampled 2008), five 400-m reaches, spaced ≥ 4 km apart, were sampled and each contained ten, 40-m subreaches that were sampled with single-pass electrofishing alternating between one backpack and two backpacks, with the beginning configuration being randomly selected. The subreaches were isolated with block-nets during sampling.

I examined the effect of increasing sampling intensity by increasing the number of electrofishing passes with 34 sites on second- to fourth-order streams in the New River basin and 49 sites on first- to fifth-order streams in the upper Wabash River basin. The New River sites were sampled using triple-pass depletion electrofishing on fixed reach lengths of 120, 150, 180, or 240 meters, depending on stream width. These reach lengths were approximately 15 to 20 times the mean stream width at the wetted perimeter and are representative of reach lengths commonly used for bioassessment purposes (Ohio EPA 1987). Two backpack units were used for all reaches except the smallest streams (those sampled with a 120m reach length) on which only one backpack unit was deployed. The upper Wabash River sites were sampled with a single

backpack unit with reach lengths of 15 to 20 mean stream widths (Frimpong et al. 2005), with total reach lengths approximating those in the New River samples.

I also used the protocol outlined above for Reed Creek to examine the effect of increasing stream length on the number of rare species. Because reaches in this system were sampled in 40-m increments, the protocol allowed me to compare the trends observed for increasing the number of backpack units or electrofishing passes with those produced by increasing reach length.

Rarity Criteria and Assessment Metrics

I examined different proportional and numerical rarity criteria in my analysis. Because the appropriate cutoff for neither of these criteria has not been determined, I included numerical rarity criteria ranging from 1 to 25 individuals and proportional rarity criteria ranging from 0.5% to 20% of the community sample. To compare community assessment metrics between sampling intensities, I calculated a variety of common community metrics including Shannon Diversity index, Simpson Index (as a measure of evenness), and IBI metrics such as species richness, number of minnow species, number of sunfish species, number of benthic species, percent of individuals that are insectivores and percent of individuals that are lithophilic spawners (Smogor and Angermeier 2001). These metrics are representative of diversity, structural, and functional metrics that are frequently employed in community assessment. Also included in my community metrics were the number of singletons (species with an abundance of 1, Novotny and Bassett 2000; Kanno et al. 2009) and “ecologically rare” species that meet at least two of the following three criteria based on previous analysis (Pritt and Frimpong 2010): 1) numerical abundance of <20 individuals, 2) proportional abundance of <5%, and 3) proportional abundance of <1/species richness (Camargo 1993). The latter definition of rarity was derived

through an analysis of patterns of abundance at the site level and thus has more ecological significance than an arbitrarily defined cutoff.

Statistical Analysis

The number of rare species observed at increasing numerical and increasing proportional abundance rarity criteria for the one- versus two-backpack electrofishing configurations, increasing electrofishing pass, and increasing stream length were compared using linear mixed models (Der and Everitt 2002). A linear mixed model allows for repeated measures (rarity criteria) along longitudinal data (intensity treatment). The linear mixed model also allowed us to include the effects of covariates such as watershed area, conductivity, and the effects of the different systems (New River vs. upper Wabash River) used in the comparison of electrofishing passes. The model included fixed effects such as gear configuration (one- vs two-backpack) and watershed area, and random factors such as rarity criteria (I use multiple rarity criteria at each site that cannot be viewed as independent from each other). I also used mixed models to account for the effect of using a one- or two-backpack protocol in my analysis of electrofishing pass and reach length because both backpack protocols were used during sampling (see above). I used linear mixed models with both unstructured and structured covariance assumptions and selected the most appropriate model based on Akaike's Information Criteria (AIC). Models were implemented in SAS 9.2 using the mixed procedure (PROC MIXED).

I compared metrics between one-backpack and two-backpack configurations, and single-pass and multiple-pass electrofishing with the Hotelling T^2 test on paired multivariate responses (Cite Johnson and Wichern 2002). If a globally significant difference was detected (i.e., $p \leq 0.05$), Bonferroni-adjusted confidence limits were used to determine significance of differences between individual variables. The Bonferroni confidence limits provided a conservative

criterion for significance and allowed us to account for multiplicity in the multivariate analysis. I did not compare changes in community assessment metrics with increasing reach length (Reed Creek protocol) because the small sample size did not lend itself to the Hotelling T^2 test; however, a previous study indicated that structural IBI metrics increased with increased reach lengths while functional metrics were inconsistently influenced (Dauwalter and Pert 2003b).

To provide a case study of assessment of rarity of fishes with conservation interest, I compared the assessment of the four New River endemic species that I found during my sampling for one-, two-, and three-pass electrofishing. I compared the number of sites where each species was found, the number of sites where each species was considered a singleton, the number of sites where each species met my ecological rarity criteria, the average total abundance and proportional abundance of each species at sites where they were found among passes.

Results

Linear mixed models with unstructured covariance provided a better fit to my data based on AIC. The significant factors retained in the model comparing the one-backpack protocol to the two-backpack protocol were rarity criteria (random factor) and the gear configuration (fixed factor). Watershed (Reed vs. Toms) was not a significant fixed factor. Because of the paired nature of the backpack comparison, factors such as watershed area and conductivity were controlled by the sampling design. There was no significant difference in the number of numerically rare species between one- and two-backpack protocols but there were more species that met proportional abundance rarity criteria with the two-backpack protocol than with the one backpack protocol ($p < 0.0001$) (Figure 2.2).

Significant factors that were retained in the model comparing the effect of electrofishing pass were watershed area and system (New River vs. upper Wabash) (fixed factors), and rarity criterion and pass (random factors). Non-significant factors that were excluded from the final mixed model were gear configuration and conductivity. There was a small increase in the number of rare species between one-pass and multiple-pass electrofishing protocols; however, this effect was not found to be significant (Figure 2.3). The number of species that met the proportional abundance criterion increased with electrofishing pass ($p < 0.0001$) (Figure 2.3).

The significant fixed factors in the model comparing reach length was number of backpacks and the significant random factors were rarity criterion and reach length. The number of numerically rare species increased with increasing stream length but this result was not significant (Figure 2.4). As with the comparison between electrofishing pass and backpack configuration, the number of species that met a proportional abundance criterion increased with increasing reach length ($p = 0.0036$) (figure 2.4).

The Hotelling T^2 test did not detect a significant difference in community assessment metrics between one-backpack and two-backpack protocols, however there was a significant difference in community assessment between one-pass and two-pass electrofishing ($p < 0.0001$), one-pass and three-pass electrofishing ($p < 0.0001$), and two-pass and three-pass electrofishing ($p < 0.0001$). The number of singletons, biologically rare species, species richness, sunfish species, minnow species, and benthic species were found to be greater in the double and triple-pass protocol than the single-pass protocol (Table 2.1). In addition, species richness, the number of minnow species, and the number of benthic species were greater with three-pass electrofishing than with two-passes (Table 2.1).

In the assessment of New River endemic species, increasing the number of electrofishing passes increased observed presence for three of the four species, increased numerical abundance for each species, and decreased the proportional abundance for each species (Table 2.2). There was no meaningful change in the number of times a species was observed as a singleton among one-, two, or three-pass samples. All of these endemic species were also considered ecologically rare in every site that they occurred.

Discussion

Numerical rarity criteria were not influenced by sampling intensity whereas the number of species labeled as rare by proportional abundance criteria showed an increase with sampling intensity; this is likely because individuals from common species were added faster than individuals from rare species as sampling intensity increased. Adding more common species increases the number of rare species in two ways: 1) as individuals of the most common species are added, the proportional abundance of other species is driven down below the threshold for rarity and 2) when new species are added with increased sampling intensity, these species are usually observed as rare. Because the numerical rarity criteria are not sensitive to sampling intensity, I suggest using some numerical criterion to define rarity for statistical or bioassessment purposes such as the deletion of a species for multivariate analysis. If a proportional abundance criterion is instead used, researchers must be careful to ensure that sampling intensity and total number of fish sampled is similar between sites.

The comparison between the one- and two-backpack approaches can be attributed to only the electrofishing protocol as a whole because the ratio of backpacks to netters was changed between protocols. As a result, I cannot determine if the change in netters or backpack units was

the mechanism for any differences between the protocols. The ratio was adjusted because maintaining a two netter per backpack ratio would have necessitated more field crew members for the two-backpack protocol. My aim was to provide an optimal way to utilize a field crew; expanding the number of crew members would have caused an increase in the resources needed to conduct sampling.

Because greater sampling intensity results in a greater number of species and individuals, more information is available to researchers and managers as they interpret stream electrofishing data. However, as Smith and Jones (2008) point out, efficient use of resources is of utmost importance for any sampling protocol. From my analysis, I can draw several important recommendations for future sampling in wadeable streams. First, a one-backpack approach was sufficient for characterizing fish communities, and hence this approach is recommended because of the obvious high costs associated with electrofishing units. It is important to point out that my one-backpack approach was to meticulously sample all available habitats with the single unit; if a more rapid approach (such as that in Reynolds et al. 2003) is utilized, the effect of adding a second backpack could be more substantial. Although this finding corroborates many of the backpack electrofishing protocols currently employed, I suggest that researchers and managers that wish to gain more information from their sampling protocols explore other alternatives to an additional electrofishing unit.

Furthermore, there was a substantial difference in community assessment metrics and observed rarity between one-pass and multiple-pass electrofishing protocols but the difference between double- and triple-pass electrofishing protocols was minimal. As a result, researchers may strongly consider the merits of using a double-pass protocol; however a triple-pass protocol may provide little new information and a diminishing return for sampling resources. Careful

consideration of the tradeoffs between information gained from increased sampling intensity and cost of sampling should precede any sampling program (Smith and Jones 2008).

The multiple-pass protocol generally improves stability of assemblage composition and functional metrics (Dauwalter and Pert 2003b) and therefore it is likely that management decisions based on a multiple-pass electrofishing will be less prone to error. In addition, sampling for imperiled species is likely to provide a different result if a low-intensity protocol is used instead of a high-intensity protocol. In the example of the New River endemic species, three of the four endemics were found in more sites using a multiple-pass protocol in a fixed reach and the numerical abundance of these species was slightly increased. The assessment of the New River endemic species could be considerably altered based on the number of electrofishing passes used in the sampling process. For example, increasing the number of electrofishing passes increased the likelihood that an endemic species would be observed at a site and could have potential management implications, such as setting up conservation easements based on the endemic diversity or listing these endemics on an endangered species list.

Several programs and agencies could potentially apply the findings of this study. For example, monitoring for conservation purposes (e.g. Edwards et al. 2002) depend on the assumption that sampling methods provide an accurate representation of the species or group of species of concern. I demonstrated that increasing sampling intensity increases the observed abundance and number of sites occupied for endemic species. Conservationists may come to different conclusions about suitable habitat, areas to designate for protection, and species dispersal abilities, depending on the intensity of the sampling protocol employed.

This study can be reasonably applied to most eastern US wadeable streams that have species richness similar to the New River and upper Wabash River basins. Different patterns

may exist in systems that have low species richness common in many western streams (Reynolds et al. 2003), or in systems with very high species richness. Also, detection probabilities are much lower in larger streams (Meador 2005) as a function of a decreased chance of capturing individuals. In these systems, increasing sampling intensity may cause an effect that is greater in magnitude than a similar increase in sampling intensity in a smaller stream. In very species rich and larger systems, it may be necessary to increase sampling intensity more than determined in this study.

My study further highlights the importance of considering sampling intensity for any survey of stream fishes. I encourage researchers and managers to give thoughtful consideration to their objectives in order to use sampling resources in the most efficient manner. Future research is necessary to examine if the trends found in this study hold true for other regions with different faunas and sampling conditions, such as the western United States.

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Table 1. Means of community assessment metrics for one-, two-, and three-pass electrofishing.

Different letters indicate significant differences with Bonferroni confidence limits.

Metric	One-Pass	Two-Pass	Three-Pass
Shannon Diversity	1.79 ^a	1.83 ^b	1.84 ^b
Simpson Evenness	0.76 ^a	0.76 ^a	0.76 ^a
Species Richness	13.07 ^a	14.70 ^b	15.30 ^c
Singletons	2.88 ^a	2.66 ^a	2.40 ^a
Biologically Rare Species	8.98 ^a	10.25 ^b	10.13 ^b
Minnow Species	6.14 ^a	6.78 ^b	6.99 ^c
Sunfish Species	1.58 ^a	1.77 ^b	1.86 ^b
Benthic Species	2.59 ^a	2.90 ^b	3.02 ^c
Proportion of invertivores	0.57 ^a	0.57 ^a	0.57 ^a
Prop. of lithophilic spawners	0.34 ^a	0.33 ^a	0.33 ^a

Table 2. Assessment of four New River endemic species for one-, two-, and three-pass electrofishing. Average abundance represents the average number of individuals observed in a sample and average proportion is the average proportional abundance observed in a sample.

Passes	Appalachian Darter (<i>Pecina gymnocephalus</i>)			Kanawha Darter (<i>Etheostoma kanawhae</i>)			Kanawha Minnow (<i>Phenacobius teratulus</i>)			New River Shiner (<i>Notropis scabiriceps</i>)		
	One	Two	Three	One	Two	Three	One	Two	Three	One	Two	Three
Sites occurred	9	12	13	12	13	14	11	13	15	4	4	4
%Sites	26	35	38	35	38	41	32	38	44	12	12	12
Sites as singleton	1	2	3	4	4	5	2	2	1	1	1	1
Sites as rare	9	12	13	12	14	14	11	13	15	4	4	4
Avg. abundance	3.9	5.2	6.3	3.4	4.9	5.4	5.5	6.4	5.8	4.3	5.3	8.5
Avg. proportion	1	0.9	0.8	0.7	0.6	0.5	1.5	1	0.7	0.9	0.7	0.6

Figures

Figure 2.1. Four theoretical outcomes of sampling intensity on numerically rare species. Circles indicate a common species in a population while triangles represent a rare species. Box a indicates that a species is rare at low levels of sampling intensity (area within the ellipse) and high levels of sampling (area within the rounded rectangle), and in this case sampling has a neutral effect on numerical rarity. Box b indicates that sampling intensity has a positive effect on the number of numerically rare species. Box c represents a situation in which a species is numerically rare at a low level of intensity but not at a high level, a negative effect of sampling intensity on the number of rare species. Finally, box d represents a species that is not numerically rare but may appear to be rare in samples because of sampling inefficiencies as some individuals (denoted by hollow triangles) are not detected.

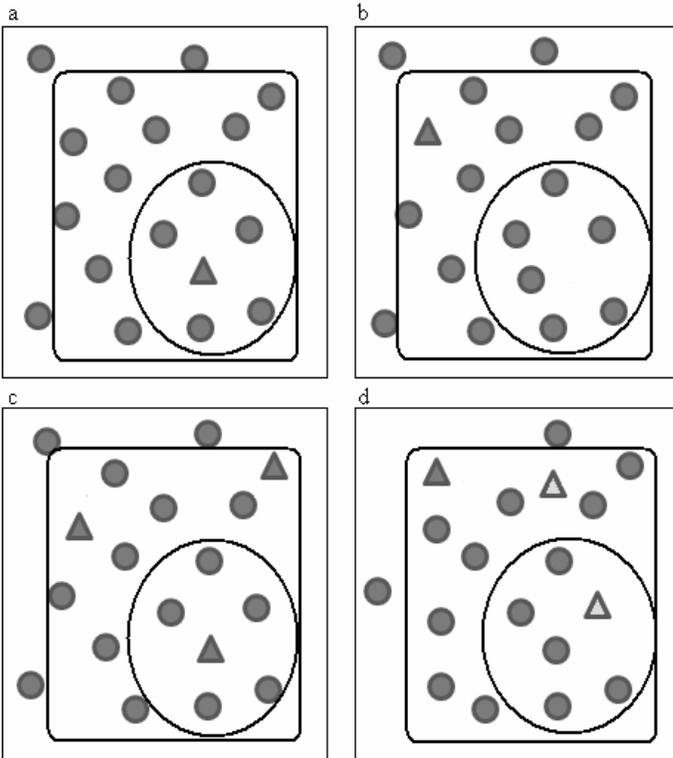


Figure 2.2. The number of rare species at increasing numerical rarity criteria for one-backpack and two-backpack electrofishing protocols (a), and the number of rare species at increasing proportional abundance criteria for one- and two-backpack protocols (b). Error bars represent standard error.

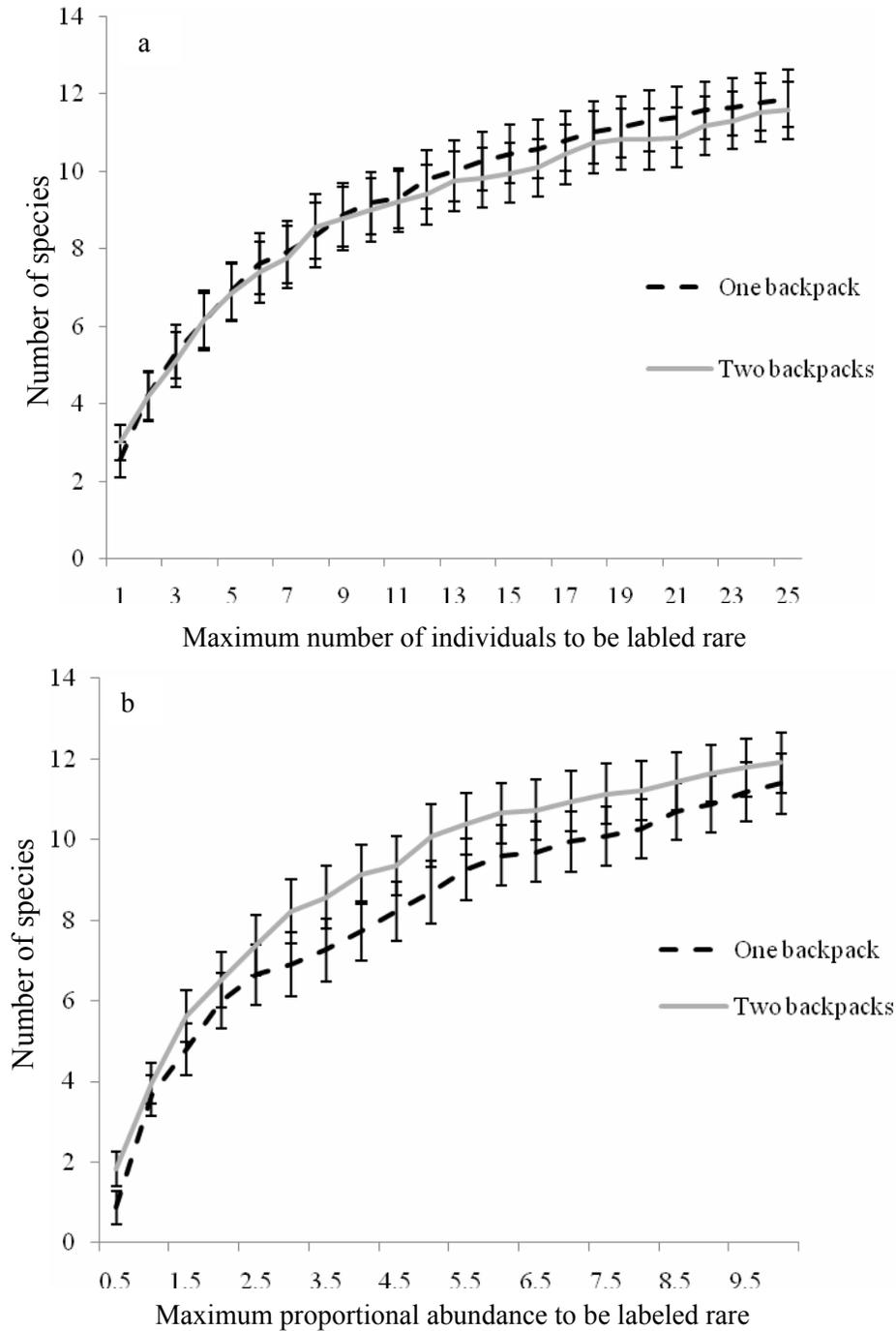


Figure 2.3. The number of rare species at increasing numerical rarity criteria for one-pass, two-pass, and three-backpack electrofishing protocols (a), and the number of rare species at increasing proportional abundance criteria for one-, two-, and three-pass protocols (b). Error bars represent standard error.

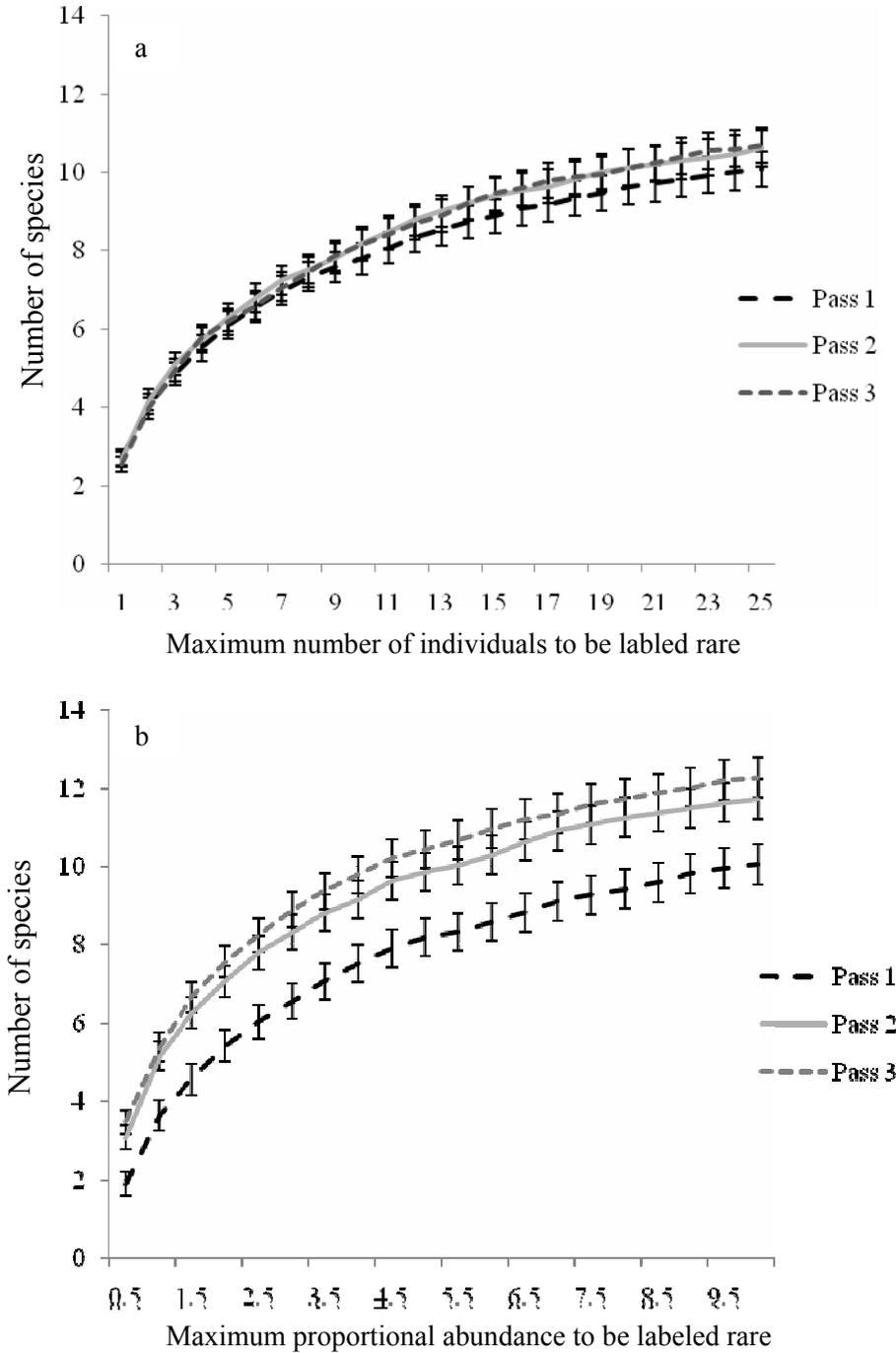
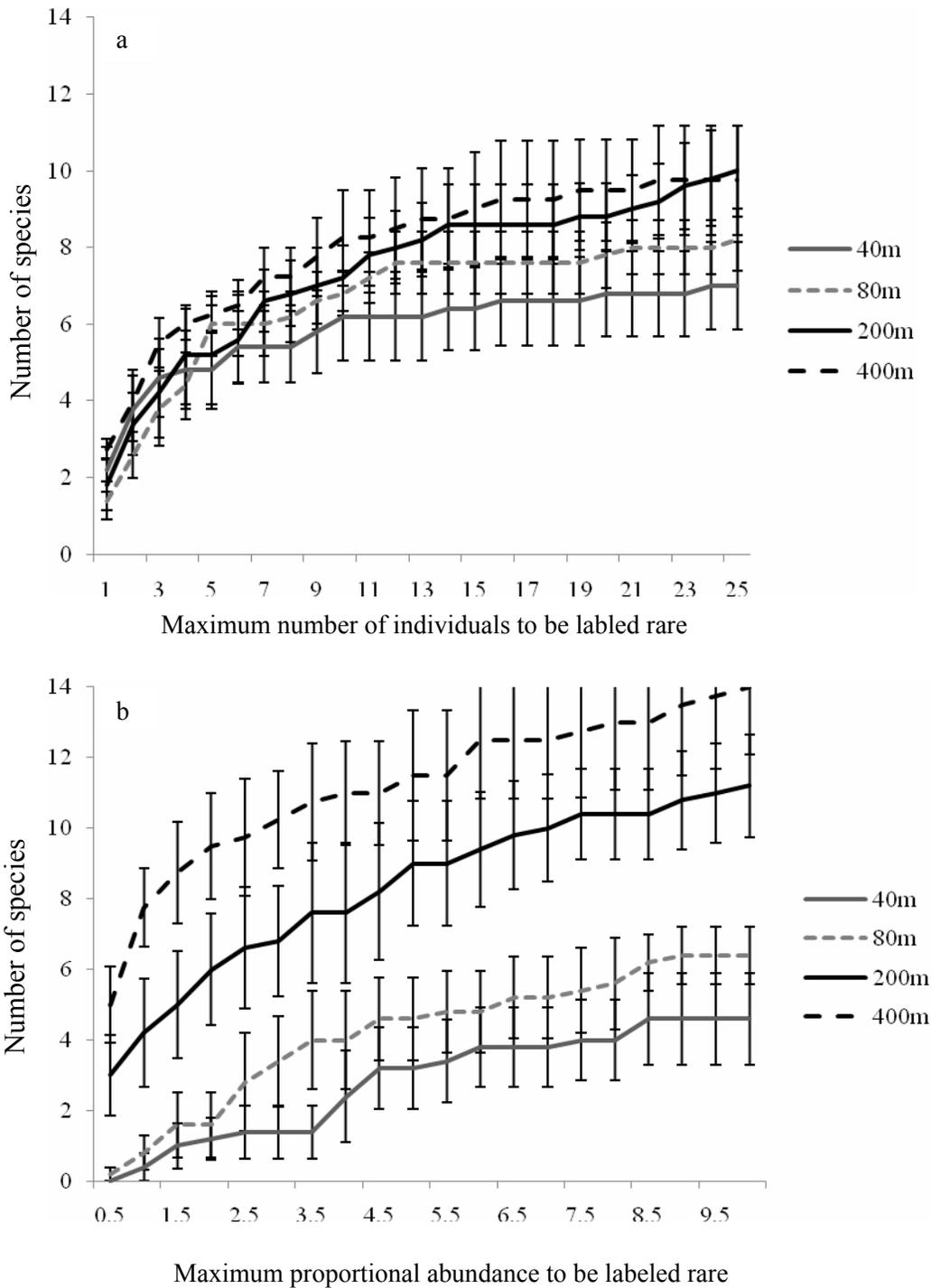


Figure 2.4. The number of rare species at increasing numerical rarity criteria for increasing reach length (a), and the number of rare species at increasing proportional abundance criteria for increasing reach length (b). Error bars represent standard error



Chapter 3

Habitat factors associated with rarity in fishes and biological traits of rare fish species

Abstract

Many fishes are rare in some locations but common in others and the factors that produce these patterns are not well understood for most species. In addition, the biology of rarity in freshwater fishes has not been studied in much detail. I used logistic regression models to examine the effect of 1) regional habitat variables such as temperature, and precipitation, 2) watershed habitat variables such as slope, land use, and stream order, 3) instream habitat variables, and 4) biotic interaction variables on the rare or common status on 23 North American freshwater fishes found in a national database. I also compared biological and reproductive traits among species classified into a rarity framework based on range extent, habitat breadth, and site abundance. Rare or common status was successfully modeled in 19 of the 23 species and I found that regional and watershed habitat variables were the most important predictors of rarity while biotic interaction variables were significant predictors of rarity in a only few species. Significant explanatory variables varied greatly between species. I also found that species with large body size, high fecundity, and late age at maturity were generally considered common based on range extent, habitat breadth and site abundance while species that did not guard nests were more frequently rare by site-abundance. These results indicate that habitat variables at large spatial grains can be used to successfully model species rarity and rare fishes differ in their biology and reproduction from common fishes. Understanding the potential mechanisms driving rarity is an important step for conserving rare fishes and could serve to inform captive breeding and translocation programs.

Introduction

Rarity is important to many community ecology studies and understanding what environmental and anthropogenic factors lead to species rarity is vital to directing conservation efforts (Mace and Kershaw 1997). Not surprisingly, examining the factors that lead to species rarity or commonness is a classic theme in community ecology (Kunin and Gaston 1993). Many factors have been attributed to rarity including biogeography and macroecological factors (Harcourt 2006), habitat type or availability (Novotny and Basset 2000), interspecific competition (Thiollay 1994), and species' biology and ecology (Gaston and Kunin 1997). Because of the great number of possible causes of rarity, and possible interactions among these causes, many factors ranging from environmental and habitat factors to species traits must be considered to infer the mechanisms that produce patterns of commonness and rarity in a particular species.

North American freshwater fishes represent a diverse temperate fauna, with almost 800 species (Page and Burr 1992) and this group is characterized by a great deal of variation in traits among species (Balon 1975) that allow for detailed comparison based on species traits. Available abundance data, as well as detailed information on species traits for many freshwater fishes in the United States, make this group a useful study taxon for examining possible biological and environmental causes and correlates of rarity.

Pritt and Frimpong (2010) developed a classification of rarity for fishes, following the model of Rabinowitz (1981), in which species are defined as rare or common based on range extent, habitat breadth, and site abundance. This leads to the creation of eight groups, seven of which display rarity across at least one dimension (table 3.1). With respects to site abundance, they found that approximately 35% of species were rare at every site at which they occurred

while ~10% of species were common at every site at which they occurred; therefore almost half of the species were rare at some sites but common at others. This phenomenon, known as diffusive rarity, has been documented in other taxa (Shoener 1987), but the mechanisms producing this pattern are unclear.

Examining factors at different spatial grains is important for understanding rarity (Hartley and Kunin 1993) and stream habitats can be classified in a hierarchy of spatial grains. Frissell et al. (1986) classified stream habitat by: 1) stream system or watershed, 2) stream segment, 3) stream reach, 4) pool/riffle sequence, and finally by 5) microhabitat. Different geological and environmental factors act to shape habitat attributes at each of these spatial grains. For example, geological events such as tectonic shifts and glaciation drive habitat at the stream system grain while annual floods and deposition events determine habitat at the pool/riffle and microhabitat scales. Habitat features at each of these spatial grains are likely to influence fish populations and communities (Frissell et al. 1986; Schlosser 1991; Poff 1997). Few researchers have examined rarity in fishes at different spatial grains but many researchers have documented changes in species diversity, distributions, and abundance along gradients at different spatial grains (e.g. Angermeir and Winston 1998). Many of these well-documented factors that drive species occurrences and assemblage patterns may also drive species rarity. In stream fish, species occurrences can be predicted at the reach, watershed, and landscape based on environmental suitability and species dispersal ability (Angermeir et al. 2002). As patterns of presence and absence can be predicted by environmental factors, it is likely that patterns of rarity or commonness can be predicted by many of the same factors.

At large spatial grains, macroecological gradients have often been linked to species distributions and abundance. For example, fishes are often distributed along temperature and

precipitation gradients (Barbour and Brown 1974, Latta et al. 2008). Species abundance is related to distribution (Gaston and Kunin 1997) and a species' abundance generally decreases towards the periphery of that species' range (Brown 1984). Furthermore, species diversity decreases as latitude increases possibly because of a corresponding drop in ecosystem productivity and a shorter growing season, a trend which has been demonstrated for fish diversity in North American lakes (Barbour and Brown 1974) and Michigan streams (Latta et al. 2008). Through neutral metacommunity models, patterns of biodiversity have also been explained by annual runoff production (Muneepeerakul et al. 2008) and river topology (Bertuzzo et al. 2009). Also, introductions have expanded the ranges of many species far beyond their native ranges (Gido and Brown 1999) and potentially into a set of conditions and selective forces that are much different than those within the native range. Separating a species from its native range could create patterns of rarity that are different from those observed in the species' native range. For example, a transplanted species may exhibit lower abundance because conditions are different from those to which the species has adapted and the genetic diversity of transplanted species is sometimes limited from a bottleneck effect (Sakai et al. 2001). By contrast, the species may have greater abundance because of release from competitors or predators (Keane and Crawley 2002). The rare or common status of individual species may also vary because of these landscape and regional factors.

In stream systems, the watershed represents an intermediate spatial grain. Fish assemblages have been documented to change across the longitudinal gradient of a watershed (Ostrand and Wilde 2002; Grubbs 2007), as hypothesized by the river continuum concept (Vannote et al. 1980). Several researchers have found that downstream areas contain greater numbers of rare fish and macroinvertebrate species (Cucherousset et al. 2008; Santoul et al.

2005). Cucherousset et al. (2008) also noted that the number of common species peaked in the middle of the river continuum indicating that the areas with the highest number of common species may not be the same as those with the highest number rare species. Furthermore, understanding which areas contain great numbers of rare species could allow for these areas to be targeted for conservation in the case that these rare species face threats of extinction or serve as source populations (Lawler et al. 2003). However, the spatial patterns of commonness and rarity for individual species along longitudinal watershed gradients have not been documented.

In watersheds, physical and anthropogenic disturbance gradients that change through space can be defined as habitat templates (Poff and Ward 1990). These habitat templates control local processes and selective forces that can be important for determining biotic structure and functioning (Poff 1997). Spatial patterns of fish rarity could be influenced by instream conditions, and the interaction between these large-scale and local factors could influence rarity. At local grains, habitat heterogeneity has a great importance in explaining species diversity, (Eadie et al. 1986; Baldi 2008) and local geomorphologic and habitat characteristics have been linked with species richness and assemblage composition at the local level (Smiley and Dibble 2005). Similarly, the localized effects of anthropogenic disturbance could play an important role in determining spatial patterns of species richness and rarity. Many researchers have documented the deleterious effects of anthropogenic practices, such as agriculture, deforestation, and urbanization, on stream fish assemblages (Wang et al. 2001; Burcher et al. 2008). Anthropogenic disturbance has also been shown to negatively affect species considered rare by extent criteria (Fagan et al. 2005). The intensity and extent of anthropogenic disturbance, as well as the type of disturbance (urbanization vs. agriculture,) could interrupt naturally occurring patterns of rarity and species richness across landscape and watershed gradients. For example,

Guenther and Spacie (2006) demonstrated that impoundments along an Indiana river altered fish assemblages in both the mainstem and its tributaries.

At local spatial grains such as the stream reach, biotic interactions may also be important in explaining patterns of rarity in stream fishes. Interspecific competition has been shown to be important in structuring stream fish communities by some researchers (Strange et al. 1993; Taylor 1996; Herder and Freyhof 2006); however, others have concluded that competition plays a minimal role in organizing these fish communities (Jackson et al. 2001; Perez-Neto 2004). Possible competition may be discerned from phylogenetic relationships as closely related species are more likely to compete because of greater niche overlap. This phenomenon has been documented by Strauss et al. (2006) who found that successful invasive species have few native relatives. As a result, I hypothesize that species which have greater taxonomic relatedness with a great number of other species within a community are more likely to be rare than those species that have few close relatives.

Species traits have been used to explain species' associations with landscape variables and habitat templates (Goldstein and Meador 2004). The study of stream fish communities through a trait-based approach has become an important and useful method for identifying environmental variables responsible for structuring the community and understanding the response of fishes to environmental gradients and disturbance (Frimpong and Angermeier 2010). Species traits can be categorized as biological traits which include life-history and morphological characteristics, and ecological traits which include feeding, reproductive, and habitat associations. Both categories of traits could serve as mechanisms of rarity.

Life-history traits have been linked to rarity in plants (Murray et al. 2002) and birds (Cofre et al. 2007). Fishes can be grouped into three life-history groups that include: 1) periodic,

characterized by long life spans, high fecundity, and low juvenile survival, 2) opportunistic, which include species that are short lived, and have low fecundity and low juvenile survival, and 3) equilibrium, species that have low fecundity, moderate life spans, and high juvenile survival (Winemiller 2005). Life-history traits in fishes may be an important factor determining rarity and have been used to characterize imperiled species. Olden et al. (2008) found that fishes in the Colorado River that had life-histories similar to that of the periodic group are often associated with a small range extent, greater local extirpation rate, and greater risk of extinction. Similar examination among fishes across North America should reveal the life-history traits that contribute to rarity.

Ecological traits can also be important in determining specialization in habitat use, reproduction and feeding. Specialization in ecological traits has also been associated with local extirpations (Angermeier 1995). Reproductive ecology has been of particular importance in explaining rarity in taxa ranging from plants to fishes to mammals (Gaston and Kunin 1997). Minimal parental care to offspring has been correlated to extinction risk in fishes (Olden et al. 2008) and to rarity in darters (Paine 1990) and birds (Cofre et al. 2007). Parental care may also offset adverse conditions that negatively affect juvenile survivorship and again allow species that offer more parental care to be more common than species not offering parental care. Similarly, nest building may mitigate against a limiting habitat type and thus make nest building species reproductive generalists and allow these species to be more common than those that do not build nests (Peoples and Frimpong, in review).

In this study, my goal is to understand what factors produce patterns of rarity or commonness in stream fishes. My objectives are to 1) examine landscape, watershed, and local habitat factors that predict rarity at the site-level, and 2) examine differences in biological traits

among North American freshwater fishes that differ in rare or common status across the rarity dimensions of range size, habitat breadth, and site abundance (Rabinowitz 1981).

Methods

Spatial, habitat, and biotic predictions of site-level rarity

I used 1,025 sites from the United States Geological Survey (USGS) National Water Quality Assessment Program (NAWQA) database that contained fish abundance, landscape, and habitat data (USGS 2008). The NAWQA database is well suited for this study, as it represents sites that span the entire conterminous United States and encompasses a large number of species.

At each site, species were defined as rare if they met two of the three following criteria: 1) <20 individuals in the sample, 2) relative abundance of <5%, and 3) relative abundance of <1/species richness (Pritt and Frimpong 2010). More than 200 species in the NAWQA database were rare at some sites and common at others. In order to examine mechanisms that produce rarity or commonness in individual species, I chose a subset of species that met the following criteria: 1) rare at 30-70 percent of sites occupied (to provide enough rare and common observations for statistical modeling), 2) present at 30 or more sites (to provide enough power for statistical modeling), and 3) NAWQA samples well-distributed around the species' range centroid (centroid found from FishTraits database (Frimpong and Angermeier 2009); site distributions visually estimated using ArcGIS). I also sought to represent as many families as possible in the analysis. A total of 23 species representing 10 families met these criteria and were selected for analysis. I then classified landscape and habitat variables as 1) regional habitat variables such as distance to the species' range centroid, annual temperature, annual precipitation, latitude, longitude, and status as native or nonnative species, 2) watershed variables

such as amount of watershed disturbance, watershed area, road density, slope, elevation, and 3) assemblage variables such as total species richness, family-level richness, and genus-level richness (table 3.2). These assemblage variables represent proxy variables for interspecific competition as species that are most closely related have the greatest amount of niche overlap and are therefore most likely to compete for common resources. Some of the NAWQA sites (508) also had available instream habitat data including percentage pool, riffle, and run habitat, average depth, maximum depth, wetted width, and the width to depth ration (table 3.2).

I used multiple logistic regression with stepwise model selection and Akaike's Information Criterion (AIC) to select environmental variables that best explained a species common or rare status at a given site. The models were constructed with the binary response variables, "0" representing rarity and "1" representing commonness, which were explained by the continuous variables from the NAWQA sites described above. The significance, effect, and magnitude of the predictor variables included in each model were determined from odds ratios. I then validated the logistic regression model derived for each species using reduced models that evaluate the predictive ability of each selected model. In this technique, observations (rare or common status at a site) are withheld from the model and forwardly predicted with the selected independent variables. I used several fit and validation statistics to gage the success of the logistic regression models. To measure fit, I obtained the maximum rescaled R^2 and Somer's D statistic which measures the correlation between predicted and actual observations. To validate the predictive ability of each model, I used the percent of observations correctly predicted, sensitivity, which measures the success of predicting commonness, and specificity, which measures the success of predicting rarity. I also found the percent of false positives (incorrectly

predicted commonness), and false negatives (incorrectly predicted rarity) for each model. The validation statistics were obtained using a 0.5 probability cutoff.

Traits as mechanisms for rarity

To determine which biological traits are associated with rarity, traits for North American fishes were taken from the FishTraits database (Frimpong and Angermeier 2009) and included fecundity (number of eggs), maximum total length (cm), age at maturity (years), maximum age (years), and larval size (mm). Species from FishTraits were organized into the framework of Pritt and Frimpong (2010) in which species were placed into one of eight rarity groups based on range extent, habitat breadth, and site abundance (table 3.1). I then constructed boxplots of biological trait values for each rarity group and analyzed the boxplots visually to examine the differences in descriptive statistics in the above biological traits among rarity groups for the 399 species classified by Pritt and Frimpong (2010). I then used correlates of natural-log-transformed biological traits with adjusted range values, habitat breadth as given by an index of habitat breadth score (Pritt and Frimpong 2010), and site abundance to examine the relationships between these biological traits with the three dimensions of rarity in the framework.

Reproductive traits were also taken from FishTraits and were used to form reproductive groups of non-guarders, guarders, serial spawners, and live bearers. The frequency of each of these traits among species in each rarity group was determined. I then analyzed the distribution of these binary-scored traits (“1” if present, “0” if absent) within the rarity framework with a Chi-squared test of independence and compared the distribution of traits in rarity groups to the distribution of traits in all fish to understand which traits are more often associated with rarity.

Results

Habitat and biotic predictors of site-level rarity

Instream habitat variables were significant explanatory variable for only one of the 23 species in the original logistic regression models (blacknose dace rarity was partially explained by the percent of run habitat). Because these instream variables had little significance, and introduced colinearity with regional and watershed habitat variables, they were removed from the models. The AIC and maximum rescaled R^2 fit statistic indicated that removing these variables and including only regional habitat, watershed habitat, and interspecific variables provided a better fit.

Of the 23 species used for the logistic regression analysis, 19 were successfully explained as rare or common by a statistically significant logistic regression model; sand shiner (*Notropis stramineus*), Alabama hogsucker (*Hypentilium etowanum*), hornyhead chub (*Nocomis biguttatus*), and gizzard shad (*Dorosoma cepedianum*) were not successfully modeled. The significant models were evaluated for fit and predictive ability.

The fit of the logistic regression models varied among species as maximum rescaled R^2 ranged from 0.12 (rock bass) to 0.75 (margined madtom) (table 3.3). In logistic regression models, R^2 tends to be much lower than values in more familiar, linear regression (even a value of 0.2 indicates a strong fit) (Myers 1990). The predictive ability of the logistic regression models also varied among species. In general, the models had greater specificity (accuracy predicting rarity) than sensitivity (accuracy predicting commonness) and there were more false positives than false negatives (table 3.3), indicating that the models predicted rarity more accurately than commonness. For species with significant models, the logistic models predicted an average of 72.6 percent of observations correctly with striped shiner having the least accurate

model (54.1 percent of observations correctly predicted) and margined madtom having the most accurate model (84.8 percent of observations correctly predicted) (table 3.3). The square of Somer's D statistic provides a measurement of correlation between the observed and predicted responses in each model and was again highly variable among species, ranging from 0.15 (rock bass) to 0.85 (margined madtom) (table 3.3).

Regional habitat variables were the most frequent predictors of rare or common status among species (table 3.4). Decreased mean annual precipitation significantly explained rarity for six species in three families (cyprinidae, centrarchidae, poeciliidae) and a positive effect (explained commonness) for one cyprinid, the striped shiner (*Luxilus chrysocephalus*). Mean annual temperature was a significant explanatory variable for two species of cyprinids. High mean annual temperatures were related to commonness in striped shiner and rarity in blacknose dace (*Rhynchithyes atratalus*). The central stoneroller (*Campostoma anomalum*) was most likely to be rare at higher latitudes while the striped shiner and pirate perch were most likely to be rare at low latitudes.

Watershed habitat variables were also important for many species (table 3.4). Large watershed area was associated with rarity of blacknose dace creek chub (*Semotilus atromaculatum*) and commonness for western mosquitofish. High slope was associated with commonness of the banded sculpin (*Cottus carolinae*), margined madtom (*Noturus insignis*), and blacknose dace and rarity for redbreast sunfish and western mosquitofish. Largescale sucker (*Catostomus macrocheilus*) was likely to be common at high elevation while striped shiner and western mosquitofish (*Gambusia affinis*) were likely to be rare at high elevations. High amounts of riparian disturbance explained commonness of western mosquitofish while high watershed disturbance explained commonness of striped shiner and blacknose dace. Conversely, high

watershed disturbance explained rarity of rosyside dace (*Clinostomus funduloides*), margined madtom and rainbow darter (*Etheostoma caeruleum*) while high road density explained rarity of banded sculpin.

Biotic variables were significant for only a few species (table 3.4). Redbreast sunfish (*Lepomis auritus*), longear sunfish (*Lepomis megalotis*), and margined madtom were more common at sites with high richness of members of their family or genus. Brook trout (*Salvelinus fontinalis*) and johnny darter (*Etheostoma nigrum*) were likely to be rare as their family-level richness increased, indicating that these species may be negatively influenced by interspecific competition from closely related species.

Traits as mechanisms of rarity

There were substantial differences in biological traits among rarity groups. Longevity, age at maturity, maximum total length and fecundity were all greater in groups with large range sizes than in groups with small range sizes (Figure 3.1). Also, longevity, age at maturity, and maximum total length were greater in groups with small site abundances than in groups with large site abundances (Figure 3.1). The correlation analysis showed that the natural logs of longevity ($r=0.31$; $p<0.0001$), fecundity ($r=0.45$; $p<0.0001$), age at maturity ($r=0.30$; $p<0.0001$), and maximum total length ($r=0.46$; $p<0.0001$) were positively correlated with range extent (Figure 3.2). Similarly, the natural logs of longevity ($r=0.16$; $p<0.0001$), fecundity ($r=0.28$; $p<0.0001$), age at maturity ($r=0.16$; $p<0.0001$), and maximum total length ($r=0.32$; $p<0.0001$) were positively correlated with index of habitat of breadth scores (Figure 3.2). There weak correlations between biological traits and site abundance as fecundity ($r=0.10$; $p=0.0419$),

longevity ($r=0.11$; $p=0.0257$) and maximum total length ($r=0.10$; $p=0.0418$) were positively related to large site abundance (Figure 3.2).

The Chi-squared analysis of reproductive traits showed that a significant difference in spawning strategies among groups. Overall, more species were considered non-gaurders than gaurders while a small proportion of the total species were live-bearers ($p<0.05$). There was significantly greater proportion of non-gaurding species in group B (large extent, wide habitat breadth, and small site abundance) and in groups G (small extent, narrow habitat breadth, large site abundance) and group H (small extent, narrow habitat breadth, small site abundance) (Figure 3.3). In addition, there was a significantly greater proportion of live bearing species in group H (Figure 3.3). These results indicate that reproductive traits may also contribute to a species' rarity or commonness.

Discussion

The mechanistic plausibility of the logistic regression models differed among species and is likely a result of a difference in biological significance among these models. Some species had models with significant predictors that made intuitive sense. For example, the blacknose dace, which is often found in headwater streams and in small, coldwater systems (Page and Burr 1992), is predicted to be rare in streams with large watershed areas and high mean annual temperatures while it is predicted to be common in streams with high slope. Other species characterized as associates of small headwater streams (Page and Burr 1992) show similar patterns. For example, the creek chub is predicted be rare in streams with large watershed areas and margined madtom and banded sculpin, are predicted to be rare in streams with low slope.

Many of the species that were predicted best by regression models were often associated with small streams including species such as the blacknose dace, creek chub, and banded sculpin.

As predicted by the River Continuum Concept (Vannote et al. 1980), these small streams have the most interaction with the adjacent landscape and as a result their rarity or commonness may be intimately linked to landscape and watershed variables more so than species in larger systems. In addition, catchability decreases in large systems (Bayley and Peterson 2001) and as a result, rarity in large streams may be a result of sampling inefficiencies rather than a reflection of true rarity. In addition, a species that is truly rare in a large system may not be detected at all and hence observed as absent rather than rare (see again figure 2.1).

The models also highlight several species that may be able to tolerate anthropogenic disturbance but are rarer in disturbed environments. These species include the rosyside dace, banded sculpin, margined madtom, and rainbow darter. Not surprisingly, three of these species are benthic species and all are lithophilic in their spawning requirements; benthic and lithophilic species have been shown to be typically vulnerable to anthropogenic disturbances such as agriculture, deforestation, and urbanization (Wang et al. 2001). Relatively little information can be ascertained by the observed absence of a species and as a result, these species may be useful to bioassessment as their presence and status as rare or common may indicate assemblages undergoing adjustments in composition in response to anthropogenic disturbance. For example, rainbow darter observed in low abundance is likely to indicate watershed disturbance while the observed absence of another darter species can be only indirectly attributed to disturbance.

The biotic interaction variables used in this modeling showed some mixed results. Counter to my initial expectations, some species had positive relationships with closely related species that could serve as competitors. I believe that this observation is likely the result of favorable habitat conditions to multiple species in the family or genus and the good habitat conditions override the negative effect to that of interspecific competition. Also, this

phenomenon could be explained by competitive coexistence, in which coevolution of similar species results in niche partitioning and coexistence (Amarasekare 2003). I did find possible evidence that interspecific competition has a negative impact on two species, brook trout and johnny darter that are more likely to be rare as the richness of closely related taxa increases. The brook trout has been shown by several studies to be an inferior competitor with introduced salmonids (Dewald and Wilzbach 1992).

My results show that for most species, models can be derived to explain and even predict rarity or commonness and this has several implications to fish ecology and conservation. For example, taking predictors of rarity into account can help researchers understand patterns in fish assemblages while identifying sites where a species is rare or likely to be rare can streamline conservation efforts to those sites. In addition, these models can be used to predict rarity or commonness in stream sites that have not been sampled. In this way, large-scale models can be built to form ecological hypotheses and to help inform landscape- and site-level conservation decisions. Predicting rarity also has applicability to harvest for research, captive breeding, and translocation programs. For example, if researchers wish to sacrifice individuals of a species for further study or remove individuals to start a broodstock for captive breeding, rarity models can help researchers identify areas where a species is most likely to be common and avoid unnecessarily removing individuals from, and possibly damaging, a small population. Models of rarity and commonness could also be used to guide translocation by identifying areas favorable areas that a reintroduced species may become common, which may improve the likelihood of success for translocation programs.

Interestingly, the status as a native or transplanted species did not influence the rare or common status of any species in this analysis. I had originally expected that some transplanted

species would be more likely to be rare because they would face competition for niches that were already filled and face conditions different from those that the species is adapted. Conversely, other species may be more common in nonnative areas because they are released from competitors and predators in their native ranges. Instead, neither of these scenarios is apparent. This could be because many transplantations of North American freshwater fish species have happened some time ago (Jenkins and Burkhead 1993) and as such many generations have passed and these are no longer recent invasions. Also, I did not examine any species that were not native to North America and as a result, the species used in this analysis can be considered to be adapted to conditions on this continent.

The lack of significance of the instream habitat variables could have several explanations. I had instream habitat measurements for about half of the total sites, although most of the species were still represented by >20sites, which could reduce the power of models that included the instream habitat variables. Also, the watershed and landscape variables used in this study can serve as proxies for instream habitat. For example, watershed area, slope, and annual precipitation may control stream width and depth. As a result, these larger-scale variables may be more useful than instream habitat variables and are also advantageous because they can be easily measured with spatial software instead of requiring field measurements. These results suggest that future modeling efforts should focus on landscape and watershed variables rather than instream habitat measurements.

Biological traits differed between rarity groups. This indicates that there are biological mechanisms driving rarity, which is an important step for understanding the rarity and the causes of rarity in fishes. Several important differences in biological and reproductive traits among rarity classification groups are apparent. First, the most rare group, H (small extent, narrow

habitat breadth, small local abundance and group G (small extent, narrow habitat breadth, large local abundance), have a much greater proportion of non-guarding spawning species than the other group, a finding that corroborates past rarity biology studies (Gaston and Kunin 1997). As a consequence, the species that are already in the two rarest groups may be at a greater risk from anthropogenic disturbance as siltation has been shown to have the greatest effect on non-guarding broadcast spawning species (Walters et al. 2002). However, in contradiction to the hypothesis that rare species provide minimal parental care to offspring, group H had the greatest abundance of live-bearing species. This reproductive trait requires a great energetic input which could indicate that the relationship between parental investment and rarity is nonlinear. As a result, species that have a moderate energetic investment may be more likely to be common while those offering high or low levels of investment are more likely to be rare.

The association of commonness with longevity, high fecundity, and high investment in progeny indicates that commonness is a characteristic of periodic and equilibrium life-histories (see Winemiller 2005). By contrast, short longevity, low fecundity, and low parental investment were associated with rarity, meaning that rarity characteristic of the opportunistic life-history. The moderate, positive relationship between range extent and biological traits such as longevity, fecundity, age at maturity, and maximum total length indicates that species with these features have a greater ability to disperse than other species (Pyron 1999). The positive relationship between these traits and the index of habitat breadth (habitat generalists) could be explained by the ability of larger, more fecund species to take advantage of a greater array of niches.

This study has several limitations. First, the species list used for my logistic regression analysis was dominated by those species with large ranges and a high number of occurrences and this reflects the statistical necessity of choosing such species. Also, because of my use of an

existing dataset and a large number of sites and variables for an arbitrary list of species, it is likely that I did not include some important data that may have served to better predict rarity or commonness for some species. In the future, this approach can be used for species of interest and careful consideration can be taken to include the best possible predictor variables for those species to achieve the best model. Future research is needed to test the applicability of this approach to more species and also to test if rarity modeling can predict rarity or commonness at a site known to have a species but lacking available samples.

Understanding the reasons a species is common or rare is important to assessing the status of, or making any conservation decisions about, that species. This study provides an example of methodology linking biological traits, spatial and habitat features, and biotic interactions to species rarity and this methodology could be readily applied to other taxa.

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Tables

Table 3.1. Eight permutations of the rarity classification framework of Rabinowitz (1982) broken down by three dimensions of rarity: extent, habitat breadth, and local population size. Seven of the eight groups display rarity on at least one dimension while one group (A) is common across all three dimensions.

Range Extent		Large		Small	
Habitat breadth		Wide	Narrow	Wide	Narrow
Site abundance	Large	A	C	E	G
	Small	B	D	F	H

Table 3.2. Description of regional, watershed, and instream habitat variables used to model the rarity or commonness of fishes.

Category	Variable	Description
Regional	Annual temperature	Mean annual temperature (Celsius)
	Annual precipitation	Mean annual precipitation (com)
	Latitude	Latitude of site
	Longitude	Longitude of site
	Native status	Status as a native or introduced species at site
	Distance to range centroid	Distance from site to the center of a species' range (km)
Watershed	Watershed disturbance	Percent of watershed in agricultural or urban use
	Road density	Density of roads in a watershed
	Watershed area	The total area drained at a site (km ²)
	Slope	Amount of slope at a site
	Elevation	Elevation of a site
Instream	Pool	Percent of pool habitat at a site
	Riffle	Percent of riffle habitat at a site
	Run	Percent of run habitat at a site
	Average depth	Average depth of a site (cm)
	Maximum depth	Maximum depth at a site (cm)
	Average width	Average width at a site (m)
	Depth/width ratio	Average depth divided by average width

Table 3.3. Model details of species successfully predicted as rare or common by logistic regression models. Sensitivity, specificity, false positive, and false negative statistics were obtained from a 0.5 cutoff probability.

Family	Species	p-value	n	rescaled r ²	Somer's D(2)	%correctly predicted	sensitivity	specificity	false pos.	false neg.
Aphredoderidae	Pirate perch	<0.0001	77	0.3387	0.430336	83.1	57.1	92.9	25	14.8
Catostomidae	Alabama hogsucker	0.5884	50		0					
	Largescale sucker	0.0047	19		0.515524	84.2	66.7	92.3	20	14.3
Centrarchidae	Longear sunfish	0.0002	95	0.1815	0.173889	62.1	76.5	45.5	38.1	37.7
	Redbreast sunfish	<0.0001	148	0.2091	0.186624	68.9	83.7	44.6	28.7	37.5
	Rock bass	0.0003	62	0.1217	0.146689	66.1	30	83.3	53.8	28.6
Clupeidae	Gizzard shad	0.4804	40		0					
Cottidae	Banded sculpin	<0.0001	52	0.5092	0.511225	73.1	80	63.6	25	30
Cyprinidae	Blacknose dace	0.0031	63	0.3333	0.314721	65.1	80.8	54.1	44.7	20
	Central stoneroller	0.3738	144		0					
	Creek chub	<0.0001	95	0.2478	0.265225	70.5	66.7	72.3	47.4	17.5
	Hornyhead chub	0.3356	16		0					
	Redside shiner	0.004	55	0.2427	0.218089	63.6	63	64.3	37	35.7
	Roseyside dace	0.0049	21	0.4272	0.427716	81	75	84.6	25	15.4
	Sand shiner	0.3575	11		0					
	Spotfin shiner	0.0006	32	0.4552	0.501264	78.1	62.5	83.3	44.4	13
	Striped shiner	0.0021	61	0.3878	0.386884	54.1	80	36.1	53.5	27.8
Ictaluridae	Margined madtom	<0.0001	33	0.7511	0.850084	84.8	80	87	27.3	9.1
Percidae	Blackbanded darter	0.0012	77	0.1691	0.160801	67.5	72.5	62.2	32.6	32.4
	Johnny darter	0.0072	37	0.2574	0.265225	78.4	40	92.6	33.3	19.4
	Rainbow darter	0.0036	34	0.3322	0.3969	76.5	37.5	88.5	50	17.9
	Western mosquitofish	<0.0001	121	0.4401	0.49	74.4	75.6	73.7	37	16.4
Poeciliidae	Brook trout	0.0012	62	0.2047	0.206116	75.8	41.2	88.9	41.7	20
Salmonidae	Mudminnow	0.2414	18		0					
Umbridae										

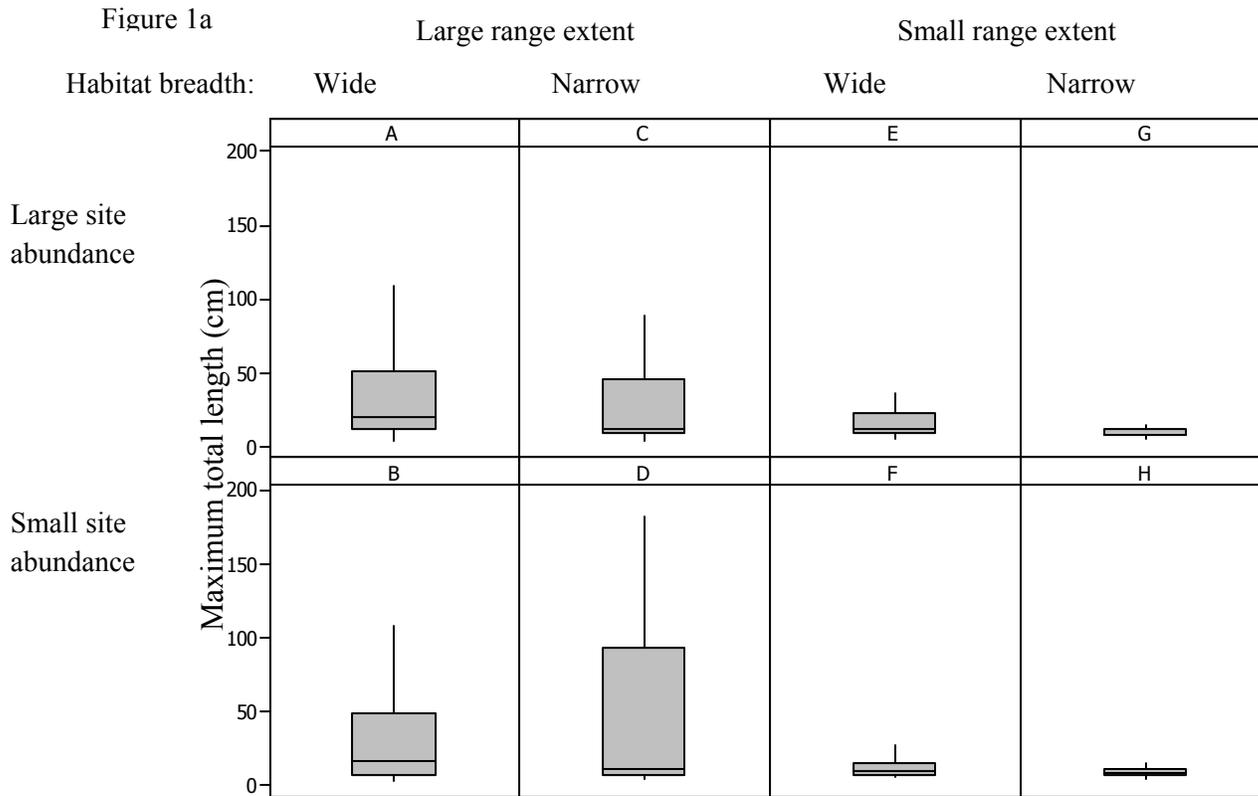
Table 4. Significant explanatory variables of the rare or common status of 19 fishes

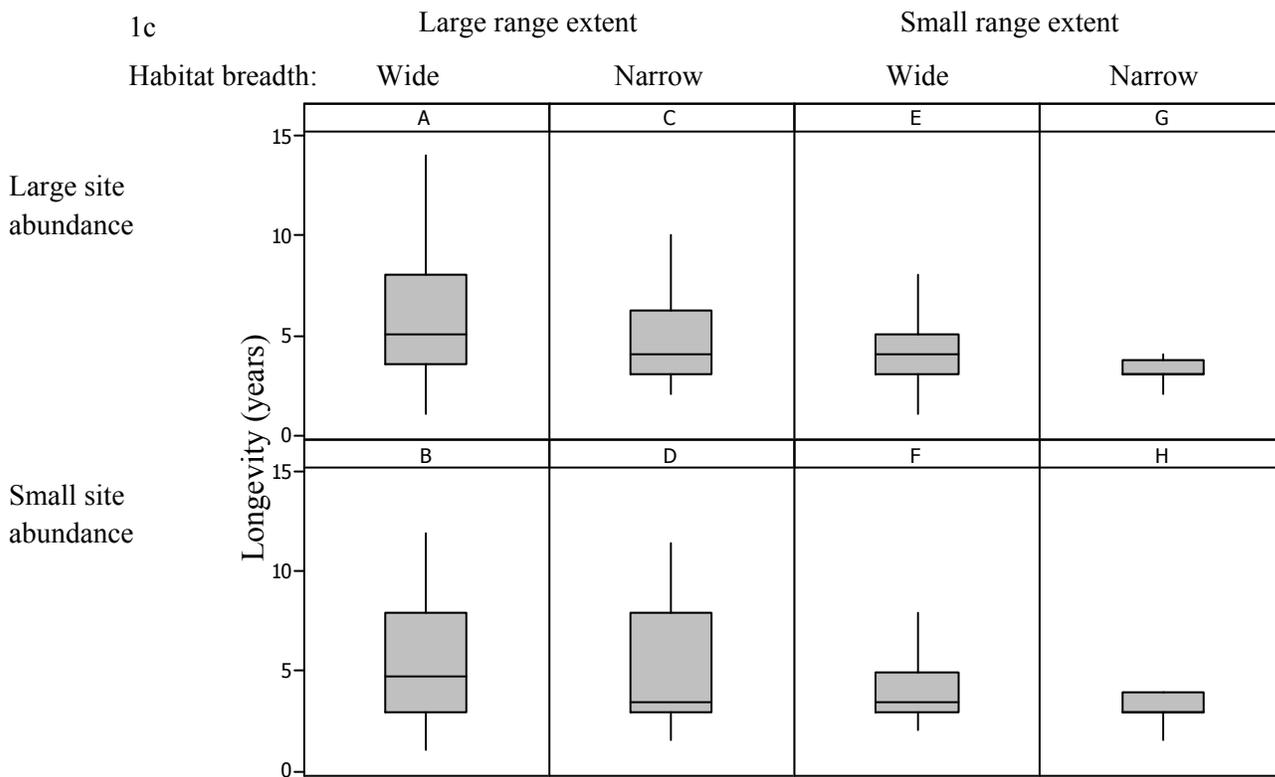
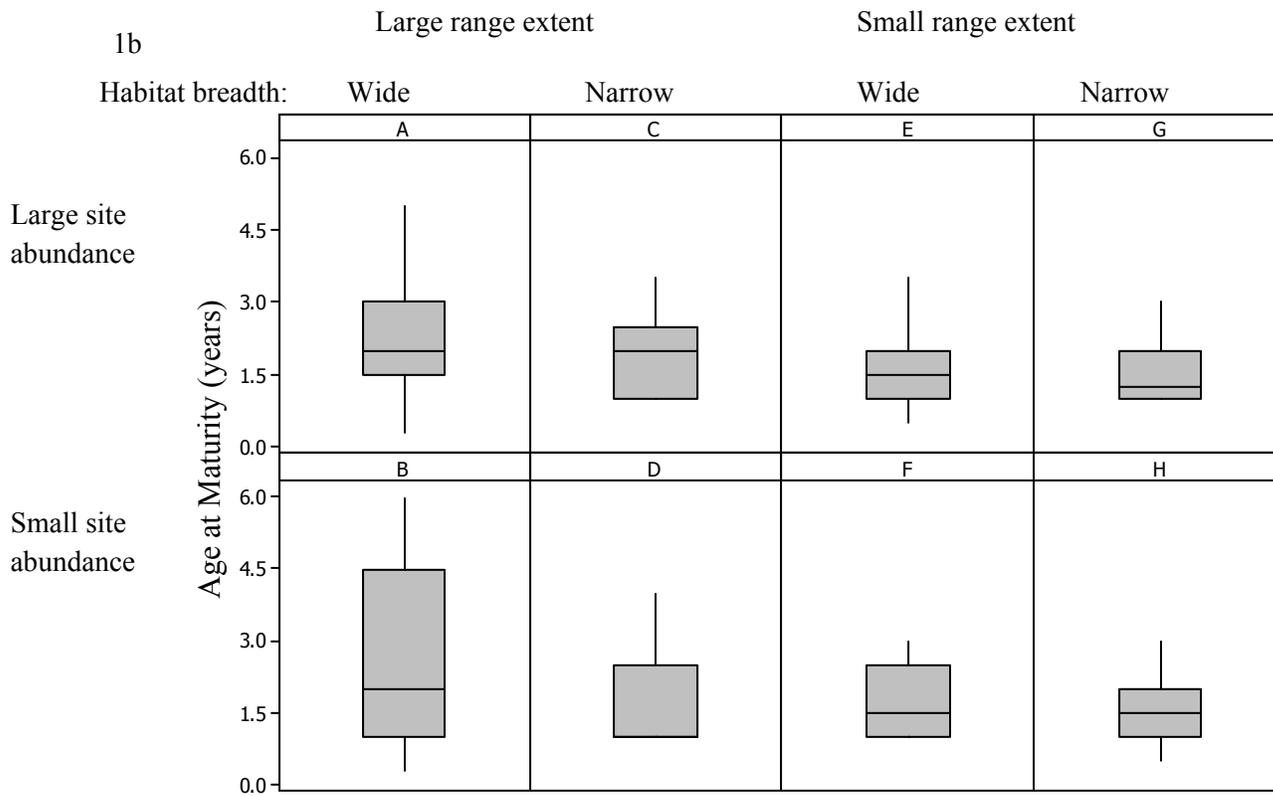
Family	Species	Variable	p-value	Point estimate	Left CL	Right CL	
Aphredoderidae	Pirate perch	lat	0.1312	0.801	0.601	1.068	
		elevation	0.0016	0.973	0.957	0.99	
Catostomidae	Largescale sucker	latitude	0.0125	1.002	1	1.004	
Centrarchidae	Longear sunfish	family richness	0.0007	1.576	1.21	2.053	
		Redbreast sunfish	Genus richness	0.001	1.684	1.234	2.297
	Rock bass	annual precipitation	0.0426	0.963	0.929	0.999	
		slope	0.0453	0.869	0.758	0.997	
		annual precipitation	0.0205	0.981	0.966	0.997	
Cottidae	Banded sculpin	species richness	0.0351	0.866	0.757	0.99	
		road density	0.0024	0.177	0.058	0.542	
		slope	0.0181	1.472	1.068	2.028	
Cyprinidae	Blacknose dace	Genus richness	0.0138	5.641	1.424	22.35	
		watershed disturbance	0.0117	1.028	0.998	1.058	
		watershed area	0.064	0.13	0.027	0.635	
		annual temperature	0.0086	0.657	0.481	0.899	
		slope	0.0223	1.188	1.025	1.376	
		Creek chub	watershed area	0.0039	0.287	0.123	0.67
			annual precipitation	0.0002	0.956	0.933	0.979
	Redside shiner	longitude	0.0298	1.057	1.005	1.11	
		annual precipitation	0.0054	0.973	0.954	0.992	
	Roseyside dace	watershed disturbance	0.047	0.905	0.82	0.999	
	Spotfin shiner	annual precipitation	0.0201	0.942	0.896	0.991	
	Striped shiner	latitude	0.0143	1.554	1.075	2.245	
		watershed disturbance	0.0032	1.086	1.028	1.147	
annual precipitation		0.0363	1.15	1.009	1.331		
annual temperature		0.0603	0.29	0.08	1.055		
elevation		0.0216	0.984	0.97	0.998		
Ictaluridae	Margined madtom	slope	0.0047	1.76	1.189	2.606	
		family richness	0.0469	7.297	1.027	51.822	
		watershed disturbance	0.0268	0.884	0.793	0.986	

		slope	0.0299	1.865	1.324	2.452
Percidae	Blackbanded darter	latitude	0.0041	1.372	1.105	1.702
Percidae	Johnny darter	family richness	0.0183	0.41	0.196	0.86
Percidae	Rainbow darter	watershed disturbance	0.018	0.944	0.899	0.99
Poeciliidae	Western mosquitofish	longitude	<0.0001	0.824	0.762	0.89
		elevation	<0.0001	0.994	0.99	0.997
Salmonidae	Brook trout	family richness	0.0051	0.287	0.12	0.688

Figures

Figure 3.1. a) Boxplot of maximum total length, b) age at maturity, c) longevity, d) fecundity, and e) larval size, for species in each of the eight rarity groups established by Pritt and Frimpong (2010).





1d

Large range extent

Small range extent

Habitat breadth:

Wide

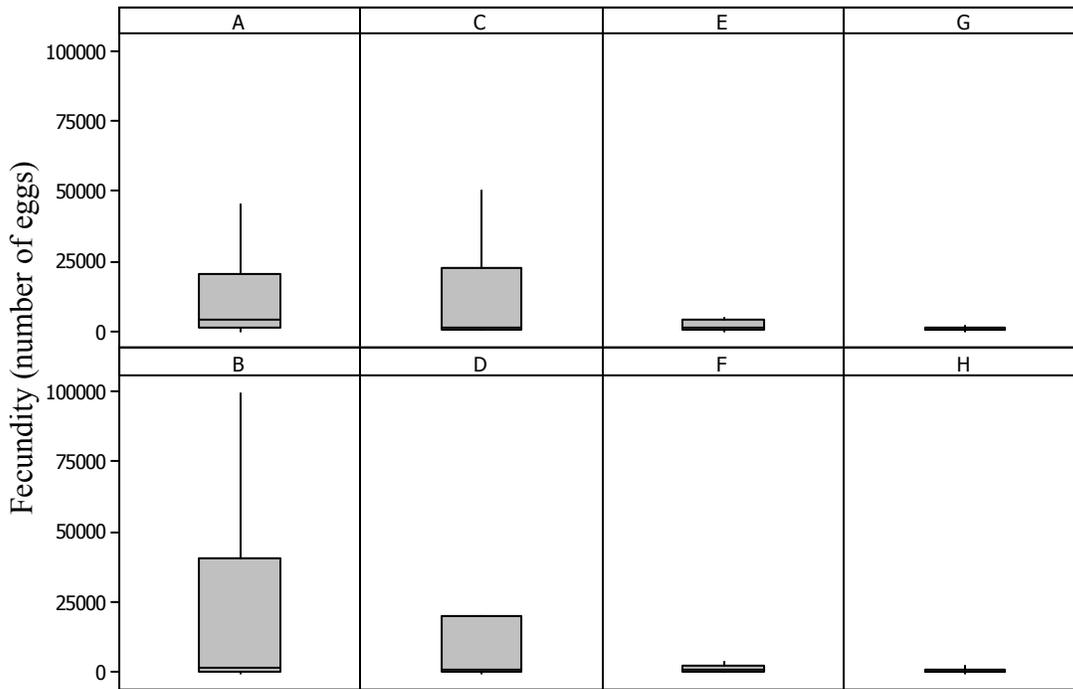
Narrow

Wide

Narrow

Large site abundance

Small site abundance



1e

Large range extent

Small range extent

Habitat breadth:

Wide

Narrow

Wide

Narrow

Large site abundance

Small site abundance

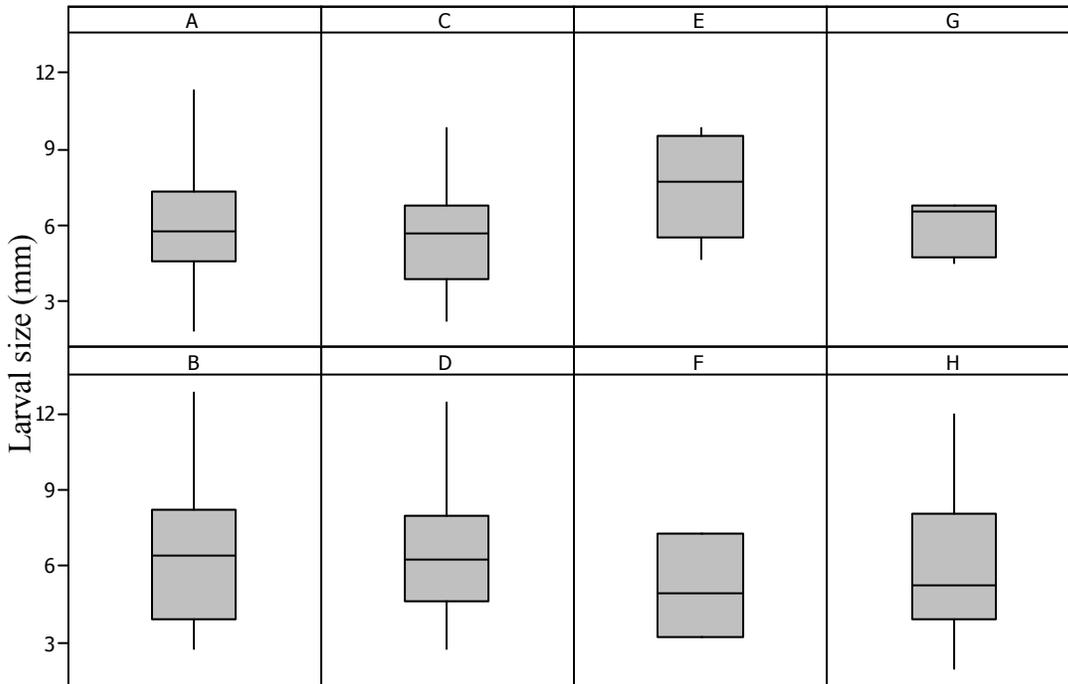


Figure 3.2 Scatterplots of life-history traits with adjusted range size (a-c), index of habitat breadth scores (d-f), and percent of sites at which a species occurs as rare (g-i).

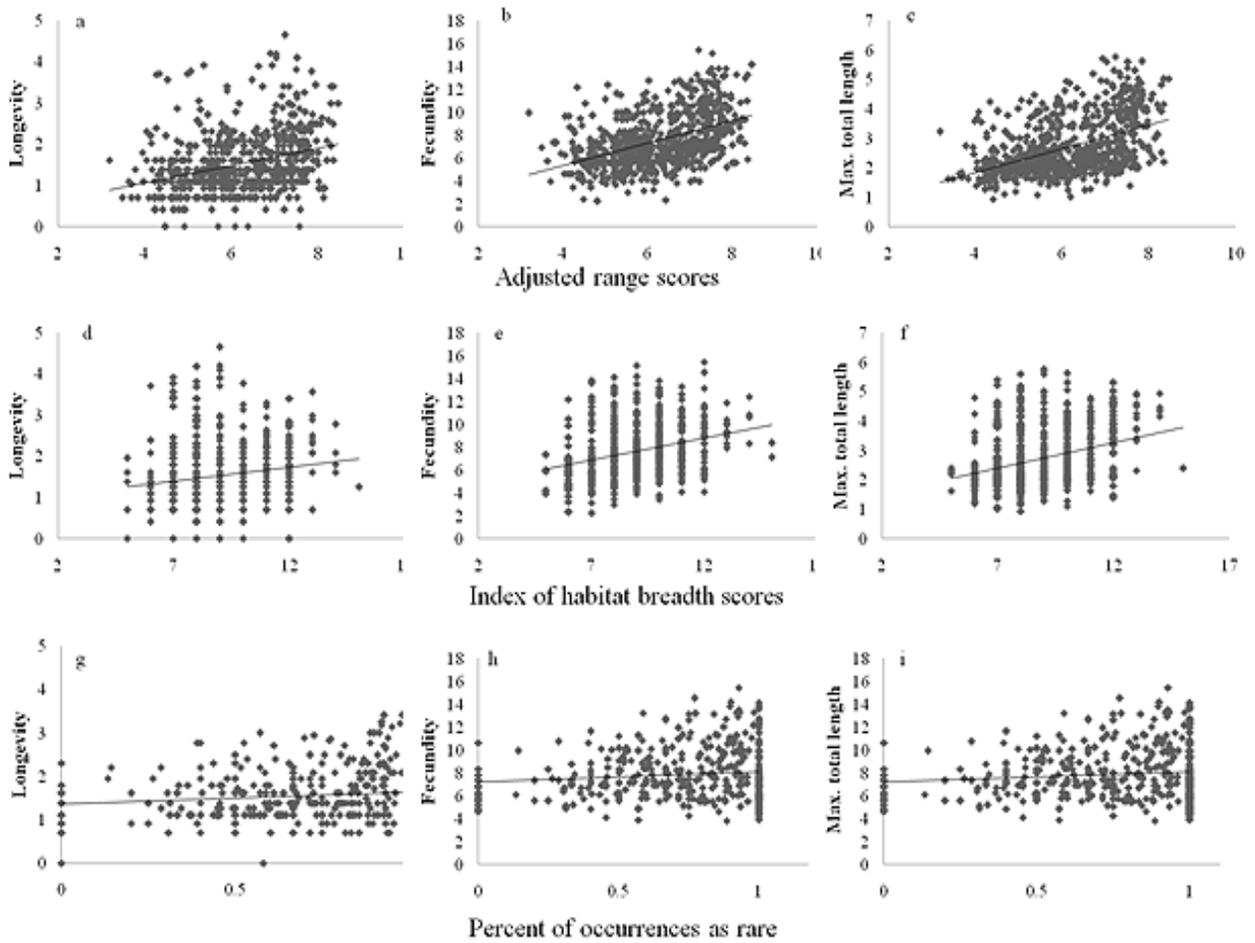
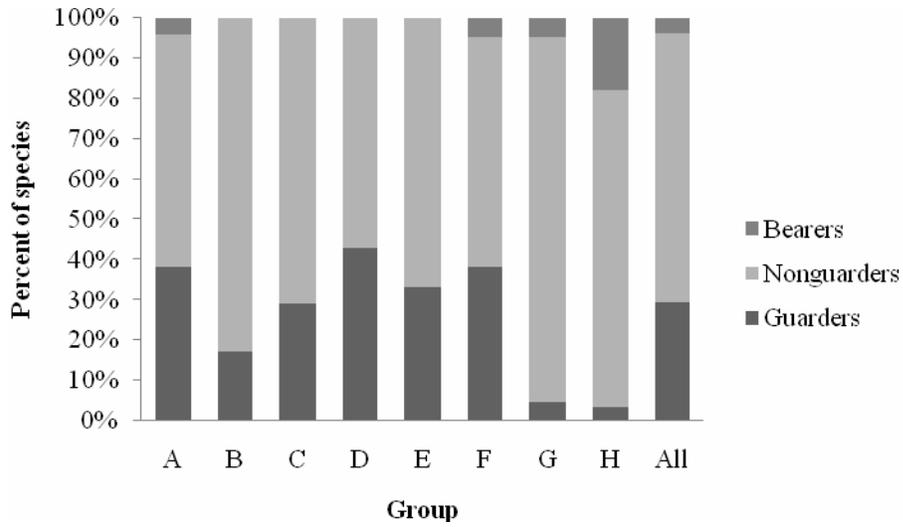


Figure 3.3. Percent of non-guarder, guarder, and bearer species in each rarity group (A-H) and all species.



Summary/Conclusion

In summary, I first defined rarity based on a classification of species' range extents, habitat associations, and site abundances, and used this classification to describe rarity in fish and examine how rarity is associated with species imperilment. I found that the most populated groups were the group that displayed commonness across all three dimensions of the classification and the group that displayed rarity across all three dimensions of the classification. However, species with extremely small range sizes were likely underrepresented by the databases I used. As a result, the large number of species appearing in the most common group may have resulted from sampling bias. Species that were on the imperiled species list of Jelks et al. (2008) were the most likely to fall into the most rare group. I also identified 30 species that were rare across all three dimensions of the classification but were not on the Jelks et al. (2008) list.

Next, I examined the influence of sampling intensity on observed rarity and community assessment of stream fish. I compared a single- versus a multiple-pass electrofishing protocol, a one- versus two-backpack electrofishing protocol, and increasing the stream length sampled as means of increasing sampling intensity. I found that proportional abundance rarity criteria were increased by an increase in sampling intensity while numerical abundance rarity criteria were not affected by sampling intensity. Taxonomic richness community assessment metrics, such as species richness and the number of minnow species, were increased with increasing number of electrofishing pass and increasing passes led to a greater observed abundance and occurrence of endemic species in the New River basin. Also, increasing sampling intensity increased the number of species that met my definition of site abundance rarity from Chapter 1. This indicates

that sampling intensity must be considered before applying that definition to other sampling protocols.

Finally, I examined species traits that could serve as mechanisms of rarity and the macroecological, habitat template, instream habitat, and biotic interaction factors that could explain site-level rarity in those species that exhibit diffusive rarity (rare at some sites but common at others). I found that species with small range extents were likely to have shorter life spans, smaller body size, lower fecundity, and lower age at maturity. Also, species that were rare at the site-level were also more likely to be non-guarders. The limited parental investment corroborates the findings of other researchers (Gaston and Kunin 1997). The rare or common status of species that displayed diffusive rarity was most frequently explained by macroecological variables such as temperature and precipitation or habitat template variables such as elevation, slope, watershed area, or watershed disturbance. Instream habitat variables and biotic interaction variables were significant for only a few species. These results show that the variables predicting rare or common status varies greatly among species but rarity can be successfully predicted for most species.

In conclusion, I was able to define rarity and describe rarity in stream fishes. However, I also demonstrated that sampling intensity could play an important role in species occurrence and status as rare or common at a site. Specifically, I determined that the number of rare species at a site increases between single pass and multiple-pass electrofishing. In addition, the number of occurrences for New River endemic species increased when multiple passes were used. This effect should be considered for future research of rare species. The protocols used for defining rarity (Chapter 1) were the same as those used to predict site abundance rarity (Chapter 3) and thus sampling intensity was constant for those two components of this study.

Finally, I conclude that differences in biological and reproductive traits among species influence, but not exclusively, their rarity or commonness at extent, habitat requirements, and site abundances. Also, regional and watershed habitat factors heavily influence the site-level rare or common status of species that exhibit diffusive rarity. Understanding rarity is a crucial step towards conserving fish biodiversity. The results of this study show that most fishes are rare in some way, and mechanisms of rarity can be attributed to biological traits, regional habitat factors, and watershed habitat factors. These factors can be used to inform conservation programs such as captive breeding and translocation efforts.

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Appendix

Appendix A. Species used for the rarity classification of freshwater fishes of the conterminous US. Listed status from Jelks et al. (2008) but excluding species that have listed subspecies.

Scientific name	Common name	Listed	Rare Extent	Rare Habitat	Rare Local
<i>Acantharchus pomotis</i>	mud sunfish	No	No	No	Yes
<i>Acipenser brevirostrum</i>	shortnose sturgeon	Yes	No	No	
<i>Acipenser fulvescens</i>	lake sturgeon	Yes	No	No	Yes
<i>Acipenser medirostris</i>	green sturgeon	Yes	No	Yes	
<i>Acipenser oxyrinchus</i>	Atlantic sturgeon	No	No	No	
<i>Acipenser transmontanus</i>	white sturgeon	Yes	No	No	
<i>Acrocheilus alutaceus</i>	chiselmouth	No	No	No	No
<i>Agosia chrysogaster</i>	longfin dace	Yes	No	Yes	No
<i>Alosa aestivalis</i>	blueback herring	No	No	No	Yes
<i>Alosa alabamae</i>	Alabama shad	Yes	No	No	
<i>Alosa chrysochloris</i>	skipjack herring	No	No	No	Yes
<i>Alosa mediocris</i>	hickory shad	No	No	Yes	
<i>Alosa pseudoharengus</i>	alewife	No	No	No	No
<i>Alosa sapidissima</i>	American Shad	No	No	No	No
<i>Ambloplites ariommus</i>	shadow bass	No	No	No	No
<i>Ambloplites cavifrons</i>	Roanoke bass	Yes	Yes	No	Yes
<i>Ambloplites constellatus</i>	Ozark bass	No	Yes	No	Yes
<i>Ambloplites rupestris</i>	rock bass	No	No	No	No
<i>Amblyopsis rosae</i>	Ozark cavefish	Yes	Yes		
<i>Amblyopsis spelaea</i>	northern cavefish	Yes	Yes	Yes	
<i>Ameiurus brunneus</i> *	snail bullhead	Yes	No	No	No
<i>Ameiurus catus</i>	white catfish	No	No	No	No
<i>Ameiurus melas</i>	black bullhead	No	No	No	No
<i>Ameiurus natalis</i>	yellow bullhead	No	No	No	No
<i>Ameiurus nebulosus</i>	brown bullhead	No	No	No	No
<i>Ameiurus platycephalus</i>	flat bullhead	Yes	No	No	Yes
<i>Ameiurus serracanthus</i>	spotted bullhead	Yes	Yes		
<i>Amia calva</i>	bowfin	No	No	No	Yes
<i>Ammocrypta beanii</i>	naked sand darter	No	No	Yes	
<i>Ammocrypta bifascia</i>	Florida sand darter	No	Yes	Yes	
<i>Ammocrypta clara</i>	western sand darter	Yes	No	Yes	Yes
<i>Ammocrypta meridiana</i>	southern sand darter	No	Yes	Yes	
<i>Ammocrypta pellucida</i>	eastern sand darter	Yes	No	Yes	Yes

<i>Ammocrypta vivax</i>	scaly sand darter	No	No	Yes	No
<i>Apeltes quadracus</i>	fourspine stickleback	No	No		
<i>Aphredoderus sayanus</i>	pirate perch	No	No	No	No
<i>Aplodinotus grunniens</i>	freshwater drum	No	No	No	No
<i>Archoplites interruptus</i>	Sacramento perch	Yes	Yes	No	
<i>Astronotus ocellatus</i>	oscar	No		Yes	
<i>Astyanax mexicanus</i>	Mexican tetra	No	No	No	
<i>Atractosteus spatula</i>	alligator Gar	Yes	No	No	Yes
<i>Belonesox belizanus</i>	pike killifish	No		No	
<i>Betta splendens</i>	Siamese fighting fish	No			
<i>Brachydanio rerio</i>	zebra danio	No			
<i>Callichthys callichthys</i>	casarudo	No		Yes	
<i>Campostoma anomalum</i>	central stoneroller	No	No	No	No
<i>Campostoma oligolepis</i>	largescale stoneroller	No	No	Yes	No
<i>Campostoma ornatum</i>	Mexican stoneroller	Yes	No	No	
<i>Campostoma pauciradii</i>	bluefin stoneroller	No	Yes	No	No
<i>Carassius auratus</i>	goldfish	No		No	
<i>Carpiodes carpio</i>	river carpsucker	No	No	Yes	No
<i>Carpiodes cyprinus</i>	quillback	No	No	No	No
<i>Carpiodes velifer</i>	highfin carpsucker	No	No	Yes	No
<i>Catostomus ardens</i>	Utah sucker	No	Yes	No	No
<i>Catostomus bernardini</i>	Yaqui sucker	Yes	Yes	No	
<i>Catostomus catostomus</i>	longnose sucker	No	No	No	No
<i>Catostomus clarkii</i>	desert sucker	No	No	No	No
<i>Catostomus columbianus</i>	bridgelip sucker	No	No	No	No
<i>Catostomus commersonii</i>	white sucker	No	No	No	No
<i>Catostomus discobolus</i>	bluehead sucker	No	No	No	No
<i>Catostomus fumeiventris</i>	Owens sucker	No	Yes	No	
<i>Catostomus insignis</i>	Sonora sucker	Yes	Yes	No	Yes
<i>Catostomus latipinnis</i>	flannelmouth sucker	No	No	No	No
<i>Catostomus macrocheilus</i>	largescale sucker	No	No	No	No
<i>Catostomus microps</i>	Modoc sucker	Yes	Yes	Yes	
<i>Catostomus platyrhynchus</i>	mountain sucker	No	No	No	No
<i>Catostomus plebeius</i>	Rio Grande sucker	Yes	Yes	No	No
<i>Catostomus rimiculus</i>	Klamath smallscale sucker	No	Yes	No	
<i>Catostomus santaanae</i>	Santa Ana sucker	Yes	Yes	No	No
<i>Catostomus snyderi</i>	Klamath Largescale sucker	Yes	Yes	No	
<i>Catostomus sp.</i>	Salish sucker	Yes	Yes		
<i>Catostomus sp.</i>	Wall Canyon sucker	Yes	Yes	No	
<i>Catostomus sp.</i>	Little Colorado River sucker	No	Yes	Yes	
<i>Catostomus tahoensis</i>	Tahoe sucker	No	Yes	No	No
<i>Catostomus warnerensis</i>	Warner sucker	Yes	Yes	Yes	

<i>Centrarchus macropterus</i>	flier	No	No	No	No
<i>Channa argus</i>	snakehead	No			
<i>Channa maculata</i>	blotched snakehead	No			
<i>Channa marulius</i>	great snakehead	No			
<i>Channa micropeltes</i>	giant snakehead	No			
<i>Chasmistes brevirostris</i>	shortnose sucker	Yes	Yes	Yes	
<i>Chasmistes cujus</i>	cui-ui	Yes	Yes	Yes	
<i>Chasmistes liorus</i>	June sucker	No	Yes	Yes	
<i>Chasmistes muriei</i>	Snake River sucker	Yes	Yes		
<i>Chitala ornata</i>	clown knifefish	No			
<i>Chologaster cornuta</i>	swampfish	No	No	No	Yes
<i>Cichlasoma bimaculatum</i>	black acara	No			
<i>Cichlasoma citrinellum</i>	midas cichlid	No			
<i>Cichlasoma cyanoguttatum</i>	Rio Grande cichlid	No	Yes	No	
<i>Cichlasoma managuense</i>	jaguar guapote	No			
<i>Cichlasoma meeki</i>	firemouth	No			
<i>Cichlasoma nigrofasciatum</i>	convict cichlid	No			
<i>Cichlasoma ocellaris</i>	butterfly peacock bass	No			
<i>Cichlasoma octofasciatum</i>	Jack Dempsey	No			
<i>Cichlasoma severum</i>	banded cichlid	No		Yes	
<i>Cichlasoma urophthalmus</i>	Mayan cichlid	No			
<i>Clarias batrachus</i>	walking catfish	No		Yes	
<i>Clinostomus elongatus</i>	reeside dace	Yes	No	Yes	No
<i>Clinostomus funduloides</i>	rosyside dace	No	No	Yes	No
<i>Colisa fasciata</i>	banded gourami	No			
<i>Colossoma macropomum</i>	Tambaqui	No			
<i>Coregonus albula</i>	vendace	No			
<i>Coregonus artedi</i>	cisco	No	No	Yes	
<i>Coregonus clupeaformis</i>	lake whitefish	No	No	Yes	
<i>Coregonus hoyi</i>	bloater	No	No	Yes	
<i>Coregonus kiyi</i>	kiyi	No	No		
<i>Coregonus lavaretus</i>	Baltic whitefish	No			
<i>Coregonus nigripinnis</i>	blackfin cisco	No			
<i>Coregonus reighardi</i>	shortnose cisco	No	Yes		
<i>Coregonus zenithicus</i>	shortjaw cisco	Yes	No	Yes	
<i>Cottus aleuticus</i>	coastrange sculpin	No	No	Yes	
<i>Cottus asper</i>	prickly sculpin	No	No		No
<i>Cottus asperrimus</i>	rough sculpin	Yes	Yes	No	
<i>Cottus baileyi*</i>	black sculpin	No	Yes	Yes	Yes
<i>Cottus bairdii</i>	mottled sculpin	No	No	No	No

<i>Cottus beldingii</i>	Paiute sculpin	No	No	Yes	No
<i>Cottus carolinae</i>	banded sculpin	No	No	No	No
<i>Cottus cognatus</i>	slimy sculpin	No	No	No	No
<i>Cottus confusus</i>	shorthead sculpin	No	No	No	No
<i>Cottus echinatus</i>	Utah Lake sculpin	Yes	Yes		
<i>Cottus extensus</i>	Bear Lake sculpin	Yes	Yes		
<i>Cottus girardi</i>	Potomac sculpin	No	Yes	No	No
<i>Cottus greenei</i>	Shoshone sculpin	Yes	Yes		No
<i>Cottus gulosus</i>	riffle sculpin	No	No	No	No
<i>Cottus hypselurus</i>	Ozark sculpin	No	Yes	Yes	No
<i>Cottus klamathensis</i>	marbled sculpin	No	Yes	Yes	
<i>Cottus leiopomus</i>	Wood River sculpin	Yes	Yes	Yes	No
<i>Cottus marginatus</i>	marginated sculpin	Yes	Yes		
<i>Cottus paulus</i>	pygmy sculpin	Yes	Yes	Yes	
<i>Cottus perplexus</i>	reticulate sculpin	No	Yes	No	No
<i>Cottus pitensis</i>	Pit sculpin	No	Yes	Yes	
<i>Cottus princeps</i>	Klamath Lake sculpin	No	Yes	Yes	
<i>Cottus rhotheus</i>	torrent sculpin	No	No	Yes	No
<i>Cottus ricei</i>	spoonhead sculpin	No	No	Yes	
<i>Cottus tenuis</i>	slender sculpin	Yes	Yes	No	
<i>Couesius plumbeus</i>	lake chub	No	No	No	No
<i>Crenichthys baileyi</i>	White River springfish	No	Yes	Yes	
<i>Crenichthys nevadae</i>	Railroad Valley springfish	Yes	Yes	Yes	
<i>Cromileptes altivelis</i>	humpback grouper	No			
<i>Crystallaria asprella</i>	crystal darter	Yes	No	Yes	
<i>Ctenopharyngodon idella</i>	grass carp	No		Yes	
<i>Culaea inconstans</i>	brook stickleback	No	No	No	
<i>Cycleptus elongatus</i>	blue sucker	No	No	Yes	Yes
<i>Cyprinella analostana</i>	satinfish shiner	No	No	No	No
<i>Cyprinella caerulea</i>	blue shiner	Yes	Yes	No	
<i>Cyprinella callisema</i>	Ocmulgee shiner	No	Yes	No	No
<i>Cyprinella callistia</i>	Alabama shiner	No	Yes	No	Yes
<i>Cyprinella callitaenia</i>	bluestripe shiner	Yes	Yes	No	
<i>Cyprinella camura</i>	bluntnose shiner	No	No	No	No
<i>Cyprinella chloristia</i>	greenfin shiner	No	Yes	No	
<i>Cyprinella formosa</i>	beautiful shiner	Yes	Yes	No	
<i>Cyprinella galactura</i>	whitetail shiner	No	No	No	No
<i>Cyprinella gibbsi</i>	Tallapoosa shiner	No	Yes	Yes	
<i>Cyprinella labrosa</i>	thicklip chub	No	Yes	Yes	
<i>Cyprinella leedsii</i>	bannerfin shiner	No	Yes	Yes	No
<i>Cyprinella lepida</i>	Plateau shiner	Yes	Yes	Yes	
<i>Cyprinella lutrensis</i>	red shiner	No	No	No	No

<i>Cyprinella proserpina</i>	proserpine shiner	Yes	Yes	Yes	
<i>Cyprinella pyrrhomelas</i>	fieryblack shiner	No	Yes	No	Yes
<i>Cyprinella spiloptera</i>	spotfin shiner	No	No	Yes	No
<i>Cyprinella trichroistia</i>	tricolor shiner	No	Yes	No	No
<i>Cyprinella venusta</i>	blacktail shiner	No	No	No	No
<i>Cyprinella whipplei</i>	steelcolor shiner	No	No	No	No
<i>Cyprinella xaenura</i>	Altamaha shiner	Yes	Yes	Yes	Yes
<i>Cyprinella zanema</i>	Santee chub	No	Yes	Yes	
<i>Cyprinidae .</i>	sawfin shiner	No	Yes	No	
<i>Cyprinodon bovinus</i>	Leon Springs pupfish	Yes	Yes	Yes	
<i>Cyprinodon diabolis</i>	Devils Hole pupfish	Yes	Yes	No	
<i>Cyprinodon elegans</i>	Comanche Springs pupfish	Yes	Yes	Yes	
<i>Cyprinodon eximius</i>	Conchos pupfish	No	Yes	No	
<i>Cyprinodon macularius</i>	desert pupfish	Yes	Yes	No	
<i>Cyprinodon nevadensis</i>	Amargosa pupfish	No	Yes		
<i>Cyprinodon pecosensis</i>	Pecos pupfish	Yes	Yes	Yes	
<i>Cyprinodon pisteri</i>	Palomas pupfish	No	Yes	No	
<i>Cyprinodon radiosus</i>	Owens pupfish	Yes	Yes	No	
<i>Cyprinodon rubrofluviatilis</i>	Red River pupfish	No	Yes	Yes	
<i>Cyprinodon salinus</i>	Salt Creek pupfish	No	Yes	No	
<i>Cyprinodon tularosa</i>	White Sands pupfish	Yes	Yes	Yes	
<i>Cyprinodon variegatus</i>	sheepshead minnow	No		Yes	
<i>Cyprinus carpio</i>	common carp	No		No	
<i>Deltistes luxatus</i>	Lost River sucker	Yes	Yes	Yes	
<i>Dionda diaboli</i>	Devils river minnow	Yes	Yes	Yes	
<i>Dionda episcopa</i>	roundnose minnow	No	No	No	
<i>Dorosoma cepedianum</i>	gizzard shad	No	No	No	No
<i>Dorosoma petenese</i>	threadfin shad	No	No	No	No
<i>Elassoma alabamae</i>	spring pygmy sunfish	Yes	Yes	Yes	
<i>Elassoma boehlkei</i>	Carolina pygmy sunfish	No	Yes	Yes	
<i>Elassoma evergladei</i>	Everglades pygmy sunfish	No	No	Yes	No
<i>Elassoma okatie</i>	bluebarred pygmy sunfish	No	Yes	No	
<i>Elassoma okefenokee</i>	Okefenokee pygmy sunfish	No	Yes	Yes	
<i>Elassoma zonatum</i>	banded pygmy sunfish	No	No	Yes	No
<i>Empetrichthys latos</i>	Pahrump poolfish	No	Yes	Yes	
<i>Empetrichthys merriami</i>	Ash Meadows poolfish	Yes	Yes	Yes	
<i>Enneacanthus chaetodon</i>	blackbanded sunfish	Yes	No	Yes	No
<i>Enneacanthus gloriosus</i>	bluespotted sunfish	No	No	No	No
<i>Enneacanthus obesus</i>	banded sunfish	No	No	Yes	No
<i>Eremichthys acros</i>	desert dace	Yes	Yes	Yes	
<i>Erimonax monachus</i>	spotfin chub	Yes	Yes	Yes	

<i>Erimystax cahni</i>	slender chub	Yes	Yes	Yes	
<i>Erimystax dissimilis</i>	streamline chub	No	No	Yes	Yes
<i>Erimystax harryi</i>	Ozark chub	Yes	Yes		No
<i>Erimystax insignis*</i>	blotched chub	No	Yes	Yes	Yes
<i>Erimystax x-punctatus</i>	gravel chub	No	No	Yes	No
<i>Erimyzon oblongus</i>	creek chubsucker	No	No	No	No
<i>Erimyzon sucetta</i>	lake chubsucker	No	No	No	Yes
<i>Erimyzon tenuis</i>	sharpfin chubsucker	No		Yes	
<i>Esox americanus</i>	redfin pickerel	No	No	No	No
<i>Esox lucius</i>	northern pike	No	No	Yes	Yes
<i>Esox masquinongy</i>	muskellunge	No	No	Yes	Yes
<i>Esox niger</i>	chain pickerel	No	No	No	No
<i>Esox reicherti</i>	Amur pike	No			
<i>Etheostoma .</i>	Red snubnose (firebelly) darter	No			
<i>Etheostoma acuticeps</i>	sharphead darter	Yes	Yes	Yes	
<i>Etheostoma akatulo</i>	jewel darter, bluemask darter	No	Yes	Yes	
<i>Etheostoma aquali</i>	coppercheek darter	Yes	Yes	Yes	Yes
<i>Etheostoma asprigene</i>	mud darter	No	No	Yes	Yes
<i>Etheostoma baileyi</i>	emerald darter	No	Yes	Yes	
<i>Etheostoma barbouri</i>	teardrop darter	No	Yes	Yes	
<i>Etheostoma barrenense</i>	splendid darter	No	Yes	Yes	
<i>Etheostoma bellator</i>	Warrior darter	No	Yes	Yes	
<i>Etheostoma bellum</i>	orange-fin darter	No	Yes	Yes	
<i>Etheostoma blennioides</i>	greenside darter	No	No	No	No
<i>Etheostoma blennius</i>	blenny darter	No	Yes	Yes	No
<i>Etheostoma boschungii</i>	slackwater darter	Yes	Yes	No	Yes
<i>Etheostoma brevirostrum</i>	holiday darter	No	Yes	No	
<i>Etheostoma caeruleum</i>	rainbow darter	No	No	No	No
<i>Etheostoma camurum</i>	bluebreast darter	No	No	Yes	Yes
<i>Etheostoma chlorbranchium</i>	greenfin darter	No	Yes	Yes	
<i>Etheostoma chlorosoma</i>	bluntnose darter	No	No	Yes	No
<i>Etheostoma cinereum</i>	ashy darter	No	Yes	Yes	
<i>Etheostoma collettei</i>	creole darter	No	Yes	Yes	
<i>Etheostoma collis</i>	Carolina darter	Yes	Yes	Yes	
<i>Etheostoma colorosum</i>	coastal darter	No	Yes	Yes	
<i>Etheostoma coosae</i>	Coosa darter	No	Yes	Yes	No
<i>Etheostoma corona</i>	crown darter	Yes	Yes	Yes	
<i>Etheostoma cragini</i>	Arkansas darter	Yes	Yes	Yes	
<i>Etheostoma crossopterygum</i>	fringed darter	No	Yes	No	Yes
<i>Etheostoma davisoni</i>	Choctawhatchee darter	No	Yes	Yes	

<i>Etheostoma denoncourti</i>	golden darter	Yes	Yes	Yes	
<i>Etheostoma ditrema</i>	coldwater darter	No	Yes	Yes	
<i>Etheostoma duryi</i>	blackside snubnose darter	No	Yes	No	No
<i>Etheostoma edwini*</i>	brown darter	No	Yes	Yes	Yes
<i>Etheostoma etnieri</i>	cherry darter	No	Yes	Yes	
<i>Etheostoma euzonum*</i>	Arkansas saddled darter	No	Yes	Yes	Yes
<i>Etheostoma exile</i>	Iowa darter	No	No	No	No
<i>Etheostoma flabellare</i>	fantail darter	No	No	Yes	No
<i>Etheostoma flavum</i>	saffron darter	No	Yes	Yes	No
<i>Etheostoma fonticola</i>	fountain darter	Yes	Yes	No	
<i>Etheostoma fricksium</i>	Savannah darter	No	Yes	No	Yes
<i>Etheostoma fusiforme</i>	swamp darter	No	No	No	Yes
<i>Etheostoma gracile</i>	slough darter	No	No	Yes	Yes
<i>Etheostoma grahami</i>	Rio Grande darter	Yes	Yes	No	
<i>Etheostoma histrio</i>	harlequin darter	No	No	No	Yes
<i>Etheostoma hopkinsi*</i>	Christmas darter	No	Yes	Yes	Yes
<i>Etheostoma inscriptum</i>	turquoise darter	No	Yes	No	No
<i>Etheostoma jessiae</i>	blueside darter	No	Yes		Yes
<i>Etheostoma jordani*</i>	greenbreast darter	No	Yes	Yes	Yes
<i>Etheostoma juliae*</i>	yoke darter	No	Yes	Yes	Yes
<i>Etheostoma kanawhae</i>	Kanawha darter	No	Yes	No	Yes
<i>Etheostoma kennicotti*</i>	stripetail darter	No	Yes	Yes	Yes
<i>Etheostoma lepidum</i>	greenthroat darter	Yes	Yes	Yes	
<i>Etheostoma longimanum*</i>	longfin darter	No	Yes	Yes	Yes
<i>Etheostoma luteovinctum</i>	redband darter	No	Yes	No	
<i>Etheostoma lynceum</i>	brighteye darter	No	Yes		Yes
<i>Etheostoma maculatum</i>	spotted darter	Yes	Yes	Yes	
<i>Etheostoma mariae</i>	pinewoods darter	Yes	Yes	Yes	
<i>Etheostoma microlepidum</i>	smallscale darter	Yes	Yes	Yes	
<i>Etheostoma microperca</i>	least darter	No	No	No	Yes
<i>Etheostoma moorei</i>	yellowcheek darter	Yes	Yes	Yes	
<i>Etheostoma neopterum</i>	lollypop darter	Yes	Yes		Yes
<i>Etheostoma nianguae</i>	Niangua darter	Yes	Yes	Yes	
<i>Etheostoma nigripinne*</i>	blackfin darter	No	Yes	Yes	Yes
<i>Etheostoma nigrum</i>	johnny darter	No	No	No	No
<i>Etheostoma nivea</i>	whitefin shiner	No	Yes	No	
<i>Etheostoma nuchale</i>	watercress darter	No	Yes	Yes	
<i>Etheostoma obeyense</i>	barcheck darter	No	Yes	Yes	
<i>Etheostoma okaloosae</i>	Okaloosa darter	Yes	Yes	Yes	
<i>Etheostoma olivaceum</i>	dirty darter	No	Yes	Yes	
<i>Etheostoma olmstedi</i>	tessellated darter	No	No	No	No
<i>Etheostoma oophylax*</i>	guardian darter	No	Yes	Yes	Yes

<i>Etheostoma osburni</i>	candy darter	Yes	Yes	No	Yes
<i>Etheostoma pallidorsum</i>	paleback darter	Yes	Yes	No	
<i>Etheostoma parvipinne</i>	goldstripe darter	No	No	No	
<i>Etheostoma percnum</i>	duskytail darter	No	Yes	Yes	
<i>Etheostoma perlongum</i>	Waccamaw darter	Yes	Yes	Yes	
<i>Etheostoma podostemone</i>	riverweed darter	No	Yes		Yes
<i>Etheostoma proeliare</i>	cypress darter	No	No	Yes	Yes
<i>Etheostoma punctulatum</i> *	stippled darter	No	Yes	Yes	Yes
<i>Etheostoma pyrrhogaster</i>	firebelly darter	Yes	Yes		
<i>Etheostoma radiosum</i>	orangebelly darter	No	Yes	Yes	
<i>Etheostoma rafinesquei</i>	Kentucky darter	No	Yes	Yes	
<i>Etheostoma ramseyi</i>	Alabama darter	No	Yes	Yes	No
<i>Etheostoma raneyi</i>	Yazoo darter	Yes	Yes		
<i>Etheostoma rubrum</i>	bayou darter	Yes	Yes	No	
<i>Etheostoma rufilineatum</i>	redline darter	No	Yes	Yes	No
<i>Etheostoma rupestre</i> *	rock darter	No	Yes	Yes	Yes
<i>Etheostoma sagitta</i>	arrow darter	No	Yes	Yes	
<i>Etheostoma sanguifluum</i>	bloodfin darter	No	Yes	Yes	
<i>Etheostoma scotti</i>	Cherokee darter	No	Yes	Yes	
<i>Etheostoma sellare</i>	Maryland darter	Yes	Yes	Yes	
<i>Etheostoma serrifer</i>	sawcheek darter	No	No	Yes	No
<i>Etheostoma simoterum</i>	snubnose darter	No	Yes	Yes	No
<i>Etheostoma smithi</i>	slabrock darter	No	Yes	Yes	
<i>Etheostoma sp.</i>	sunburst darter	No	Yes		
<i>Etheostoma spectabile</i>	orangethroat darter	No	No	Yes	No
<i>Etheostoma squamiceps</i>	spottail darter	No	Yes	Yes	
<i>Etheostoma stigmaeum</i>	speckled darter	No	No	No	No
<i>Etheostoma striatulum</i>	striated darter	Yes	Yes	Yes	
<i>Etheostoma swaini</i>	Gulf darter	No	No	Yes	Yes
<i>Etheostoma swannanoa</i>	Swannanoa darter	No	Yes	Yes	
<i>Etheostoma tecumsehi</i>	Tallapoosa darter	Yes	Yes	Yes	
<i>Etheostoma tetrazonum</i>	Missouri saddled darter	No	Yes	Yes	
<i>Etheostoma thalassinum</i>	seagreen darter	No	Yes	Yes	No
<i>Etheostoma tippecanoe</i>	Tippecanoe darter	Yes	Yes	Yes	Yes
<i>Etheostoma trisella</i>	trispot darter	Yes	Yes	Yes	
<i>Etheostoma tuscumbia</i>	Tuscumbia darter	Yes	Yes	Yes	
<i>Etheostoma variatum</i>	variegate darter	No	No	No	No
<i>Etheostoma virgatum</i>	striped darter	No	Yes	Yes	No
<i>Etheostoma vitreum</i>	glassy darter	No	Yes	No	
<i>Etheostoma vulneratum</i>	wounded darter	Yes	Yes	Yes	
<i>Etheostoma wapiti</i>	boulder darter	Yes	Yes	Yes	
<i>Etheostoma whipplei</i>	redfin darter	No	No	No	No

<i>Etheostoma zonale</i>	banded darter	No	No	No	No
<i>Etheostoma zonifer</i>	backwater darter	No	Yes	Yes	No
<i>Etheostoma zonistium</i>	bandfin darter	No	Yes	Yes	
<i>Eucyclogobius newberryi</i>	tidewater goby	Yes	Yes	No	
<i>Exoglossum laurae*</i>	tonguetied minnow	No	Yes	Yes	Yes
<i>Exoglossum maxillingua</i>	cutlips minnow	No	No	No	No
<i>Forbesichthys agassizii</i>	spring cavefish	Yes	Yes	Yes	Yes
<i>Fundulus albolineatus</i>	whiteline topminnow	Yes	Yes	Yes	
<i>Fundulus bifax</i>	stippled studfish	Yes	Yes	No	
<i>Fundulus blairae</i>	western starhead topminnow	No	No	Yes	
<i>Fundulus catenatus</i>	northern studfish	No	No	No	Yes
<i>Fundulus chrysotus</i>	golden topminnow	No	No	No	Yes
<i>Fundulus cingulatus</i>	banded topminnow	No	No	No	
<i>Fundulus confluentus</i>	marsh killifish	No	Yes		Yes
<i>Fundulus diaphanus</i>	banded killifish	No	No	No	No
<i>Fundulus dispar</i>	starhead topminnow	No	No	Yes	
<i>Fundulus escambiae*</i>	russetfin topminnow	No	Yes	Yes	Yes
<i>Fundulus euryzonus</i>	broadstripe topminnow	Yes	Yes	Yes	
<i>Fundulus heteroclitus</i>	mummichog	No	No	No	No
<i>Fundulus julisia</i>	Barrens topminnow	Yes	Yes	Yes	
<i>Fundulus lineolatus</i>	lined topminnow	No	No	No	Yes
<i>Fundulus luciae</i>	spotfin killifish	No	Yes		
<i>Fundulus majalis</i>	striped killifish	No	Yes		
<i>Fundulus notatus</i>	blackstripe topminnow	No	No	No	No
<i>Fundulus notti</i>	southern starhead topminnow	No	Yes	Yes	
<i>Fundulus olivaceus</i>	blackspotted topminnow	No	No	No	No
<i>Fundulus rathbuni</i>	speckled killifish	No	Yes	Yes	No
<i>Fundulus sciadicus</i>	plains topminnow	No	No	Yes	Yes
<i>Fundulus seminolis</i>	Seminole killifish	No	Yes	No	Yes
<i>Fundulus stellifer</i>	southern studfish	No	Yes	No	No
<i>Fundulus waccamensis</i>	Waccamaw killifish	Yes	Yes		
<i>Fundulus zebrinus</i>	plains killifish	No	No	No	No
<i>Gambusia affinis</i>	western mosquitofish	No	No	No	No
<i>Gambusia amistadensis</i>	Amistad gambusia	Yes	Yes	Yes	
<i>Gambusia gaigei</i>	Big Bend gambusia	No	Yes	Yes	
<i>Gambusia geiseri</i>	largespring gambusia	No	Yes	Yes	
<i>Gambusia georgei</i>	San Marcos gambusia	Yes	Yes	Yes	
<i>Gambusia heterochir</i>	Clear Creek gambusia	Yes	Yes	No	
<i>Gambusia holbrooki</i>	eastern mosquitofish	No		Yes	
<i>Gambusia nobilis</i>	Pecos gambusia	Yes	Yes	Yes	
<i>Gambusia senilis</i>	blotched gambusia	Yes	Yes	No	
<i>Gasterosteus aculeatus</i>	threespine stickleback	No	No	No	No

<i>Geophagus surinamensis</i>	redstriped eartheater	No				
<i>Gila alvordensis</i>	Alvord chub	Yes	Yes	No		
<i>Gila atraria</i>	Utah chub	No	No	No		Yes
<i>Gila bicolor</i>	tui chub	No	No	No		
<i>Gila boraxobius</i>	Borax Lake chub	Yes	Yes	No		
<i>Gila coerulea</i>	blue chub	No	Yes	Yes		
<i>Gila crassicauda</i>	thicktail chub	Yes	Yes	Yes		
<i>Gila cypha</i>	humpback chub	Yes	Yes	Yes		
<i>Gila ditaenia</i>	Sonora chub	Yes	Yes	Yes		
<i>Gila elegans</i>	bonytail chub	Yes	No	No		
<i>Gila intermedia</i>	Gila chub	Yes	Yes	No		
<i>Gila nigrescens</i>	Chihuahua chub	Yes	Yes	Yes		
<i>Gila orcuttii</i>	arroyo chub	Yes	Yes	No		No
<i>Gila pandora*</i>	Rio Grande chub	Yes	No	No		No
<i>Gila purpurea</i>	Yaqui chub	Yes	Yes	No		
<i>Gila robusta</i>	roundtail chub	No	No	No		No
<i>Gobionellus oceanicus</i>	highfin goby	No				
<i>Gymnocephalus cernuus</i>	ruffe	No		No		
<i>Hemichromis bimaculatus</i>	jewelfish	No				
<i>Hemichromis letourneuxi</i>	African jewelfish	No		Yes		
<i>Hemitremia flammea</i>	flame chub	Yes	Yes	No		Yes
<i>Hesperoleucus symmetricus</i>	California roach	No	No	No		No
<i>Heterandria formosa</i>	least killifish	No	No	No		Yes
<i>Hiodon alosoides</i>	goldeye	No	No	No		No
<i>Hiodon tergisus</i>	mooneye	No	No	Yes		Yes
<i>Hoplosternum littorale</i>	brown hoplo	No				
<i>Hybognathus amarus</i>	Rio Grande silvery minnow	Yes	Yes	No		Yes
<i>Hybognathus argyritis</i>	western silvery minnow	Yes	No	Yes		No
<i>Hybognathus hankinsoni</i>	brassy minnow	No	No	No		No
<i>Hybognathus hayi</i>	cypress minnow	No	No	Yes		Yes
<i>Hybognathus nuchalis</i>	Mississippi silvery minnow	No	No	Yes		No
<i>Hybognathus placitus*</i>	plains minnow	Yes	No	No		No
<i>Hybognathus regius</i>	eastern silvery minnow	No	No	No		No
<i>Hybopsis amblops</i>	bigeye chub	No	No	Yes		No
<i>Hybopsis amnis</i>	pallid shiner	Yes	No	Yes		Yes
<i>Hybopsis hypsinotus</i>	highback chub	No	Yes	Yes		
<i>Hybopsis lineapunctata</i>	lined chub	Yes	Yes	No		
<i>Hybopsis rubrifrons</i>	rosyface chub	No	Yes	Yes		
<i>Hybopsis winchelli</i>	clear chub	No	No	No		
<i>Hypentelium etowanum</i>	Alabama hog sucker	No	Yes	Yes		No
<i>Hypentelium nigricans</i>	northern hog sucker	No	No	No		No

<i>Hypentelium roanokense</i>	Roanoke Hogsucker	No	Yes	No	Yes
<i>Hypomesus nipponensis</i>	wakasagi	No			
<i>Hypomesus transpacificus</i>	delta smelt	Yes	Yes		
<i>Hypophthalmichthys molitrix</i>	silver carp	No		Yes	
<i>Hypophthalmichthys nobilis</i>	bighead carp	No		Yes	
<i>Hypostomus plecostomus</i>	suckermouth catfish	No		No	
<i>Hypsoblennius ionthas</i>	freckled blenny	No			
<i>Hysterocarpus traskii</i>	tule perch	No	Yes	No	No
<i>Ichthyomyzon bdellium</i>	Ohio lamprey	No	No	No	Yes
<i>Ichthyomyzon castaneus</i>	chestnut lamprey	No	No	Yes	Yes
<i>Ichthyomyzon fossor</i>	northern brook lamprey	No	No	No	Yes
<i>Ichthyomyzon gagei</i>	southern brook lamprey	No	No	No	Yes
<i>Ichthyomyzon greeleyi</i>	mountain brook lamprey	No	No	No	Yes
<i>Ichthyomyzon unicuspis</i>	silver lamprey	No	No	No	Yes
<i>Ictaluridae .</i>	broadtail madtom	Yes	Yes	No	
<i>Ictalurus furcatus</i>	blue catfish	No	No	Yes	No
<i>Ictalurus lupus</i>	headwater catfish	No	Yes	No	
<i>Ictalurus pricei</i>	Yaqui catfish	Yes	Yes	No	
<i>Ictalurus punctatus</i>	channel catfish	No	No	No	No
<i>Ictiobus bubalus</i>	smallmouth buffalo	No	No	Yes	No
<i>Ictiobus cyprinellus</i>	bigmouth buffalo	No	No	No	No
<i>Ictiobus niger</i>	black buffalo	No	No	Yes	No
<i>Iotichthys phlegethontis</i>	least chub	Yes	Yes	No	
<i>Jordanella floridae</i>	flagfish	No	Yes	No	No
<i>Labidesthes sicculus</i>	brook silverside	No	No	No	No
<i>Lampetra aepyptera</i>	least brook lamprey	No	No	No	No
<i>Lampetra appendix</i>	American brook Lamprey	No	No	No	No
<i>Lampetra ayresii</i>	river lamprey	Yes	No	No	
<i>Lampetra hubbsi</i>	Kern brook lamprey	Yes	Yes	No	Yes
<i>Lampetra lethophaga</i>	Pit-Klamath brook Lamprey	Yes	Yes		
<i>Lampetra macrostoma</i>	Vancouver lamprey	Yes	Yes	Yes	
<i>Lampetra minima</i>	Miller Lake lamprey	Yes	Yes	No	
<i>Lampetra richardsoni</i>	western brook lamprey	No	No	No	Yes
<i>Lampetra tridentata</i>	Pacific lamprey	Yes	No	No	Yes
<i>Lavinia exilicauda</i>	hitch	No	Yes	No	No
<i>Lepidomeda albivallis</i>	White River spinedace	Yes	Yes	No	
<i>Lepidomeda altivelis</i>	Pahrnagat spinedace	Yes	Yes	Yes	
<i>Lepidomeda mollispinis</i>	Virgin spinedace	No	Yes	No	
<i>Lepidomeda vittata</i>	Little Colorado spinedace	Yes	Yes	Yes	
<i>Lepisosteus oculatus</i>	spotted gar	No	No	Yes	No

<i>Lepisosteus osseus</i>	longnose gar	No	No	No	No
<i>Lepisosteus platostomus</i>	shortnose gar	No	No	Yes	No
<i>Lepisosteus platyrhincus</i>	Florida gar	No	No		No
<i>Lepomis auritus</i>	redbreast sunfish	No	No	No	No
<i>Lepomis cyanellus</i>	green sunfish	No	No	No	No
<i>Lepomis gibbosus</i>	pumpkinseed	No	No	No	No
<i>Lepomis gulosus</i>	warmouth	No	No	No	No
<i>Lepomis humilis</i>	orangespotted sunfish	No	No	No	No
<i>Lepomis macrochirus</i>	bluegill	No	No	No	No
<i>Lepomis marginatus</i>	dollar sunfish	No	No	No	No
<i>Lepomis megalotis</i>	longear sunfish	No	No	No	No
<i>Lepomis microlophus</i>	redear sunfish	No	No	No	No
<i>Lepomis miniatus</i>	redspotted sunfish	No	No	Yes	No
<i>Lepomis punctatus</i>	spotted sunfish	No	No	No	No
<i>Lepomis symmetricus</i>	bantam sunfish	No	No	Yes	Yes
<i>Leptolucania ommata</i>	pygmy killifish	No	No	Yes	
<i>Leuciscus idus</i>	ide	No		Yes	
<i>Lota lota</i>	burbot	No	No	No	No
<i>Lucania goodei</i>	bluefin killifish	No	No	No	No
<i>Lucania parva</i>	rainwater killifish	No	No	No	
<i>Luxilus albeolus</i>	white shiner	No	Yes	Yes	No
<i>Luxilus cardinalis</i>	cardinal shiner	No	Yes	No	No
<i>Luxilus cerasinus</i>	crescent shiner	No	Yes	No	No
<i>Luxilus chrysocephalus</i>	striped shiner	No	No	No	No
<i>Luxilus coccogenis</i>	warpaint shiner	No	Yes	No	No
<i>Luxilus cornutus</i>	common shiner	No	No	No	No
<i>Luxilus pilsbryi</i>	duskystripe shiner	No	Yes	No	No
<i>Luxilus zonatus</i>	bleeding shiner	No	Yes	No	No
<i>Luxilus zonistius</i>	bandfin shiner	No	Yes	No	No
<i>Lythrurus ardens</i>	rosefin shiner	No	No	No	Yes
<i>Lythrurus atrapiculus*</i>	blacktip shiner	No	Yes	Yes	Yes
<i>Lythrurus bellus</i>	pretty shiner	No	Yes	Yes	No
<i>Lythrurus fasciolaris</i>	scarlet shiner	No	No	Yes	No
<i>Lythrurus fumeus</i>	ribbon shiner	No	No	Yes	No
<i>Lythrurus lirus</i>	mountain shiner	No	Yes	No	No
<i>Lythrurus matutinus</i>	pinewoods shiner	No	Yes	Yes	
<i>Lythrurus roseipinnis</i>	cherryfin shiner	No	Yes	Yes	
<i>Lythrurus snelsoni</i>	Ouachita shiner	Yes	Yes	No	
<i>Lythrurus umbratilis</i>	redfin shiner	No	No	No	No
<i>Macrhybopsis aestivalis</i>	speckled chub	No	No	No	Yes
<i>Macrhybopsis gelida</i>	sturgeon chub	Yes	No	No	Yes
<i>Macrhybopsis meeki</i>	sicklefin chub	Yes	No	Yes	

<i>Macrhybopsis storeriana</i>	silver chub	No	No	Yes	No
<i>Margariscus margarita</i>	pearl dace	No	No	No	No
<i>Meda fulgida</i>	spikedace	Yes	Yes	No	
<i>Menidia beryllina</i>	inland silverside	No	No	No	No
<i>Menidia conchorum</i>	key silverside	Yes	Yes		
<i>Menidia extensa</i>	Waccamaw silverside	Yes	Yes		
<i>Microphis brachyurus</i>	opossum pipefish	No		No	
<i>Micropterus cataractae</i>	shoal bass	Yes	Yes	No	
<i>Micropterus coosae</i>	redeye bass	No	Yes	No	No
<i>Micropterus dolomieu</i>	smallmouth bass	No	No	No	No
<i>Micropterus notius</i>	Suwannee bass	No	Yes	No	
<i>Micropterus punctulatus</i>	spotted bass	No	No	No	Yes
<i>Micropterus salmoides</i>	largemouth bass	No	No	No	No
<i>Micropterus treculii</i>	Guadalupe bass	Yes	Yes	No	No
<i>Minytrema melanops</i>	spotted sucker	No	No	No	No
<i>Misgurnus anguillicaudatus</i>	oriental weatherfish	No			
<i>Moapa coriacea</i>	Moapa dace	Yes	Yes	Yes	
<i>Monopterus albus</i>	Asian swamp eel	No		No	
<i>Morone americana</i>	white perch	No	No	No	No
<i>Morone chrysops</i>	white bass	No	No	Yes	No
<i>Morone mississippiensis</i>	yellow bass	No	No	Yes	No
<i>Morone saxatilis</i>	striped bass	No	No	No	No
<i>Moxosoma sp.</i>	grayfin redhorse	No	Yes	Yes	
<i>Moxostoma anisurum</i>	silver redhorse	No	No	No	No
<i>Moxostoma ariommum</i>	bigeye jumprock	No	Yes	Yes	
<i>Moxostoma austrinum</i>	Mexican redhorse	Yes	Yes	Yes	
<i>Moxostoma carinatum</i>	river redhorse	No	No	Yes	No
<i>Moxostoma cervinum</i>	blacktip jumprock	No	Yes	No	Yes
<i>Moxostoma congestum</i>	gray redhorse	Yes	No	No	
<i>Moxostoma duquesnei</i>	black redhorse	No	No	No	No
<i>Moxostoma erythrurum</i>	golden redhorse	No	No	No	No
<i>Moxostoma hubbsi</i>	copper redhorse	Yes	Yes		
<i>Moxostoma lacerum</i>	harelip sucker	Yes	Yes	Yes	
<i>Moxostoma lachneri</i>	greater jumprock	No	Yes	Yes	
<i>Moxostoma macrolepidotum</i>	shorthead redhorse	No	No	No	No
<i>Moxostoma occidentalis</i>	Sacramento sucker	No	Yes	No	
<i>Moxostoma pappillosum*</i>	V-lip redhorse	No	Yes	Yes	Yes
<i>Moxostoma poecilurum</i>	blacktail redhorse	No	No	No	No
<i>Moxostoma robustum</i>	robust redhorse	No	Yes	No	
<i>Moxostoma rupiscartes</i>	striped jumprock	No	Yes	Yes	

<i>Moxostoma valenciennesi</i>	greater redhorse	Yes	No	Yes	No
<i>Myleus rubripinnis</i>	redhook myleus	No			
<i>Mylocheilus caurinus</i>	peamouth	No	No		Yes
<i>Mylopharodon conocephalus</i>	hardhead	No	Yes	No	No
<i>Myoxocephalus thompsonii</i>	deepwater sculpin	No	No		
<i>Neogobius melanostomus</i>	round goby	No			
<i>Nocomis asper</i>	redspot chub	No	Yes	No	No
<i>Nocomis biguttatus</i>	hornyhead chub	No	No	No	No
<i>Nocomis effusus</i>	redtail chub	No	Yes	No	Yes
<i>Nocomis leptocephalus</i>	bluehead chub	No	No	No	No
<i>Nocomis micropogon</i>	river chub	No	No	No	No
<i>Nocomis platyrhynchus</i>	bigmouth chub	No	Yes	No	No
<i>Nocomis raneyi</i>	bull chub	No	Yes	No	No
<i>Notemigonus crysoleucas</i>	golden shiner	No	No	No	No
<i>Notropis albizonatus</i>	palezone shiner	Yes	Yes	Yes	
<i>Notropis alborus</i>	whitemouth shiner	No	Yes	Yes	No
<i>Notropis altipinnis</i>	highfin shiner	No	Yes	No	No
<i>Notropis amabilis</i>	Texas shiner	No	Yes	No	
<i>Notropis ammophilus</i>	orangefin shiner	No	Yes	No	Yes
<i>Notropis amoenus</i>	comely shiner	No	No	Yes	No
<i>Notropis anogenus</i>	pugnose shiner	Yes	No	No	
<i>Notropis ariommus</i>	popeye shiner	Yes	No	Yes	
<i>Notropis asperifrons*</i>	burrhead shiner	No	Yes	Yes	Yes
<i>Notropis atherinoides</i>	emerald shiner	No	No	No	No
<i>Notropis atrocaudalis</i>	blackspot shiner	No	Yes	No	
<i>Notropis baileyi</i>	rough shiner	No	Yes	No	No
<i>Notropis bairdi</i>	Red River shiner	No	Yes	Yes	
<i>Notropis bifrenatus</i>	bridle shiner	Yes	No	No	Yes
<i>Notropis blennioides</i>	river shiner	No	No	No	No
<i>Notropis boops</i>	bigeye shiner	No	No	No	No
<i>Notropis braytoni</i>	Tamaulipas shiner	Yes	No	No	
<i>Notropis buccatus</i>	silverjaw minnow	No	No	No	Yes
<i>Notropis buccula</i>	smalleye shiner	Yes	Yes	No	
<i>Notropis buechanani</i>	ghost shiner	No	No	Yes	No
<i>Notropis cahabae</i>	Cahaba shiner	Yes	Yes	Yes	
<i>Notropis candidus</i>	silverside shiner	No	Yes	Yes	No
<i>Notropis chalybaeus</i>	ironcolor shiner	Yes	No		No
<i>Notropis chihuahua</i>	Chihuahua shiner	Yes		Yes	
<i>Notropis chiliticus</i>	redlip shiner	No	Yes	Yes	
<i>Notropis chlorocephalus</i>	greenhead shiner	No	Yes	Yes	

<i>Notropis chrosomus</i>	rainbow shiner	No	Yes	No	No
<i>Notropis cummingsae</i>	dusky shiner	No	No	No	No
<i>Notropis dorsalis</i>	bigmouth shiner	No	No	No	No
<i>Notropis edwardraneyi</i>	fluvial shiner	No	Yes	Yes	No
<i>Notropis girardi</i>	Arkansas River shiner	Yes	No	Yes	
<i>Notropis greenei*</i>	wedgespot shiner	No	Yes	Yes	Yes
<i>Notropis harperi</i>	redeye chub	No	Yes	No	No
<i>Notropis heterodon</i>	blackchin shiner	No	No	No	No
<i>Notropis heterolepis</i>	blacknose shiner	No	No	No	No
<i>Notropis hudsonius</i>	spottail shiner	No	No	No	No
<i>Notropis hypsilepis</i>	highscale shiner	Yes	Yes	No	No
<i>Notropis jemezianus</i>	Rio Grande shiner	Yes	No	No	
<i>Notropis leuciodus</i>	Tennessee shiner	No	Yes	No	No
<i>Notropis longirostris</i>	longnose shiner	No	No	No	No
<i>Notropis lutipinnis</i>	yellowfin shiner	No	Yes	No	No
<i>Notropis maculatus</i>	taillight shiner	No	No	No	Yes
<i>Notropis mekistocholas</i>	Cape Fear shiner	Yes	Yes	Yes	
<i>Notropis melanostomus</i>	blackmouth shiner	Yes	Yes	No	
<i>Notropis nubilus</i>	Ozark minnow	No	No	Yes	No
<i>Notropis orca</i>	phantom shiner	Yes	No	Yes	
<i>Notropis ortenburgeri</i>	Kiamichi shiner	Yes	Yes	Yes	
<i>Notropis oxyrhynchus</i>	sharpnose shiner	Yes	Yes	Yes	
<i>Notropis ozarcanus</i>	Ozark shiner	Yes	Yes	No	Yes
<i>Notropis perpallidus</i>	peppered shiner	Yes	Yes	No	
<i>Notropis petersoni</i>	coastal shiner	No	No	No	No
<i>Notropis photogenis</i>	silver shiner	No	No	No	No
<i>Notropis potteri</i>	chub shiner	No	No	Yes	
<i>Notropis procne</i>	swallowtail shiner	No	No	No	No
<i>Notropis rubellus</i>	rosyface shiner	No	No	No	No
<i>Notropis rubricroceus</i>	saffron shiner	No	Yes	No	No
<i>Notropis rupestris</i>	bedrock shiner	Yes	Yes	Yes	
<i>Notropis sabinae</i>	Sabine shiner	No	Yes	Yes	No
<i>Notropis scabriceps</i>	New River shiner	No	Yes	No	Yes
<i>Notropis szepticus</i>	sandbar shiner	No	Yes	No	Yes
<i>Notropis semperasper</i>	Roughhead shiner	Yes	Yes	No	
<i>Notropis shumardi</i>	silverband shiner	No	No	Yes	
<i>Notropis simus</i>	bluntnose shiner	No	Yes	No	
<i>Notropis spectrunculus</i>	mirror shiner	No	Yes	Yes	
<i>Notropis stilbius</i>	silverstripe shiner	No	Yes	No	Yes
<i>Notropis stramineus</i>	sand shiner	No	No	No	No
<i>Notropis telescopus</i>	telescope shiner	No	No	No	No
<i>Notropis texanus</i>	weed shiner	No	No	No	No

<i>Notropis topeka</i>	Topeka shiner	Yes	No	Yes	
<i>Notropis uranoscopus*</i>	skygazer shiner	No	Yes	Yes	Yes
<i>Notropis volucellus</i>	mimic shiner	No	No	No	No
<i>Notropis xaenocephalus</i>	Coosa shiner	No	Yes	Yes	No
<i>Noturus albater*</i>	Ozark madtom	No	Yes	Yes	Yes
<i>Noturus baileyi</i>	smoky madtom	Yes	Yes	Yes	
<i>Noturus elegans*</i>	elegant madtom	No	Yes	Yes	Yes
<i>Noturus eleutherus</i>	mountain madtom	No	No	Yes	Yes
<i>Noturus exilis</i>	slender madtom	No	No	Yes	No
<i>Noturus flavater</i>	checkered madtom	Yes	Yes		
<i>Noturus flavipinnis</i>	yellowfin madtom	Yes	Yes	Yes	
<i>Noturus flavus</i>	stonecat	No	No	No	Yes
<i>Noturus funebris</i>	black madtom	No	Yes	No	Yes
<i>Noturus furiosus</i>	Carolina madtom	Yes	Yes	No	Yes
<i>Noturus gilberti</i>	orangefin madtom	Yes	Yes	Yes	Yes
<i>Noturus gyrinus</i>	tadpole madtom	No	No	No	No
<i>Noturus hildebrandi</i>	least madtom	No	Yes		
<i>Noturus insignis</i>	margined madtom	No	No	No	No
<i>Noturus lachneri</i>	Ouachita madtom	Yes	Yes	Yes	
<i>Noturus leptacanthus</i>	speckled madtom	No	No	No	No
<i>Noturus miurus</i>	brindled madtom	No	No	No	Yes
<i>Noturus munitus</i>	frecklebelly madtom	No	Yes	No	
<i>Noturus nocturnus</i>	freckled madtom	No	No	No	No
<i>Noturus phaeus</i>	brown madtom	No	Yes		
<i>Noturus placidus</i>	Neosho madtom	Yes	Yes	Yes	
<i>Noturus stanauli</i>	pygmy madtom	Yes	Yes	No	
<i>Noturus stigmosus</i>	northern madtom	Yes	No	No	
<i>Noturus taylori</i>	Caddo madtom	Yes	Yes	Yes	
<i>Noturus trautmani</i>	Scioto madtom	Yes	Yes	Yes	
<i>Novumbra hubbsi</i>	Olympic mudminnow	Yes	Yes	No	
<i>Oncorhynchus clarkii</i>	cutthroat trout	No	No	No	No
<i>Oncorhynchus gilae</i>	Gila trout	No	Yes	Yes	
<i>Oncorhynchus gorbuscha</i>	pink salmon	No	No	No	
<i>Oncorhynchus keta</i>	chum salmon	No	No	No	
<i>Oncorhynchus kisutch</i>	coho salmon	No	No	No	No
<i>Oncorhynchus mykiss</i>	rainbow trout	No	No	No	No
<i>Oncorhynchus nerka</i>	sockeye salmon	No	No	No	No
<i>Oncorhynchus tshawytscha</i>	Chinook salmon	No	No	No	No
<i>Opsopoeodus emiliae</i>	pugnose minnow	No	No	No	Yes
<i>Oregonichthys crameri</i>	Oregon chub	Yes	Yes	No	
<i>Oreochromis aureus</i>	blue tilapia	No		No	

<i>Oreochromis mossambicus</i>	Mozambique tilapia	No			
<i>Oreochromis niloticus</i>	Nile tilapia	No			
<i>Oreochromis urolepis</i>	Wami tilapia	No			
<i>Orthodon microlepidotus</i>	Sacramento blackfish	No	Yes	No	No
<i>Oryzias latipes</i>	Japanese rice fish	No		Yes	
<i>Osmerus mordax</i>	rainbow smelt	No	No	No	
<i>Osteoglossum bicirrhosum</i>	arawana	No		Yes	
<i>Perca flavescens</i>	yellow perch	No	No	No	No
<i>Percina antesella</i>	amber darter	Yes	Yes	No	
<i>Percina aurantiaca</i>	tangerine darter	No	Yes	No	Yes
<i>Percina aurolineata</i>	goldline darter	Yes	Yes	Yes	
<i>Percina aurora</i>	pearl darter	Yes	Yes	Yes	
<i>Percina breviceauda</i>	coal darter	Yes	Yes	Yes	
<i>Percina burtoni</i>	blotchside darter	Yes	Yes	Yes	Yes
<i>Percina caprodes</i>	logperch	No	No	No	No
<i>Percina carbonaria*</i>	Texas logperch	No	Yes	Yes	Yes
<i>Percina copelandi</i>	channel darter	No	No	No	
<i>Percina crassa*</i>	piedmont darter	No	Yes	Yes	Yes
<i>Percina cymatotaenia</i>	bluestripe darter	Yes	Yes	Yes	
<i>Percina evides</i>	gilt darter	No	No	Yes	No
<i>Percina gymnocephala</i>	Appalachia darter	No	Yes	Yes	
<i>Percina jenkinsi</i>	Conasauga logperch	Yes	Yes		Yes
<i>Percina kathae</i>	Mobile logperch	No	Yes	No	No
<i>Percina lenticula</i>	freckled darter	Yes	Yes	Yes	
<i>Percina macrocephala</i>	longhead darter	Yes	No	No	Yes
<i>Percina macrolepida</i>	bigscale logperch	No	No	No	No
<i>Percina maculata</i>	blackside darter	No	No	No	No
<i>Percina nasuta</i>	longnose darter	No	Yes	No	
<i>Percina nigrofasciata</i>	blackbanded darter	No	No	No	No
<i>Percina notogramma</i>	stripeback darter	No	Yes	Yes	
<i>Percina oxyrhynchus</i>	sharpnose darter	No	Yes	No	No
<i>Percina palmaris</i>	bronze darter	No	Yes	Yes	
<i>Percina pantherina</i>	leopard darter	Yes	Yes	No	
<i>Percina peltata</i>	shield darter	No	No	No	Yes
<i>Percina phoxocephala</i>	slenderhead darter	No	No	Yes	No
<i>Percina rex</i>	Roanoke logperch	Yes	Yes	Yes	Yes
<i>Percina roanoka</i>	Roanoke darter	No	Yes	No	No
<i>Percina sciera</i>	dusky darter	No	No	Yes	Yes
<i>Percina shumardi</i>	river darter	No	No	Yes	Yes
<i>Percina smithvanizi</i>	Muscadine darter	No	Yes	Yes	
<i>Percina sp.</i>	Warrior brindled darter	No			
<i>Percina squamata</i>	olive darter	Yes	Yes	Yes	Yes

<i>Percina stictogaster</i>	frecklebelly darter	No	Yes	Yes	
<i>Percina tanasi</i>	snail darter	Yes	Yes	Yes	
<i>Percina uranidea</i>	stargazing darter	Yes	Yes	Yes	
<i>Percina vigil</i>	saddleback darter	No	No	Yes	
<i>Percopsis omiscomaycus</i>	trout-perch	No	No	No	No
<i>Percopsis transmontana</i> *	sand roller	No	Yes	Yes	Yes
<i>Petromyzon marinus</i>	sea lamprey	No	No	No	Yes
<i>Phenacobius catostomus</i>	rifle minnow	No	Yes	No	Yes
<i>Phenacobius crassilabrum</i> *	fatlips minnow	No	Yes	Yes	Yes
<i>Phenacobius mirabilis</i>	suckermouth minnow	No	No	No	Yes
<i>Phenacobius teretulus</i> *	Kanawha minnow	No	Yes	Yes	Yes
<i>Phenacobius uranops</i> *	stargazing minnow	No	Yes	Yes	Yes
<i>Phoxinus cumberlandensis</i>	blackside dace	Yes	Yes	Yes	
<i>Phoxinus eos</i>	northern redbelly dace	No	No	No	Yes
<i>Phoxinus erythrogaster</i>	southern redbelly dace	No	No	Yes	No
<i>Phoxinus neogaeus</i>	finescale dace	No	No	No	
<i>Phoxinus oreas</i>	mountain redbelly dace	No	Yes	No	No
<i>Phoxinus tennesseensis</i>	Tennessee dace	Yes	Yes	Yes	Yes
<i>Piaractus brachypomus</i>	pirapitinga	No			
<i>Pimephales notatus</i>	bluntnose minnow	No	No	No	No
<i>Pimephales promelas</i>	fathead minnow	No	No	No	No
<i>Pimephales tenellus</i>	slim minnow	No	No		
<i>Pimephales vigilax</i>	bullhead minnow	No	No	No	No
<i>Plagopterus argentissimus</i>	woundfin	Yes	Yes	No	
<i>Platygobio gracilis</i>	flathead chub	No	No	No	No
<i>Poecilia formosa</i>	Amazon molly	No	Yes	Yes	No
<i>Poecilia latipinna</i>	sailfin molly	No	No	No	
<i>Poecilia mexicana</i>	shortfin molly	No			
<i>Poecilia reticulata</i>	guppy	No			
<i>Poeciliopsis gracilis</i>	porthole livebearer	No		No	
<i>Poeciliopsis occidentalis</i>	Gila topminnow	No	No	No	Yes
<i>Pogonichthys ciscoides</i>	Clear Lake splittail	Yes	Yes		
<i>Pogonichthys macrolepidotus</i>	splittail	Yes	Yes	Yes	Yes
<i>Polyodon spathula</i>	paddlefish	Yes	No	Yes	Yes
<i>Pomoxis annularis</i>	white crappie	No	No	No	No
<i>Pomoxis nigromaculatus</i>	black crappie	No	No	No	Yes
<i>Prosopium abyssicola</i>	Bear Lake whitefish	Yes	Yes		
<i>Prosopium coulterii</i>	pygmy whitefish	No	No	Yes	
<i>Prosopium cylindraceum</i>	round whitefish	No	No	No	
<i>Prosopium gemmifer</i>	Bonneville cisco	Yes	Yes		

<i>Prosopium williamsoni</i>	mountain whitefish	No	No	No	No
<i>Pterois volitans/miles</i>	red lionfish	No			
<i>Pteronotropis euryzonus</i>	broadstripe shiner	Yes	Yes	Yes	
<i>Pteronotropis hubbsi</i>	bluehead shiner	Yes	Yes	Yes	Yes
<i>Pteronotropis hypselopterus</i>	sailfin shiner	No	No	Yes	No
<i>Pteronotropis signipinnis</i>	flagfin shiner	No	Yes	No	Yes
<i>Pteronotropis welaka</i>	bluenose shiner	Yes	No	Yes	
<i>Pterygoplichthys anisitsi</i>	southern sailfin catfish	No			
<i>Pterygoplichthys disjunctivus</i>	vermiculated sailfin catfish	No			
<i>Pterygoplichthys multiradiatus</i>	Orinoco sailfin catfish	No			
<i>Pterygoplichthys pardalis</i>	Amazon sailfin catfish	No			
<i>Ptychocheilus grandis</i>	Sacramento pikeminnow	No	Yes	No	No
<i>Ptychocheilus lucius</i>	Colorado pikeminnow	Yes	No	Yes	Yes
<i>Ptychocheilus oregonensis</i>	northern pikeminnow	No	No	No	No
<i>Ptychocheilus umpqua</i>	Umpqua pikeminnow	No	Yes	Yes	
<i>Pungitius pungitius</i>	ninespine stickleback	No	No	Yes	
<i>Pygocentrus nattereri</i>	red piranha	No		Yes	
<i>Pyloodictis olivaris</i>	flathead catfish	No	No	No	Yes
<i>Relictus solitarius</i>	relict dace	Yes	Yes	No	
<i>Rhinichthys atratulus</i>	eastern blacknose dace	No	No	No	No
<i>Rhinichthys cataractae</i>	longnose dace	No	No	No	No
<i>Rhinichthys cobitis</i>	loach minnow	Yes	Yes	No	
<i>Rhinichthys deaconi</i>	Las Vegas dace	Yes	Yes		
<i>Rhinichthys evermanni</i>	Umpqua dace	Yes	Yes	Yes	
<i>Rhinichthys falcatus</i>	leopard dace	No	No	No	
<i>Rhinichthys osculus</i>	speckled dace	No	No	No	No
<i>Rhinichthys umatilla</i>	Umatilla dace	Yes	No	Yes	
<i>Rhodeus sericeus</i>	bitterling	No		Yes	
<i>Richardsonius balteatus</i>	redside shiner	No	No	No	No
<i>Richardsonius egregius</i>	Lahontan redside	No	Yes	No	No
<i>Rivulus marmoratus</i>	mangrove rivulus	No	Yes	No	
<i>Salmo salar</i>	Atlantic salmon	No	No	No	No
<i>Salmo trutta</i>	brown trout	No		No	
<i>Salvelinus alpinus</i>	Arctic charr	No	No	No	
<i>Salvelinus aureolus</i>	Sunapee trout	No			
<i>Salvelinus confluentus</i>	bull trout	No	No	No	Yes
<i>Salvelinus fontinalis</i>	brook trout	No	No	No	No
<i>Salvelinus malma</i>	Dolly Varden	No	No		
<i>Salvelinus namaycush</i>	lake trout	No	No	Yes	

<i>Sander canadensis</i>	sauger	No	No	No	No
<i>Sander lucioperca</i>	zander	No			
<i>Sander vitreus</i>	walleye	No	No	No	No
<i>Sarotherodon melanotheron</i>	blackchin tilapia	No		Yes	
<i>Satan eurystomus</i>	widemouth blindcat	Yes	Yes		
<i>Scaphirhynchus albus</i>	pallid sturgeon	Yes	No		Yes
<i>Scaphirhynchus platorynchus</i>	shovelnose sturgeon	No	No	Yes	
<i>Scaphirhynchus suttkusi</i>	Alabama sturgeon	Yes	Yes	Yes	
<i>Scardinius erythrophthalmus</i>	rudd	No		No	
<i>Scartomyzon cervinus</i>	black jumprock	No	No	Yes	Yes
<i>Semotilus atromaculatus</i>	creek chub	No	No	No	No
<i>Semotilus corporalis</i>	fallfish	No	No	No	No
<i>Semotilus lumbee</i>	sandhills chub	Yes	Yes	Yes	
<i>Semotilus thoreauianus</i>	Dixie chub	No	Yes	No	
<i>Serrasalmus rhombeus</i>	redeye piranha	No			
<i>Snyderichthys copei</i>	leatherside chub	No	Yes	Yes	
<i>Speoplatyrhinus poulsoni</i>	Alabama cavefish	Yes	Yes		
<i>Spirinchus thaleichthys</i>	longfin smelt	No	No	Yes	
<i>Strongylura marina</i>	Atlantic Needlefish	No	No	Yes	Yes
<i>Telmatochromis bifrenatus</i>	dward cichlid	No			
<i>Thaleichthys pacificus</i>	eulachon	No	No	Yes	
<i>Thoburnia atripinnis</i>	blackfin sucker	Yes	Yes	Yes	
<i>Thoburnia hamiltoni</i>	rustyside sucker	Yes	Yes	Yes	
<i>Thoburnia rhothoeca</i>	torrent sucker	No	Yes	Yes	No
<i>Thymallus arcticus</i>	Artic grayling	No	No	No	
<i>Tilapia buttikoferi</i>	zebra tilapia	No			
<i>Tilapia mariae</i>	spotted tilapia	No			
<i>Tilapia zillii</i>	redbelly tilapia	No	No		Yes
<i>Tinca tinca</i>	tench	No		Yes	
<i>Trichopsis vittata</i>	croaking gourami	No			
<i>Trogloglanis pattersoni</i>	toothless blindcat	Yes	Yes		
<i>Typhlichthys subterraneus</i>	southern cavefish	Yes	No		
<i>Umbra limi</i>	central mudminnow	No	No	No	No
<i>Umbra pygmaea</i>	eastern mudminnow	No	No	No	No
<i>Xiphophorus hellerii</i>	green swordtail	No			
<i>Xiphophorus maculatus</i>	southern platyfish	No			
<i>Xiphophorus variatus</i>	variable platyfish	No			
<i>Xyrauchen texanus</i>	razorback sucker	Yes	No	No	

*Species that are rare at all levels of the classification but are not listed by Jelks et al. (2008)

