Detection probabilities and local population demographics of fishes in urbanized and forested streams of the New River basin, Virginia

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ABSTRACT

Aquatic biodiversity continues to decline as humans modify the landscape. A

population-level approach is necessary to address the mechanisms of impairment in urban stream

habitats. When estimating population-level parameters, incomplete detection of individuals must

be accounted for to ensure unbiased estimates. In this thesis, I examined differences in the

detection probabilities of stream fishes, and used estimates of size/age-specific detection

probabilities to reduce bias in estimates of the reproductive success of various fish species in

urban and forested stream habitats. In Chapter 1, I examined differences in detection

probabilities of stream fishes among electrofishing passes and size/age groups in the middle New

River basin, Virginia. I also examined differences in detection probabilities between two

physiographic regions: the middle New River basin, and the upper Wabash River basin, Indiana;

and evaluated differences between single- and multiple-season estimation methods. I found that

for most species, detection probabilities do not differ among electrofishing passes, size/age

classes, between the two regions, or between single- and multiple-season estimation methods. I

used size/age-specific estimates of detection probabilities to remove bias from relative

abundance estimates of steam fish populations in Chapter 2. In Chapter 2, I examined the

reproductive success of six lithophilic and speleophilic fishes in urban and forested reaches of

2nd-4th Strahler-order streams in the middle New River basin. I found that binary classification is

a poor method of quantifying reproductive success, that the age distributions of many lithophilic

and speleophilic species are dominated by adult individuals in urban habitats, and that the population growth rates of speleophils is reduced in urban habitats. These results suggest that although detection probabilities may be equal among various sources of variation, managers should verify this assumption before assuming equal detectability. The results also suggest that reduced reproductive success of speleophilic and lithophilic species in urban stream habitats may be a mechanism of their impairment.

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Attribution

Emmanuel Frimpong co-authored Chapter 1. This paper is currently in review for

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Emmanuel's contributions to the paper include assistance in developing the testing framework,

evaluation of the statistical analysis, and editing the manuscript for publication.

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General introduction

The characteristics of streams are strongly influenced by the land cover of their valleys (Hynes 1975). Land cover influences many of the processes that affect stream habitat, water quality, and stream fish communities (Johnson and Gage 1997; Allan 2004). These processes operate at multiple scales, with varied effects (Allan 2004; Lowe et al. 2006). Anthropogenic land cover disturbances affect the physical, chemical, and biological processes that influence the characteristics of streams. Alterations of these processes affect stream habitat (Leopold et al. 2005), food webs (Malmqvist and Rundle 2002; Singer and Battin 2007), and biotic communities (Taylor and Roff 1986; Weaver and Garman 1994).

Urbanization is a large-scale perturbation that affects stream ecosystems (Paul and Meyer 2001; Scott 2006). The term "urbanization" is often used to describe increasingly populated areas and associated loss of agriculture or forest to development (Lussier et al. 2008). Road building, which often occurs in the initial stages of urbanization, has similar effects and is often categorized with urbanization (Angermeier et al. 2004; Wheeler et al. 2005). In terms of long term, large-scale disturbances, urbanization is often considered one of the most detrimental land use types for stream ecosystems (Leopold 1968; Malmqvist and Rundle 2002; DeFries and Eshleman 2004; Fleming 2007).

Urbanization affects instream habitat in many ways. At the watershed scale, increased impervious surface coverage (ISC) alters natural hydrologic cycles, which contributes to the frequency and magnitude of flood events, as well as unnaturally low flows during periods of low precipitation (Leopold et al. 2005; Fleming 2007). Flash flood events associated with urban hydrology contribute to channel incision, which exposes bare stream banks and mobilizes fine sediments that eventually settle and cover coarse substrates (Wolman 1967; Davies et al. 2005).

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These events also wash away medium-sized substrate particles (mainly gravels) (Pizzuto et al. 2000) and contribute to channel widening, filling, and straightening (Booth 1990; Trimble 1997). When combined, these processes usually result in the overall homogenization of instream habitat (Wang et al. 2001). Additionally, surface runoff from urban areas during storm events can carry harmful chemical pollutants and sediments exposed by development (Chester et al. 1996; Wang et al. 2001). Watershed-scale percentages of impervious surface coverage are often used as a measure of urbanization (Chester et al. 1996), and ISC of 10-20% have been identified as hydrologic (Booth and Jackson 1997) and biological (Klein 1979; Yoder et al. 1999) thresholds of degradation (Paul and Meyer 2001).

In urban areas, riparian vegetation is often reduced or completely removed (Booth and Jackson 1997). This accentuates the watershed-scale effects of urbanization, and contributes to losses of hydrologic (Karr and Schlosser 1978) and thermal buffering (Galli 1991) capacity, channel incision (Wolman 1967; Davies et al. 2005), increased loads of chemical and sedimentary pollutants, (Karr and Schlosser 1978; Davies et al. 2005), and reduced allochthonous energy input (McNeeley 1987; McTammany et al. 2007). Many studies have shown the importance of riparian vegetation to the persistence of stream dwelling organisms (Bunn et al. 1999; Jones et al. 1999; Roy et al. 2005). It has also been suggested that biotic communities in streams with urbanizing watersheds that whose riparian corridors remain intact tend to be much less affected than those whose riparian corridors have been removed (Yoder et al. 1999).

The past few decades have seen the development and implementation of bioassessment protocols to evaluate the ecological condition of streams using fishes (Karr 1981; Karr et al. 1986; Joy and Death 2002; Carlisle et al. 2008). Such methods characterize ecological integrity

by comparing proportional abundance changes of fishes of various trophic or reproductive guilds along gradients of habitat degradation, or by comparing observed assemblages with those in reference sites. Bioassessment also gives managers substantial evidence to justify conservation strategies, as well as relevant findings to present at public hearings. As current trends push toward total ecosystem management, the need for effective biological monitoring has been placed on the forefront of many agencies' agendas (Angermeier and Karr 1986; Yoder and Smith 1999).

Although assemblage-level bioassessment protocols provide replicable results to assess the impairment of biological communities, their framework does not allow users to assess the mechanisms of biological impairment. Multimetric and observed/expected indices estimate biological impairment by producing a single numerical value to represent the "health" of the community. These approaches provide a coarse resolution for assessing impairment, at which much species-specific information cannot be obtained. Furthermore, some have argued that when metrics of fish assemblage response to habitat degradation are combined, information regarding the mechanisms of impairment may be lost and causality may not be inferred (Suter 1993; Hughes et al. 1998).

The structure of any biological community is a representation of the performance of its constituent populations. Likewise, the performance of any population is a culmination of the reproductive performance of its constituent individuals (Shipley et al. 2006; Power 2007). The performance of individuals is affected by habitat through biological and ecological traits evolved by the species, and is expressed as fitness (Merigoux et al. 2001; Shipley et al. 2006). Therefore, anthropogenic disturbances affect stream fish communities by altering the habitat and biotic characteristics fishes have evolved to exploit. An assessment of the reproductive performance of

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fish populations in stream habitats that experience various levels of anthropogenic degradation may provide insight into the mechanisms of their impairment and persistence in degraded habitats (Power 2007). Population parameters such as size/age structure, the population growth rate (λ), density, age-specific fecundity, and condition factors (i.e. relative weight, gonadosomatic indices, etc…), can be more informative measures of the mechanisms of biological impairment than community-level measures (Power 2007). These parameters are not included in community-level approaches to bioassessment because their estimation requires more effort, and because community-level approaches are designed to identify impairment, rather than assess the mechanisms of impairment. Despite the existing knowledge of the effects of urbanization of stream fishes (Suren 2000; Brown et al. 2005; Walsh et al. 2005), much of the mechanisms of their impairment and persistence in urban habitats remain unexplored, and mechanistic studies are vastly underrepresented in the literature (Suren 2000; Paul and Meyer 2001).

Bioassessment protocols require the estimation of assemblage structure, and many methods for assessing the reproductive performance require the examination of age structure. However, the inconspicuous nature of fishes, scarcity within their ranges, and the heterogeneity of their habitats seldom allow for all individuals in an assemblage to be surveyed (Zalewski and Cowx 1990; Dolloff et al. 1996). These phenomena cause unequal detection probabilities (p, the probability of encountering a species in a given sample, given its presence) among species and among length/age classes within species (MacKenzie et al. 2002; Dauwalter and Fisher 2007). Detection probabilities may differ among species due to differences in size, shape, behavior, or color (Mahon 1980; Bayley and Austen 2002), or similarly within species due to size (Bayley and Austen 2002; Dauwalter and Fisher 2007) or stage-specific habitat partitioning (Schlosser

and Angermeier 1995). Additionally, multiple-pass depletion electrofishing protocols that are designed to estimate assemblage composition yield decreasing species' catch with subsequent passes, and could influence pass-specific detection probabilities (Bayley and Peterson 2001; Wilson 2008). Accordingly, any empirical study of fish ecology should account for inter- and/or intraspecific differences in detection probability (Bayley and Peterson 2001; MacKenzie and Kendall 2002; Royle et al. 2007). Not accounting for unequal detection probabilities among species can result in the biased estimation of assemblage composition and demographic parameters, and can lead to poor management decisions (Slaski et al. 1983; Bayley and Dowling 1993; Thompson et al. 1998; Bayley and Austen 2002).

Estimates of detection probabilities for various species are being increasingly presented in literature. However, most studies that estimate detection probabilities only do so for one or a few species (Albanese et al. 2007; Dauwalter and Fisher 2007; Reid et al. 2008a; Korman et al. 2009). Furthermore, most of these studies are restricted to estimates within single drainages or physiographic regions (Ruiz and Peterson 2007; Hayer and Irwin 2008). As studies continue to incorporate and report detection probabilities, intraspecific overlap and differences among regions is inevitable. Because detection probabilities for the same species are often evaluated with different objectives in mind, they are usually estimated with different covariates or models among studies. Differences in reported estimates due to covariate and model discrepancies may prevent their application to management scenarios in other regions. Furthermore, range-wide estimates of detection probability would provide insight into each species' inherent detectability, which is largely determined by that species' traits (e.g. color, size, habitat preferences, etc…), and may be applicable across basins and/or regions.

Multiple-pass depletion sampling, commonly used to survey stream fish assemblages, does not meet the ideal criteria to serve as a protocol for estimating patch occupancy. Most sampling protocols for estimating detection probabilities are designed to estimate patch occupancy, and require multiple visits to sites over a period during which the sites are not subject to extinction or colonization of the species of concern, or that potential differences between sampling events be accounted for as coefficients of extinction and colonization (MacKenzie et al. 2002). Although detection probabilities may vary within or among years, this variation is accounted for by incorporating data from a large number of diverse sites across a species' range (at a spatial scale that is appropriate for the given study). Interannual replication of sampling of stream fishes is often absent or applied to only a limited number of sites, and single-year, single-pass sampling is still prevalent among state and federal agency protocols (Barbour et al. 1999; Moulton et al. 2002). Because many stream fish conservation efforts are bound to agency-wide protocols, adequate time and resources for estimating detection probabilities and patch occupancies separately may not always be available. Although protocols have been defined to estimate assemblage composition and detection probabilities based on temporally replicated sampling, the application of single-season, multiple-pass depletion data to estimates of detection probability has not been evaluated. If this approach is found to be efficient, it would give fisheries managers and conservationists a wider set of options to estimate and incorporate detection probabilities in the parameters they estimate to develop and justify management strategies.

In this thesis, I examined differences in the detection probabilities of stream fishes, and used estimates of size/age-specific detection probabilities to reduce bias in estimates of the reproductive success of various fish species in urban and forested stream habitats. In Chapter 1,

I examined differences in detection probabilities of stream fishes among electrofishing passes and size/age groups in the middle New River basin, Virginia. I also examined differences in detection probabilities between two physiographic regions: the middle New River basin, and the upper Wabash River basin, Indiana; and evaluated differences between single- and multiple-season estimation methods. I found that for most species, detection probabilities do not differ among electrofishing passes, size/age classes, between the two regions, or between single- and multiple-season estimation methods. I used size/age-specific estimates of detection probabilities to remove bias from relative abundance estimates of steam fish populations in Chapter 2. In Chapter 2, I examined the reproductive success of six lithophilic and speleophilic fishes in urban and forested reaches of 2nd-4th Strahler-order streams in the middle New River basin. I found that binary classification is a poor method of quantifying reproductive success, that the age distributions of many lithophilic and speleophilic species are dominated by adult individuals in urban habitats, and that the population growth rates of speleophils is reduced in urban habitats. These results suggest that although detection probabilities may be equal among various sources of variation, managers should verify this assumption before assuming equal detectability. The results also suggest that reduced reproductive success of speleophilic and lithophilic species in urban stream habitats may be a mechanism of their impairment (e.g. decreased relative abundance in assemblages), and that species with more resilient life-history strategies (e.g. relatively opportunistic species) are more likely to persist in urban habitats than less resilient strategists.

Chapter 1: Among-pass, interregional, and single- versus multiple-season comparisons of detection probabilities of stream fishes

Abstract.—Unequal detection of stream fishes should be accounted for when estimating assemblage composition. Detection probabilities may differ among electrofishing passes, regions, or methods of estimation. I tested for among-pass differences in detection probabilities of fishes in tributaries to the New River, Virginia. I examined interregional differences in average detection probability using data from the upper Wabash system of northern Indiana, and compared single- and multiple-season estimates using the New River and National Water Quality Assessment Program (NAWQA) datasets. I found no difference among pass-specific detection probabilities for 97% of species in the New River dataset. Average detection probability was not significantly different between regions for 73% of species that occurred in both datasets. Single-season estimates of average detection probabilities did not differ from multiple-season estimates for 86% of species found in both datasets. Two of three species whose single- and multiple-season estimates differed also had interregional differences. Differences in pass-specific detection probabilities may reflect decreased abundance or behavioral changes in subsequent passes. Interregional differences may be attributable to dissimilarities in abundance, habitat, or sampling protocols between the two systems. Similar factors may have affected single- versus multiple-season comparisons. My results show that overall detection probabilities do not significantly differ among electrofishing passes in three-pass samples for most species, and that averaged estimates of detection probabilities from single-season data are comparable to those from multiple seasons. More research is needed to determine if differences in detection probabilities across regions is a common phenomenon. My approach provides a relatively quick and reliable method for estimating detection probabilities of stream fishes, and will benefit

managers who seek to attain accurate estimates of stream fish assemblage composition, while

making best use of time and resources.

Introduction

Biological monitoring programs require accurate estimation of stream fish assemblage

structure (Karr 1981; Barbour et al. 1999). However, the inconspicuous nature of fishes, scarcity

within their ranges, and the heterogeneity of their habitats seldom allow for all individuals in an

assemblage to be surveyed (Zalewski and Cowx 1990; Dolloff et al. 1996). These phenomena

cause unequal detection probabilities (p, the probability of encountering a species in a given

sample, given its presence) among species and among length/age classes within species

(MacKenzie et al. 2002; Dauwalter and Fisher 2007). Accordingly, any empirical study of fish

ecology should account for inter- and/or intraspecific differences in detection probability (Bayley

and Peterson 2001; MacKenzie and Kendall 2002; Royle et al. 2007). Not accounting for

unequal detection probabilities among species can result in the biased estimation of assemblage

composition and demographic parameters, and can lead to poor management decisions (Slaski et

al. 1983; Bayley and Dowling 1993; Thompson et al. 1998; Bayley and Austen 2002). To ensure

sound management strategies are developed and implemented, differences in detection of species

must be quantified and accounted for.

The past decade has seen a rapidly developing body of literature that addresses unequal

detection probabilities among species. Methods have been developed for estimating species

richness (Boulinier et al. 1998; Bayley and Peterson 2001; Humpl and Lusk 2006), patch

occupancy (MacKenzie et al. 2002; Wenger and Freeman 2008), and the effects of habitat

heterogeneity on species occurrence (Hayer and Irwin 2008; Wenger et al. 2008; Korman et al.

2009). Emerging research also identifies methods of developing and selecting models to estimate detection probability, or to account for the effects of unequal detection probability on the parameters listed above (Wintle et al. 2004; Royle et al. 2007; Ruiz and Peterson 2007).

Backpack electrofishing is the most widely used method of sampling stream fishes, largely due to its great effectiveness and relative lack of selectivity among species and sizes when compared to other methods such as seining or passive gear sampling (Reynolds 1996). Furthermore, backpack electrofishing is the standard method of collecting fishes for many statewide and nationally implemented protocols. As many studies have shown the importance of conducting multiple electrofishing passes to estimate assemblage (Pusey et al. 1998; Meador et al. 2003; Reid et al. 2008b) and population (Kruse et al. 1998; Kennard et al. 2006) parameters, many protocols require multiple passes (Moulton et al. 2002; Rabeni et al. 2009).

Multiple-pass depletion electrofishing protocols that are designed to estimate assemblage composition yield decreasing species' catch with subsequent passes, and could influence pass-specific detection probabilities (Bayley and Peterson 2001; Wilson 2008). Despite advances in the realms of estimating species occurrence and patch occupancy, most fish bioassessment protocols do not account for unequal detection probabilities among species or electrofishing passes. Instead, many assume that, given the sampling technique and reach length, raw estimates of assemblage composition are accurate (Angermeier and Karr 1986; Barbour et al. 1999). Recently, several studies have evaluated the effects of additional electrofishing passes on estimates of stream fish assemblage composition, and have found that, although comparable to multiple-pass estimates of species richness, single-pass electrofishing samples typically miss some species (Simonson and Lyons 1995; Pusey et al. 1998; Meador et al. 2003).   Additionally, indices of biological integrity are calibrated based upon unadjusted sample data (Angermeier and

Karr 1986; Joy and Death 2002). However, Bayley and Peterson (2001) note that the detectability of a species is a function of the number of vulnerable individuals in the sample area. Additionally, Riley and Fausch (1992) expound upon the influence of unequal detectability among subsequent passes on estimates of trout abundance. Despite this knowledge, the fact that multiple-pass depletion protocols may incorporate inequalities among pass-specific detection probabilities has been largely unrecognized and, until recently, unevaluated (Riley and Fausch 1992; Scheurer et al. 2003; Reid et al. 2008a).

Similarly, detection probability may differ within species. Although intraspecific variations of detection probability can be controlled by many of the same variables that influence differences among species, these variables may operate at different degrees. For instance, the effect of individual fish length on electrofishing capture probability has been well documented (Bayley and Austen 2002; Dauwalter and Fisher 2007). Additionally, variation in habitat preference among age classes of the same species can alter detection probability. Throughout their development from juveniles to adults, fishes utilize a variety of habitat types (Werner and Gilliam 1984; Schlosser 1991; Orth and Newcomb 2002). This stage-based habitat partitioning distributes members of the same species nonrandomly within stream reaches (Schlosser and Angermeier 1995), and thus affects their likelihood of being captured. If unaccounted for, length/age-specific differences may result in biased estimates of the length/age structure of lotic fish populations (Dauwalter and Fisher 2007).

Estimates of detection probabilities for various species are being increasingly presented in literature. However, most studies that estimate detection probabilities only do so for one or a few species (Albanese et al. 2007; Dauwalter and Fisher 2007; Reid et al. 2008a; Korman et al. 2009). Furthermore, most of these studies are restricted to estimates within single drainages or

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physiographic regions (Ruiz and Peterson 2007; Hayer and Irwin 2008). As studies continue to incorporate and report detection probabilities, intraspecific overlap and differences among regions is inevitable. Because detection probabilities for the same species are often evaluated with different objectives in mind, they are usually estimated with different covariates or models among studies. Differences in reported estimates due to covariate and model discrepancies may prevent their application to management scenarios in other regions. Furthermore, range-wide estimates of detection probability would provide insight into each species' inherent detectability, which is largely determined by that species' traits (e.g. color, size, habitat preferences, etc…), and may be applicable across basins and/or regions. I know of no study that has evaluated interregional differences in overall detection probability within species, or estimated range-wide detection probabilities.

Multiple-pass depletion sampling, commonly used to survey stream fish assemblages, does not meet the ideal criteria to serve as a protocol for estimating patch occupancy. Most sampling protocols for estimating detection probabilities are designed to estimate patch occupancy, and require multiple visits to sites over a period during which the sites are not subject to extinction or colonization of the species of concern, or that potential differences between sampling events be accounted for as coefficients of extinction and colonization (MacKenzie et al. 2002). Although detection probabilities may vary within or among years, this variation is accounted for by incorporating data from a large number of diverse sites across a species' range (at a spatial scale that is appropriate for the given study). Interannual replication of sampling of stream fishes is often absent or applied to only a limited number of sites, and single-year, single-pass sampling is still prevalent among state and federal agency protocols (Barbour et al. 1999; Moulton et al. 2002). Because many stream fish conservation efforts are bound to agency-wide

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protocols, adequate time and resources for estimating detection probabilities and patch occupancies separately may not always be available. Although protocols have been defined to estimate assemblage composition and detection probabilities based on temporally replicated sampling, the application of single-season, multiple-pass depletion data to estimates of detection probability has not been evaluated. If this approach is found to be efficient, it would give fisheries managers and conservationists a wider set of options to estimate and incorporate detection probabilities in the parameters they estimate to develop and justify management strategies.

This chapter addresses six objectives: 1) to determine if the detection probabilities of stream fishes differ among electrofishing passes in three-pass samples; 2) to determine if detection probabilities differ among length/age classes of species; 3) to estimate length/age-specific detection probabilities for a subset of the species in the middle New River basin; 4) to determine if species-specific detection probabilities differ between two regions; 5) to determine if single- and multiple-season estimates of detection probabilities differ; and 6) to estimate range-wide detection probabilities of species for which data are available. Addressing these objectives could provide valuable information for stream fish managers and conservationists who wish to make best use of time and resources, while obtaining the most accurate assessments of stream fish assemblages and ecological health.

Methods

Study area

The middle New River basin is in southwestern Virginia. It drains northward from North Carolina to the borders of Pulaski, Montgomery, and Giles Counties, VA, where it encounters a

steeper gradient, effectively separating it from a distinct "lower" portion. This basin

encompassing a drainage area of 7,951 km^2 in Virginia and 18,085 km^2 total (Figure 1.1)

(Jenkins and Burkhead 1993). Land use in the middle New River basin is predominately pasture

for hay and livestock grazing, with less amounts of row crop, siliviculture, suburban, and urban

land use. Suburban and urban land use occurs in a few urban centers. Three of the six streams,

Chestnut Creek, Crooked Creek, and Little Reed Island Creek, are located in the New River

Plateau region of the southern Blue Ridge province, whose geology is characterized by granite

bedrock and low relief. The other three streams, Stroubles Creek, Crab Creek, and Peak Creek,

are located in the Great Valley region of the Valley and Ridge province, which is characterized

by limestone bedrock and relatively low relief (Jenkins and Burkhead 1993). Watershed areas

upstream of sampled reaches ranged from 7.1 to 173.6 km^2 and averaged 64.6 km^2.

To examine interregional variation and transferability of detection probability, I used data

the upper Wabash River basin of Indiana (Figure 1.1) (Frimpong et al. 2005a). The upper

Wabash basin is in northern Indiana's Eastern Corn Belt Plain (ECBP) ecoregion (Omernick

1987), and encompasses a watershed area of approximately 20,000 km^2. Land use in the ECBP

is dominated by row-crop agriculture, primarily corn and soybean rotation. The entire landscape

is traversed by roads, isolated subdivisions, and few urban areas. This dataset included 50 sites

with reach lengths 15-20 times mean wetted channel width. These sites were established to

capture the range of instream habitat conditions in that region. Streams in these samples ranged

from first to fifth Strahler-order, with watershed areas of 3.1 to 256.4 km^2, averaging 65.0 km^2

(Frimpong et al. 2005a).

For comparisons between single- and multiple-season estimates of detection probability, I

used fish sample data from the United States Geological Survey's (USGS) NAWQA database

(NAWQA 1991-2009). NAWQA sites are placed in wadeable (typically 3rd-4th order) portions

of streams with reach lengths of 150-300 m, and are sampled during periods of stable flow (mid

June through early October) (Meador et al. 1993). Of 1,162 total sites, I identified 266 with fish

samples from three or more occasions between 1998 and 2006, some of which were in the New

and Wabash basins. Only one reach that was sampled multiple years was used from each site.

These data were collected annually at multiple sites, which provided an ideal sampling scheme

(MacKenzie et al. 2002) for comparing the efficacy of single-season, removal sampling for

estimating detection probabilities of fishes.

Site selection

Using data from the National Land Cover Database (NLCD), I used ArcGIS 9.2 to

reclassify land cover types into six categories: 1) urban/high density residential, 2) suburban/low

density residential/roads, 3) agriculture (row crop and pasture), 4) forest, 5) wetland/water, and

6) barren land. Potential sample segments were first selected based on stream order (2-4)

(Strahler 1957). First-order reaches were excluded because they are often subject to dryness in

southwest Virginia, and their fish communities are subject to highly variable environmental

conditions which can introduce demographic variation (Wine et al. 2008). Fifth- and higher-

order reaches were excluded because they are generally not wadeable in the middle New River

basin. Candidate segments were evaluated based on dominant adjacent land cover type and

distance from adjacent land cover types (>1 km). Sample reaches were randomly placed within

each segment that met my criteria, subject to access constraints. In order to encompass all

habitat types, reach lengths were 150-240 m (20-30 times wetted channel width) (Moulton et al.

2002). Reaches were established with riffles on each end, which serve as natural barriers that

prevent mid-sample escapement (Barbour et al. 1999). Although Strahler-orders of streams used

in the New and Wabash differ (1st to 5th in Wabash versus 2nd to 4th in the New), watershed sizes and instream habitat volume are comparable between the two regions.

My criteria allowed me to establish 36 sites that represent the range of instream habitat conditions (e.g. volume, discharge, various measures of degradation [see Chapter 2], etc…) found in 2nd-4th-order tributaries to the New River. All sites were separated by at least one fluvial kilometer, and those on the same stream were sampled within five days of one another to ensure that single sampling events did not affect the demographic composition of other sites between sampling events.

Because my protocol and that of Frimpong et al. (2005a) are largely based upon the NAWQA protocol (Moulton et al. 2002), seasons, sites, and reach lengths are comparable among datasets. These sites represent the broad range of instream habitat characteristics that observed species encounter within their ranges. As the presence of various species may be related to instream habitat features (Bayley and Austen 2002; Hayer and Irwin 2008), this allowed me to estimate basin-wide detection probabilities that included the potential effects of all habitat conditions. The middle New River and Wabash basins contain distinct geologic features, which provide a meaningful context for making interregional comparisons among species' inherent detection probabilities.

Sampling

In the New River basin, fishes were sampled from July to September 2008 using three-pass depletion, double-backpack electrofishing. Beginning at the head of the reach's most downstream riffle, a four-member crew (two shockers, one netter with each shocker) electrofished in an upstream direction. Netters remained close to shockers, who proceeded in a "zig-zag" pattern diagonally from the center of the channel to the margins, then rejoining in the

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center of the channel approximately every 20 m. Netters collected every possible fish, regardless

of size or species. After three passes, all pools in the sampled reach were seined to improve

certainty about the absence of species not detected in electrofishing.

The upper Wabash data were collected June-September 2002 and 2003. NAWQA data

was collected from 1998 to 2004. Fishes from both datasets were collected with single-backpack

electrofishing in accordance with NAWQA protocol (Moulton et al. 2002). Beginning at the

reach's downstream boundary, one shocker and up to three netters proceeded upstream in a "zig-

zag" pattern, netting all fishes regardless of size or species.

The major difference between the two protocols is the use of an additional backpack

electrofisher in my protocol. Using two backpacks allowed me to effectively sample all portions

of stream channels, which helps to reduce length/age-related bias that may arise when estimating

detection probabilities among year classes.

I evaluated differences among length/age-specific detection probabilities for six species

whose patch-specific population dynamics are examined in Chapter 2 (Table 1.1). In order to

reduce as much length/age-specific bias as possible, I incorporated these species length/age-

specific detection probabilities into estimates of their relative abundance in their respective

populations. I selected study species primarily based upon their hypothesized responses to

urbanization, given their spawning requirements (Table 1.1). I sought speleophils and lithophils,

whose reproductive success is likely inhibited by urbanization (Scott et al. 1986; Berkman and

Rabeni 1987). Secondly, I screened potential study species based upon their presence in all

study streams. Lastly, I chose six study species whose abundance was greater than or equal to 30

individuals at each site (Table 1.1). Based on these criteria, I selected speleophilic mottled

sculpin *C. bairdi* and fantail darter *E. flabellare*; broadcast lithophilic mountain redbelly dace *P.*

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oreas, rosyside dace *C. funduloides*; lithophilic pit-nesting rock bass *A. rupestris*; and gravel mound nesting bluehead chub *N. leptocephalus*.

I assigned individuals to age/year classes based on sagittal otolith analysis. Initially, I intended to use length-frequency histograms to assign individuals to year classes (Gray et al. 2002; Reid et al. 2008a). This approach produced length-at-age categories that largely agreed with published accounts (Jenkins and Burkhead 1993). However, many species displayed high relative abundances of mid-range lengths, which often displayed a slight, but noticeable "dip" in the distribution—which may represent a different year class. Originally, I hypothesized that these breaks in the median length category were an expression of discrepancies in spawning time throughout the previous year's breeding season. However, sagittal otolith analysis was necessary to verify this hypothesis. In June 2009, I collected approximately 30 individuals of each species from upper and lower sites on Chestnut Creek. Each individual was measured to the nearest mm (total length, TL) in the field, and was assigned a unique identification number. Later, I removed each individual's sagittal otoliths, and their ages were estimated by two independent readers. This approach requires two assumptions: 1) that growth (and thus length at age) did not differ among years, and 2) that growth among sites and systems is relatively uniform. Ages estimated from otoliths nearly entirely agreed with length-frequency histograms among sites and systems. Additionally, otolith analysis revealed that for *N. leptocephalus*, the noticeable "dip" in mid-range length was indeed a third year class. Consequently, I accept that for this study, the aforementioned assumptions were not violated.

Data analyses

For the New River and upper Wabash datasets, pass-specific presence-absence data were compiled into binary-coded (presence = 1, absence = 0), species-specific matrices. Each matrix

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contained three columns (one for each pass), with the number of rows equaling the number of sites where the species was encountered at least once. For length/age-specific comparisons within species (New River only), I compiled similar matrices for each age class (three for each species except *P. oreas* and *C. funduloides*, which rarely reach age-3 and were simply classified as "juvenile" or "adult"). For the NAWQA dataset, presence-absence data were compiled in similar matrices in which the number of columns equaled the maximum number of sampling occasions for the most frequently sampled site (up to eight), and the number of rows equaled the number of sites where the species was encountered at least once. Because many NAWQA sites were not always sampled in consecutive years, sampling occasions were not treated as year-specific. Instead, I identified each sampling occasion T_i with its chronological position in the sampling sequence. For example, T_1 for a site could have occurred in any year between 1998 and 2003, and may not occur in the same year for all sites. This approach allowed me to construct presence-absence matrices without gaps in the data.

Detection probabilities (p) and their standard errors (*SE*) were estimated using program PRESENCE (Hines 2006). PRESENCE estimates p using the maximum likelihood model described by MacKenzie et al (2002). Although this model was designed to estimate patch occupancy, it also estimates detection probability, and has been used by other researchers to estimate detection probabilities of stream fishes (Ruiz and Peterson 2007). For single-season data, the sampling protocol designed for the model requires that the population is closed to changes in occupancy during the study period. Multiple-season variations of the model allow for patch occupancy to differ among seasons. Because I designed the study to compare the efficiency of estimating p using a single-season sampling protocol versus a multiple-season protocol, I sampled with removal as most multiple-pass protocols require (Moulton et al. 2002;

Reid et al. 2009). Consequently, overall detection probability was likely altered with additional electrofishing passes. To account for this, I estimated detection probabilities for the New and upper Wabash datasets using a predefined model that estimates survey-specific detection probability, where individual passes are regarded as surveys (Hines 2006). Detection probabilities from the NAWQA dataset were estimated using the predefined constant p model (Hines 2006). The models assume that no species were falsely detected (MacKenzie et al. 2002). Because individuals whose species was unclear (hybrids and very small age-0 individuals) were excluded, I am confident that this assumption was not violated. As detection probability refers to the probability of encountering a species, given its presence, I assumed that a species was truly absent from sites where it was never encountered in multiple within-season sampling (passes) or multiple seasons of sampling. Thus, sites where species were never encountered were excluded when estimating detection probabilities. Accordingly, I assumed that no false absences occurred. This assumption is met by my sample size threshold (present at ≥ 3 sites), below which the precision of distinguishing between detection and non-detection is greatly reduced (MacKenzie et al. 2002).

For length/age class, interregional, and single- vs. multiple-season comparisons of detection probability, I estimated mean detection probability (p_{ave}) from three-pass data for each species in the New River and upper Wabash datasets using mathematical results for estimating the variance of a random variable formed from a linear combination of other random variables (Rencher 2000; Ross 2007). For a linear combination of the three random variables,

$$p_{ave} = ap_1 + bp_2 + cp_3 \qquad (1.1)$$

where *a, b,* and *c* are coefficients representing the weighted contribution of p_i to p_{ave} ($a = b = c = $ ⅓ for three-pass estimates). I estimated standard error for p_{ave} ($SE[p_{ave}]$) using the equations

$$s^2(p_{ave}) = a^2 s^2[p_1] + b^2 s^2[p_2] + c^2 s^2[p_3] + abCOV[p_1, p_2] + acCOV[p_1, p_3] + bcCOV[p_2, p_3] \quad (1.2)$$

and

$$SE(p_{ave}) = \sqrt{s^2(p_{ave})} \quad (1.3)$$

where $s^2[p]_i$ $COV(p_i, p_j), i \neq j$ are estimated variances of the detection probability of each pass ($i =$ 1, 2, 3) and covariances between pass-specific detection probabilities. Estimates of covariance matrices were reported by PRESENCE in each species' model output.

To examine pass-specific and among-length/age differences in detection probability, I used plots of $p_i \pm 2SE$ for each pass. Assuming approximate normal distribution of the estimated detection probabilities, the interval $p_i \pm 2SE$ represents a conservative approximate 95% confidence interval for point estimates (Lohr 1999), the plots are visual representations of tests of statistical differences among estimates with comparisonwise Type I error controlled at $\alpha =$ 0.05. Similarly, for interregional comparisons, I plotted three-pass estimates of $p_{ave} \pm 2SE(p_{ave})$ for the New River estimate beside that of the upper Wabash estimate for each species. Additionally, I used this method to compare the mean detection probability of all species between the two regions. For among-length/age class and single- versus multiple-season comparisons, I plotted three-pass estimates of $p_{ave} \pm 2SE(p_{ave})$ for the New River estimate beside p $\pm 2SE$ from the NAWQA estimate. Plots were visually examined for error bar overlap; no overlap equates to a lack of a significant difference ($p > 0.05$). All analyses were limited to species that occurred in the pairwise datasets being compared (Lohr 1999).

After individual comparisons were made, I adjusted the confidence intervals of each comparison using the Bonferroni correction method (α divided by the number of comparisons) to reduce experiment-wise Type 1 error rate. I then repeated each comparison with the Bonferroni-adjusted confidence intervals.

Five species, black jumprock *Scartomyzon cervinus*, brown bullhead *Amerius nebulosus*, crescent shiner *Luxilis cerasinus*, pumpkinseed *Lepomis gibbosus*, New River shiner *Notropis scabriceps*, and Roanoke darter *Percina roanoka* were excluded from pass-specific comparisons for two reasons. Primarily, individuals of these species were often captured in the same pass at all sites, which resulted in matrices that consisted of columns of all 0's or 1's. Consequently, the model estimated p as 1 ± 0 or 0 ± 0, rendering the estimates inappropriate for statistical comparisons. Secondly, all excluded species barely met the site presence criteria ($n = 3$ or 4 sites), which minimizes the chance of presence-absence heterogeneity within passes, and contributed to large or no standard errors. Pumpkinseed was excluded from interregional comparisons due to the complications with estimating pass-specific detection probability as described above, which likely influenced estimates of p_{ave}. Excluding these species may have influenced my conclusions by decreasing the probability of encountering a significant difference (experiment-wise Type II error). However, estimates of their detection probabilities had no standard errors, and thus no confidence intervals. Unless pass-specific detection probabilities were exactly equal (none were), this ensures that Type 1 errors are made for each species' among-pass comparison, which would be more detrimental to the validity of my conclusions than simply excluding them from analyses would be.

Results

I encountered 46 species in the New River basin, and I estimated detection probabilities for 38. Seine hauls never yielded species or length/age classes of species not captured via electrofishing. Seventeen species were present in both the New River and upper Wabash datasets, and I estimated detection probabilities for 11. Twenty-seven species were found in both

the New River and NAWQA datasets, and I estimated detection probabilities for 21. All excluded species did not satisfy the criterion of being present at three or more sites.

Estimates of pass-specific detection probabilities ranged from 0 to 1 for species in the New River dataset and from 0.33 to 1 for those in the upper Wabash dataset. Estimates of p_{ave} ranged from 0.33 to 1.0 for species in the New River dataset, and from 0.44 to 1.0 for those in the upper Wabash dataset (Table 1.2). Year class-specific estimates of p_{ave} ranged from 0.68 to 0.98 (Table 1.3). Multiple-season estimates of detection probability for species in the NAWQA dataset ranged from 0.17 to 0.89 (Table 1.2). Estimates of *SE* decreased exponentially with increasing number of sites in which each species was detected (Figure 1.2).

I found no significant differences in *p* with additional electrofishing passes for 97% of the species encountered in the New River basin whose detection probabilities were estimated (*n* = 33, 5 excluded). The pass-2 estimate of *p* for *N. leptocephalus* was equal to the pass-1 estimate, but significantly higher than that of pass 3 (Figure 1.3). I found no significant difference among year-class-specific estimates of p_{ave} for any of the six species studied.

Estimates of p_{ave} were not different between regions for 73% of the 11 species that occurred in both the New River and upper Wabash datasets whose detection probabilities were estimated (*n* = 7, 1 excluded). For creek chub *Semotilus atromaculatus*, estimates of p_{ave} were significantly higher in the Wabash system than in the New (Figure 1.4). Conversely, estimates of p_{ave} for central stoneroller *Campostoma anomalum* and *E. flabellare* were significantly higher in the New than in the Wabash (Figure 1.4). Mean detection probability of all species did not differ between the two regions. There were no pass-specific differences in detection probability for any of the species from either system, thus making p_{ave} comparable between regions.

I found no significant difference between single- and multiple-season estimates of detection probability for 86% of the species that occurred in both the New River and NAWQA datasets, whose detection probabilities were estimated ($n = 18$). Single-season estimates were lower than multiple-season estimates for brown trout *Salmo trutta*, and higher than multiple-season estimates for *C. anomalum* and *E. flabellare* (Figure 1.5).

Detection probabilities with Bonferroni-adjusted confidence intervals did not differ for any experiment-wise comparison.

Discussion

Differences among passes

I found that detection probabilities for most species did not differ among consecutive electrofishing passes. This result is consistent with Reid et al. (2008a), who found that capture probabilities of rediside dace *Clinostomus elongatus* remained constant among electrofishing passes. My results partially agree with Riley and Fausch (1992), who found that, although capture probability differed for some estimates, assumptions of equal capture probability among passes were not violated for 78% of three-pass abundance estimates for salmonids. The two measures of detectability differ slightly in implication. Detection probabilities describe the probability of encountering a species (or an age class of a species), given its presence. Although indirectly related to a species' local abundance, equations that estimate detection probability do not incorporate abundance. Catchability, or capture probability, is the slope of a "catch curve" derived from multiple-pass (more than three) depletion sampling. Catchability incorporates pass-specific measures of abundance. Additionally, detection probabilities describe species' range-wide detectability and should remain relatively constant among samples; while estimates

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of catchability are sample-specific and require distinct estimates for each sample. Although detection probability and catchability differ slightly in implication, I consider the findings to be similar and contextually relevant. Otis et al. (1978) argued that for multiple-pass removal estimates of abundance, at least four passes must be conducted to test the assumption of equal catchability. However, bioassessment protocols usually seek to describe stream fish assemblage structure rather than abundance, often use only one pass, and rarely use more than three passes. As such, I believe that an evaluation of differences in detection probabilities among three passes is of practical relevance to these protocols.

Detection probabilities differed among passes only for *N. leptocephalus*, which is ubiquitous throughout the New River basin and are typically abundant where present. It is possible that depletion sampling removed enough individuals in the first and second passes to lower third-pass estimates of detection probability (Bayley and Peterson 2001). However, this explanation would not account for the increased second-pass estimates of detection probability, or the lack of a significant difference between first- and third-pass estimates of detection probability (Figure 1.3). Alternatively, it is possible that behavioral changes in subsequent passes resulted from exposure to electricity and other disturbances related to sampling, and caused the unequal detection probabilities (Cross and Stott 1975; Bohlin and Sundstrom 1977; Mahon 1980). Riley and Fausch (1992) expounded upon decreasing trends in capture probability with subsequent electrofishing passes. Despite the lack of significant differences among passes, estimates of detection probabilities for less-abundant species often displayed a negative trend with additional passes (Figure 1.6). Likewise, detection probabilities for more-abundant species remained relatively constant among additional passes (Figure 1.7). However, detection

probabilities for many species showed little trend among passes. Although not significantly different, second-pass estimates were often lower or higher than first- or third-pass estimates.

Complications associated with small sample sizes lowered the statistical power of among-pass comparisons for several species. Standard error, as a proportion of its respective detection probability estimate, decreased exponentially with the number of sites the species was present (Figure 1.2). Large standard errors for species that were present at few sites (< 10) provided wide confidence intervals, and lowered my ability to discern differences in detection probability among passes. Additionally, low sample sizes likely decreased the probability of collecting heterogeneous presence-absence data for species that were present at only a few sites (e.g. the likelihood of both presence and absence in the same pass for all sites).

Length/age-specific differences

Detection probabilities did not differ among year classes for any of the six study species. Alternatively, Dauwalter and Fisher (2007) found that the capture probability of smallmouth bass *Micropterus dolomieui* decreased with total length. However, their study encompassed a broader range of habitat volume and types than mine, and they used multiple methods to capture fish (single-backpack electrofishing in wadeable streams, and boat electrofishing in larger ones). Additionally, they compared capture probability among habitat units (Frissell et al. 1986), while I focused on overall detectability within a given reach that encompasses multiple habitats. Nevertheless, I do not believe these results disagree. As fishes pass through different life history stages as they increase in size/age, they utilize a variety of habitat types (Schlosser 1991). Naturally, detectability of individuals of various year classes should differ among habitat types. I speculate that this study would have yielded similar results if I had compared differences in patch-specific detection probabilities.

Interregional differences

Detection probabilities were not significantly different between regions for most species. Interregional differences in detection probability for *S. atromaculatus*, *E. flabellare*, and *C. anomalum* may be attributable to several factors. Firstly, differences in abundance for each species between the two systems could have influenced estimates of p_{ave} (Angermeier and Smogor 1995; Bayley and Peterson 2001). In the Wabash system, *S. atromaculatus* are the dominant omnivore and largely outnumber *Nocomis* species; whereas *N. leptocephalus* numerically dominates in the New. Similarly, although *E. flabellare* is clearly the most abundant *Etheostoma* species in most New River tributaries, they are largely outnumbered by johnny *E. nigrum*, orangethroat *E. spectabile*, and rainbow darters *E. caeruleum* in the Wabash system (Hrodney et al. 2009). Although I speculate that differences in abundance may contribute to significant variation in detection probabilities, evidence is strictly anecdotal, as I did not directly estimate abundance. Further research on the relationship between detection probability and abundance is needed, and would be particularly insightful for managers of rare species which are often found in low abundances at all sites (Albanese et al. 2007).

Distinct habitat differences between the two regions may have also contributed to the differences in detection probability. While the upper Wabash system is heavily influenced by agricultural disturbance (Omernick 1987; Pyron and Lauer 2004), the New system is much less affected. This likely contributes to differences in habitat suitability between regions for various species. Differences in substrate composition may also contribute to the differences between the two regions, as they affect the species' visibility (due mainly to color contrast) and catchability (the tendency for stunned fishes to become lodged in coarse substrate). Higher levels of sediment input in the Wabash system could contribute to lowered abundances of lithophilous *C.*

anomalum and *E. flabellare* (Berkman and Rabeni 1987), and thus detection probabilities. Additionally, higher turbidity levels in the Wabash system could hinder algae and periphyton production, and thus inhibit stoneroller abundance. Likewise, the clear New River tributaries supported large standing crops of periphyton at most sites, and stonerollers were widely abundant. Sediment input and increased turbidity in the Wabash system could have also contributed to decreased visibility, especially of more benthic oriented fishes, and thus affected their probability of capture.

Differences in sampling protocols could have also contributed to the differences seen in interregional comparisons. In the New system I used three-pass, double-backpack depletion. The upper Wabash streams were sampled similarly, but with one backpack. If the different sampling protocols influenced detection probability, one would expect double-backpack estimates to be higher for all species. However, the significantly higher detection probability of creek chubs in the upper Wabash system contradicts this notion, and suggests that that the different sampling protocols did not significantly influence my results.

Interregional differences occurred for species that were found at many sites. Narrow confidence intervals associated with large sample sizes increased my ability to detect differences in detection probability for these species. Likewise, large confidence intervals for species that were found at few sites reduced statistical power. Due to the lack of available comparable data, I was able to compare detection probabilities between only two regions. Although my findings suggest that overall detection probabilities do not significantly differ between the two regions for most species, I do not assume that this trend holds true among all regions within a given species' range. Further research that examines interregional comparisons of overall detection probability could include additional regions.

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Single- versus multiple-season estimates

For most species, single-season estimates of detection probability did not differ from multiple-season estimates. As presence-absence data for multiple-season estimates were drawn from a larger pool of sites and occasions, sample sizes were large and most estimates of detection probabilities were less variable than single-season estimates. However, standard errors for species that were present at 20 or more sites in the New River dataset were comparable to those in the NAWQA dataset. Additionally, most species involved in single- versus multiple-season comparisons were present at more than 10 sites.

Differences for *S. trutta*, *C. anomalum*, and *E. flabellare* may be attributable to factors similar to those mentioned for regional comparisons (e.g. abundance, habitat, sampling, and/or statistical power). Additionally, interregional differences could have contributed to the results. As I found differences in detection probabilities between the New and Wabash systems for *C. anomalum* and *E. flabellare*, differences among systems in the NAWQA dataset could have also been present, and may have influenced single- versus multiple-season comparisons.

Other factors may also contribute to the difference in detection probabilities for *S. trutta*. In several New River tributaries, *S. trutta* is stocked for delayed harvest fisheries from October to May (VDGIF 2009). Because *S. trutta* is heavily harvested, presence and abundance in community samples is likely dependent upon the length of time the samples were collected after stocking. Although *S. trutta* is likely stocked near many of the NAWQA sites, I do not expect that its influences are homogenous among all sites, or even within datasets. Therefore, although I believe the estimate of detection probability for brown trout from the NAWQA dataset to be accurate, the estimate from the New River dataset should be regarded with the aforementioned

caveat. Additionally, this situation should be considered when estimating detection probabilities for any stocked and harvested species.

<u>Conclusions</u>

Overall, my findings show that for most species, detection probabilities do not differ significantly among electrofishing passes or size/age classes. Additionally, detection probabilities for most species do not differ between the New and Wabash basins. This is corroborated by the fact that when confidence intervals were adjusted using the Bonferroni method, no experiment-wise differences were found. Because most bioassessment metrics are developed with raw count data, and do not attempt to account for differences in detection probability, my findings do not present a pressing need to change protocols that require only one or two electrofishing passes. However, managers who wish to account for incomplete detection when estimating population-level parameters such as patch occupancy or population size should first confirm that these differences do not exist among or within their study species before assuming equal detection among potential sources of variation. A lack of such attention may result in biased estimates of relative abundances assessments of stream ecosystem health.

My findings provide a method for estimating detection probabilities from multiple-pass bioassessment protocols, without the need for an additional sampling regime. For most stream fishes, depletion electrofishing does not significantly alter detection probability among passes. Additionally, most single-season estimates of detection probability are comparable with the more traditional multiple-season estimates. Although detection probabilities were not different among passes for most species, I do not recommend the use of single pass estimates of detection probability, particularly for species which are found at only a few sites. Three-pass estimates of

SE([p_{ave}]) are, by definition, significantly lower than single-pass estimates of standard error (Equations 2 and 3). Additionally, three-pass estimates of $p_{ave} \pm SE([p_{ave}])$ are encompassed by $p_1 \pm SE(p_1)$, and provide a tighter, more reliable estimate of overall detection probability for species whose detection probabilities do not significantly differ among electrofishing passes.

The lack of significant interregional differences in overall detection probabilities for most species provides justification for a more widespread analysis of detection probabilities for species across regions. This information will be useful for the estimation of overall detection probabilities that managers can use for all species across their respective ranges, and thus save time, effort, and money. Managers could also capitalize on existing national and regional datasets such as NAWQA and the Regional Environmental Monitoring and Assessment Program (REMAP) to estimate detection probabilities for focal species. In addition to the species that occur in New River basin, I have included an appendix of multiple-season estimates of detection probabilities for the most common species in the NAWQA database, which will provide reference for managers and conservationists who work with those species (Appendix A). This will save time and effort for those who wish to incorporate these species' detection probabilities into their efforts, but lack the resources to implement a protocol for estimating detection probabilities. Accounting for the incomplete detection of species will provide more accurate estimates of stream fish assemblage structure, and will thus refine existing management tools to conserve aquatic biodiversity for future generations.

Table 1.1. Species selected for estimation of size/age-specific detection probabilities.

Species	Spawning mode*
Mottled sculpin *Cottus bairdi*	Speleophil
Fantail darter *Etheostoma flabellare*	Speleophil
Mountain redbelly dace *Phoxinus oreas*	Lithophilic broadcast spawner
Rosyside dace *Clinostomus funduloides*	Lithophilic broadcast spawner
Rock bass *Ambloplites rupestris*	Lithophilic pit nester
Bluehead chub *Nocomis leptocephalus*	Lithophilic mound nester

*Spawning modes from Balon 1975.

Table 1.2. Detection probabilites (*p*) and associated standard errors (*SE*) of fishes from the New River, Wabash River, and NAWQA datasets.

Family	Species	Pass 1 New *p*	*SE*	Pass 1 Wabash *p*	*SE*	Pass 2 New *p*	*SE*	Pass 2 Wabash *p*	*SE*	Pass 3 New *p*	*SE*	Pass 3 Wabash *p*	*SE*	3-pass average New *p*	*SE*	3-pass average Wabash *p*	*SE*	NAWQA *p*	*SE*	Number of sites present New	Wabash	NAWQA
Catostomidae	Black jumprock *Scartomyzon cervinus**	1	0	-	-	0.33	0.27	-	-	0	0	-	-	0.44	0.09	-	-	-	-	3	-	-
Catostomidae	Northern hogsucker *Hypentelium nigricans*	0.85	0.07	0.92	0.08	0.78	0.08	0.75	0.13	0.47	0.09	0.50	0.14	0.70	0.05	0.72	0.07	0.89	0.04	25	12	48
Catostomidae	White sucker *Catostomus commersoni*	0.88	0.05	0.89	0.05	0.97	0.03	0.87	0.05	0.72	0.08	0.76	0.07	0.85	0.03	0.84	0.03	0.84	0.02	28	38	120
Centrarchidae	Bluegill *Lepomis macrochirus*	0.86	0.13	0.71	0.10	0.86	0.13	0.67	0.10	0.43	0.19	0.33	0.10	0.71	0.09	0.57	0.06	0.79	0.02	7	21	171
Centrarchidae	Green sunfish *Lepomis cyanellus**	0.80	0.18	-	-	0.40	0.22	-	-	0.20	0.18	-	-	0.47	0.11	-	-	0.74	0.02	5	-	153
Centrarchidae	Largemouth bass *Micropterus salmoides*	0.56	0.17	-	-	0.78	0.14	-	-	0.56	0.17	-	-	0.63	0.09	-	-	0.69	0.02	9	-	163
Centrarchidae	Pumpkinseed *Lepomis gibosus**	0.67	0.27	0.33	0.27	0.00	0.00	0.33	0.27	0.33	0.27	0.67	0.27	0.33	0.13	0.44	0.16	-	-	3	3	-
Centrarchidae	Redbreast sunfish *Lepomis auritus*	0.91	0.09	-	-	0.91	0.09	-	-	0.64	0.15	-	-	0.82	0.06	-	-	0.83	0.03	11	-	65
Centrarchidae	Rock bass *Ambloplites rupestris*	0.93	0.05	0.85	0.10	0.89	0.06	0.77	0.12	0.79	0.08	0.38	0.13	0.87	0.04	0.67	0.07	0.78	0.05	28	12	56
Centrarchidae	Smallmouth bass *Micropterus dolomieui*	0.69	0.13	0.60	0.22	0.56	0.13	0.60	0.22	0.50	0.13	0.60	0.22	0.58	0.09	0.60	0.13	0.77	0.02	11	5	95
Cottidae	Mottled sculpin *Cottus bairdi*	0.86	0.07	-	-	0.91	0.06	-	-	0.86	0.07	-	-	0.88	0.04	-	-	-	-	22	-	-
Cyprinidae	Blacknose dace *Rhinichthys atratulus*	0.82	0.09	-	-	1	0	-	-	0.88	0.08	-	-	0.90	0.04	-	-	0.83	0.03	17	-	66
Cyprinidae	Bluehead chub *Nocomis leptocephalus*	0.87	0.06	-	-	0.97	0.03	-	-	0.72	0.08	-	-	0.85	0.03	-	-	0.85	0.05	36	-	17
Cyprinidae	Bluntnose minnow *Pimephales notatus*	1	0	0.91	0.04	0.90	0.09	0.89	0.05	0.70	0.14	0.78	0.06	0.87	0.04	0.86	0.03	0.79	0.03	10	46	74
Cyprinidae	Central stoneroller *Campostoma anomalum*	0.89	0.05	0.79	0.08	0.94	0.04	0.72	0.08	0.94	0.04	0.66	0.09	0.92	0.03	0.72	0.05	0.76	0.03	35	29	61
Cyprinidae	Creek chub *Semotilus atromaculatus*	0.86	0.09	1.00	0.00	0.71	0.12	0.97	0.03	0.57	0.13	0.86	0.06	0.71	0.07	0.94	0.02	0.74	0.03	14	29	95
Cyprinidae	Crescent shiner *Luxilis cerasinus*	1	0	-	-	0.67	0.16	-	-	0.67	0.16	-	-	0.78	0.07	-	-	-	-	9	-	-
Cyprinidae	Cutlips minnow *Exoglossum maxillingua*	0.57	0.19	-	-	0.86	0.13	-	-	0.43	0.19	-	-	0.62	0.10	-	-	0.89	0.04	7	-	18
Cyprinidae	Kanawha minnow *Phenacobius tetratulus*	0.69	0.12	-	-	0.56	0.12	-	-	0.56	0.12	-	-	0.60	0.07	-	-	-	-	16	-	-
Cyprinidae	Longnose dace *Rhinichthys cataractae*	0.85	0.08	-	-	0.85	0.08	-	-	0.75	0.10	-	-	0.82	0.05	-	-	0.81	0.03	70	-	73
Cyprinidae	Mountain redbelly dace *Phoxinus oreas*	0.87	0.06	-	-	0.90	0.05	-	-	0.83	0.07	-	-	0.87	0.04	-	-	-	-	30	-	-
Cyprinidae	New River shiner *Notropis scabriceps**	1	0	-	-	0.50	0.25	-	-	0.25	0.22	-	-	0.58	0.11	-	-	-	-	4	-	-
Cyprinidae	Rosefin shiner *Lythrurus ardens**	1	0	-	-	0.50	0.25	-	-	0.50	0.25	-	-	0.67	0.12	-	-	0.25	0.22	4	-	1
Cyprinidae	Rosyface shiner *Notropis rubellus*	0.83	0.09	-	-	0.72	0.11	-	-	0.50	0.12	-	-	0.69	0.06	-	-	0.78	0.06	18	-	-
Cyprinidae	Rosyside dace *Clinostomus funduloides*	0.96	0.04	-	-	0.82	0.07	-	-	0.75	0.08	-	-	0.85	0.04	-	-	-	-	28	-	-
Cyprinidae	Saffron shiner *Notropis rubricoceous*	0.95	0.05	-	-	0.89	0.07	-	-	0.95	0.05	-	-	0.93	0.03	-	-	0.17	0.15	19	-	1
Cyprinidae	Spottail shiner *Notropis hudsonius**	0.83	0.15	-	-	0.67	0.19	-	-	0.33	0.19	-	-	0.61	0.10	-	-	-	-	6	-	-
Cyprinidae	White shiner *Luxilis albeolus*	1	0	-	-	0.90	0.07	-	-	0.95	0.05	-	-	0.95	0.03	-	-	-	-	20	-	-
Ictaluridae	Margined madtom *Noturus insignis*	0.86	0.09	-	-	1	0	-	-	0.86	0.09	-	-	0.90	0.05	-	-	0.89	0.05	14	-	17
Percidae	Appalachia darter *Percina gymnocephala*	0.62	0.13	-	-	0.77	0.12	-	-	0.62	0.13	-	-	0.67	0.07	-	-	-	-	13	-	-
Percidae	Fantail darter *Etheostoma flabellare*	0.93	0.05	0.82	0.12	0.93	0.05	0.45	0.15	0.96	0.04	0.36	0.15	0.94	0.02	0.55	0.08	0.72	0.07	29	11	18
Percidae	Greenside darter *Etheostoma blennoides**	1	0	0.89	0.07	1	0	0.67	0.11	0.67	0.19	0.61	0.11	0.89	0.06	0.72	0.06	-	-	6	18	-
Percidae	Kanawha darter *Etheostoma kanawhae*	0.73	0.11	-	-	0.60	0.13	-	-	0.67	0.12	-	-	0.67	0.07	-	-	-	-	15	-	-
Percidae	Roanoke darter *Percina roanoka**	1	0	-	-	1	0	-	-	0.33	0.27	-	-	0.78	0.09	-	-	-	-	3	-	-
Salmonidae	Brook trout *Salvelinus fontinalis**	0.80	0.18	-	-	0.60	0.22	-	-	0.40	0.22	-	-	0.60	0.12	-	-	0.80	0.06	5	-	21
Salmonidae	Brown trout *Salmo trutta*	0.63	0.17	-	-	0.25	0.15	-	-	0.38	0.17	-	-	0.42	0.10	-	-	0.81	0.03	8	-	57
Salmonidae	Rainbow trout *Oncorynchus mykiss*	0.89	0.10	-	-	0.44	0.17	-	-	0.44	0.17	-	-	0.59	0.09	-	-	0.68	0.07	9	-	56

* indicates species with low sample sizes whose detection probabilities may be inaccurately estimated.

Table 1.3. Year class/length-specific detection probabilities (p) and their standard errors (SE) for six fish species in tributaries to the middle New River basin, Virginia.

Species	Year class	Total length (mm)	Pass1 p	SE	Pass 2 p	SE	Pass 3 p	SE	Average p	SE	Number of sites present
N. leptocephalus	0	0-55	0.91	0.05	0.97	0.03	1.00	0.00	0.91	0.03	34
N. leptocephalus	1	56-110	0.91	0.05	1.00	0.00	1.00	0.00	0.97	0.02	35
N. leptocephalus	2^+	>110	0.92	0.05	0.97	0.03	0.91	0.05	0.93	0.04	36
P. oreas	0	0-60	0.92	0.05	0.92	0.05	0.92	0.05	0.92	0.03	26
P. oreas	1^+	>55	0.90	0.06	0.93	0.05	0.90	0.06	0.93	0.03	29
C. funduloides	0	0-60	0.94	0.05	0.89	0.07	0.72	0.11	0.85	0.05	18
C. funduloides	1^+	>60	0.96	0.04	0.85	0.07	0.73	0.09	0.85	0.04	26
E. flabellare	0	0-40	0.89	0.06	0.93	0.05	0.92	0.05	0.91	0.03	27
E. flabellare	1	41-55	0.96	0.04	0.96	0.04	1.00	0.00	0.98	0.02	27
E. flabellare	2^+	>55	0.86	0.06	0.90	0.06	0.93	0.05	0.90	0.03	29
C. bairdi	0	0-65	0.63	0.12	0.94	0.06	0.50	0.13	0.69	0.06	16
C. bairdi	1	66-78	0.94	0.05	0.94	0.05	0.78	0.10	0.89	0.04	18
C. bairdi	2^+	>78	0.85	0.08	0.95	0.05	0.80	0.09	0.87	0.04	20
A. rupestris	0	0-90	0.81	0.07	0.74	0.08	0.62	0.10	0.72	0.05	27
A. rupestris	1	91-130	0.80	0.08	0.76	0.09	0.67	0.10	0.74	0.05	25
A. rupestris	2^+	>130	0.83	0.08	0.79	0.08	0.43	0.10	0.69	0.05	24
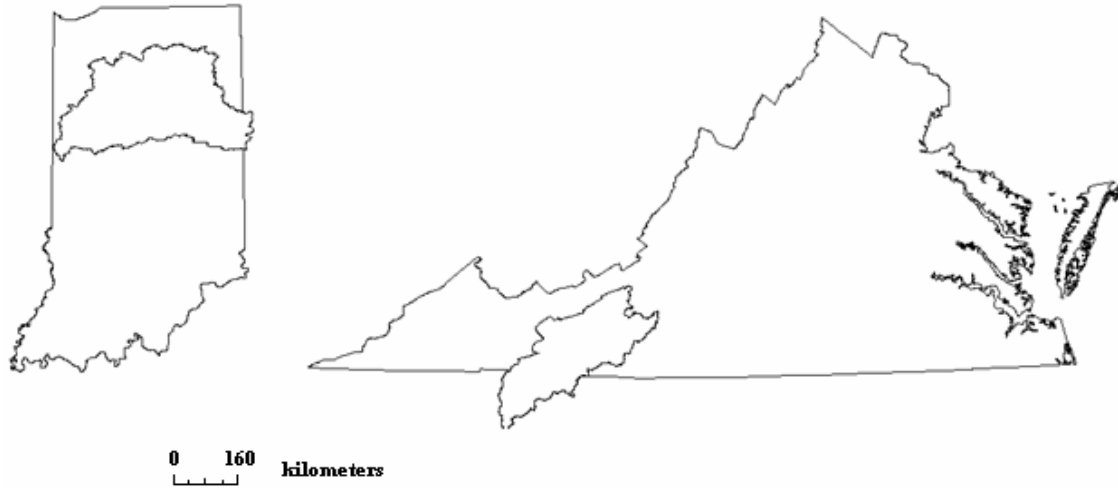
Figure 1.1. The middle New River basin, Virginia and upper Wabash River basin, Indiana.
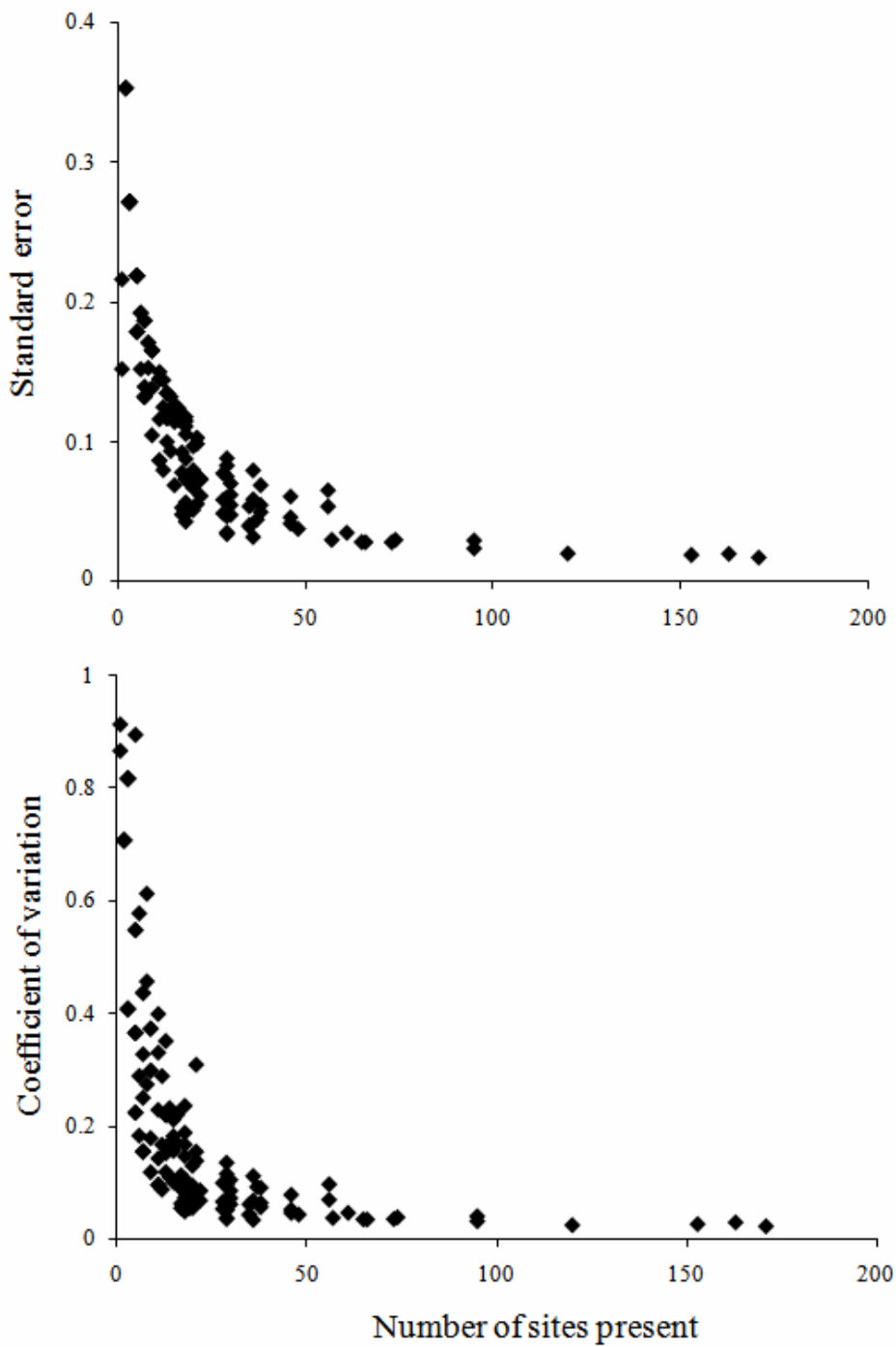
Figure 1.2. Standard errors (above) and coefficients of variation (below) of detection probability estimates as functions of the number of sites where a species is present. Points represent individual estimates of detection probability.
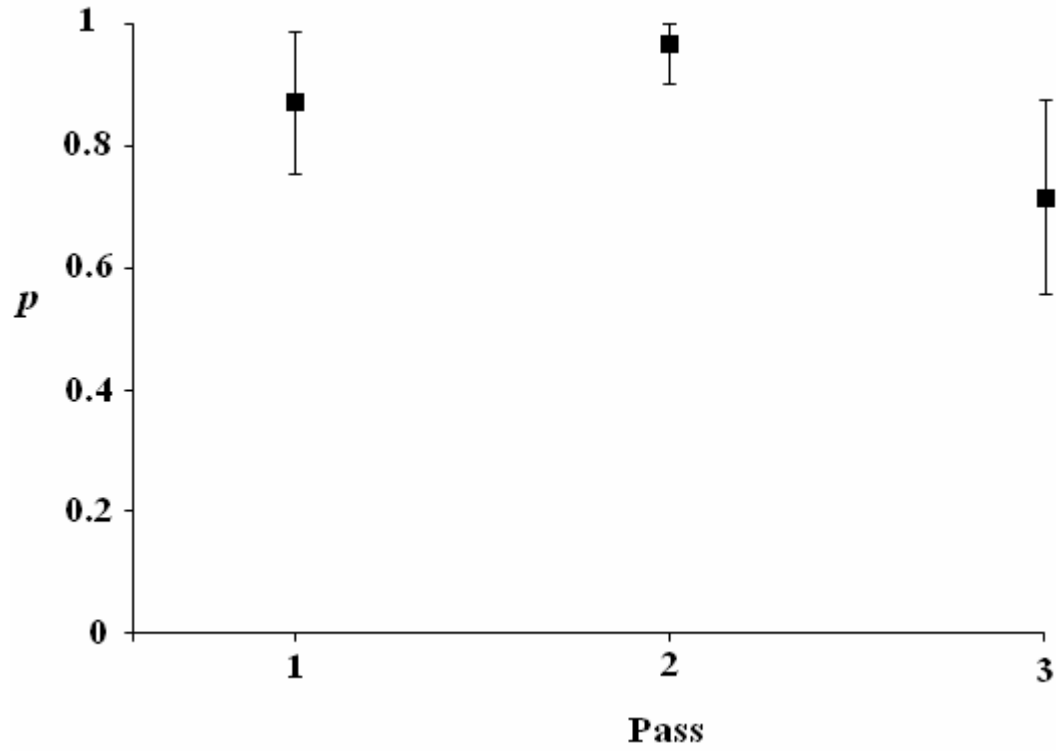
Figure 1.3. Comparison of pass-specific detection probabilities (*p*) for *N. leptocephalus*. Error bars are ± 2 standard errors.
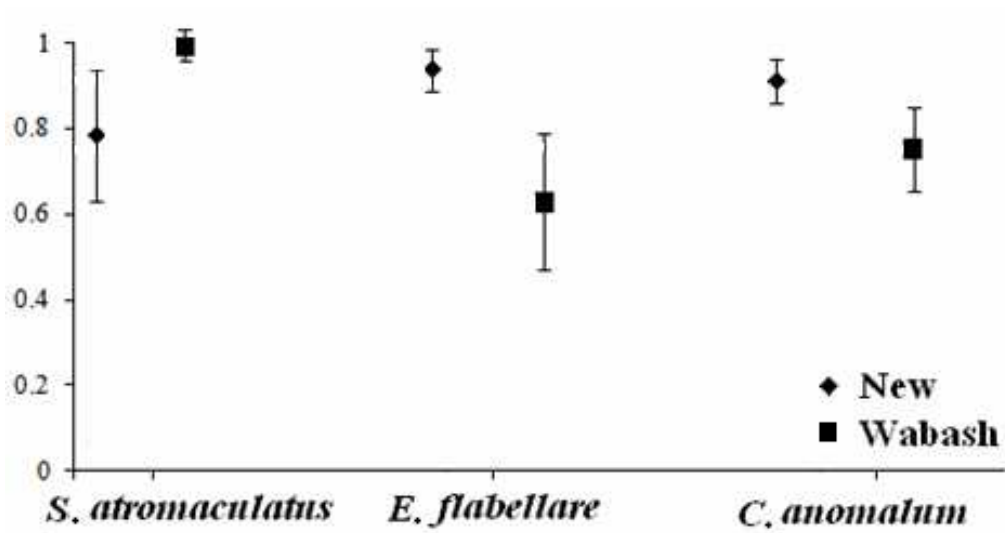
Figure 1.4. Interregional comparisons of detection probabilities (*p*) for *S. atromaculatus*, *E. flabellare*, and *C. anomalum*. Error bars are ± 2 standard errors.
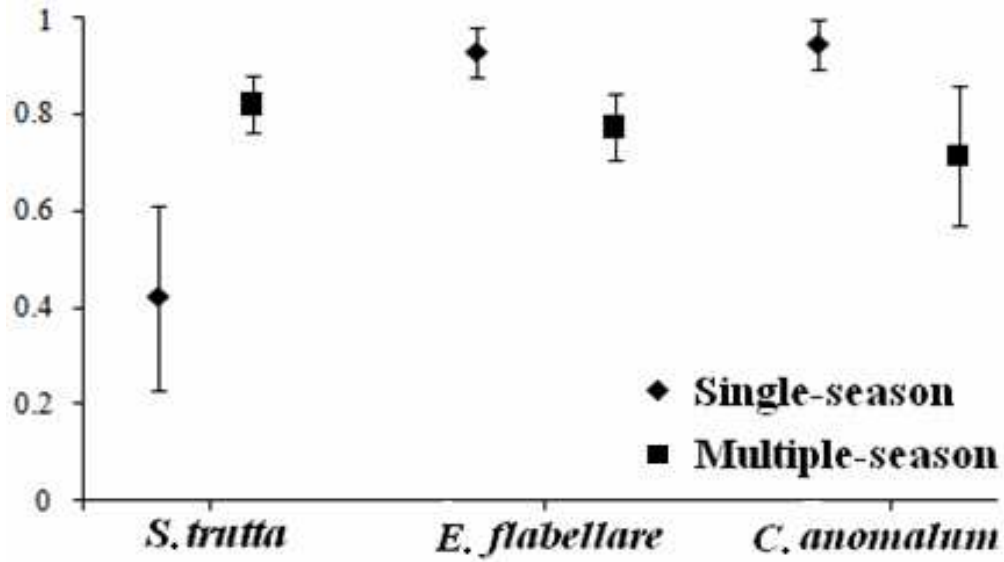
Figure 1.5. Comparison of single- vs. multiple-season estimates of detection probability for *S. trutta*, *C. anomalum*, and *E. flabellare*. Error bars are ± 2 standard errors
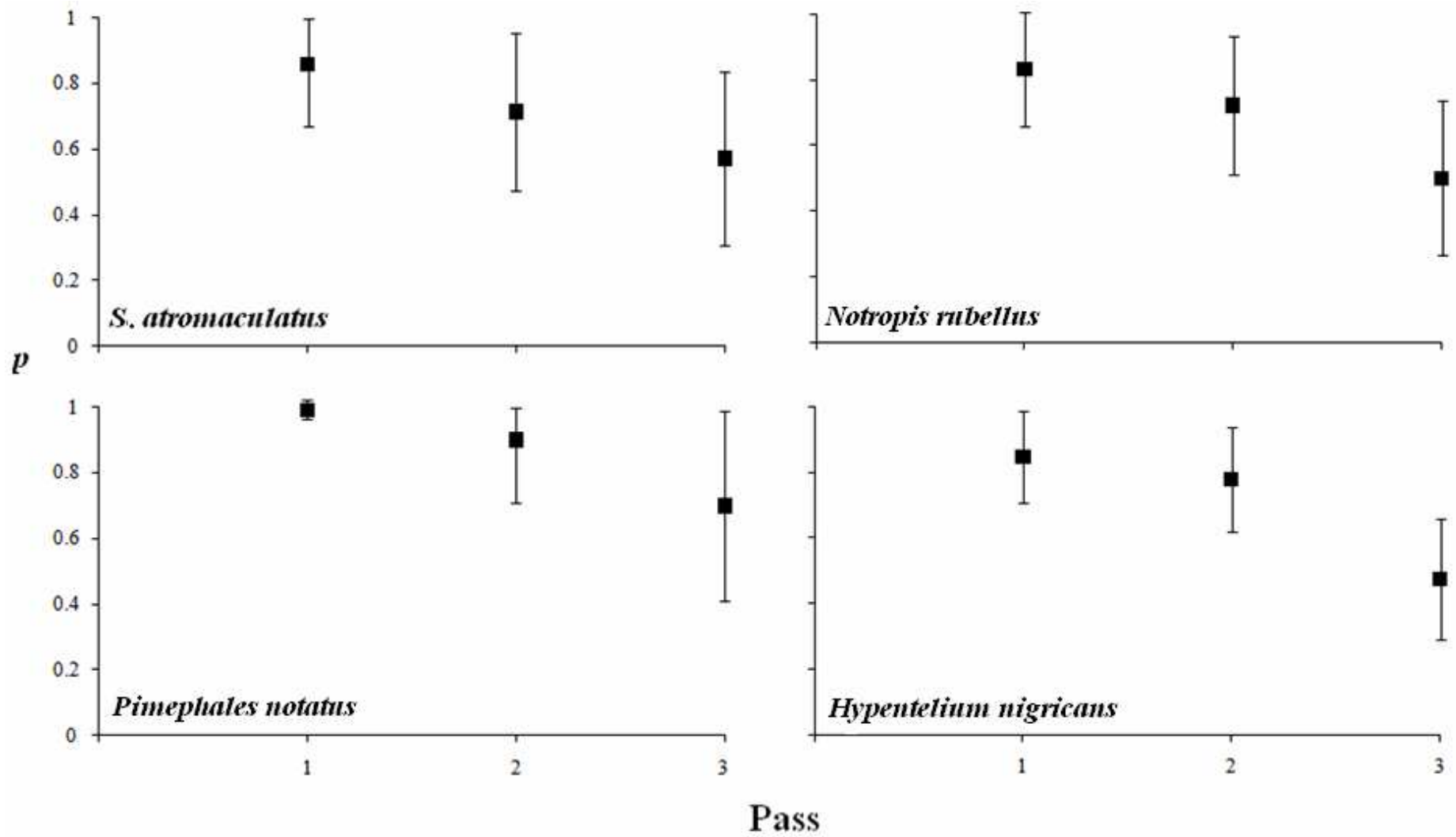
Figure 1.6. Trends of decreasing detection probability (p) with increasing fishing effort for some less abundant species in the New River basin. Error bars are ± 2 standard errors.
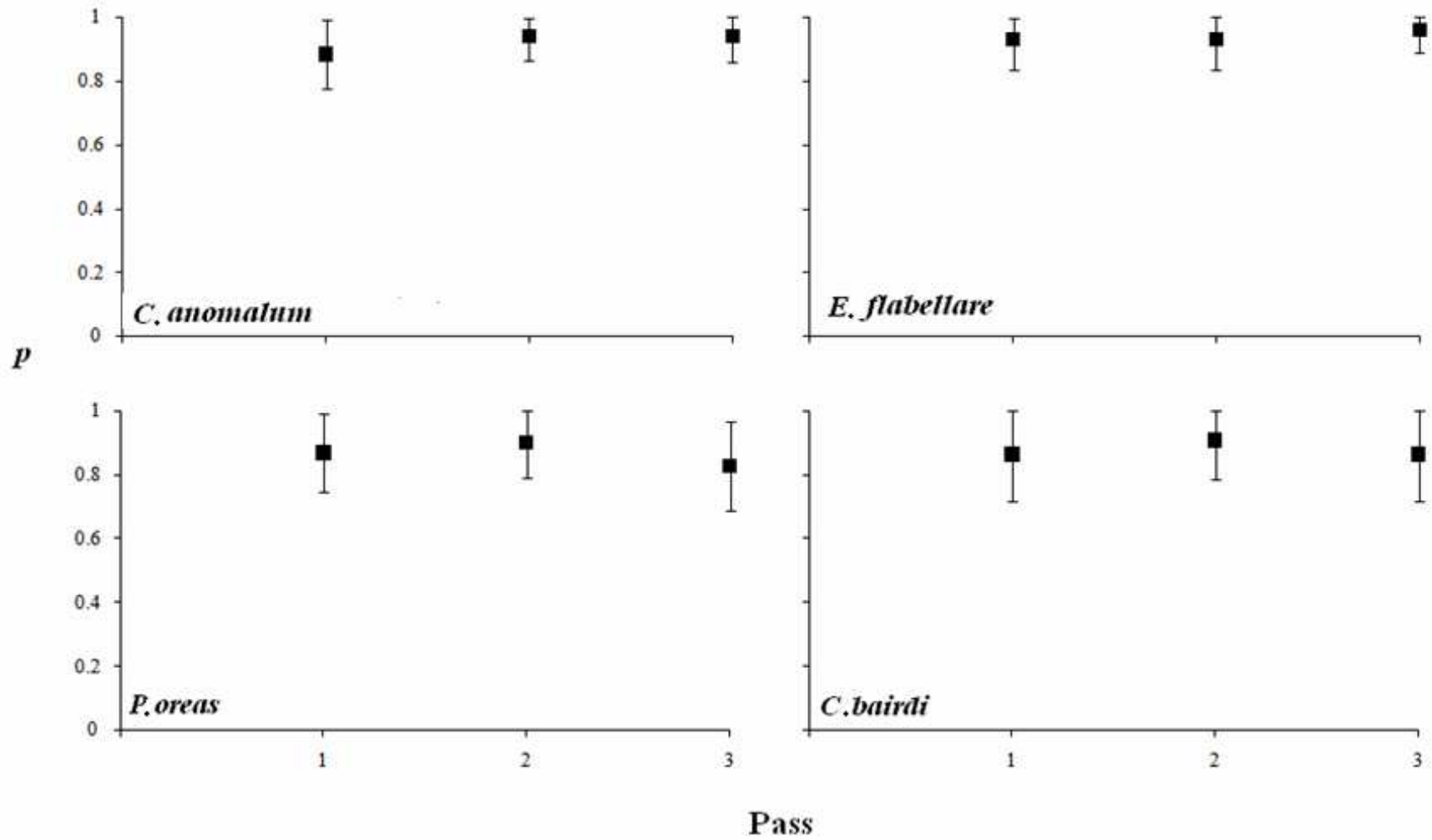
Figure 1.7. Trends of relatively constant detection probability (*p*) with increasing electrofishing effort for some abundant species in the New River basin. Error bars are ± 2 standard errors.

Chapter 2: Evaluating the population-level reproductive performance of six fish species in forested and urban stream habitats

Abstract.—Urbanization is a primary contributor to lotic fish imperilment. A population-level approach is necessary to address the mechanisms of impairment in urban stream habitats. I evaluated the reproductive success of several speleophilic and lithophilic fishes in urban and forested tributaries to the New River, Virginia. I electrofished at 18 sites (5 urban, 13 forested) on three tributaries to the New River, Virginia during the summer and fall of 2008. The total lengths of all individuals were measured to the nearest mm; length-at-age was determined using sagittal otoliths. I evaluated reproductive success using a 3-tiered approach: 1) predicting age-0 presence/absence, 2) predicting differences in age distributions (as an ordinal polytomous response) using multiple logistic regression, and 3) predicting changes in species' population growth rates (λ) using multiple linear regression. I accounted for the effects of watershed area and spatial autocorrelation by including them in all models. Age-0 presence/absence was the least sensitive measure of reproductive success, and only responded to measures of urbanization in instances of complete reproductive failure at sites. Age distributions of most speleophils and lithophils were dominated by adults in urban reaches, while those in forested reaches were more balanced. The λ values of speleophils were negatively correlated with urbanization, while those of broadcast lithophils and gravel mound nesters were positively correlated with urbanization. The positive influences of urbanization on the reproductive performance of broadcast lithophils may be explained by the species' relatively opportunistic life-history strategies, or by the benefits received from nest association. A *post-hoc* survival analysis showed that age-0 survival of speleophils was negatively correlated with urbanization, while that of other lithophils and gravel

mound nesters was not. Reduced reproductive performance may be a mechanism of lotic fish imperilment in urban stream reaches.

<u>Introduction</u>

Aquatic biodiversity continues to decline as humans modify the landscape (Allendorf 1988; Moyle and Williams 1990). Due primarily to anthropogenic land use changes resulting in habitat fragmentation and loss, extinction rates of 4% per decade have been predicted for North American freshwater fishes (Ricciardi and Rasmussen 1999). Urbanization, a term that is often used to describe increasingly populated areas (cities) and associated loss of agriculture or forest to development (Lussier et al. 2008), has been considered one of the greatest threats to stream ecosystem health (Leopold 1968; Malmqvist and Rundle 2002; DeFries and Eshleman 2004; Fleming 2007).

The detrimental effects of urbanization on instream habitat are vast. At the watershed scale, increased impervious surface coverage (ISC) alters the hydrologic cycle, contributing to the frequency and magnitude of flood events, as well as unnaturally low flows during periods of low precipitation (Leopold et al. 2005; Fleming 2007). Flash flood events associated with urban hydrology contribute to channel incision, which exposes stream banks and mobilizes sediments that eventually settle and cover coarse substrates (Wolman 1967; Davies et al. 2005). These events also wash away medium-sized substrate particles (mainly gravels) (Pizzuto et al. 2000) and contribute to channel widening, filling, and straightening (Booth 1990; Trimble 1997). When combined, these processes usually result in the overall homogenization of instream habitat (Wang et al. 2001). Additionally, surface runoff from urban areas during storm events can carry harmful chemical pollutants and sediments exposed by development (Chester et al. 1996; Wang

et al. 2001). Watershed-scale percentages of impervious surface coverage are often used as a measure of urbanization (Chester et al. 1996), and ISC of 10-20% have been identified as hydrologic (Booth and Jackson 1997) and biological (Klein 1979; Yoder et al. 1999) thresholds of degradation (Paul and Meyer 2001).

In urban areas, riparian vegetation is often intentionally removed (Booth and Jackson 1997). This accentuates the watershed-scale effects of urbanization, and contributes to losses of hydrologic (Karr and Schlosser 1978) and thermal buffering (Galli 1991) capacity, channel incision (Wolman 1967; Davies et al. 2005), increased loads of chemical and sedimentary pollutants, (Karr and Schlosser 1978; Davies et al. 2005), and reduced allochthonous energy input (McNeeley 1987; McTammany et al. 2007). Many studies have shown the importance of riparian vegetation to the persistence of stream dwelling organisms (Bunn et al. 1999; Jones et al. 1999; Roy et al. 2005). Additionally, some have shown that biota in streams with urbanizing watersheds that have intact riparian corridors tend to be much less affected than those without intact riparian corridors (Yoder et al. 1999).

The effects of urbanization on stream organisms have been well-documented. Studies have identified higher densities of microbes (Porcella and Sorensen 1980; Duda et al. 1982) and decreased diversity of algae (Chessman et al. 1999), macrophyte (Suren 2000), invertebrate (Seager and Abrahams 1990; Wright et al. 1995), and fish taxa (Weaver and Garman 1994; Boet et al. 1999; Onorato et al. 2000) in urban reaches. Urbanization has been shown to decrease the abundance of many benthic invertebrate taxa (Resh and Grodhaus 1983; Wiederholm 1984), which reduces food resources for many fishes (Taylor and Roff 1986). Sediment input from urbanization covers coarse substrates with silt, which degrades spawning habitat for fishes (Wood and Armitage 1997). Sedimentation has also been shown to contribute to behavioral

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changes of spawning fishes, increased egg mortality, and decreased larval growth (Berkman and

Rabeni 1987). The high levels of thermal variability associated with urbanization have also been

attributed to dissolved oxygen deficiencies, which can cause fish kills (Boet et al. 1999; Gafny et

al. 2000).

The past few decades have seen the development of methods to evaluate the ecological

condition of streams using fish communities (Karr 1981; Karr et al. 1986; Joy and Death 2002;

Carlisle et al. 2008). Such methods characterize ecological integrity by comparing proportional

abundance changes of fishes of various trophic or reproductive guilds along gradients of habitat

degradation, or by comparing observed assemblages with those in reference sites. However,

some have argued that when metrics of fish assemblage response to habitat degradation are

combined, information regarding the mechanisms of impairment may be lost and causality may

not be inferred (Suter 1993; Hughes et al. 1998).

The structure of any biological community is a representation of the performance of its

constituent populations. Likewise, the performance of any population is a culmination of the

reproductive performance of its constituent individuals (Shipley et al. 2006; Power 2007). The

performance of individuals is affected by habitat through biological and ecological traits evolved

by the species, and is measured as fitness (Merigoux et al. 2001; Shipley et al. 2006). Therefore,

anthropogenic disturbances affect stream fish communities by altering the habitat and biotic

characteristics fishes have evolved to exploit. This influences individual members of

populations, and is evident as proportional differences in communities. Consequently, an

assessment of the reproductive performance of fish populations in stream habitats that experience

various levels of anthropogenic degradation may provide insight into the mechanisms of their

impairment and persistence, rather than coarsely identifying local assemblages (good, fair, poor,

etc…) (Power 2007). Despite the existing knowledge of the effects of urbanization on stream

fishes (Suren 2000; Brown et al. 2005; Walsh et al. 2005; Nelson et al. 2009), much of the

mechanisms are still unknown, and mechanistic studies are vastly underrepresented in the

literature (Suren 2000; Paul and Meyer 2001).

Population-level reproductive performance may be evaluated in many ways, most of

which involve estimating parameters associated with juvenile (age-0) members of populations.

Because of their small size and habitat preferences, age-0 individuals are often difficult to

sample, which complicates the process of estimating their abundance (Reynolds 1996). In cases

where a species is not locally abundant, or when traditional sampling methods such as

electrofishing or seining may cause significant damage to populations, the presence of age-0

individuals is used as a qualitative indicator of local reproductive success (CFI 2008).   Many

stock assessment programs quantitatively evaluate reproductive success as relative year-class

"strength", which are usually estimates of indices of abundance or biomass that are compared to

reference or previous conditions (Smith 1985; Jensen and Johnsen 1999; Power 2007). Age

distributions are also indicative of population-level reproductive success (Scott et al. 1986; Gray

and Munkittrick 2005). Age distributions that are proportionally dominated by adults often

indicate decreasing "momentum" (trajectory of population growth). Growth of populations with

similar proportional abundances of year classes is usually stable; and age distributions that are

proportionally dominated by age-0 individuals typically indicate population growth (Mills 2007)

(Figure 2.1).

One of the most descriptive measures of population reproductive performance is the

population growth rate (λ). Population growth rates incorporate species' age-at-first

reproduction, age-specific fecundity and survivorship, brood frequency, and longevity effects

(Power 2007). Population growth rates also quantitatively describe differences in momentum

that are evident in age distributions. It has been argued that λ values describe the effects of all or

most environmental factors that influence populations over the life spans of its constituent

individuals, and account for the effects of compensatory mechanisms such as density-dependent

mortality (Daniels and Allan 1981; Walthall and Stark 1997). In some cases, λ values can

provide evidence of source-sink dynamics that may sustain populations that persist in reaches

that are unsuitable for reproduction (Pulliam 1988). Population growth rates can be estimated

from life table analyses, which require multiple years' worth of data (Wooton 1998; Krebs

1999); or from matrix modeling (Leslie 1945), which require only one season's worth of data if

age-specific survival and fecundity parameters are known (Aalto and Newsome 1980; Caswell

1989).

Although oftentimes similar, every species has evolved and displays unique biological

traits. As a result, it is intuitive to expect varying levels of responses to urbanization among

species. However, from the foundation of multimetric community-level approaches to

bioassessment, expected population-level responses to urbanization may be comparable among

species of similar trophic (Goldstein and Simon 1999), reproductive, (Balon 1975), or life-

history strategies (Winemiller and Rose 1992).

Many studies have shown that lithophils (non-guarding open gravel substrate spawners)

and speleophils (cavity spawners) are negatively affected by anthropogenic development.

Berkman and Rabeni (1987) reported that among Balon's (1975) reproductive guilds, the relative

abundance of simple lithophils in assemblages are most likely to be reduced by increased

siltation associated with anthropogenic development. Additionally, the relative abundance of

lithophils and speleophils is often used as a metric in several indices of biotic integrity, with low

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relative abundances negatively affecting scores (Oberdoff and Hughes 1992; Hughes et al. 1998; Lyons et al. 2001). Given this evidence, it is intuitive to expect population-level responses of lithophils and speleophils to be similar. Accordingly, I hypothesize that the reproductive success of simple lithophils and speleophils will be negatively affected by urbanization because of reductions of suitable spawning habitat.

In this study, I evaluated the reproductive success of several speleophilic and lithophilic stream fishes in relation to urbanization. I evaluated reproductive success using a three-tiered approach: 1) age-0 presence/absence, 2) age distributions, and 3) population growth rates. Descriptive power increased with each subsequent tier, which allowed me to assess the population-level mechanisms of lotic fish impairment in urban stream habitats.

Methods

Site selection and land use estimation

I conducted this study on three tributaries to the middle New River, Virginia: Chestnut, Crooked, and Peak (Figure 2.2). These streams were chosen to capture the range of physical instream habitat conditions associated with urban and forested streams in this basin. Land use in upper and lower portions of Chestnut and Peak's watersheds are dominated by deciduous forest with small patches of pastureland. Riparian vegetation corridors in these areas are largely intact, and instream habitats contain relative lower (than in urban reaches) amounts of embedded coarse substrate and a variety of mesohabitat types (Frissell et al. 1986). Chestnut and Peak's midreaches are heavily affected by urbanization from the cities of Galax and Pulaski, Virginia, respectively. Channels in urban areas are highly modified; they have been artificially straightened and widened and primarily consist of shallow run habitats. These reaches contain

little or no riparian vegetation, and coarse substrates are heavily embedded with silt. Crooked Creek's watershed is adjacent to that of Chestnut, and is much less affected by anthropogenic degradation. Upstream portions of Crooked Creek's watershed are nearly entirely forested, and lower portions contain relatively small amounts of pastureland. Physical instream habitats and thermal regimes throughout Crooked Creek are comparable to forested portions of Chestnut and Peak.

Using data from the National Land Cover Database (NLCD), I used ArcGIS 9.2 to reclassify land cover types into six categories: 1) urban/high density residential, 2) suburban/low density residential/roads, 3) agriculture (row crop and pasture), 4) forest, 5) wetland/water, and 6) barren land. Potential sample segments (approximately one fluvial km of relatively homogenous land use and instream habitat features) were first selected based on stream order (2-4) (Strahler 1957). Next, candidate segments were evaluated based on dominant adjacent land cover type and distance from adjacent land cover types (>1 km) in order to remove some effects of spatial autocorrelation that may be associated with dispersal among adjacent land cover types. Sample reaches of 180-240 m (20 to 30 times mean wetted channel width) were randomly placed within each segment that met my criteria, subject to access constraints. All reaches were separated by one kilometer or more so that single sampling events did not affect the demographic composition of other sites between sampling events. All sites on each stream were sampled within five days of one another. These criteria allowed me to establish 18 sites: ten on Chestnut, four on Crooked, and four on Peak.

I used a digital elevation model to delineate each reach's watershed and riparian buffer (30 m on each side and 600 m upstream) (Frimpong et al. 2005b). I then calculated the percentage of each land cover type in each watershed and riparian buffer (Appendix B).

Percentages of wetland/water and barren land were negligible (<1), and were excluded from

analyses. Watershed areas ranged from 12.1 to 173.6 km^2 and averaged 81.9 km^2.

Study species

I selected study species primarily based upon their hypothesized responses to

urbanization, given their spawning requirements (Table 1.1). I sought speleophils and lithophils,

whose reproductive success is likely inhibited by urbanization (Scott et al. 1986; Berkman and

Rabeni 1987). Secondly, I screened potential study species based upon their presence in all three

study streams. Lastly, I chose species whose abundance was greater than or equal to 30

individuals at each site where they were present (Table 1.1). These criteria allowed me to choose

six species: mottled sculpin *C. bairdi*, fantail darter *E. flabellare*, mountain redbelly dace *P.*

oreas, rosyside dace *C. funduloides*, rock bass *A. rupestris*, and bluehead chub *N. leptocephalus*.

Sampling

I quantified instream habitat using methodology based on the United States

Environmental Protection Agency (USEPA) Rapid Bioassessment Protocol (RBP) (Barbour et

al. 1999) and the United States Geologic Survey (USGS) National Water-Quality Assessment

Program (NAWQA) protocol (Moulton et al. 2002). At each site, I measured wetted channel

width and determined mesohabitat type along transects spaced 7 m apart ($n \approx 20$ for each reach).

I measured depth and visually estimated dominant substrate type at 10 equidistant points along

each transect (Table 2.1). I visually estimated substrate embeddedness at three points (33% of

channel width from left bank, thalweg, and 33% of channel width from right bank) along each

transect.

Fishes were sampled from July to September 2008 using three-pass depletion, double-

backpack electrofishing. Beginning at the head of the reach's most downstream riffle, a four-

member crew (two shockers, one netter with each shocker) electrofished in an upstream direction. Netters remained close to shockers, who proceeded in a zig-zag pattern diagonally from the center of the channel to the margins, then rejoining in the center of the channel approximately every 20 m. Netters collected every possible fish, regardless of size or species. After three passes, all pools in the sampled reach were seined to improve our certainty about the absence of species not detected in electrofishing.

Age/year class designation

I assigned individuals to age/year classes based on sagittal otolith analysis. Initially, I intended to use length-frequency histograms to assign individuals to year classes (Gray et al. 2002; Reid et al. 2008a). This approach produced length-at-age categories that largely agreed with published accounts (Jenkins and Burkhead 1993). However, many species displayed high relative abundances of mid-range lengths, which often displayed a slight, but noticeable "dip" in the distribution—which may represent a different year class. Originally, I hypothesized that these breaks in the median length category were an expression of discrepancies in spawning time throughout the previous year's breeding season. However, sagittal otolith analysis was necessary to verify this hypothesis. In June 2009, I collected approximately 30 individuals of each species from upper and lower sites on Chestnut Creek. Each individual was measured to the nearest mm total length, (TL) in the field, and was assigned a unique identification number. Later, I removed each individual's sagittal otoliths, and their ages were estimated by two independent readers. This approach requires two assumptions: 1) that growth (and thus length-at-age) did not differ among years, and 2) that growth among sites and systems is relatively uniform. Ages estimated from otoliths nearly entirely agreed with length-frequency histograms among sites and systems. Additionally, otolith analysis revealed that for longer-lived species such as *A. rupestris* and *N.*

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leptocephalus, the noticeable "dip" in mid-range length was indeed a third year class. Consequently, I accept that for this study, the aforementioned assumptions were not violated.

Data analyses

I measured reproductive success in three ways: 1) presence of age-0 individuals, 2) relative abundance of age-0 individuals in the age distribution, and 3) population growth rates. I evaluated the effects of urbanization on the reproductive success of the study species using a three-tiered approach: 1) predicting age-0 presence/absence using multiple logistic regression, 2) predicting differences in size/age distributions using polytomous logistic regression with multiple predictors, and 3) predicting differences in λ values using multiple linear regression. This approach allowed for increasingly complex descriptions of population performance with each subsequent tier, while providing meaningful results to revert to in case assumptions could not be met for a more complex tier.

Model selection

I calculated several composite variables to simplify the process of selecting regression models. To form a metric of overall anthropogenically developed land cover at the watershed and riparian scales, I summed the percentages of urban and suburban land cover. I also summed the percentages of pebble, gravel, and cobble as a metric of coarse substrate. Watershed areas were log-transformed to achieve approximate normal distribution. To account for the potential effects of spatial autocorrelation (namely dispersal) among sites, I calculated an index of dispersal/proximity by determining presence/absence in adjacent sites, which conformed to the dependent variable types in each tier. For *Tier 1*, the value of this variable for a given site was the presence/absence of age-0 individuals in the nearest site. For *Tier 2*, the value of a given site's measure of spatial autocorrelation was calculated as the average relative abundance of a

length/age class in both adjacent sites. Mean λ values in adjacent sites served as measures of spatial autocorrelation in *Tier 3*.

Each of the tiers employed two types of independent variables: categorical (forest, urban) and continuous measures of urbanization and physical instream habitat degradation. I accounted for the effects of watershed area and spatial autocorrelation (dispersal/proximity) by including these variables in all models. I selected models for each response and independent variable type using Akaike's information criterion (AIC) (Akaikie 1974). I sought parsimonious models that maximized descriptive power and minimized AIC, while retaining significance at $\alpha \leq 0.05$. I used these criteria to check models from decreasing AIC by adding more variables. I used automated procedures in SAS to run all possible subsets of models given hypothesized independent variables. The SAS output ranked all models by AIC and so enabled me to easily select candidate models meeting my criteria. After performing the regressions, I removed extraneous variables that poorly predicted dependent variables ($p<0.05$). Within tiers, I compared AIC values to determine the optimal independent variable type.

Tiers 1 and 2: Predicting age-0 presence and changes in age distributions

For analyses in Tier 1, I utilized the length/age-specific presence/absence dataset that I used to estimate detection probabilities in Chapter 1 (see *Data analyses* section). To prepare data for Tier 2, I first divided the abundance of each size/year class by its respective detection probability, which was estimated in Chapter 1 (Table 3), to remove as much length/age-specific bias as possible from estimates of relative abundance. I then modeled the adjusted abundances as ordinal polytomous response variables in SAS 9.2 (PROC LOGISTIC), which converted the abundances to relative abundances. Given the interspecific variability in growth rates, sexual dimorphism, and length/age at maturity of some of the study species, the "age-1" year class may

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represent a combination of reproductively mature and immature individuals (Jenkins and

Burkhead 1993). To avoid confusion, I assigned age-1 relative abundance as a reference

category. The resulting outputs were interpreted as the odds of habitat variables describing the

relative domination of adults in a site's age distribution, which is the hypothesized characteristic

of age distributions in habitats where reproductive success is reduced (Jennings et al. 2010).

Tier 3: Predicting changes in population growth rates

Fecundity estimation

      Tier 3 involved using age-based matrix population modeling (Leslie 1945) to estimate λ,

and required estimates of survival and fecundity. To estimate fecundity, I first conducted a

literature review. I incorporated fecundity estimates in localities as close to the study areas as

possible. Only one species, *C. bairdi*, has a published fecundity-at-length equation (Table 2.2)

(Grossman et al. 2002). Although the fecundity of *P. oreas* has not been studied in detail,

Hamed et al. (2008) provide a fecundity-at-length equation for Tennessee dace *P. tennesseensis*,

which is closely related to *P. oreas* (Starnes and Jenkins 1988). Given the close proximity of the

phylogenetic relationship and study area (northeastern Tennessee), I used *P. tennesseensis* as a

surrogate for *P. oreas*. Detailed fecundity-at-length information was available for *C. funduloides*

(R. Davis 1972). Fecundity information for *E. flabellare*, *N. leptocephalus*, and *A. rupestris*

were limited to a few records.

      I derived fecundity-at-length equations from primary literature for four species without

published equations. For *E. flabellare*, I used data from an ongoing graduate project at Virginia

Tech (M. L. Henebry, Virginia Tech, unpublished data). These data were collected in March of

2009 in 2nd-4th-order tributaries to the New River (Crab and Toms), and likely provide an

accurate (or as close as possible) representation of the fecundity of *E. flabellare* in my study

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streams. Because many life history studies report standard length (SL) of fishes, rather than total length (TL, which I measured in the field), I first developed conversion factors for each species by measuring standard and total length of preserved specimens. I estimated mean TL-to-SL ratios, and divided each individual's TL by the ratio. For each species, I plotted reported mean fecundity as a function of length, and fit the data with linear models (Table 2.2). Using the length-at-age relationships estimated in Chapter 1 and the fecundity-at-length estimates, I estimated mean fecundity-at-age (Appendix C).

Survival estimation

Although survival may vary among or within populations, each species exhibits an inherent pattern of survival based on its life history strategy (Winemiller 1989). Using Winemiller's (1989) model of relationships among fecundity, longevity, and survivorship, I derived an equation to estimate each species' survival rate:

$$S_x = \frac{f}{10^{Log(f)-[Log(f)/t]x}}$$
(2.1)

where S_x is the proportion of individuals surviving to age x, f is fecundity, and t is the longevity (y+0.5) of the species at this approximate locality, as reported by Jenkins and Burkhead (1993). Adding 0.5 y to each species' longevity allows for longevity to be expressed as the number of breeding seasons, rather than calendar years. For example, a species with longevity of 2.5 y breeds for two seasons, and then typically dies before the third reproductive season.

Matrix modeling

To construct life-history (survival and fecundity) vectors for matrix modeling, I first multiplied each year class' fecundity estimate by its adjusted relative abundance (relative abundance divided by detection probability). This allowed me to estimate the potential number

of juveniles (as eggs) that could be contributed to site-specific populations. Next, I constructed

life-history vectors for each species at each site in the following form:

$$
\begin{bmatrix}
F_0 & F_1 & F_{2+} \\
S_0 & 0 & 0 \\
0 & S_1 & 0 \\
0 & 0 & S_{2+}
\end{bmatrix}
\tag{2.2}
$$

where F_x and Sx are the estimated median fecundity and survival values of age-class x. I then

constructed site-specific population demography matrices for each species:

$$
\begin{bmatrix}
N_0 \\
N_1 \\
N_{2+}
\end{bmatrix}
\tag{2.3}
$$

where Nx is the adjusted relative abundance of each species' age class.

To calculate λ values, an estimate of the population size one time step (in this case, one

breeding season) into the future is needed.   This is achieved by multiplying the life-history and

population vectors. Population growth rates are then calculated using the equation,

$$
\lambda = \frac{N_0}{N_{0+1}}
\tag{2.4}
$$

where N_0 is the original population size, and N_{0+1} is the population size one time step into the

future. Because λ values may vary annually due to environmental factors, population growth

rates must be projected far enough into the future (time scales vary, depending on demographic

variability) that they converge on a dominant eigenvalue (λ), which characterizes the overall

trajectory of population growth or decline (Caswell 1989; Mills 2007). Estimates of λ center at

1.0; $\lambda \leq 1.0$ indicates population decline, $\lambda \approx 1.0$ indicates stable momentum, and $\lambda \geq 1.0$ indicates

population growth.

Once the vectors were assembled, I used MathCAD 14 to calculate their dominant

eigenvalues (Caswell 1989). I then used the λ values as response variables in multiple linear

regression models, which were selected using the aforementioned process.

Individual sample reaches spaced so closely together cannot be treated as separate

biological populations. However, for this study, I treat them as separate statistical populations.

This allows for trends in local demographics to be evaluated along a gradient of physical habitat

degradation.

Assumptions

All tiers rely on several assumptions. Firstly, I assume that no age-0 individuals of any

species were falsely identified, and that detectability does not differ among length/age classes.

The distance of phylogenetic relationships among study species (no two species were of the same

genus) reduced the probability of species-level misidentification of age-0 individuals. By

sampling all channel portions (margins, thalweg, etc…) and mesohabitat types equally, and

adjusting the relative abundances of size/age classes by their respective detection probabilities, I

removed as much length/age-specific bias as possible. By treating each site as a separate

population, I must assume that dispersal among sites is limited to the point that it would not

confound my results. Studies have shown that *N. leptocephalus* and *P. oreas* are highly mobile

species (Albanese et al. 2004), and *N. leptocephalus* is capable of moving more than a kilometer

during dispersal events (Garrick and Gilliam 2000). These dispersal events are often associated

with high temperatures, pool intermittency, and/or flood events. Alternatively, *C. bairdi* and *E.

flabellare* typically disperse less than 300 m throughout their life (Petty and Grossman 2004;

Roberts and Angermeier 2007). Less is known about the movement of *A. rupestris* and *C.

funduloides*. I accounted for the potential effects of dispersal in several ways. Firstly, I

separated sites by at least one fluvial kilometer, and sampled them within five days of one another. Secondly, I introduced measures of spatial autocorrelation into all models. Additionally, no flood events occurred, and instream flow was continuous (no dry riffles were observed) during the sample season.

Similarly to estimating detection probability, the use of the presence of age-0 individuals as a measure of reproductive success assumes that no false absences occurred. My criteria for selecting study species helps to meet the first assumption. I selected species that are relatively ubiquitous and abundant within their range, which decreases the likelihood of non-detection (Bayley and Peterson 2001).

The methods in *Tier* 3 rely on several assumptions. Firstly, my approach for estimating fecundity assumes that the fecundity of species in other studies is approximately equal to those in my study area. As several studies have shown intraspecific latitudinal clines in fecundity (Bagenal 1978; McGurk 2000), this may be a concern. I accounted for this by using fecundity estimates from studies that were conducted as close to my study area as possible (Table 2.2). The approach also assumes that within species, fecundity does not change along gradients of habitat quality or volume. Given that urbanization alters food resources for fishes (Weaver and Garman 1994; Singer and Battin 2007), and implicitly, available energy to devote to growth and reproduction (Gray and Munkittrick 2005), this assumption may also need investigation. Ideally, I would have estimated the study species' fecundity from the sites I sampled. This would have allowed me to examine site-specific variation. However, this would be expensive and time consuming, and was not feasible given the scope of this project. Although there may be intraspecific differences in fecundity among study areas or sites, readers should bear in mind that my estimates are more of an approximation of the fecundity inherent to the species (as a species

trait), rather than an exact calculation of their actual fecundity. Finally, I assume that length-specific fecundity behaves in a linear manner. Although the fecundity-at-length of most fishes follows a positive exponential function (Morse 1980; Wooton 1998), my fecundity estimates are limited by the range of lengths reported by other studies, which were better fit (consistently higher R^2) by linear, rather than exponential functions.

My approach also implicitly assumes that age-0 survival is approximately equal along a gradient of habitat quality or volume. Of all the aforementioned assumptions, this one would affect my results most strongly if not satisfied. Studies have shown that the survival of some age-0 lithophilic stream fishes can be reduced in reaches that are influenced by anthropogenic development (Varanasi et al. 1993; Able et al. 1998). Accordingly, maintaining constant survival values among sites may result in over-generalized estimates of λ. Ideally, I would have estimated site-specific survival of each age class of every species. Estimating differences in age-0 survival among habitat types would have been difficult and time-consuming, and was not feasible given the scope of this project. However, keeping all survival parameters constant allows for λ to fluctuate based on the measurable effects of urbanization on fishes' population structure, and provides an effective method of estimating λ with limited life-history information.

Alternatively, a relatively simple approach (Boreman 1997) allowed me to perform a *post-hoc* analysis to explore the potential for urbanization-related differences in approximated site-specific survival using the data I collected. To estimate site-specific age-0 survival (S_0), I used the equation proposed by Boreman (1997):

$$S_0 = \frac{N_S / N_E}{S_0 \cdot S_2 \cdot \ldots S_N} \tag{2.5}$$

where N_S is the total number of mature individuals at a site, N_E is the total number of potentially spawned eggs at a site (N_E multiplied by size/age-specific fecundity), and S_x is age-specific

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survival. I then log-transformed the survival estimates to achieve approximate normality and regressed them on continuous measures of urbanization using the model selection process as described above.

An underlying assumption of matrix population modeling is that the vector parameters (rates of fecundity and survival) are summed so that estimated population parameters implicitly assume that the parameters of all individuals of a given group (in this case, size/year class) in the population are equal (Power 2007). As stressors may act on different portions of a population unequally, this lack of individuals' ability to influence λ can cause inaccurate results (Crouse et al. 1987; Adams 2002). However, Power (2007) notes that age-structured matrix models provide a descriptive method of estimating λ that allows for more size/age-related variation among population parameters, which is optimal for this study.

Results

Tier 1: Predicting age-0 presence

Age-0 presence/absence of most species responded poorly to both categorical and continuous measures of urbanization. Categorical and continuous models predicted the presence of age-0 individuals of one species each. Absences of age-0 *C. funduloides*, the only species with a significant model of categorical independent variables in this tier, were significantly higher at urban sites ($p=0.0002$). In fact, age-0 *C. funduloides* were absent at all urban sites. Likewise, *C. bairdi* was the only species with a significant presence/absence model of continuous measures of urbanization. The presence of age-0 *C. bairdi* was positively related to the percentage of watershed-scale development ($p=0.0260$), and negatively related to watershed

area (p=0.0420). Given the low number of species predicted by these models, I could not make valid comparisons between the two types of independent variables (Tables 2.3 and 2.6).

Tier 2: Predicting changes in age distributions

Age distributions, as polytomous response variables were more sensitive to urbanization than their binary counterparts from *Tier 1*. The age distributions of most speleophilic and simple lithophilic species were dominated by adult individuals in urban habitats, while those in forested habitats were more balanced and contained relatively higher proportions of age-0 and age-1 individuals (Figures 2.3 through 2.8).

Categorical and continuous independent variables predicted differences in all species' age distributions. "Urban" site classification negatively affected the relative abundances of age-0 *P. oreas* (p<0.0001); while it positively affected those of age-0 *E. flabellare* (p<0.0001) and *N. leptocephalus* (p<0.0001), and age-2$^+$ *C. bairdi* (p<0.0001) and *E. flabellare* (p=0.0010) (Tables 2.3 through 2.8).

Watershed area positively affected the relative abundances of age-0 *P. oreas* (p=0.004) and *C. bairdi* (p<0.0001), and age-2$^+$ *N. leptocephalus* (p<0.0001); while it negatively affected those of age-0 *E. flabellare* (p=0.0100), *C. funduloides* (p<0.0001), *A. rupestris* (p=0.0320), and *N. leptocephalus* (p<0.0001). Dispersal/proximity positively affected the relative abundances of age-2$^+$ *N. leptocephalus* (p=0.0360), and negatively affected that of age-0 *C. funduloides* (p=0.0150) (Tables 2.3 through 2.8).

Percentages of riparian-scale development and thalweg embeddedness were the most prevalent continuous predictors of polytomous responses, each of which having influenced the age distributions of five species. The percentage of watershed development, which was highly correlated with that of riparian development (R^2=0.49, p=0.0008), was often an insignificant

predictor of reproductive success, and was excluded from final polytomous models. The percentage of riparian scale development negatively affected the relative abundances of age-0 *C. bairdi* (*p*=0.0003), *P. oreas* (*p*<0.0001), and *C. funduloides* (*p*<0.0001), and age-2$^+$ *A. rupestris* (*p*=0.0030); while it positively affected those of age-0 *E. flabellare* (*p*<0.0001) and *N. leptocephalus* (*p*<0.0001), and age-2$^+$ *C. bairdi* (*p*=0.0005). The percentage of thalweg embeddedness negatively affected the relative abundances of age-0 *E. flabellare* (*p*=0.0470), *C. funduloides* (*p*=0.011), and *N. leptocephalus* (*p*<0.0001), and age-2$^+$ *E. flabellare* (*p*=0.0240); while it positively affected those of age-0 *P. oreas* (*p*<0.0001), and age-2$^+$ *N. leptocephalus* (*p*=0.0002) (Tables 2.3 through 2.8).

Watershed area exhibited significance in three species' continuous polytomous models, where it negatively affected the relative abundances of age-0 *E. flabellare* (*p*<0.0001) and *P. oreas* (*p*<0.0001); and positively affected those of age-0 *C. bairdi* (*p*<0.0001) and age-2$^+$ *E. flabellare* (*p*<0.0001). Percentages of pool habitat and coarse substrate also influenced the age distributions of three species. Dispersal/proximity did not retain significance in any species' continuous polytomous models (Tables 2.3 through 2.8).

For this tier, models with continuous independent variables outperformed their categorical counterparts by having consistently lower AIC values. Additionally, when modeled alongside other continuous independent variables, the effects of watershed area were rendered insignificant for *C. funduloides*, *N. leptocephalus*, and *A. rupestris*. Furthermore, the effects of spatial autocorrelation were also insignificant in models with continuous measures of urbanization for *C. funduloides* and *N. leptocephalus* (Tables 2.3 through 2.8).

Tier 3: Predicting changes in population growth rates

Population growth rates of speleophils and most lithophils were negatively influenced by riparian-scale measures of urbanization, while those of gravel mound nesting *N. leptocephalus* were not. Multiple linear regression models that incorporated categorical and continuous measures of urbanization predicted changes in the λ values of three and five species, respectively. All of these models were free of the effects of watershed area and spatial autocorrelation. "Urban" site classification positively affected the λ values of *E. flabellare* (*p*=0.0008), *P. oreas* (*p*<0.0001), and *C. funduloides* (*p*=0.0210) (Tables 2.3 through 2.8).

The percentage of riparian-scale development was the most prevalent continuous independent variable, having negatively affected the λ values of *C. bairdi* (*p*=0.0250), *E. flabellare* (*p*=0.0110), and *A. rupestris* (*p*=0.0020); and positively affected those of *P. oreas* (*p*=0.0050), and *C. funduloides* (*p*=0.0040). Moreover, this variable was the only continuous predictor of the λ values of *E. flabellare*, *P. oreas*, and *C. funduloides*. The percentages of pool habitat and coarse substrate also influenced the λ values of two species. Models with categorical variables outperformed those with continuous variables for two (*E. flabellare* and *P. oreas*) of the three species whose λ values were predicted by both variable types (Tables 2.3 through 2.8).

The *post-hoc* survival analysis showed that the survival of age-0 *C. bairdi* and *E. flabellare* was negatively affected solely by the percentage of riparian-scale development (*p*<0.0001, R^2=0.87, *b*=-0.93 and *p*=0.0250, R^2=0.29, *b*=-0.54, respectively). Age-0 survival of other species was not predicted by any variable.

Model comparisons

Within tiers, continuous measures of urbanization are clearly better predictors of reproductive success. Firstly, AIC values of models with continuous variables were lower than

75% of their categorical counterparts. Additionally, excluding presence/absence models, continuous measures of urbanization sometimes predicted a species' reproductive performance when categorical models failed to do so (Tables 2.3 through 2.8).

Among tiers, the presence of age-0 individuals served as the worst metric of reproductive success. On the whole, these variables responded poorly to both categorical and continuous measures of urbanization. Age distributions, as polytomous responses, were much more sensitive to both categorical and continuous measures of urbanization. Although only three species' λ values were predicted by categorical measures of urbanization, continuous variables predicted differences in λ for the same number of species as they did for polytomous responses, generally with the same variables predicting both types of responses. Consequently, making comparisons between the two types of response variables is difficult. On the one hand, polytomous responses were predicted by multiple continuous measures of urbanization, while most λ values were predicted by one variable. On the other hand, AIC values of models with λ responses were orders of magnitude lower than those with polytomous responses. Additionally, λ values were not affected by watershed area or spatial autocorrelation.

Discussion

Tier 1: Predicting age-0 presence

The presence of age-0 individuals served as a poor measure of most species' reproductive success. Because this type of response variable treats all levels of reproductive success equally, reproductive inhibition can only be detected in instances of complete reproductive failure at a site. This situation arose most often for *C. bairdi* and *C. funduloides* which, of the six study species, seem to be the most responsive to urbanization given that the various measures of

reproductive success in subsequent tiers were consistently negatively affected by both categorical and continuous measures of urbanization. Because the results of *Tier 2* demonstrate that at least some successful reproduction occurs in urbanized reaches for most species (excluding *C. funduloides*), it is clear that complete reproductive failure in urban reaches is an infrequent occurrence for my study species. Although my metrics of spatial autocorrelation were not significant predictors of age-0 presence of *C. bairdi* and *C. funduloides*, it is very likely that this approach can be heavily influenced by dispersal from adjacent reaches, given that one encountered immigrant can equate to site-specific reproductive success. Binary classification of reproductive success did not provide unique results, and lacked the descriptive power provided by more detailed approaches. This approach provides an undesirably coarse resolution for assessing these species' patch-specific reproductive success.

Tier 2: Predicting changes in age distributions

Much of the polytomous model results support the hypothesis that the age distributions of most of the study species contain significantly higher proportions of adults in urbanized reaches. Firstly, the negative effects of both categorical and continuous measures of urbanization on the relative abundances of age-0 *P. oreas*, *C. funduloides*, and *A. rupestris* demonstrate that these variables contribute to the relative exclusion of age-0 individuals in favor of adults. This is corroborated by the negative influences of thalweg embeddedness on age-0 *E. flabellare* and *C. funduloides*. Likewise, categorical and continuous measures of urbanization positively influenced the relative abundance of age-2^+ *C. bairdi* and, consequently, the relative exclusion of age-0 individuals. These consistent patterns among speleophilic and lithophilic species suggest that their reproductive success is reduced in urbanized reaches, which is expressed through their unbalanced age distributions.

Some polytomous response models yielded slightly counterintuitive results. Urbanization positively influenced the relative abundance of age-0 *E. flabellare*, which contradicts my hypothesis that all age-0 speleophils would be relatively excluded by age-2^+ individuals in urban reaches. However, urbanization also positively influenced the relative abundances of age-2^+ *E. flabellare*, which suggests that it did not contribute to the relative exclusion of either age class by the other. As a result, the relative abundance of age-1 *E. flabellare* was negatively influenced by urbanization. Male and female *E. flabellare* mature at distinctly different rates. Accordingly, this age class may represent a mixture of both mature and immature individuals (Jenkins and Burkhead 1993). Because age-1 *E. flabellare* may be immature, this may in fact represent a negative effect of urbanization on its reproductive success. Alternatively, some authors have considered *E. flabellare* to be relatively tolerant of anthropogenic degradation (Trautman 1981; Gatz and Harig 1993), which suggests that the positive effect of urbanization may be accurate.

Tier 3: Predicting changes in population growth rates

As hypothesized, various measures of urbanization negatively influenced the population growth rates of speleophils *C. bairdi* and *E. flabellare*. However, λ values of lithophilic broadcast spawners *P. oreas* and *C. funduloides* were positively influenced by urbanization, which contradicts my hypothesis that they would be negatively affected. These results may be explained by differences in the species' life history strategies (Winemiller and Rose 1992; Winemiller 2005). *C. bairdi* and *E. flabellare* exhibit the relatively low fecundity, high parental care, and long life spans more closely associated with equilibrium life history strategies; while *P. oreas* and *C. funduloides* exhibit the relatively low parental care, and short life spans associated with more opportunistic life history strategies (Winemiller 2005). The persistence of species that exhibit relatively equilibrium life-history strategies must rely more heavily on juvenile

survivorship than relatively opportunistic species; while that of more opportunistic species relies less on juvenile survivorship, and more on their iteroparous spawning habits, early age-at-maturity, and short generation time. Opportunistic life-history strategists are typically more resilient to disturbances, and are capable of quickly recolonizing areas from which they are extirpated (Winemiller 2005). Furthermore, Albanese et al. (2004) considered *P. oreas* a "superior colonist". Consequently, λ values of *C. bairdi* were substantially lower at urban sites where lower proportions of age-0 individuals were present, as demonstrated in *Tier 2*. Additionally, the negative influences of urbanization on the λ values of *E. flabellare* suggest that age-1 *E. flabellare* are mostly immature. Conversely, λ values of *P. oreas* and *C. funduloides* were higher at urban sites where age-0 individuals were relatively excluded by adults because their higher fecundities compensate for low age-0 survivorship, and thus relative abundance.

In agreement with my hypothesis, λ values of *A. rupestris* were negatively influenced by urbanization. *A. rupestris* has been described as being less tolerant of anthropogenic disturbances than other centrarchids (Jenkins and Burkhead 1993). Unlike other centrarchids, *A. rupestris* is not a polyphilic nester, but instead prefers to nest in shallow gravely portions of streams that are often less abundant, or covered by silt, in urban reaches. The positive effects of the percentage of coarse substrate, accompanied by the negative effects of the percentage of pool habitat on the λ values of *A. rupestris* seem to support this. Additionally, as a species that exhibits a relatively equilibrium life-history strategy, *A. rupestris* does not mature until age-2^+ and expends relatively larger amounts of energy on parental care than more opportunistic species. Accordingly, the persistence of *A. rupestris* likely depends more heavily on juvenile survivorship than more opportunistic strategists. Similar to the species that exhibit relatively

equilibrium life-history strategies, the relative abundance of age-0 *A. rupestris* was significantly reduced at urban sites, which in turn was expressed through its λ values.

Gravel mound nest building and association

The nesting activities of *N. leptocephalus* may explain some seemingly counterintuitive relationships between urbanization and its reproductive success. I hypothesized that as a lithophil, the age distributions of *N. leptocephalus* would contain significantly lower proportions of age-0 individuals than those of age-2^+, and that λ values would be negatively influenced by urbanization. This was clearly not the case, as urbanization positively influenced the relative abundance of age-0 *N. leptocephalus*, and did not predict its λ values. However, unlike other lithophils, *N. leptocephalus* builds gravel mound nests for spawning, and continuously tends them to keep them free of silt (Maurikis et al. 1991; Wallin 1992). Unlike *A. rupestris*, which constructs saucer-shaped depression nests in gravel (Jenkins and Burkhead 1993), the nests of *N. leptocephalus* are strategically placed in the tails of pools where water flows in an upward direction, which allows for much of the suspended sediment load to pass over them (Maurikis et al. 1992). These nesting activities create elevated microhabitats of clean gravel substrate, which are often the only silt-free portions urbanized reaches. Peoples and Frimpong (Environmental Biology of Fishes, *in review*) identified the mitigating effects of the nesting activities of *N. leptocephalus* on their persistence in urbanized reaches. They found that although age-0 abundance was slightly lower in urban than in forested reaches, the strong positive effect of nest abundance on the reproductive success of *N. leptocephalus* dampened the overall negative effect of habitat degradation, and that the nesting activity of *N. leptocephalus* is likely a mechanism of their persistence in urbanized stream reaches whose instream habitats are seemingly degraded. Given these circumstances, it is likely that the negative effects of urbanization on the measures

of the reproductive success of *N. leptocephalus* used in this study are masked by the positive

effects of nesting activity.

The benefits of nest association (one or more species utilizing another species' nest for

spawning, Johnston 1994b) may have contributed to the positive effects of urbanization on the

population growth rates of *P. oreas* and *C. funduloides*, which are nest associates of *Nocomis*.

Johnston (1994a) suggested that nest associates achieve increased juvenile survivorship due to

the provision of clean gravel substrate for spawning, increased parental care, and the dilution

effect (decreased probability of predation). Furthermore, a side analysis of Peoples and

Frimpong's study identified the strong positive effects of the abundance of *N. leptocephalus*

nests on the reproductive success of various nest associates. In this study, the positive effects of

nest abundance dampened the negative effects of habitat degradation on the reproductive success

of nest associates. Similarly to *N. leptocephalus*, the benefits of nest association to the

reproductive success of *P. oreas* and *C. funduloides* may outweigh the negative influences of

urbanization.

Response variable comparisons

Among tiers, the presence/absence of age-0 individuals served as the worst metric of

reproductive success. On the whole, these variables responded poorly to urbanization and did

not provide unique results. However, this does not dismiss presence/absence modeling as a poor

approach to assessing the impacts of anthropogenic land use disturbance on stream fishes. The

reproductive success of species that are difficult to sample, or whose abundances are naturally

low throughout systems cannot be predicted using the approaches in *Tiers 2* and *3*. For these

species, presence/absence modeling can be an effective tool for assessing range-wide impairment

(Albanese et al. 2007; Ruiz and Peterson 2007; Hayer and Irwin 2008).

Of the three dependent variable types, age distributions seemed to be most sensitive to urbanization. Age distributions were more sensitive to both categorical and continuous measures of urbanization than binary classified responses, and were more sensitive to categorical measures of urbanization than λ values. Continuous variables predicted differences in λ for the same number of species as they did for polytomous responses, generally with the same variables (namely riparian-scale development) predicting both types of responses. Consequently, making comparisons between the two types of response variables is difficult. On the one hand, polytomous responses were predicted by multiple continuous measures of urbanization, while most λ values were predicted only by urbanization itself. On the other hand, AIC values of models with λ responses were orders of magnitude lower than those with polytomous responses, which suggests better model fit. Additionally, λ values seem to be free of the effects of watershed area and spatial autocorrelation.

In its own way, each type of response variable provides insight into the characteristics and/or mechanisms of population-level impairment in urban stream reaches. The absence of age-0 individuals can indicate complete reproductive failure at sites for species that are highly sensitive to urbanization, which can potentially make strong statements about population impairment in the most drastic of cases. Age distributions provide a characteristic of the patch-specific reproductive success of many stream fish populations. As demonstrated in *Tier 2*, the age distributions of most speleophils and lithophils in urban reaches were dominated by adults, while those in forested reaches were more balanced. These results are corroborated by Scott et al. (1986) , who documented this aspect of the population structure of cutthroat trout *Oncorhynchus clarki* in an urbanized Washington stream; and by Gray and Munkittrick (2005), who found a similar pattern in populations of slimy sculpin *C. cognatus* in heavily impacted

agricultural streams in Canada. Although not a definitive measure of reproductive success, this seems to be a relatively consistent pattern among the more sensitive study species, and should be thoroughly investigated to determine if this characteristic is applicable among species and systems.

Patch-specific population growth rates provide detailed insight into the local population dynamics of lotic fish populations and mechanisms of their impairment and persistence in urban reaches (Roff 1992; Power 2007). This approach incorporates the major components of fishes' life-history strategies (fecundity, survival, and longevity) into a useful description of overall population performance (Walthall and Stark 1997; Forbes and Calow 1999). Reduced population growth rates of more sensitive species in urban habitats may be a mechanism driving their decreased relative abundance or extirpation in urban assemblages that have been widely documented (Gatz and Harig 1993; Weaver and Garman 1994; Forbes and Calow 1999). Although they persist in lower abundances, species that are relatively intolerant of urbanization cannot replenish their populations in urban habitats as well as they can in forested ones, resulting in decreased relative abundance in assemblages.

Post-hoc survival analysis

Much of this study's results suggest significant reductions in the survival of age-0 individuals of some species in urban habitats, which has been described by other authors (Varanasi et al. 1993; Able et al. 1998). A simple *post-hoc* analysis showed that survival of age-0 *C. bairdi* and *E. flabellare* was negatively influenced by the percentage of riparian-scale development, while the survival of age-0 individuals in other species was not predicted by any variable. Although this approach provided rather coarse estimates of site-specific age-0 survival, it provides an interesting perspective on these species' population dynamics which helps to

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explain the trends in their reproductive success. As urbanization degrades spawning habitat for speleophils, those that are unable to disperse (possibly due to isolation caused by wetted channel desiccation) are likely forced to make sub-optimal spawning habitat choices, which in turn decreases age-0 survival and is reflected through the species' λ values. Additionally, the null effects of urbanization on the survival of age-0 *P. oreas* and *C. funduloides* seem to corroborate the notion that their resilient life history strategies make them better suited to persist in degraded reaches; and/or that nest association may dampen the negative effects of urbanization on these species' reproductive success. Alternatively, the null effects may be attributable to the coarseness of my age-0 survival estimates, which are largely determined by assumption-laden estimates of size/age-specific fecundity and survival. This study was not designed to quantify age-0 survival, and my *post-hoc* survival analysis is clearly limited by data availability. A more descriptive study that employs more quantitative methods of estimating age-0 survival (Vaughan and Salia 1976; Aalto and Newsome 1980) is necessary to determine the effects of urbanization on various species' age-0 survival. Such a study would provide vital insight into the patch-specific population dynamics and mechanisms of various species' impairment and persistence in urban stream habitats.

Other mechanisms of impairment

This study clearly shows that the degradation of physical instream habitat in urban stream reaches can reduce the reproductive success of speleophilic and lithophilic fishes, which may be a mechanism of the impairment of their populations. However, I do not assume that reduced reproductive success is the only mechanism of impairment, and that physical habitat degradation is the only pathway. Firstly, urbanization has been shown to alter the food webs of stream ecosystems (Ulseth and Hershey 2005; Singer and Battin 2007). These changes in available food

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resources may alter some fishes' energy uptake (Gatz and Harig 1993; Weaver and Garman 1994), thus allowing for less energy to be devoted to reproduction. Secondly, water quality is also greatly affected in urban stream reaches. Many studies have identified harmful levels of temperature (Galli 1991), dissolved oxygen (Boet et al. 1999; Gafny et al. 2000), metals (Wilber and Hunter 1979; Neal et al. 1997), pesticides (Daniels et al. 2000; Hoffman et al. 2000), and organic pollutants (Smart et al. 1985; Winger and Duthie 2000) in urbanized portions of streams, which surely contributes to reduced reproductive success of fishes through various physiological pathways (Forbes and Calow 1999). These processes likely operate independently of, or in conjunction with physical habitat degradation to impair lotic fish populations (Walsh et al. 2005). Although this study focuses on the effects of physical habitat degradation, the other aforementioned affects are likely captured in the measures of reproductive success used in all three tiers.

Temporal variation

The patterns of reproductive success I observed surely vary over time. As these data were collected during a relatively short time period (four months), they cannot be regarded as more than a description of population characteristics at that time. Stochastic events such as floods, droughts, or freezing play a large role in the annual reproductive performance of lotic fish populations (Moyle and Vondracek 1985; Schlosser 1985; Noltie and Keenleyside 1986; Bayley and Osborne 2006; Huusko et al. 2007), and may contribute to, dampen, or even counteract the effects of urbanization. However, the patterns of reproductive success were relatively consistent among species, largely explainable by urbanization, and corroborated the results of other studies (Scott et al. 1986; Gray and Munkittrick 2005). Additionally, many studies point out that in comparative ecological studies, time is often substituted by space. By capturing a wide range of

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habitat conditions, comparative studies capture a temporal range of demographic patterns (Allan 2004; Fitzpatrick et al. 2004; Frimpong et al. 2005a). Future research should address temporal variation in the reproductive success of fish populations in urban stream reaches.

Conclusions

As lotic fishes become increasingly threatened by anthropogenic development, a detailed understanding of the mechanisms that contribute to their imperilment and persistence in degraded habitats is crucial for future conservation efforts (Paul and Meyer 2001). This study demonstrates that the reproductive success of many fishes is inhibited by the detrimental effects of urbanization on physical instream habitat, which can express itself through the absence of age-0 individuals, unbalanced age distributions, and altered population growth rates. Additionally, reduced reproductive success is likely a mechanism of population-level impairment in urbanized stream reaches. These characteristics should be further evaluated among species and systems.

Although none of the species in this study receive state or federal protection, urbanization likely influences closely-related species similarly due to similarities in various aspects of their life-histories. Accordingly, knowledge of the factors that affect populations of *C. funduloides*, *P. oreas*, and *A. rupestris* can be applied to the conservation of endangered species such as *C. elongatus* and *P. tennessensis*, and to Roanoke bass *A. cavrifons*, whose status is considered vulnerable in Virginia. Because many governmental species protection programs often limit sampling and/or sacrifice of individuals for life-history studies, the species used in this study may serve as surrogates for more protected species. Furthermore, given the strong negative effects of the percentage of riparian-scale development, I echo the call of many authors (Wang et

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al. 2001; Snyder et al. 2003; Roy et al. 2005) that in urbanizing watersheds, forested riparian

corridors must be maintained to conserve populations of stream fishes for future generations.

Table 2.1. Substrate types, particle size ranges (mm), and identification codes.

Substrate type	Size range (mm)	Code
Boulder	>256	Bo
Cobble	16 - 256	Co
Gravel	2 to 15	Gr
Sand	0.06-1	Sa
Silt/clay	<0.06	Si
Detritus	Dead organic material	De

Table 2.2. Fecundity-at-length equations derived from primary literature for six study species in the middle New River basin, Virginia; where y is the estimated fecundity value of any standard length x.

Species	Locality	Equation	Source
Mottled sculpin *Cottus bairdi*	Northeast North Caronia	$y = 2.64x - 84.54$	Grossman et al. 2002
Fantail darter *Etheostoma flabellare*	Southwest Virginia	$y=10.04x-303.83$	M. L. Henebry, unpublished data
Mountain redbelly dace *Phoxinus oreas*	Northeast Tennessee	$y=19.89x-390.51$	Hamed et al. 2008
Rosyside dace *Clinostomus funduloides*	Western Maryland	$y=16.24x-854.06$	R. Davis 1972
Rock bass *Ambloplites rupestris*	Southern Wisconsin	$y=75.38x-8795.4$	Becker 1983
Bluehead chub *Nocomis leptocephalus*	Southwest Virginia	$y=9.04x-28.82$	Jenkins and Burkhead 1993

Table 2.3. Categorical and continuous predictors of changes in age-0 presence, age distributions, and population growth rates of *C. bairdi* in urban and forested tributaries to the middle New River, Virginia.

	Tier			
	2: Demographic proportions			
Model type	Multiple logistic, polytomous response			
Habitat descriptors	Continuous	Categorical	Continuous	Continuous
AIC	20.8	1589	1525	4.5
Significant variables (p-value, lower Wald confidence limit<*point estimate*<upper Wald confidence limit)	Watershed area (*p*=0.026, 0.001<*0.002*<0.08) % Watershed development (*p*=0.042, 11.61<*999.99*<999.99)	Land use (age-2+) (*p*<0.0001, 5.02<*12.63*<31.54) Watershed area (age-0) (*p*<0.0001, 3.54<*5.63*<9.22)	Watershed area (age-0) (*p*<0.0001, 2.78<*4.58*<7.54) % Riparian development (age-0) (*p*=0.0003, 0.007<*0.04*<0.22) % Riparian development (age-2+) (*p*=0.0005, 1.86<*8.03*<34.64) % Coarse substrate (age-2) (*p*=0.0045, 1.14<*35.49*<999.99) % Pool (age-0) (*p*=0.0015, 16.01<*49.41*<152.50) % Pool (age-2+) (*p*=0.034, 1.10<*4.02*<14.59)	% Coarse substrate (*p*=0.022, R^2=0.04, *b*=0.66) % Watershed development (*p*=0.006, R^2=0.17, *b*=-1.94) % Riparian development (*p*=0.025, R^2=0.20, *b*=-0.74) % Pool (*p*=0.014, R^2=0.38, *b*=1.03)
Somer's D	8			
Gamma	8			
Global R^2				0.79
Global *p*	0.007	<0.0001	<0.0001	0.045

Table 2.4. Categorical and continuous predictors of changes in age-0 presence, age distributions, and population growth rates of *E. flabellare* in urban and forested tributaries to the middle New River, Virginia.

	Tier			
	2: Demographic proportions		**3: Rate of population growth**	
Model type	Multiple logistic, polytomous response		Multiple linear, continuous response	
Habitat descriptors	Categorical	Continuous	Categorical	Continuous
AIC	2942	2925	-18.3	-12.7
Significant variables (p-value, lower Wald confidence limit<*point estimate*<upper Wald confidence limit)	Land use (age-0) ($p<0.0001$, 1.66<*2.82*<4.61) Land use (age-2+) ($p=0.001$, 1.36<*2.12*<3.33) Watershed area (age-0) ($p=0.010$, 0.35<*0.55*<0.87)	Watershed area (age-0) ($p<0.0001$, 0.20<*0.37*<0.66) Watershed area (age-2+) ($p<0.0001$, 1.69<*2.93*<5.06) % Riparian development (age-0) ($p<0.0001$, 1.97<*3.70*<6.97) Thalweg embeddedness (age-0) ($p=0.047$, 0.96<*0.98*<0.99) Thalweg embeddedness (age-2+) ($p=0.024$, 0.96<*0.98*<0.99)	Land use ($p=0.0008$, $R^2=0.54$, $b=0.73$)	% Riparian development ($p=0.011$, $R^2=0.36$, $b=-0.60$)
Somer's D				
Gamma				
Global R^2				0.36
Global p	<0.0001	<0.0001	0.0008	0.011

Table 2.5. Categorical and continuous predictors of changes in age-0 presence, age distributions, and population growth rates of *P. oreas* in urban and forested tributaries to the middle New River, Virginia.

	Tier			
	2: Demographic proportions		3: Rate of population growth	
Model type	Multiple logistic, polytomous response		Multiple linear, continuous response	
Habitat descriptors	Categorical	Continuous	Categorical	Continuous
AIC	955	929	2.2	6.3
Significant variables (p-value, lower Wald confidence limit<point estimate<upper Wald confidence limit)	Land use (age-0) ($p<0.0001$, $0.02<0.03<0.04$) Watershed area (age-0) ($p=0.004$, $1.51<3.67<8.96$)	Watershed area (age-0) ($p<0.0001$, $11.39<52.29<240.15$) % Riparian development (age-0) ($p<0.0001$, $0.001<0.002<0.004$) Thalweg embeddedness (age-0) ($p<0.0001$, $1.02<1.05<1.08$) % Pool (age-0) ($p=0.0042$, $2.30<13.99<85.34$)	Land use ($p<0.0001$, $R^2=0.74$, $b=0.86$)	% Riparian development ($p=0.0005$, $R^2=0.65$, $b=0.81$)
Somer's D		0.75		
Gamma		0.81		
Global R^2				0.39
Global p	<0.0001	<0.0001	<0.0001	0.026

Table 2.6. Categorical and continuous predictors of changes in age-0 presence, age distributions, and population growth rates of *C. funduloides* in urban and forested tributaries to the middle New River, Virginia.

	Tier				
	1: Juvenile presence/absence	2: Demographic proportions		3: Rate of population growth	
Model type	Multiple logistic, binary response	Multiple logistic, polytomous response		Multiple linear, continuous response	
Habitat descriptors	Categorical	Categorical	Continuous	Categorical	Continuous
AIC	10.1	2259	2218	1.6	-2.2
Significant variables (p-value, lower Wald confidence limit<point estimate<upper Wald confidence limit)		Watershed area (age-0) ($p<0.0001$, $0.25<0.37<0.55$) Proximity (age-0) ($p=0.015$, $0.33<0.54<0.89$)	Proximity (age-0) ($p=0.005$, $3.81<86.40<999.99$) % Riparian development (age-0) ($p=0.0003$, $0.0002<0.019<0.162$) Thalweg embeddedness (age-0) ($p=0.011$, $0.83<0.90<0.98$)	Land use ($p=0.021$, $R^2=0.35$, $b=0.59$)	% Riparian development ($p=0.004$, $R^2=0.49$, $b=0.70$)
	Land use ($p=0.0002$, $0.002<0.003<0.004$)				
Somer's D	0.78		0.18		
Gamma	0.78		0.22		
Global R^2					0.65
Global p	0.0002	<0.0001	<0.0001	0.021	0.0005

Table 2.7. Categorical and continuous predictors of changes in age-0 presence, age distributions, and population growth rates of *A. rupestris* in urban and forested tributaries to the middle New River, Virginia.

	Tier		
	2: Demographic proportions		3: Rate of population growth
Model type	Multiple logistic, polytomous response		
Habitat descriptors	Categorical	Continuous	Continuous
AIC	537	527	6.4
Significant variables (p-value, lower Wald confidence limit<point estimate<upper Wald confidence limit)	Watershed area (age-0) (p=0.032, 0.01<*0.59*<0.78)	Watershed area (age-0) (p=0.001, 0.001<*0.003*<0.09)	% Coarse substrate (p=0.002, R^2=0.13, b=0.85)
		% Riparian development (age-2+) (p=0.003, 0.04<*0.14*<0.52)	% Riparian development (p=0.002, R^2=0.38, b=-0.91)
		% Coarse substrate (age-0) (p<0.0001, 1.82<*181.67*<999.99)	% Pool (p=0.01, R^2=0.29, b=-0.56)
		% Pool (age-2+) (p=0.005, 0.01<*0.07*<0.45)	
Somer's D			
Gamma			
Global R^2			0.80
Global p	0.004	<0.0001	0.004

Table 2.8. Categorical and continuous predictors of changes in age-0 presence, age distributions, and population growth rates of *N. leptocephalus* in urban and forested tributaries to the middle New River, Virginia.

	Tier	
	2: Demographic proportions	
Model type	Multiple logistic, polytomous response	
Habitat descriptors	Categorical	Continuous
AIC	6254	6198
Significant variables (p-value, lower Wald confidence limit<*point estimate*<upper Wald confidence limit)	Land use (age-0) (*p*<0.0001, 2.22<*2.69*<3.26)	Proximity (age-2) (*p*=0.0024, 0.14<*0.30*<0.65)
	Watershed area (age-0) (*p*<0.0001, 0.24<*0.34*<0.46)	% Riparian development (age-0) (*p*<0.0001, 2.18<*2.74*<3.44)
	Watershed area (age-2) (p<0.0001, 1.69<*2.54*<3.86)	Thalweg embeddedness (age-0) (*p*<0.0001, 0.95<*0.96*<0.97)
	Proximity (age-2+) (*p*=0.036, 0.23<*0.47*<0.95)	Thalweg embeddedness (age-2+) (*p*<0.002, 1.01<*1.03*<1.04)
Somer's D		
Gamma		
Global R^2		
Global *p*	<0.0001	<0.0001
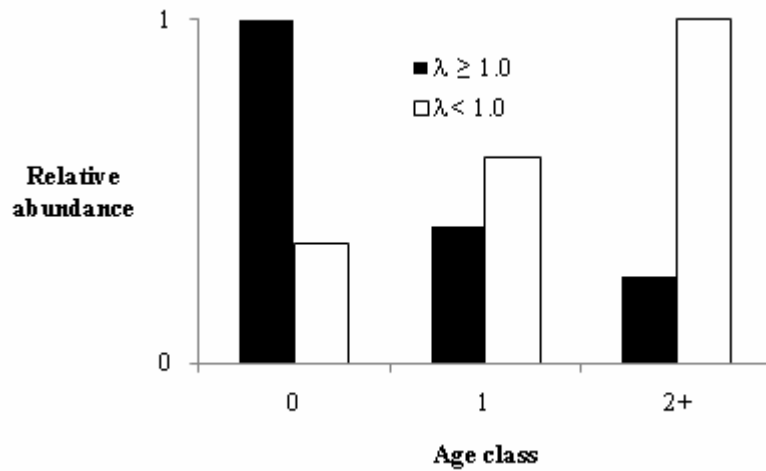
Figure 2.1. Conceptual age distributions of self-sustaining populations (λ ≥ 1.0) and non self-sustaining populations (λ < 1.0).
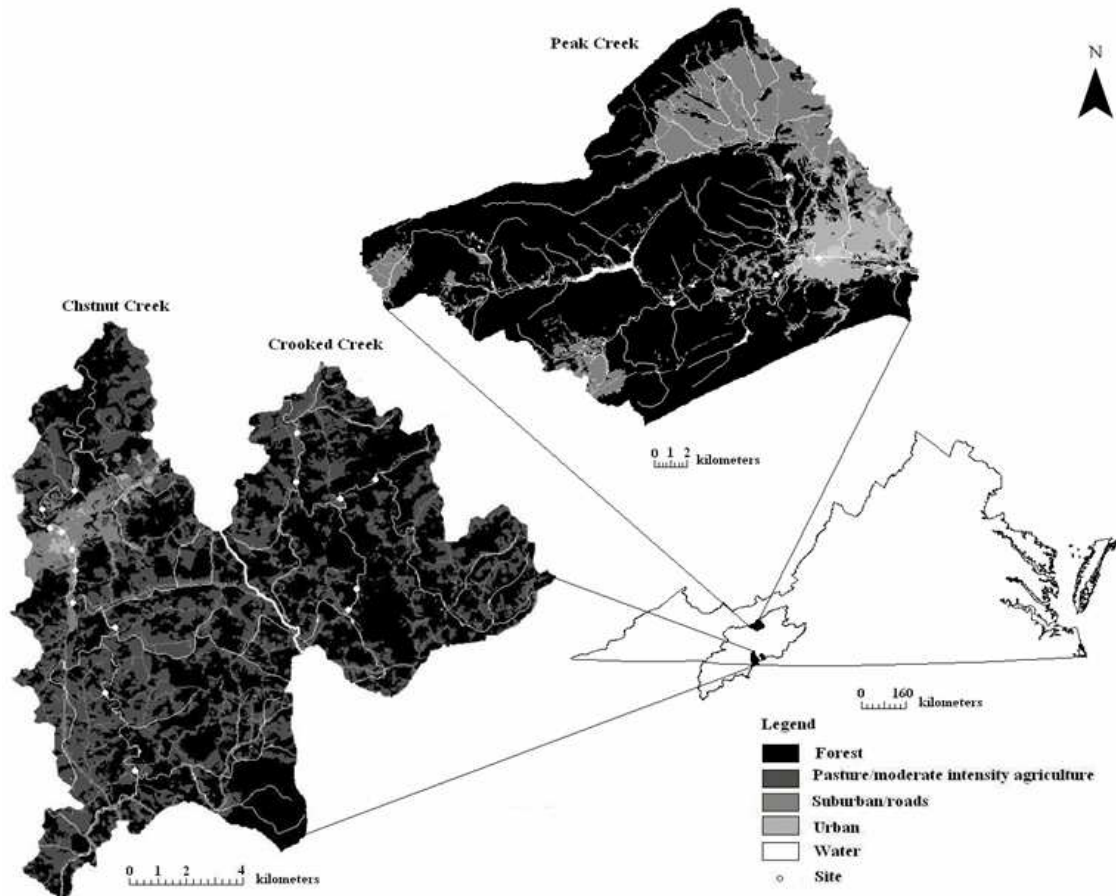
Figure 2.2. Land use of Chestnut, Crooked, and Peak Creeks, and their locations in the middle New River basin, Virginia.

Figure 2.3. Averaged age distributions of *C. bairdi* in urban and forested reaches of tributaries to the New River, Virginia. Error bars represent standard errors.
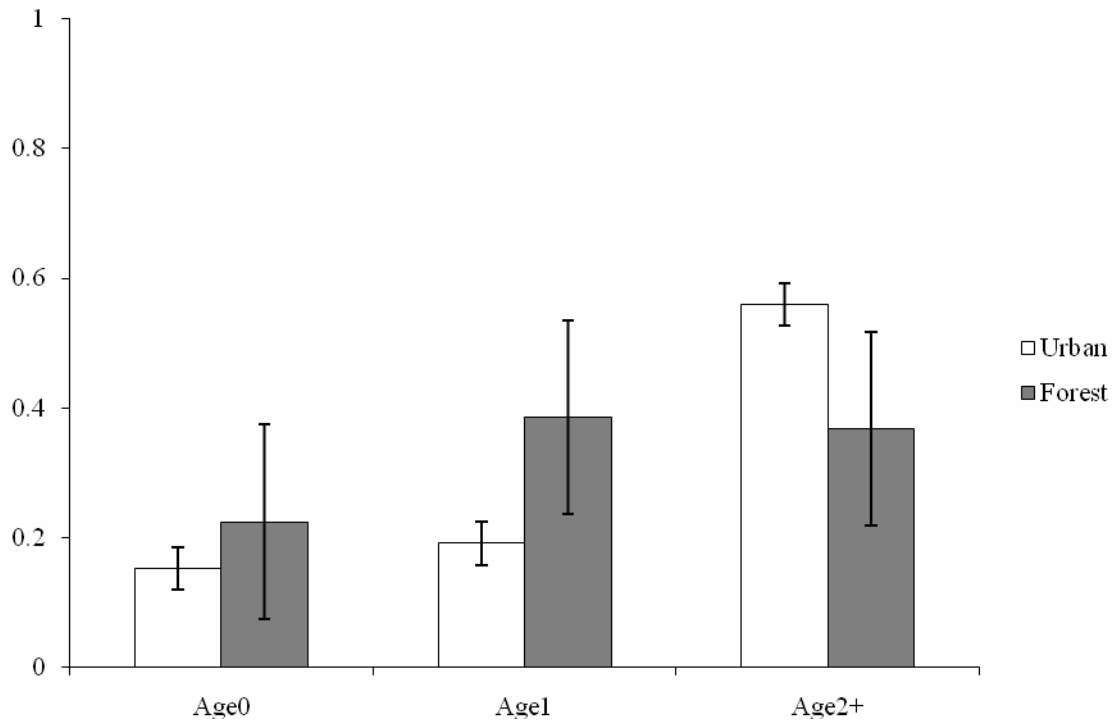
Figure 2.4. Averaged age distributions of *E. flabellare* in urban and forested reaches of tributaries to the New River, Virginia. Error bars represent standard errors.
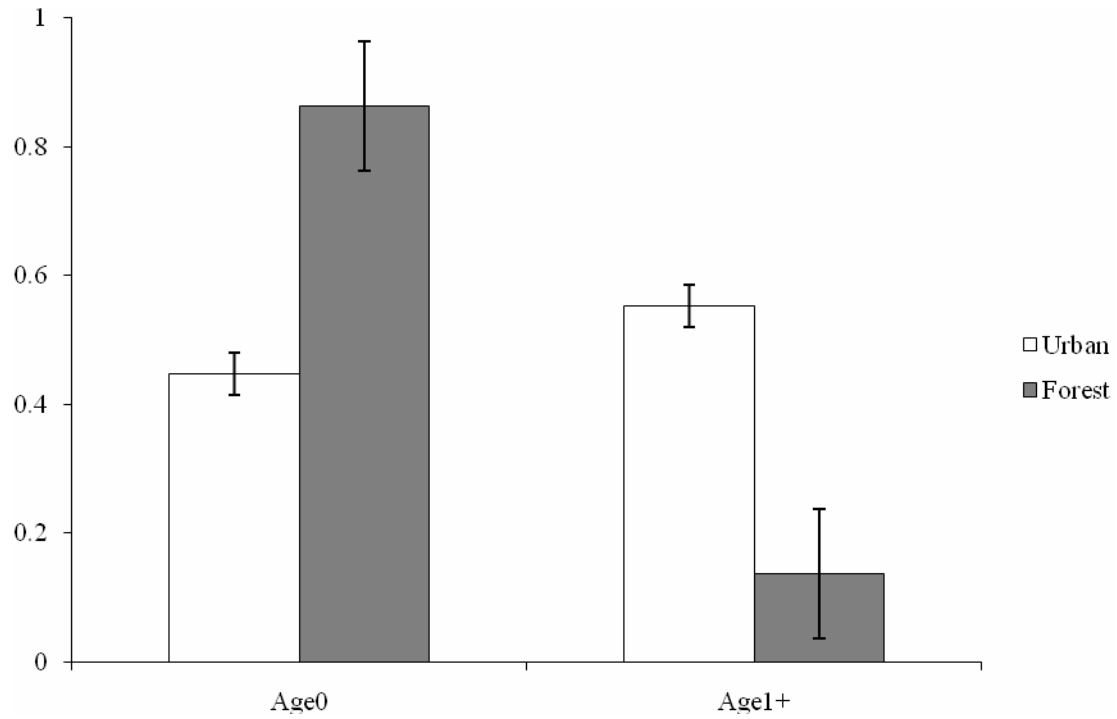
Figure 2.5. Averaged age distributions of *P. oreas* in urban and forested reaches of tributaries to the New River, Virginia. Error bars represent standard errors.

Figure 2.6. Averaged age distributions of *C. funduloides* in urban and forested reaches of tributaries to the New River, Virginia. Error bars represent standard errors.

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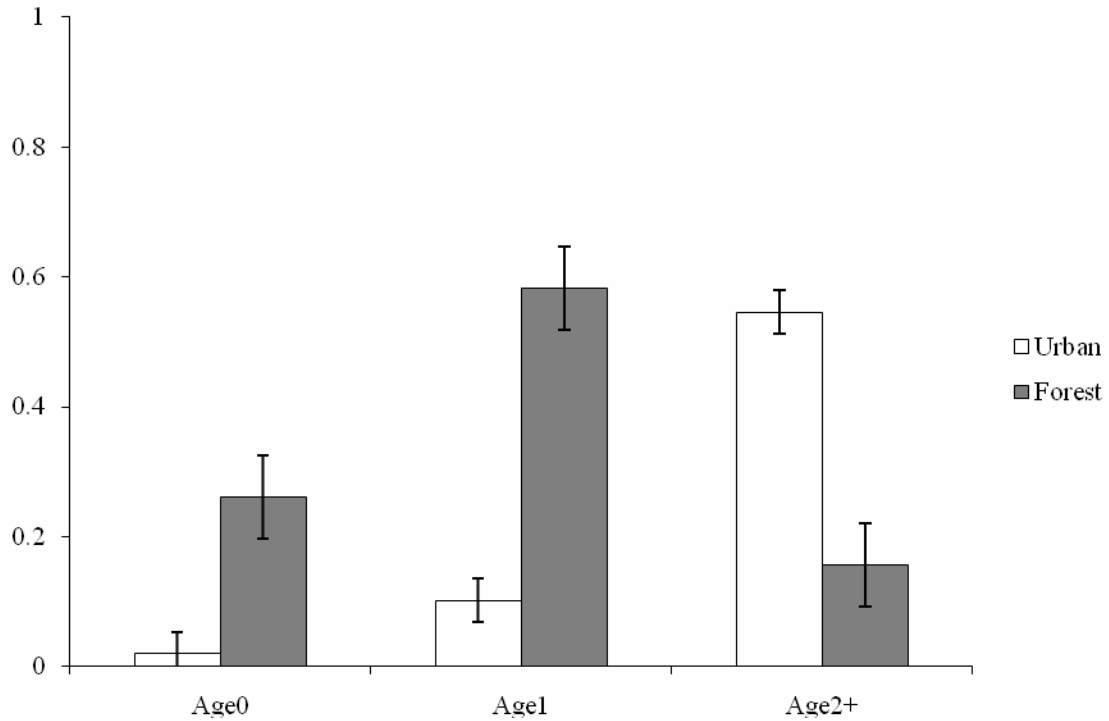**Figure 2.7**. Averaged age distributions of *A. rupestris* in urban and forested reaches of tributaries to the New River, Virginia. Error bars represent standard errors.

Figure 2.8. Averaged age distributions of *N. leptocephalus* in urban and forested reaches of tributaries to the New River, Virginia. Error bars represent standard errors.
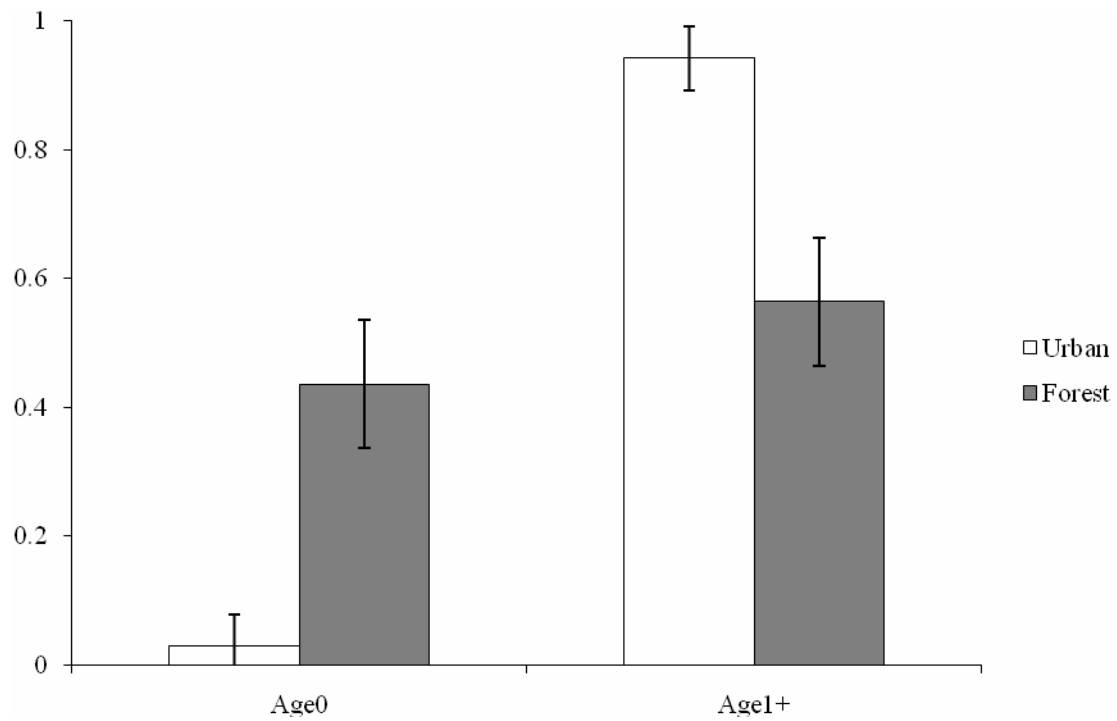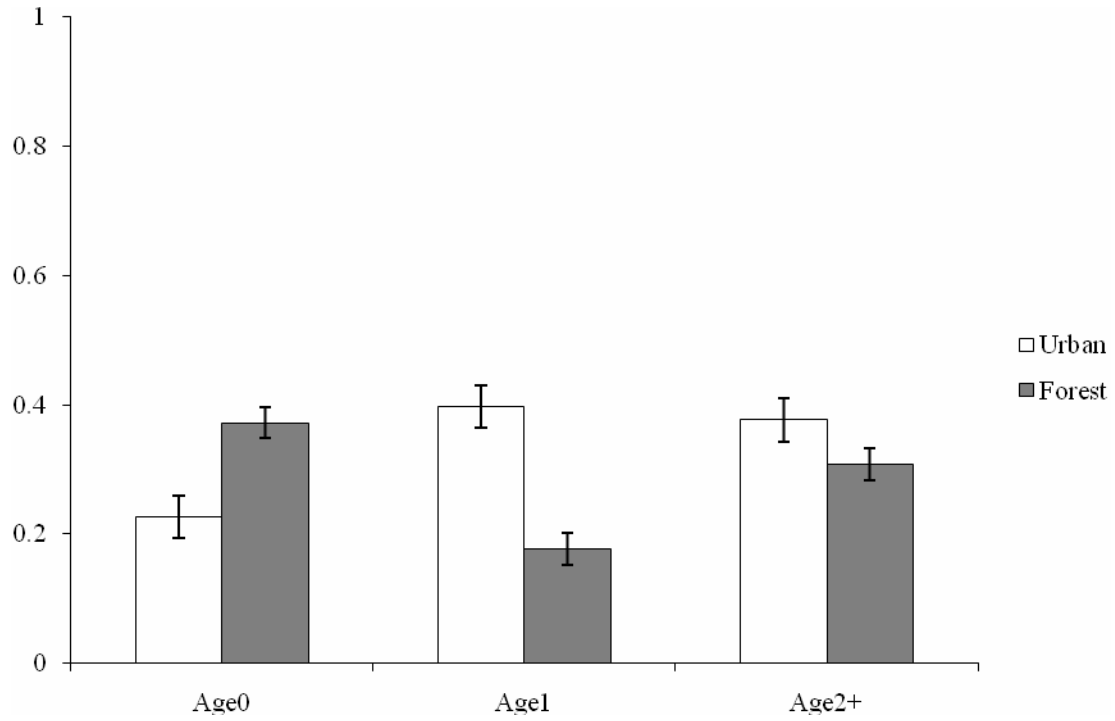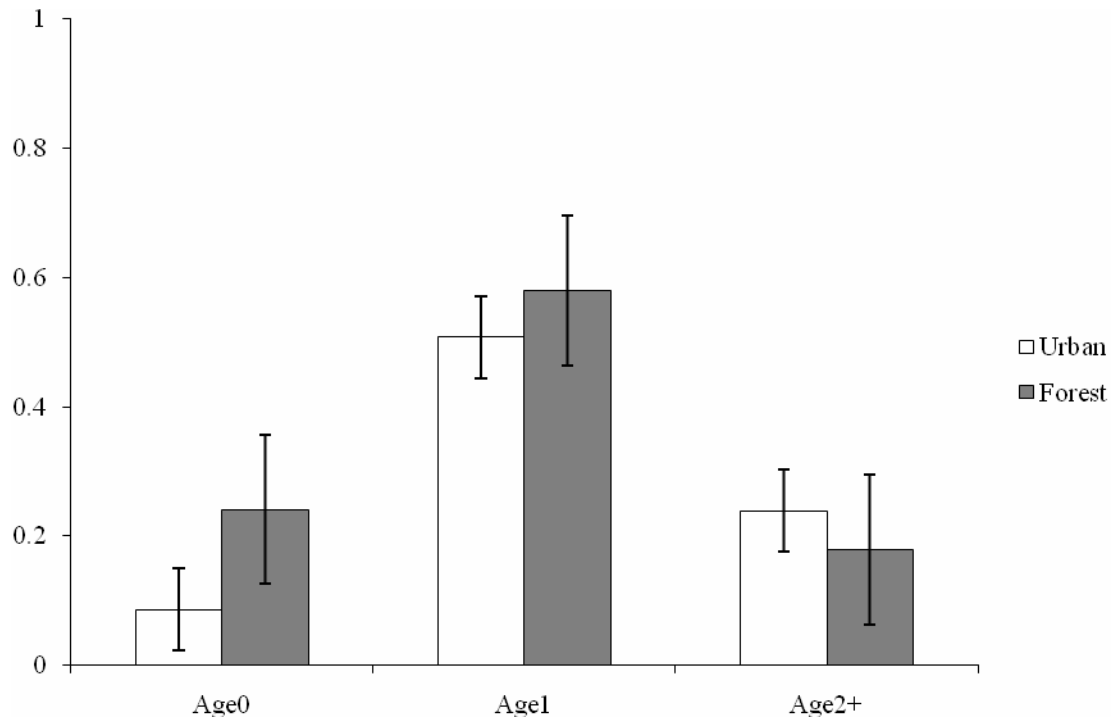
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Appendix A. Multiple-season estimates of detection probability (p) and associated standard errors (SE) for species in the NAWQA dataset.

Species	p	SE	Number of sites present
Common carp *Cyprinus carpio*	0.74	0.02	124
Yellow bullhead *Amerius natalis*	0.50	0.03	94
Spotted sunfish *Lepomis punctatus*	0.76	0.02	89
Bigmouth shiner *Notropis dorsalis*	0.75	0.05	72
Longear sunfish *Lepomis megalottis*	0.87	0.02	65
Fathead minnow *Pimephales promelas*	0.68	0.03	65
Black crappie *Pomoxis nigromaculatus*	0.42	0.03	65
Warmouth *Lepomis gulosus*	0.59	0.04	64
Threadfin shad *Dorosoma cepedinium*	0.67	0.03	62
Yellow perch *Perca flavescens*	0.36	0.06	53
Spotfin shiner *Cyprinella spiloptera*	0.80	0.03	49
Flathead catfish *Pylodictis olivaris*	0.62	0.04	49
Johnny darter *Etheostoma nigrum*	0.74	0.04	48
Sand shiner *Notropis stramineus*	0.76	0.04	48
Redear sunfish *Lepomis microlophus*	0.63	0.04	48
Golden redhorse *Moxostoma erythrurum*	0.79	0.03	45
Shorthead redhorse *Moxostoma macrolepidotum*	0.74	0.04	41
Smallmouth buffalo *Ictiobus bubalus*	0.59	0.04	41
White crappie *Pomoxis annularis*	0.47	0.05	40
Freshwater drum *Aplodinotus grunniens*	0.77	0.04	40
Tesselated darter *Etheostoma olmstedi*	0.86	0.03	38
Bullhead minnow *Pimephales vigilax*	0.63	0.04	38
Black bullhead *Amerius melas*	0.50	0.04	37
Longnose gar *Lepisosteus osseus*	0.60	0.05	37
Emerald shiner *Notropis ahterinoides*	0.70	0.05	36
Orangespotted sunfish *Lepomis humilis*	0.60	0.04	36
American eel *Anguilla rostrata*	0.77	0.03	35
Blacktail shiner *Cyprinella venusta*	0.64	0.05	35
Brook silverside *Labidesthes sicculus*	0.50	0.04	34
Blackside darter *Percina maculata*	0.74	0.05	33
Striped shiner *Luxilis chrysocephalus*	0.90	0.03	32
River carpsucker *Carpoides carpio*	0.66	0.05	31
Logperch *Percina caprodes*	0.71	0.04	30
Mottled sculpin *Cottus bairdi*	0.83	0.04	29
Blackstripe topminnow *Fundulus notatus*	0.40	0.04	29
Redfin pickerel *Esox americana*	0.50	0.06	28
Silver redhorse *Moxostoma anisurum*	0.51	0.06	27

Pirate perch *Aphredoderus sayanus*	0.61	0.05	26
Stonecat *Noturus flavus*	0.63	0.07	26
Quillback *Carpoides cyprinus*	0.54	0.06	26
Black redhorse *Moxostoma duquesni*	0.68	0.04	25
Spotted gar *Lepisosteus oculatus*	0.62	0.05	25
Blackbanded darter *Percina nigrofasciata*	0.88	0.04	23
Spotted sucker *Minitrena melanops*	0.63	0.05	23
Speckled dace *Rhinichthys osculus*	0.72	0.04	22
Walleye *Sander vitreum*	0.54	0.07	22
Bowfin *Amia calva*	0.54	0.05	22
Orangethroat darter *Etheostoma spectabile*	0.50	0.05	22
Rainbow darter *Etheostoma caeruleum*	0.84	0.05	21
Chain pickerel *Esox niger*	0.44	0.06	21
Longnose sucker *Catostomus catostomus*	0.78	0.05	21
Northern pike *Esox lucius*	0.66	0.51	21
White bass *Morone chrysops*	0.67	0.05	21
Blackspotted topminnow *Fundulus olivaceus*	0.61	0.06	20
Largescale stoneroller *Campostoma oligolepis*	0.78	0.05	19
Goldfish *Carasius auratis*	0.46	0.06	18
Silverjaw minnow *Erycrimba buccata*	0.55	0.05	18
Fallfish *Semotilus corporalis*	0.75	0.05	18
Brook stickleback *Culaea inconstans*	0.52	0.06	18
Central mudminnow *Umbra limi*	0.58	0.06	17
Dusky darter *Percina sciera*	0.43	0.06	17
White catfish *Amerius catus*	0.48	0.06	17
Creek chubsucker *Erimyozon oblongus*	0.40	0.06	17
Satinfin shiner *Cyprinella analostoma*	0.87	0.04	17
Cutthroat trout *Oncorhynchus clarki*	0.78	0.05	16
River chub *Nocomis micropogon*	0.71	0.06	15
Shortnose gar *Lepisosteus platostomus*	0.74	0.05	15
Blue catfish *Ictaluris furcatus*	0.59	0.06	15
Bigmouth buffalo *Ictiobus cyprinellus*	0.52	0.06	15
Suckermouth minnow *Phenacobius mirabilis*	0.42	0.06	15
Slender madtom *Noturus exilis*	0.69	0.06	14
Mountain sucker *Catostomus platyrynchus*	0.42	0.06	14
Slenderhead darter *Percina phoxocephala*	0.58	0.06	14
Dollar sunfish *Lepomis marginatus*	0.50	0.07	14
Striped bass *Morone saxatilis*	0.42	0.06	14
Brassy minnow *Hybognathus hankinsoni*	0.54	0.07	13
Yellowfin shiner *Notropis lutipinnis*	0.73	0.06	13

Bluefin stoneroller *Campostoma pauciradii*	0.62	0.07	13
Blacktail redhorse *Moxostoma poecilurum*	0.61	0.06	12
Coastal shiner *Notropis petersoni*	0.62	0.07	12
Black buffalo *Ictiobus niger*	0.47	0.07	12
Redfin shiner *Lythrurus umbratilis*	0.53	0.07	12
Pugnose minnow *Opsopoeodus emiliae*	0.47	0.07	12
Rhinohorn goby *Redigobius balteatus*	0.64	0.08	11
Alabama hogsucker *Hypentelium etowanum*	0.89	0.05	11
Sailfin molly *Poecilia latipinna*	0.77	0.07	11
Banded killifish *Fundulus diaphanus*	0.72	0.07	11
Freckled madtom *Noturus nocturnus*	0.55	0.08	11
Highfin carpsucker *Carpiodes velifer*	0.49	0.08	11
Grass carp *Ctenopharyngodon idella*	0.28	0.06	11
Southern brook lamprey *Ichthyomyzon gagei*	0.40	0.07	11
Largescale sucker *Catostomus macrocheilus*	0.71	0.07	10
Mountain whitefish *Prosopium williamsoni*	0.83	0.06	10
Northern studfish *Fundulus catenatus*	0.70	0.07	10
Sacramento sucker *Catostomus occidentalis*	0.75	0.07	10
Inland silverside *Menida beryllina*	0.56	0.07	10
Sauger *Sander canadensis*	0.60	0.08	10
Yellow bass *Morone mississippiensis*	0.26	0.06	10
Flathead chub *Platygobio gracilis*	0.78	0.07	9
Longnose shiner *Notropis longirostris*	0.74	0.07	9
Bigscale logperch *Percina macrolepida*	0.48	0.08	9
Bandfin shiner *Luxilus zonistius*	0.83	0.06	9
Silver chub *Macrhybopsis storeriana*	0.51	0.08	9
Chestnut lamprey *Ichthyomyzon castaneus*	0.37	0.08	9
River shiner *Notropis blennius*	0.29	0.07	9
Bigeye shiner *Notropis boops*	0.53	0.09	9
Swamp darter *Etheostoma fusiforme*	0.33	0.08	9
Piute sculpin *Cottus beldingi*	0.79	0.07	8
Redspotted sunfish *Lepomis miniatus*	0.59	0.09	8
Weed shiner *Notropis texanus*	0.83	0.07	8
Speckled madtom *Noturus leptacanthus*	0.62	0.08	8
Dusky shiner *Notropis cummingsae*	0.45	0.08	8
Florida gar *Lepisosteus platyrhincus*	0.88	0.07	8
Burbot *Lota lota*	0.55	0.09	8
Goldeye *Hiodon alosoides*	0.47	0.08	8
Texas cichlid Herichthys cyanoguttatum	0.69	0.09	8
Ozark minnow *Notropis nubilus*	0.77	0.08	8

Bigeye jumprock *Scartomyzon congestus*	0.61	0.09	8
Golden topminnow *Fundulus chrysotus*	0.58	0.10	8
Notropis amblops *Bigeye shiner*	0.77	0.11	7
Northern pikeminnow *Ptychocheilus oregonense*	0.65	0.08	7
Eastern silvery minnow *Hybognathus regius*	0.63	0.09	7
Shadow bass *Ambloplites ariommus*	0.61	0.09	7
Brindled madtom *Noturus miurus*	0.67	0.09	7
Ribbon shiner *Lythrurus fumeus*	0.46	0.08	7
Bluefin killifish *Lucania goodei*	0.64	0.10	7
Hogchoker *Trinectes maculatus*	0.44	0.10	7
White perch *Morone americana*	0.44	0.10	7
Stippled darter *Etheostoma punctulatum*	0.54	0.09	7
Blind cavefish *Astyanax mexicanus*	0.44	0.10	7
Guadalupe bass *Micropterus treculii*	0.57	0.10	7
Wedgespot shiner *Notropis greenei*	0.50	0.10	7
River redhorse *Moxostoma carinatum*	0.67	0.10	6
Flathead mullet *Mugil cephalus*	0.67	0.10	6
Bridgelip sucker *Catostomus columbianus*	0.84	0.07	6
Shield darter *Percina peltata*	0.78	0.09	6
Flier *Centrarchus macropterus*	0.40	0.10	6
Steelcolor shiner *Cyprinella whipplii*	0.43	0.09	6
American brook lamprey *Lampetra appendix*	0.60	0.10	6
Dwarf livebearer *Heterandria formosa*	0.84	0.08	6
Mississippi silvery minnow *Hybognathus nuchalis*	0.48	0.09	6
Comely shiner *Notropis amoenus*	0.52	0.14	6
Striped jumprock *Scartomyzon rupiscartes*	0.60	0.11	6
Speckled chub *Macrhybopsis aestivalis*	0.48	0.10	6
Ozark madtom *Noturus albater*	0.60	0.09	6
Lake chubsucker *Erimyzon sucetta*	0.78	0.10	6
Banded pygmy sunfish *Elassoma zonatum*	0.36	0.10	6
Clear chub *Notropis winchelli*	0.52	0.10	6
Ghost shiner *Notropis buchanani*	0.43	0.09	6
Seminole killifish *Fundulus seminolis*	0.53	0.11	6
Shovelnose sturgeon *Scaphirhynchus platorynchus*	0.43	0.09	6
Bluntface shiner *Cyprinella camura*	0.52	0.09	6
Greater jumprock *Scartomyzon lachneri*	0.44	0.10	6
American shad *Alosa sapidissima*	0.52	0.11	6
American flagfish *Jordanella floridae*	0.47	0.11	6

Appendix B. Watershed areas, land use classification type, and watershed- and riparian-scale percentages of land use for sites in Chestnut, Crooked, and Peak Creeks, Virginia.

System	Site	Watershed area (km^2)	Adjacent land use	Watershed				Riparian buffer			
				Urban	Suburban/ road	Agriculture	Forest	Urban	Suburban/ road	Agriculture	Forest
Chestnut Creek	1	138.8	Forest	0.7	11.6	38.7	48.9	0.0	4.2	0.0	95.8
Chestnut Creek	2	125.5	Forest	0.7	12.5	39.1	47.6	0.0	3.4	20.2	76.4
Chestnut Creek	3	110.0	Forest	0.6	11.6	39.3	48.5	0.0	31.0	27.6	41.4
Chestnut Creek	4	104.0	Urban	0.5	10.1	39.9	49.4	5.9	94.1	0.0	0.0
Chestnut Creek	5	101.2	Urban	0.2	8.6	40.7	50.4	17.6	82.4	0.0	0.0
Chestnut Creek	6	99.0	Urban	0.0	7.9	41.4	50.5	0.0	87.1	0.0	12.9
Chestnut Creek	7	97.1	Forest	0.0	7.6	41.9	50.3	0.0	27.1	31.4	41.4
Chestnut Creek	8	79.3	Forest	0.0	6.9	42.5	50.5	0.0	35.7	50.0	14.3
Chestnut Creek	9	44.4	Forest	0.0	7.2	33.9	58.8	0.0	12.1	27.3	60.6
Chestnut Creek	10	32.9	Forest	0.0	7.8	29.7	62.4	0.0	12.5	0.0	87.5
Crooked Creek	3	27.2	Forest	0.0	5.2	27.8	66.8	0.0	11.6	0.0	88.4
Crooked Creek	4	33.5	Forest	0.0	5.8	31.7	62.3	0.0	20.0	31.4	48.6
Crooked Creek	5	15.9	Forest	0.0	6.3	26.6	67.0	0.0	5.6	30.6	63.9
Crooked Creek	6	12.1	Forest	0.0	6.9	30.6	62.3	0.0	6.6	34.2	59.2
Peak Creek	1	173.6	Urban	0.6	8.0	18.3	72.7	0.0	50.9	3.8	45.3
Peak Creek	2	164.3	Urban	0.4	6.4	18.5	74.3	18.2	81.8	0.0	0.0
Peak Creek	4	49.5	Forest	0.0	2.3	8.5	88.4	0.0	2.8	8.3	88.9
Peak Creek	5	66.8	Forest	0.0	2.1	9.1	88.0	0.0	0.0	1.5	98.5

Appendix C. Age-specific fecundity and survival rates, and longevity of six fishes in tributaries to the middle New River, Virginia.

Species	Year class	Fecundity			Survival			Longevity (y)*
		Minimum	Median	Maximum	Minimum	Median	Maximum	
C. bairdi	0	0	0	0	0.524	0.602	0.524	
C. bairdi	1	27	54	82	0.274	0.363	0.274	6.5
C. bairdi	2$^+$	84	93	247	0.144	0.218	0.144	
E. flabellare	0	0	0	0	0.313	0.408	0.370	
E. flabellare	1	138	178	228	0.098	0.167	0.137	5.5
E. flabellare	2$^+$	238	298	599	0.031	0.068	0.051	
P. oreas	0	0	0	0	0.064	0.072	0.070	2.5
P. oreas	1$^+$	718	767	979	0.004	0.005	0.005	
C. funduloides	0	0	0	0	0.135	0.394	0.199	2.5
C. funduloides	1$^+$	1098	26	282	0.018	0.155	0.040	
A. rupestris	0	0	0	0	0.246	0.345	0.296	
A. rupestris	1	0	0	0	0.061	0.119	0.088	5.5
A. rupestris	2$^+$	1004	2738	8995	0.015	0.041	0.026	
N. leptocephalus	0	0	0	0	0.122	0.182	0.150	
N. leptocephalus	1	388	577	804	0.015	0.033	0.023	2.5
N. leptocephalus	2$^+$	811	940	1567	0.002	0.006	0.003	

*As reported by Jenkins and Burkhead (1993)