EFFECTS OF NATURAL FLOW VARIABILITY OVER SEVEN YEARS ON THE OCCURRENCE OF SHOAL-DEPENDENT FISHES IN THE ETOWAH RIVER

by

MEGAN M. HAGLER

(Under the Direction of Mary C. Freeman)

ABSTRACT

Annual fish surveys at ten shoals on the Etowah River, Georgia were conducted to assess the probability of occurrence of adult and young-of-year fish species under natural flow conditions over seven years, 1998-2004. Hierarchical logistic regression was used to simultaneously model factors thought to influence the occurrence of ten species from three families, Cyprinidae, Ictaluridae, and Percidae, including three imperiled species, at the microhabitat, survey, year and site levels. Microhabitat features were the strongest predictors of species occurrence. Increasing variability in summer stream flow (the number of days that stream flow exceeded the long-term average plus one standard deviation) reduced the odds of occurrence of most species. These findings suggest the need for stable summer flows in warmwater rivers to allow for strong species recruitment, with implications for the management of regulated rivers and possible response of natives fishes to climate change predictions for the southeastern United States.

INDEX WORDS: Natural flow variability, unregulated, Etowah River, *Podostemum*, *Percina antesella*, *Noturus munitus*, *Macrhybopsis aestivalis,* stream fishes

# EFFECTS OF NATURAL FLOW VARIABILITY OVER SEVEN YEARS ON THE OCCURRENCE OF SHOAL-DEPENDENT FISHES IN THE ETOWAH RIVER

by

MEGAN M. HAGLER

B.S., The University of Georgia, 2000

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2006

EFFECTS OF NATURAL FLOW VARIABILITY OVER SEVEN YEARS ON THE OCCURRENCE OF SHOAL-DEPENDENT FISHES IN THE ETOWAH RIVER

by

MEGAN M. HAGLER

| | |
|---|---|
| Major Professor: | Mary C. Freeman |
| Committee: | Byron J. Freeman<br>James T. Peterson |

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
May 2006

ACKNOWLEDGMENTS

Thanks to Bud Freeman and Mary Freeman for teaching me about fishes and streams, and for their guidance, steadfast support and friendship. Thanks to the members of the Freeman Lab, past and present, for all their help in conducting this research and making it fun. Thanks to Jim Peterson, whose statistical expertise improved my data analysis. Thanks to Bud Freeman and the Native Fish Conservancy Becker Grant for financial support.

Thanks to Curtiss Pernice for always being on my side and reminding me not to take myself too seriously.

My family has never hesitated to voice their love, support and encouragement throughout my life and academic career, and I am grateful. I know they are proud to see the first Garrison-Smith or Hagler-Shelton descendant get a graduate degree, especially my grandfather, Truman Hagler, who has lived 93 years to bear witness.

TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

Page

## INTRODUCTION

Stream flow variability is widely recognized to operate over multiple spatial and temporal scales and to influence species composition and diversity by sustaining different components of stream communities based on individual life-histories (Resh et al. 1988, Poff et al. 1997, Bunn and Arthington 2002, Biggs et al. 2005, Doyle et al. 2005). Much primary production, as well as feeding, growth and reproduction of aquatic fauna occur at low or base flows. Bank-full to moderate floods help flush sediment from gravel, connect the river to the floodplain and are responsible for most sediment transport over time, while catastrophic floods may significantly alter channel shape, displace biota downstream and essentially reset the system for new colonizers to rebuild the community. High-flow events can be a large source of mortality for larval and juvenile fishes in unregulated rivers, strongly influencing year-class strength (Starrett 1951, Schlosser 1985, Mion et al. 1998, Peterson and Kwak 1999, Magalhaes et al. 2003). Spring and summer flow conditions, especially the intensity and frequency of storm flow events, can influence population sizes by allowing for, or hampering, spawning activity and young-of-year (YOY) recruitment.

Quantifying relations between flow variables and biological processes has been recognized as essential to improving our understanding of the function of stream ecosystems (Mulholland et al. 1997, Poff et al. 1997, Bunn and Arthington 2002). Stream hydrology, controlled by climate, geology and land-cover, varies naturally from year-to-year and in relation to land use, with consequences to biota. Geographic variation in stream flow patterns may strongly influence fish community structure, for example, so that sites prone to harsh conditions (i.e., high temporal variability) may contain more trophic and habitat generalists (Poff and Allan 1995). Temporal flow variation within a stream influences ecological processes that shape communities (Poff et al. 1997, Richter et al. 1997, Bunn and Arthington 2002, Doyle et al. 2005). Human uses directly alter flow regimes by water withdrawal, water diversion and by regulation of river flow by dams, often with profound effects on river biota (Postel 2000, Baron et al. 2002). Understanding biotic responses to natural flow variability can help us to make predictions about how stream ecosystems and biota may respond to human alterations in flow regimes, and to prioritize management alternatives for regulated systems that will be most beneficial to native biota.

My objective was to evaluate how natural flow variability influences the probability of occurrence of shoal-dependent fish species in the mainstem of a southeastern U.S. river. The Etowah River is located in the Piedmont region of north Georgia, has relatively high diversity and species endemism and for it's length, harbors more imperiled fishes and invertebrates than any other southeastern system (Burkhead et al. 1997). This research was conducted as part of a monitoring plan required by the US Fish and Wildlife Service (USFWS) to assess potential effects of the operation of a water-supply reservoir, located on a tributary to the Etowah, on protected fish species in the Etowah River. Water from the reservoir (completed in 2002) would be released during low flow periods for municipal withdrawal from the Etowah River downstream. This analysis described baseline conditions in the Etowah mainstem and tested for differences in study shoals that will need to be addressed in future monitoring analyses. Moreover, the establishment of this monitoring plan provided the opportunity to assess effects of natural flow variability on fishes.

I selected ten fish species from three families (Cyprinidae, Ictaluridae and Percidae), including the federally endangered amber darter (*Percina antesella*), to assess how species with variable life-history traits might differ in their response to flow conditions. Using hierarchical logistic regression, probability of occurrence of target species was modeled as a function of spring and summer flow condition, microhabitat features, discharge at the time of the survey, watershed area and shoal position within the study reach. Microhabitat characteristics are known to strongly influence species occurrence (Aadland 1993, Bain 1995, Peterson and Rabeni 2001b, Fausch et al. 2002) and were essential to building credible models. Data were collected for individual seine samples (<4 $m^2$), providing fine-scale resolution of species occurrence within shoals. I included flow variables likely to be altered by the operation of the water-supply reservoir, including average discharge and the number of days of high flow within each spring and summer. Sampling was conducted from 1998-2004, including four consecutive years of drought (1999-2002), followed by an above-average (2003) and average (2004) water-year. I evaluated model results for evidence of differences among and within families in how species responded to varying flow conditions, accounting for effects of microhabitat and longitudinal shoal position on species occurrence in samples. Finally, I considered implications of these results with regard to future monitoring efforts and to effects of hydrologic alteration and habitat change on species persistence.

## METHODS

### <u>The Etowah River and study sites</u>

The Etowah River is a major headwater tributary to the Coosa River (Mobile River basin) that lies entirely within Georgia. The Etowah basin (4823 $km^2$) harbors 91 native fish species, including four endemic species and seventeen imperiled species, nine of which are thought to be extirpated from the system (Burkhead et al. 1997). Burkhead et al. (1997) have thoroughly reviewed works suggesting the high sedimentation rates that contributed to the loss of biodiversity in the Etowah occurred within the last 200 years as a result of upland erosion from poor agricultural practices (Trimble 1974) and gold mining (Leigh 1994). Current threats to aquatic biota come in the suite of changes resulting from urban development (Paul and Meyer 2001), as agricultural, forest and rural lands in the expanding metro-Atlanta area are converted to suburban or urban uses (Walters et al. 2003a, Roy et al. 2005). Urban stream systems have increased non-point source pollution and sedimentation from poor development practices and in-channel erosion, altered hydrologic and temperature regimes, and are fragmented by culvert installation at road crossings and by water supply reservoirs (Trimble 1997, Warren and Pardew 1998, Paul and Meyer 2001, Schaefer et al. 2003, Walters et al. 2003a, Roy et al. 2005). Urban stressors on biological communities may be most severe in small watersheds where the percent urban land-use may be relatively high and the terrestrial-aquatic interface greatest. Percent urban land-use in the upper Etowah River basin is low (6.5% urban upstream of Canton, GA based on 2001 land cover classified from satellite imagery; NARSAL 2003), yet the mainstem community is exposed to urban stressors coincident with increasing population growth in the basin.

The Etowah River is free flowing for 218 km (136 miles) upstream of Canton, GA and Allatoona Reservoir (a 1659 $km^2$ impoundment completed in 1950). Nevertheless, a portion of the free-flowing reach is potentially subject to altered flow and temperature regimes through the operation of Yellow Creek Reservoir. The reservoir was built to store water for release during low-flow periods, to augment flows at a municipal water intake on the Etowah River, 32 river-km (20 river-miles) downstream of the Yellow Creek confluence and upstream of Canton, GA. The watershed area of Yellow Creek is 43 $km^2$ (16.6 square miles) and Yellow Creek Reservoir covers 135 hectares (334 acres). The dam on Yellow Creek is located two river-miles upstream from its confluence with the Etowah River. As a condition of the 404 permit, USFWS requires annual monitoring of federally protected fishes in the Etowah mainstem. To the best of my knowledge, use of Yellow Creek Reservoir to augment downstream flows has been limited up to this point; reservoir releases during droughts and the potential for effects on biota in the Etowah mainstem may increase with regional population growth and increased water demand.

Monitoring on the Etowah mainstem was designed to support inferences on the response of fish species to flow and habitat alteration. Beginning in 1997, annual fish surveys were conducted at ten shoals within a 42 km (26 mile) reach of the Etowah River in Dawson and Cherokee Counties (Figure 1). Five shoals were selected upstream and five downstream of the mouth of Yellow Creek to allow for a comparison of changes resulting from the operation of the reservoir. Shoals are areas of coarse bed sediments (cobble, gravel and bedrock) with increased water velocity and decreased stream depth. Each site was located at a shoal and those terms are used interchangeably. Watershed area at the study shoals ranged from 460 $km^2$ (site 1) to 1500 $km^2$ (site 10; Table 1). Shoals were selected based on access, results of historical collections and preliminary sampling conducted to determine which shoals harbored populations of target fish species. Site 5 and site 6 were selected based on the additional criteria of proximity to the mouth of Yellow Creek. Sites 1-5 (upstream of the mouth of Yellow Creek) were more closely spaced than sites 6-10; in addition to the factors listed above, the spacing of the upper set of sites was restricted by the distributions of some target species (e.g., site 1 was the upstream-most known occurrence of the amber darter). Sampling was conducted annually between late August and early November, beginning in 1997, except that sites 3, 5 and 8 were not sampled in 1998, giving a total of 77 surveys between 1997 and 2004.

Target species

I chose ten shoal-dependent species that are relatively common in annual surveys for the analysis. The target species include four minnows (Cyprinidae), all of which are commonly found in fast riffle habitat as adults, two madtoms (small-bodied catfishes, Ictaluridae) and four darters (Percidae, Table 2). All target darter species are considered benthic-obligate, however the speckled darter (*Etheostoma stigmaeum*) is more frequently found over sandy habitat, along stream margins and in slower velocities than the other darters and it may respond differently to flow and habitat variation. Three target species are considered imperiled: the amber darter (*Percina antesella*) is federally endangered, the undescribed Coosa madtom (*Noturus sp. cf. N. munitus*) is listed as threatened in Georgia and is a likely candidate for federal listing and the undescribed Coosa chub (*Macrhybopsis* sp. cf. *M. aestivalis*), believed to be endemic to the Coosa River basin, is a likely candidate for listing. I have not included other imperiled Etowah fishes, such as the federally endangered Etowah darter (*E. etowahae*) or the Georgia endangered freckled darter (*P. lenticula*), in the analysis because they are encountered relatively rarely during annual surveys.

Peak spawning periods for the target fish species generally occur during summer for the cyprinids and ictalurids, and during spring for the percids (Etnier and Starnes 1993, Jenkins and Burkhead 1994, Boschung and Mayden 2004; Table 2). Detailed life-history studies of the target species are lacking, or if available, have been conducted outside of the Coosa River basin (except for unpublished observations by P. O'Neil on the speckled darter (*E. stigmaeum*); Boschung and Mayden 2004). Speckled darters have been observed spawning over coarse sandy substrate in an eddy in Stamp Creek, a tributary to the Etowah River, where the eggs were shallowly buried in sand by means of the spawning activity (B. J. Freeman, personal communication). The bronze darter (*P. palmaris*) is thought to behave similarly to the gilt darter (*P. evides*), which buries its eggs in coarse substrate (Boschung and Mayden 2004). No information has been reported for amber darters or rock darters (*E. rupestre*). The speckled madtom (*N. leptacanthus*) is known from the Pascagoula River system to spawn in cavities, with males guarding the nest (Clark 1978 *in* Boschung and Mayden 2004), behavior typical of the genus; however, the reproductive behavior of the Coosa madtom is not known. The Alabama shiner (*Cyprinella callistia*) and tricolor shiner (*C. trichroistia*) are known to be crevice spawners. There is no information on the spawning behavior of the riffle minnow (*Phenacobius catostomus*), although congeners are known to spawn over gravel (Jenkins and Burkhead 1994). Life history of the Coosa chub is not known. Two congeners reportedly have different strategies: *M. aestivalis hyostoma* (shoal chub) broadcasts eggs in pools, and female *M. storeriana* (silver chub) in spawning condition have been seen over coarse bed sediments in swiftly flowing water in the Upper Tombigbee River, but are also thought to spawn in pools in more northern parts of their range (Boschung and Mayden 2004).

Survey methods

Sampling was conducted using kick-set and seine-hauling techniques; to minimize the potential for mortality of imperiled fishes, no electrofishing equipment was employed. Sampling was generally conducted in a zig-zag fashion, proceeding upstream across the shoal. A kick-set consisted of two people holding a 2.4 m x 1.8 m (0.64 cm mesh) seine perpendicular to stream flow against the stream bottom, while two or three additional people disturbed the substrate in the area immediately upstream to displace fishes. Each kick-set sampled an area approximately 3.5 $m^2$. Seine-hauls, consisting of pulling the seine through areas with low current velocity and fine sediments, were variable in sample area depending on haul-length, which was estimated. Data for each kick-set/seine-haul (hereafter sets) were maintained separately, so that each was a distinct record. In 1997, fishes in each set were identified, counted and released without measurement and no fishes were preserved. Beginning in 1998, the fishes collected in each set were identified, measured to standard length and released, or were preserved in 10% formalin for identification and measurement in the lab (each set in a separate jar). Preservation of some fishes was necessary due to the additional time constraint of measuring each collected individual, but most fishes were released. All individuals not readily identifiable were preserved in 10% formalin. All preserved fishes were accessioned into the Ichthyology Collection at the Georgia Museum of Natural History at the University of Georgia. Federally protected fishes were measured and released in the field. Beginning in 2003, all protected fishes collected were retained in an aerated cooler until the completion of the fish survey to ensure that no animals were re-captured; there was no mortality associated with the temporary retention of these animals.

An alphanumeric depth and habitat code was recorded at each set. Depth was coded as: (A) less than 20cm, (B) 20-50cm, (C) greater than 50cm. The habitat codes included four categories: (1) coarse - gravel to cobble with medium to swift velocity, (2) less coarse - silt, sand and gravel with medium to slow velocity, (3) fines – sand and silt in slow velocity or backwater,

(4) boulders and bedrock with medium to swift velocity. The alphanumeric codes were used in the predictive models to differentiate two general habitat types: fast and shallow over cobble- and gravel-sized sediment, and backwater or slow habitat. All sets coded as A or B and 1 or 2 were coded as fast-shallow (FS), including 39% of all sets. All sets coded with a 3 were considered backwater (BW), including 6% of all sets. The presence of riverweed (*Podostemum ceratophyllum*) in a set was noted (58% of all sets). Moveable gravel is associated with the occurrence of amber darters (Freeman and Freeman 1994) and its presence in a set was noted (14% of all sets). The study shoals ranged in size and sampling effort (number of sets; Figure 2) was greater at larger shoals. Sampling effort at each shoal has varied among years in relation to fluctuations in water level, and was higher in 1997 and since 2001, than in other sample years.

Analysis methods

I sought to evaluate how abiotic factors at multiple spatial and temporal levels influence the probability of occurrence of adult and young-of-year (YOY) individuals in a set, especially the response of fish species to natural variability in flow condition (i.e., year-level variables representing river discharge characteristics in spring and summer months), using hierarchical logistic regression. Species occurrence and microhabitat data were collected at the set level (each set-of-the-seine). Multiple sets composed a survey (30-190 sets depending on shoal size and water level at the time of the survey). Surveys occurred at a particular site and in a particular year (year-site level). Antecedent flow conditions operated at the year level, while shoal location was site-specific. Hierarchical logistic regression was used to accommodate the nested structure of the data, allowing all levels of influence to be incorporated in a single model. I have assumed that frequency of species or life-stage occurrence in sets is positively correlated with abundance and that probability of species detection is relatively high and consistent across individual sets.

Young-of-year (YOY) were distinguished based on size- frequency distributions of captured individuals; for each species I estimated a minimum standard length for adults (Table 2). Because individual fish were not measured in 1997, those data were omitted from further analysis. At the set-level, I included as many as three binary terms in each predictive model (Table 3). For all darters, both madtoms and all adult minnows, I included fast-shallow (FS) habitat as a predictor of species occurrence. Fast-shallow habitat is known to be predictive of benthic-obligate fishes (Lobb and Orth 1991, Bain 1995, Bowen et al. 1998). For the same group, I included a term for presence of the aquatic macrophyte *Podostemum ceratophyllum* (riverweed) in the set. *Podostemum* (Pod) increases habitat complexity, supports a high abundance and biomass of macroinvertebrates that fishes can forage on, and is known to be associated with some fish species (Grubaugh and Wallace 1995, Freeman et al. 1997, Connelly et al. 1999, Hutchens et al. 2004). For amber darters and Coosa madtoms (adults and YOY), I included a term indicating the presence of moveable gravel (MG) in a set. Previous research has shown that amber darters are commonly associated with small, loose, clean gravel (Freeman and Freeman 1994). I frequently observed that the Coosa madtom also occurs in this habitat, and because they have a similar and distinct color pattern to the amber darter (broad dark saddles over a light background), I hypothesized they might also be predictably associated with this habitat feature. For all YOY minnow species, I included backwater habitat (BW) as a predictor of occurrence (Lobb and Orth 1991, Aadland 1993). In all cases, a coding of one indicated the presence of a condition and zero indicated its absence.

I included four year-level terms in the predictive set describing flow variability. These were average spring (March-May) and average summer (June-August) discharge and a count of the number of high-flow days in each spring and summer (Table 3). Flow data were obtained from the USGS (U.S. Geologic Survey) gage at Canton, GA for the period of record (1897-1905 and 1937-2004). I calculated high-flow days by summing the number of days that the average daily discharge was more than one standard deviation above the monthly average for the period of record.  For example, over the period of record, the average discharge plus one standard deviation for the month of June was 1805 cfs.  Each day in June that exceeded that discharge was considered a high-flow day and was counted as one.  Within each year, I summed the number of high-flow days for spring and summer months (Table 4).  I hypothesized that there could be a one-year lag in the effect of flow variation on adult population size; that is, if YOY recruitment was high in 2000, adult abundance might be high in 2001.  To account for this, I included the same four flow terms for the year prior to the sample year in the predictive set for the adults of each species, for a total of eight flow variables.

I included two site-level variables in the models: a continuous term for watershed area and a binary term that indicated whether a site was located in the downstream group of five sites, downstream of the mouth of Yellow Creek (Table 3).  One survey-level term, discharge at the USGS Canton gage on the date of the sample, was included to account for variation in detection of species or life-stages related to water level on the survey date.  With increasing stream discharge, fishes could be more dispersed across available habitat, leading to lower probability of detection in a set.  By incorporating this term in the model, I was able to test for differences in probability of occurrence of a species that might result from sampling effectiveness, rather than population size.

The number of possible variables included in the predictive set ranged from eight (for YOY minnow species) to fourteen (for adult amber darters and Coosa madtoms, Table 3).  I used PROC NLMIXED in SAS to model the data for each species of interest using random effects logistic regression, with the goal of exploring factors that influence species occurrence.  A random term was included to account for the grouping of the sets into distinct surveys, because sets within each of the 67 surveys could be more similar than sets among the surveys for reasons not explicitly taken into account.  Top models were selected using the Akaike's Information Criterion (AIC), where the lowest AIC score indicated the best supported model and model weights were calculated to determine the relative support for each model in a given set

(Burnham and Anderson 2002).  A correlation analysis was performed (Pearson's r) to evaluate correlations among predictor variables; any models that contained correlated variables ($r^2 > 0.36$) would have been discarded during the model selection process, but this never occurred. All combinations of the predictor variables were modeled using a SAS macro that output top models, AIC scores, model weight and rank.  From the macro output, I selected the models with at least one-eighth of the weight of the top model as the most plausible "confidence set" of models (Burnham and Anderson 2002) and recalculated model weights for the confidence set.

In order to summarize the results of well-supported, often similar models predicting species occurrence, I assessed variable importance and calculated model-weighted average regression coefficients for each variable.  Variable importance is a measure of the relative support for each predictive term derived from the model weight (Burnham and Anderson 2002). From the confidence set of models for each species, I summed the model weights for each model in which a particular variable appeared (i.e., a variable that occurred in all models for a species would have an importance of one).  I averaged variable importance within and across families of species to identify trends.  The model-weighted average regression coefficient for each variable was calculated from model estimates.  Using the subset of models in the confidence set in which a particular variable appeared, I calculated model weights for that variable-specific set of models and then calculated the model-weighted average regression coefficient and 90% unconditional confidence interval (Burnham and Anderson 2002).  Model averaging allowed me to summarize the results of numerous plausible, often nested models, to obtain estimated effect sizes for each variable based on model weights.  I transformed the model-averaged regression coefficients and confidence intervals to produce odds ratios for probability of species or life stage occurrence in a set.  For continuous variables, odds ratios were scaled as specified below.

## RESULTS

Over 5608 sets composed the project database and more than 26,200 individual fishes of 49 different species were processed during 67 surveys from 1998-2004. Of the target fish species, Alabama shiners occurred in the most sets and YOY were in nearly as many sets as adults (Figure 3). Adults occurred in more sets than YOY for all other species, except tricolor shiners. Adult Coosa chubs, rock darters, speckled darters and amber darters were much more commonly collected than YOY, based on frequency of occurrence in sets.

Model results showed that for adult and YOY individuals (discussed below) local habitat features were more important than year- and site-level predictors. Additionally, the site-level predictor indicating position at the downstream group of five sites was more important than the year-level flow terms. There were five species for which downstream group had a clear effect on the probability of occurrence, but the YOY for one of those (Coosa chub) had a small and imprecise estimate, indicating a potentially negligible effect (Figure 4). Occurrence of tricolor shiners (which never occurred at sites 8, 9 or 10) was 29 times less likely for adults and 13 times less likely for YOY, on average, at the downstream sites compared to the upstream sites. The odds of capturing adult bronze darters were 1.4 times less for adults and 2.1 times less for YOY at the downstream five sites. The speckled madtom was more likely (3.8 times for adults and 1.9 times for YOY) to occur at the downstream sites. For amber darters, the adults were 1.6 times less likely to occur at the downstream sites, while the YOY were 2.1 times more likely to occur at those same sites.

Six independent variables never occurred in the confidence set of models for any species or life-stage, including the four terms representing average discharge in the spring and summer of the sample year and in the year prior to the sample year, discharge on the day of the survey (the only survey-level term) and watershed area. Effects of other variables differed for YOY and adults, and these results are presented separately below.

Young-of-year

All four microhabitat variables (occurrence of backwater or fast-shallow habitat, and presence of *Podostemum* and moveable gravel) were associated with occurrence of YOY, although, as expected, variables differed in effects among species and families. Backwater habitat (BW) had a higher average importance (sum of weights for models in which BW occurred) across models predicting YOY presence for the group of four minnows than *Podostemum* had for madtoms or darters (Table 5). The likelihood of capturing YOY cyprinids was always greatest in BW habitat (Figure 5). On average, tricolor shiners were 10.4 times more likely and Alabama shiners 4.1 times more likely to occur in sets with BW than in sets that were not considered BW. The effect was smaller for riffle minnows and Coosa chubs (2.7 and 1.6 times more likely to occur in BW, respectively) than for the *Cyprinella* species. The probability of collecting YOY bronze darters was 4.2 times higher, on average, when *Podostemum* was present. Young-of-year madtoms were 2.1 (speckled madtom) and 1.5 (frecklebelly madtom) times more likely to occur where *Podostemum* was present. Conversely, presence of *Podostemum* decreased the likelihood of capturing YOY rock darters (2.7 times) and speckled darters (1.9 times), and possibly YOY amber darters (1.3 times), though the confidence interval included 1.0 (no effect). Presence of moveable gravel increased the odds of capturing YOY Coosa madtoms 1.9 times and YOY amber darters 3.1 times, on average; moveable gravel occurred in all models in the confidence set for both species (importance of 1.0). Fast-shallow habitat was less important than the other set-level terms, only having a clear effect on YOY of two darter species. Rock darters were 2.1 times more likely to occur in fast-shallow habitat and speckled darters were 1.5 times less likely to occur.

The effect of flow variability (number of high flow days) on the probability of capturing individuals were clearer for YOY than for adults (reported below). Odds ratios were scaled to show the effects of an increase of seven days of high flow, compared to zero days. Summer HFD occurred in all models in the confidence set for seven of ten species across the three families (Table 5). For those seven species, the odds ratios showed that increasing the number of HFD during summer decreased the probability of capturing YOY (Figure 6). On average, the strongest effect was for speckled darters (2.7 times less likely to occur) and the weakest effect was for riffle minnows (1.1 times less likely to occur) for a 7-day increase in summer HFD. The other three species, tricolor shiners, amber darters and speckled madtoms, showed a very small negative effect of increasing summer HFD, but unconditional confidence intervals on the estimates were broad and included 1.0 (no effect). Spring HFD had a lower average importance across the three families, only occurring in all models in the confidence set for four species (Table 5). The largest positive effect of increasing spring HFD was seen for YOY Coosa madtoms and bronze darters (2.4 and 1.6 times more likely to occur, respectively; Figure 6). There was a negative effect of increasing spring HFD on occurrence of two species. Young-of-year amber darters were 3.4 times less likely to occur as spring HFD increased from zero to seven days. Young-of-year speckled darters were 1.3 times less likely to occur with increasing spring HFD, however this estimate was imprecise.

## Adults

Presence of *Podostemum* was the most important independent variable in models predicting occurrence of adults, occurring in all models in the confidence set for nine of ten species, for an average importance of 0.86 across species (Table 6). The presence of *Podostemum* decreased the probability of capturing tricolor shiners (4.8 times) and riffle minnows (1.9 times), but increased the probability of capturing Coosa chubs, both madtoms and all darters except speckled darters between 4.4 (bronze darters) and 1.5 (amber darters) times (Figure 7). Fast-shallow habitat was the second most important variable and was heavily weighted in the models for seven species (Table 6). Presence of fast-shallow habitat increased the odds of capturing Coosa chubs (1.6 times), Coosa madtoms (1.5 times), rock darters (3.1 times) and bronze darters (1.7 times), on average, but decreased the odds of capturing tricolor shiners (2.0 times), Alabama shiners (1.4 times) and speckled darters (1.2 times). The set-level term moveable gravel, only included as a potential variable in the models for amber darters and Coosa madtoms, had an importance of 1.0 and 0.94, respectively. When moveable gravel was present, the odds of occurrence of amber darters were 4.0 times higher and the odds of occurrence of Coosa madtoms were 1.6 times higher, on average, than when it was not present.

Summer HFD was heavily weighted for six species and previous year's summer HFD for four species, across all three families (Table 6). Consistent across families, the clear effect (where unconditional CI did not include 1.0) of increasing summer HFD or previous year's summer HFD in increments of one week was a decrease in the odds of adults occurring in sets (Figure 8). The strongest effect of summer HFD on the probability of occurrence of adults was similar for one species in each family: Alabama shiner, speckled madtom and bronze darter were 1.5 times less likely to occur, on average, as summer HFD increased from zero to seven days. Tricolor shiners were also 1.5 times less likely to occur with increasing summer HFD, on average, but the estimate was less precise (Figure 8). Summer HFD was heavily weighted in the confidence set of models for Coosa madtoms, rock darters and riffle minnows, but the odds ratios showed a smaller effect on the probability of occurrence (1.4 - 1.2 times less likely to occur). The largest effect of previous year's summer HFD was a decrease in the odds of occurrence of adult Alabama shiners (1.34 times) and Coosa madtoms (1.3 times); the effect size was smaller for three additional species (bronze darter, speckled darters and speckled madtoms).

Spring HFD and the previous year's spring HFD was not heavily weighted in the confidence set of models for most species (Table 6). The probability of capturing Coosa madtoms was higher with increasing spring HFD in the sample year (1.4 times) and the year prior to the sample year (1.3 times; Figure 8). There was also a small increase in the odds of capturing rock darters (1.2 times) with increasing spring HFD in the sample year. Speckled darters were less likely to occur as spring HFD increased in the sample year (1.4 times) or the year prior to the sample year (1.2 times).

## DISCUSSION

Occurrence of ten target shoal-dependent fish species in samples at ten shoals in the Etowah River during annual surveys from 1998-2004 was predicted by microhabitat conditions and flow variability in spring and summer (number of days of high flow), but not by average spring or summer discharge. River discharge on the day of each survey, taken from a USGS gage located downstream of the study reach, did not explain any variation in the occurrence of target fish species, suggesting that species detection was unrelated to discharge level, at least over the range of sampled conditions. Some fish species were more likely to occur either upstream (sites 1-5) or downstream (sites 6-10) of the mouth of Yellow Creek, an important site-level factor that must be considered in monitoring for effects of the operation of Yellow Creek Reservoir on imperiled fishes in the Etowah River. There was no evidence that watershed area was linearly related to the probability of occurrence of target species within the study shoals. These results provided evidence that microhabitat conditions strongly influence the distributions of species within shoals and that spring and summer flow variability influences the probability of occurrence of target YOY and adult fishes.

Microhabitat features, including the presence of *Podostemum*, fast-shallow or backwater habitat and moveable gravel, generally had a larger effect on the odds of species or life-stage occurrence than year-level flow characteristics. *Podostemum* and fast-shallow habitat was generally positively associated with occurrence of adult darters and madtoms, except speckled darters. Association of *Podostemum* and fast-shallow habitat with YOY darters and madtoms was less clear; only YOY rock darters were more likely to occur in fast-shallow habitat, indicating a potential shift in habitat use between life-stages for most target darters and madtoms, as also observed in other systems (Lobb and Orth 1991, Aadland 1993, Freeman et al. 1997). As predicted, the speckled darter, which is known to prefer slower, sandier habitat than the other darters, was less likely to occur in fast-shallow habitat or with *Podostemum* at both life-stages. Contrary to my initial hypothesis, the presence of *Podostemum* and fast-shallow habitat was not positively correlated with the occurrence of adult minnows. Although some large individuals were captured in fast water, the cyprinid species were more likely to occur in slower or deeper habitats, except for the Coosa chub. Adult Coosa chubs responded more similarly to adult rock darters, bronze darters and both madtoms to the set-level predictors, and this may provide a clue that Coosa chubs spawn over gravel, rather than broadcasting eggs in pools (as reported for congeners; Boschung and Mayden 2004). Similar to the other cyprinids, YOY Coosa chubs were positively associated with backwater habitat, although the effect was smaller and the confidence interval approached 1.0 (no effect). Use of backwater-type conditions, such as along channel margins, by YOY minnows has also been widely observed (Lobb and Orth 1991, Aadland 1993, Freeman et al. 1997).

Moveable gravel was highly predictive of occurrence of amber darter adults and YOY, a finding consistent with Freeman and Freeman (1994). Aside from some *Percina* species, gravel habitat has more often been associated with spawning salmonids (Kondolf et al. 1993, Kondolf 2000) and catostomids (Kwak and Skelly 1992, Cooke and Bunt 1999). Some madtoms have been reported to use gravel habitat (Peterson and Rabeni 2001a). As a group, madtoms are known to be nocturnal and to spawn in cavities, with males guarding nests (Burr and Stoeckel 1999). Thus, Coosa madtoms may be using the gravel habitat for cover, rather than for spawning substrate. Interestingly, YOY Coosa madtoms were more highly correlated with moveable gravel than with *Podostemum*, but the opposite was true for adults. Coosa madtoms (and other species of the subgenus *Rabida*) have a color pattern similar to that of the amber darter, few broad dark saddles over a light background. The amber darter is known to bury in gravel habitat (Freeman and Freeman 1994). A life-history study of the Coosa madtom would be useful to help elucidate the way in which they use gravel habitat at different life stages (i.e., do they bury as both YOY and adults?).

Young-of-year are more vulnerable than adults to mortality from being swept downstream by high flows or due to the stress of increased turbidity in storm flow (Harvey 1987, Mion et al. 1998, Lake and Hinch 1999, Sutherland 2005). Turbidity values between 50-430 NTU during storm flow in the study reach are common (personal observations and B. J. Freeman, unpublished data). Therefore, it was not surprising to see that the effect of increasing summer HFD was usually to decrease the probability of capturing the target species, consistent across all three families, and that this effect is stronger for YOY than adult fishes. Additionally, YOY amber darters are negatively associated with increasing spring HFD; the amber darter is thought to be an early spawner (late winter-April; Etnier and Starnes 1993), making spring the most vulnerable time for amber darter YOY. A direct mechanism for the positive association of high spring flows on the probability of occurrence of YOY Coosa madtoms, bronze darters and Alabama shiners is less clear. For Coosa madtoms, thought to spawn June-August, increasing spring HFD is positively associated with occurrence of both YOY and adults, suggesting an indirect benefit of high spring flows, such as flushing of fine sediment from potential spawning sites. Alabama shiners and bronze darters are both thought to spawn from March-July, a spawning period that could make YOY vulnerable to both summer and spring high flows; the positive association with spring HFD is confounded by the lack of a clear effect of increasing spring HFD on the occurrence of adults. More details on the life-histories of the target species would be useful in assessing potential mechanisms for the correlations found here, but it seems likely that most target species, especially those with extended spawning periods, would benefit from spring flows that flush sediment from spawning sites.

For adults, stream flow variability in the year prior to the sample year was less important than flows in the sample year. This could indicate that none of the species had a particularly strong year class during the study that caused a spike in the probability of occurrence of adults in the subsequent year. But it seems more likely that overall recruitment was average, since most of the years of this study had few days of high summer flow and this is the modal condition for the Etowah. Over the 77-year period of record for the Etowah River at the USGS gage at Canton, the average number of summer HFD has been 7.3. During that time, 23 years had zero summer HFD and 50 years had fewer than seven HFD. The numbers for spring HFD have been similar, with 51 years below the 77-year average. Even though 1999-2002 were drought years in Georgia, the number of spring and summer HFD during the study years was typical. Summers with relatively few days of high flow may provide the stream conditions needed for successful recruitment of many native shoal-dependent fishes, while stable periods of low flow in the spring are important for at least one early spawning species, the amber darter.

Average spring and summer discharge variables never appeared in any models, suggesting that variability, rather than average condition, is critical and that even the driest years during this study contained sufficient habitat for target species. The Etowah River is not prone to drying during low water years, in contrast to arid streams, which may dry to leave only disconnected pools where increased temperature and low dissolved oxygen may stress fishes (Labbe and Fausch 2000). A more likely mechanism for the effect of variation in average water level on target fishes in this study is via spatially variable influences on habitat availability. The study shoals differ in length and width. Some shoals have islands, some have protected backwater habitat that could be an important refuge during wet years, but non-existent in dry years and some shoals have fast and deep runs that persist during the driest years, when more elevated portions of the shoal are dry. Geomorphic differences among shoals may result in spatial variation in flow-habitat relations such that, for example, a high or low flow condition has opposite effects on habitat availability in differing shoals. In this situation, effects of varying average flow conditions on fishes could be masked by differences among shoals. I hope to expand this research to incorporate features of shoal geomorphology and channel shape, which may interact with average flow condition to make habitat availability better in some shoals than others.  Shoal slope, for example, may be a relevant background geomorphic factor; it has been shown to be an important predictor of faunal assemblages in smaller streams in the Etowah basin (Walters et al. 2003b).

Implications

The hierarchical approach taken here may be applicable to studies where inferences at multiple scales are appropriate.  In this study, the effect of microhabitat and flow variability on species and life-stage occurrence were simultaneously evaluated, and this may provide context for changes in rates of species occurrence in the future.  Occurrence of fish species in differing microhabitat conditions may be strongly influenced by annual variation in stream flow; even in the most suitable habitat, the rate of species occurrence may be low following periods of higher flow variability.  This is illustrated, for example, by estimates derived from the best-supported model predicting YOY amber darter occurrence, which contains three variables, moveable gravel present, position in the downstream group of five sites and spring HFD (Figure 9).  At approximately 20 days of high flow in the spring, the probability of occurrence of YOY amber darters approaches zero, regardless of the other conditions.

The presence of *Podostemum* increases habitat complexity in flowing waters and is associated with increased invertebrate biomass and abundance (Grubaugh and Wallace 1995, Hutchens et al. 2004).  Loss of percent cover of *Podostemum* could bring a loss of invertebrate prey, resulting in a negative effect on benthic-obligate fishes and other species that feed on drifting invertebrates.  *Podostemum* continues to persist in the Etowah, but it has visibly declined over the last decade in the neighboring Conasauga River (Upper Coosa basin; B. J. Freeman, personal communication) and in other eastern states, where it is listed as historical (Rhode Island), imperiled (New York and Ohio) or of special concern (Connecticut, Kentucky, Maine, Massachusetts; USDA NRCS 2006).  Persistence of *Podostemum* and its association with other aquatic biota should continue to be an area of future investigation.

The negative effects of summer high flow pulses on many species with contrasting life histories and habitat affinities echoes observations of depressed juvenile fish abundances in regulated rivers subjected to artificially fluctuating flow regimes (Schlosser 1985, Bain et al. 1988, Bowen et al. 1998, Freeman et al. 2001). A diversity of stream species may depend on periods of stable flow conditions, especially in juvenile stages. High flow pulses are also important to removing fine sediment from gravel and providing spawning cues and access to spawning areas (Poff et al. 1997, Bunn and Arthington 2002). Results from this study indicate that high springtime flows may benefit some riverine fishes, even in the absence of a mechanism such as floodplain inundation. Overall, these results provide a basis for predicting biological effects of management actions that could alter the frequency and duration of high flow events, such as large flow releases from storage during summer or diversion of high flows during spring (e.g., to off-stream storage).

The sensitivity of riverine fishes to high flow events observed in the Etowah River may also be relevant to understanding and predicting effects of climate change on aquatic biota. The scenario of climate change presented for the southeast by Mulholland et al. (1997) indicates more intense storms or storm clustering, especially during the summer months. This suggests the possibility of dampening of successful young-of-year recruitment in shoal-dependent species. The life-spans of many small-bodied riverine fishes, such as madtom catfishes, darters and many North American cyprinids, are typically less than four years, and numerous species have narrowly restricted geographic distributions (Burr and Stoeckel 1999, Warren et al. 2000). Those combined factors could leave species susceptible to stochastic events; several consecutive years of high flow could depress population size by hampering recruitment with little or no chance of recolonization from another source population. In the case of the Etowah species, for example, the amber darter, Coosa madtom and Coosa chub are nearly restricted to the mainstem of the Etowah River and a limited reach of one other river, the

Conasauga, in the upper Coosa River basin. Management actions or changing climate patterns that alter the occurrence of high flow events could strongly affect persistence of these species.

## Conclusions

A hierarchical modeling approach may be a useful tool in simultaneously assessing how abiotic factors influence fish populations at different scales of inference. Rates of species occurrence for many species are strongly associated with a subset of microhabitat conditions available in shoals, adding evidence of species specialization or habitat specificity. Consistent with other studies, natural flow variability can strongly influence mortality of fishes, especially at vulnerable life-stages, as reflected by the rate of species occurrence in samples taken over several years. This study showed that a relatively low number of days of high flow in spring or summer (i.e., seven days in a three month period) influenced the probability of occurrence of many target fish species. Low variability in summer flow condition was associated with an increased probability of occurrence of many native fish species, while spring pulses in river discharge were positively related to the occurrence of species that are not limited to spring months for spawning.

## REFERENCES


Aadland, L. P. 1993. Stream habitat types: their fish assemblages and relationship to flow. North American Journal of Fisheries Management 13:790-806.

Bain, M. B. 1995. Habitat at the local scale: Multivariate patterns for stream fishes. Bulletin Francais De La Peche Et De La Pisciculture:165-177.

Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Streamflow regulation and fish community structure. Ecology 69:382-392.

Baron, J. S., N. L. Poff, P. L. Angermeier, C. N. Dahm, P. H. Gleick, N. G. Hairston, R. B. Jackson, C. A. Johnston, B. D. Richter, and A. D. Steinman. 2002. Meeting ecological and societal needs for freshwater. Ecological Applications 12:1247-1260.

Biggs, B. J. F., V. I. Nikora, and T. H. Snelder. 2005. Linking scales of flow variability to lotic ecosystem structure and function. River Research and Applications 21:283-298.

Boschung, H. T., and R. L. Mayden. 2004. Fishes of Alabama. Smithsonian Institution, Italy.

Bowen, Z. H., M. C. Freeman, and K. D. Bovee. 1998. Evaluation of generalized habitat criteria for assessing impacts of altered flow regimes on warmwater fishes. Transactions of the American Fisheries Society 127:455-468.

Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492-507.

Burkhead, N. M., S. J. Walsh, B. J. Freeman, and J. D. Williams. 1997. Status and restoration of the Etowah River, an imperiled southern Appalachian river ecosystem. Pages 375-444 in G. A. Benz and D. E. Collins, editors. Aquatic fauna in peril: the southeastern perspective. Lenz Design & Communications, Decatur, GA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, Second edition. Springer-Verlag, New York.

Burr, B. M., and J. N. Stoeckel. 1999. The natural history of madtoms (Genus Noturus), North America's diminutive catfishes. Pages 51-101 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm, and T. Coon, editors. Catfish 2000: proceedings of the international ictalurid symposium. American Fisheries Society, Bethesda, MD.

Connelly, W. J., D. J. Orth, and R. K. Smith. 1999. Habitat of the riverweed darter, *Etheostoma podostemone* Jordan, and the decline of riverweed, *Podostemum ceratophyllum*, in the tributaries of the Roanoke River, Virginia. Journal of Freshwater Ecology 14:93-102.

Cooke, S. J., and C. M. Bunt. 1999. Spawning and reproductive biology of the greater redhorse, *Moxostoma valenciennesi*, in the Grand River, Ontario. The Canadian Field-Naturalist 113:497-502.

Doyle, M. W., E. H. Stanley, D. L. Strayer, R. B. Jacobson, and J. C. Schmidt. 2005. Effective discharge analysis of ecological processes in streams. Water Resources Research 41.

Etnier, D. A., and W. C. Starnes. 1993. The fishes of Tennessee. University of Tennessee Press, Knoxville.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. Bioscience 52:483-498.

Freeman, B. J., and M. C. Freeman. 1994. Habitat use by an endangered riverine fish and implications for species protection. Ecology of Freshwater Fish 3:49-58.

Freeman, M. C., Z. H. Bowen, K. D. Bovee, and E. R. Irwin. 2001. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. Ecological Applications 11:179-190.

Freeman, M. C., Z. H. Bowen, and J. H. Crance. 1997. Transferability of habitat suitability criteria for fishes in warmwater streams. North American Journal of Fisheries Management 17:20-31.

Grubaugh, J. W., and J. B. Wallace. 1995. Functional structure and production of the benthic community in a Piedmont river - 1956-1957 and 1991-1992. Limnology and Oceanography 40:490-501.
Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Transactions of the American Fisheries Society 116:851-855.
Hutchens, J. J., J. B. Wallace, and E. D. Romaniszyn. 2004. Role of *Podostemum ceratophyllum* Michx. in structuring benthic macroinvertebrate assemblages in a southern Appalachian river. Journal of the North American Benthological Society 23:713-727.
Jenkins, R. E., and N. M. Burkhead. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, MD.
Kondolf, G. M. 2000. Assessing salmonid spawning gravel quality. Transactions of the American Fisheries Society 129:262-281.
Kondolf, G. M., M. J. Sale, and M. G. Wolman. 1993. Modification of fluvial gravel size by spawning salmonids. Water Resources Research 29:2265-2274.
Kwak, T. J., and T. M. Skelly. 1992. Spawning habitat, behavior, and morphology as isolating mechanisms of the golden redhorse, *Moxostoma erythrurum*, and the black redhorse, *M. duquesnei*, two syntopic fishes. Environmental Biology of Fishes 34:127-137.
Labbe, T. R., and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774-1791.
Lake, R. G., and S. G. Hinch. 1999. Acute effects of suspended sediment angularity on juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 56:862-867.
Leigh, D. S. 1994. Mercury storage and mobility in floodplains of the Dahlonega gold belt. Technical Completion Report Project 14-08-0001-G2013-(04). U.S. Geological Survey, Atlanta.
Lobb, M. D., and D. J. Orth. 1991. Habitat use by an assemblage of fish in a large warmwater stream. Transactions of the American Fisheries Society 120:65-78.
Magalhaes, M. F., I. J. Schlosser, and M. J. Collares-Pereira. 2003. The role of life history in the relationship between population dynamics and environmental variability in two Mediterranean stream fishes. Journal of Fish Biology 63:300-317.
Mion, J. B., R. A. Stein, and E. A. Marschall. 1998. River discharge drives survival of larval walleye. Ecological Applications 8:88-103.
Mulholland, P. J., G. R. Best, C. C. Coutant, G. M. Hornberger, J. L. Meyer, P. J. Robinson, J. R. Stenberg, R. E. Turner, F. VeraHerrera, and R. G. Wetzel. 1997. Effects of climate change on freshwater ecosystems of the south-eastern United States and the Gulf Coast of Mexico. Hydrological Processes 11:949-970.
Natural Resources Spatial Analysis Lab (NARSAL). 2003. Land cover map of Georgia. University of Georgia, Athens.
Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32:333-365.
Peterson, J. T., and T. J. Kwak. 1999. Modeling the effects of land use and climate change on riverine smallmouth bass. Ecological Applications 9:1391-1404.
Peterson, J. T., and C. F. Rabeni. 2001a. Evaluating the efficiency of a one-square-meter quadrat sampler for riffle-dwelling fish. North American Journal of Fisheries Management 21:76-85.
Peterson, J. T., and C. F. Rabeni. 2001b. The relation of fish assemblages to channel units in an Ozark stream. Transactions of the American Fisheries Society 130:911-926.
Poff, N. L., and J. D. Allan. 1995. Functional-organization of stream fish assemblages in relation to hydrological variability. Ecology 76:606-627.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. Bioscience 47:769-784.
Postel, S. L. 2000. Entering an era of water scarcity: The challenges ahead. Ecological Applications 10:941-948.
Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433-455.
Richter, B. D., J. V. Baumgartner, R. Wigington, and D. P. Braun. 1997. How much water does a river need? Freshwater Biology 37:231-249.
Roy, A. H., M. C. Freeman, B. J. Freeman, S. J. Wenger, W. E. Ensign, and J. L. Meyer. 2005. Investigating hydrologic alteration as a mechanism of fish assemblage shifts in urbanizing streams. Journal of the North American Benthological Society 24:656-678.
Schaefer, J. F., E. Marsh-Matthews, D. E. Spooner, K. B. Gido, and W. J. Matthews. 2003. Effects of barriers and thermal refugia on local movement of the threatened leopard darter, *Percina pantherina*. Environmental Biology of Fishes 66:391-400.
Schlosser, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66:1484-1490.
Starrett, W. C. 1951. Some factors affecting the abundance of minnows in the Des Moines River, Iowa. Ecology 32:13-27.
Sutherland, A. B. 2005. Effects of excessive sedimentation on the stress, growth and reproduction of two southern Appalachian minnows, *Erimonax monachus* and *Cyprinella galactura*. University of Georgia, Athens.
Trimble, S. W. 1974. Man-induced soil erosion on the southern Piedmont 1700-1900. Soil Conservation Society of America, Anteny, IA.
Trimble, S. W. 1997. Contribution of stream channel erosion to sediment yield from an urbanizing watershed. Science 278:1442-1444.
USDA NRCS. 2006. The Plants Database, 6 March 2006 (http://plants.usda.gov). Data compiled from various sources by Mark W. Skinner. in. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.
Walters, D. M., D. S. Leigh, and A. B. Bearden. 2003a. Urbanization, sedimentation, and the homogenization of fish assemblages in the Etowah River Basin, USA. Hydrobiologia 494:5-10.
Walters, D. M., D. S. Leigh, M. C. Freeman, B. J. Freeman, and C. M. Pringle. 2003b. Geomorphology and fish assemblages in a Piedmont river basin, USA. Freshwater Biology 48:1950-1970.
Warren, M. L., B. M. Burr, S. J. Walsh, H. L. Bart, R. C. Cashner, D. A. Etnier, B. J. Freeman, B. R. Kuhajda, R. L. Mayden, H. W. Robison, S. T. Ross, and W. C. Starnes. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the Southern United States. American Fisheries Society 25:7-31.
Warren, M. L., and M. G. Pardew. 1998. Road crossings as barriers to small-stream fish movement. Transactions of the American Fisheries Society 127:637-644.

Table 1. Watershed area at each study shoal.

| **Site number** | **Watershed area ($km^2$)** |
|---|---|
| 1 | 460 |
| 2 | 716 |
| 3 | 717 |
| 4 | 721 |
| 5 | 730 |
| 6 | 780 |
| 7 | 967 |
| 8 | 1008 |
| 9 | 1034 |
| 10 | 1500 |

Table 2. Target fish species included in the analysis. Protected status, spawning period (often inferred from related taxa) and minimum standard length used to distinguish adults from young-of-year are given.

| **Common name** | ***Genus species*** | **Protected status** | **Spawning period*** | **Minimum standard length of adults (mm)** |
|---|---|---|---|---|
| Alabama shiner | *Cyprinella callistia* | | March - July | 41 |
| Tricolor shiner | *Cyprinella trichroistia* | | June - July (peak) | 35 |
| Riffle minnow | *Phenacobius catostomus* | | April - June | 46 |
| Undescribed speckled chub | *Macrhybopsis sp. cf. M. aestivalis* | Likely candidate for listing | May – August | 32 |
| Speckled madtom | *Noturus leptacanthus* | | May – August | 33 |
| Undescribed Coosa madtom | *Noturus sp cf. N. munitus* | GA threatened | June – August | 33 |
| Amber darter | *Percina antesella* | Federally endangered | Late winter - April | 46 |
| Bronze darter | *Percina palmaris* | | March - June | 45 |
| Rock darter | *Etheostoma rupestre* | | April - May | 32 |
| Speckled darter | *Etheostoma stigmaeum* | | March - May | 31 |

*(Etnier and Starnes 1993, Jenkins and Burkhead 1994, Boschung and Mayden 2004)

Table 3. Independent variables included in the predictive models. The hierarchical structure of the data is as follows: sets compose surveys, surveys occur in a given year (1998-2004) and at a given site (1-10). Each site is surveyed only once per year.

| **Variable** | **Code** | **Binary or continuous** | **Hierarchical level** |
|---|---|---|---|
| *Podostemum* | Pod | Binary | Set |
| Moveable gravel | MG | Binary | Set |
| Fast-shallow habitat | FS | Binary | Set |
| Backwater habitat | BW | Binary | Set |
| Discharge on the sample date | Q | Continuous | Survey |
| Summer high flow days | SummHFD | Continuous | Year |
| Spring high flow days | SprHFD | Continuous | Year |
| Previous year’s summer high flow days | PYSummHFD | Continuous | Year |
| Previous year’s spring high flow days | PYSprHFD | Continuous | Year |
| Summer discharge | SummQ | Continuous | Year |
| Spring discharge | SprQ | Continuous | Year |
| Previous year’s summer discharge | PYSummQ | Continuous | Year |
| Previous year’s spring discharge | PYSprQ | Continuous | Year |
| Watershed area | WS | Continuous | Site |
| Downstream group of five sites | Group | Binary | Site |

Table 4. Average discharge on the Etowah River at the USGS gage at Canton, GA and total number of spring and summer high flow days (HFD). High flow days had an average daily discharge that exceeded the long-term monthly average plus one standard deviation, where the monthly average was taken over the period of record (1897-1905 and 1937-2004) at the Canton gage. The number of days of high flow is given, along with frequency of excursions that where considered high flow and the duration of those excursions in days.

| Year | Average discharge (cfs) | Number of HFD | Excursions | Duration of each excursion (days) |
|---|---|---|---|---|
| | | SPRING (March-May) | | |
| 1997 | 1642 | 5 | 2 | 3, 2 |
| 1998 | 2564 | 21 | 5 | 7, 5, 4, 3, 1, 1 |
| 1999 | 996 | 2 | 1 | 2 |
| 2000 | 1111 | 3 | 1 | 3 |
| 2001 | 1169 | 0 | 0 | 0 |
| 2002 | 1042 | 2 | 2 | 1, 1 |
| 2003 | 2065 | 17 | 4 | 11, 2, 3, 1 |
| 2004 | 942 | 1 | 1 | 1 |
| | | SUMMER (June-August) | | |
| 1997 | 897 | 5 | 3 | 2, 1, 2 |
| 1998 | 874 | 2 | 2 | 1, 1, |
| 1999 | 557 | 0 | 0 | 0 |
| 2000 | 350 | 0 | 0 | 0 |
| 2001 | 860 | 7 | 5 | 1, 2, 2, 1, 1 |
| 2002 | 318 | 0 | 0 | 0 |
| 2003 | 1646 | 28 | 7 | 2, 1, 9, 8, 5, 2, 1 |
| 2004 | 656 | 0 | 0 | 0 |

Table 5. Importance of independent variables in the confidence set of models for the young-of-year of target species. Variable importance was calculated as the sum of the model weights for each model in which the variable occurred. The number of models in the confidence set, average importance of variables for each family of species, and the average importance across all target species is given.

| | Models in confidence set | Moveable gravel | *Podostemum* | Fast-shallow | Backwater | Downstream group | Summer HFD | Spring HFD |
|---|---|---|---|---|---|---|---|---|
| Alabama shiner | 2 | - | - | - | 1.00 | 0.52 | 1.00 | 1.00 |
| Tricolor shiner | 4 | - | - | - | 1.00 | 1.00 | 0.37 | 0.28 |
| Coosa chub | 8 | - | - | - | 0.6 | 0.28 | 1.00 | 0.58 |
| Riffle minnow | 4 | - | - | - | 1.00 | 0.27 | 1.00 | 0.51 |
| **Average for minnows** | **-** | **-** | **-** | **-** | **0.90** | **0.52** | **0.84** | **0.59** |
| Speckled madtom | 16 | | 1.00 | 0.39 | - | 0.58 | 0.28 | 0.36 |
| Coosa madtom | 8 | 1.00 | 0.67 | 0.33 | - | 0.35 | 1.00 | 1.00 |
| **Average for madtoms** | **-** | **1.00** | **0.84** | **0.36** | **-** | **0.47** | **0.64** | **0.68** |
| Amber darter | 13 | 1.00 | 0.35 | 0.25 | - | 0.64 | 0.24 | 1.00 |
| Bronze darter | 3 | - | 1.00 | 0.29 | - | 0.90 | 1.00 | 1.00 |
| Rock darter | 4 | - | 1.00 | 1.00 | - | 0.40 | 1.00 | 0.36 |
| Speckled darter | 4 | - | 1.00 | 1.00 | - | 0.30 | 1.00 | 0.40 |
| **Average for darters** | **-** | **1.00** | **0.84** | **0.63** | **-** | **0.56** | **0.81** | **0.69** |
| **Average across species** | **-** | **1.00** | **0.84** | **0.54** | **0.90** | **0.52** | **0.79** | **0.65** |

Table 6. Importance of independent variables in the confidence set of models for adults of target species. Variable importance was calculated as the sum of the model weights for each model in which the variable occurred. The number of models in the confidence set, average importance of variables for each family of species, and the average importance across all target species is given.

| | Models in confidence set | Moveable gravel | *Podostemum* | Fast-shallow | Downstream group | Summer HFD | PY Summer HFD | Spring HFD | PY Spring HFD |
|---|---|---|---|---|---|---|---|---|---|
| Alabama shiner | 11 | - | 0.36 | 1.00 | 0.36 | 1.00 | 1.00 | 0.35 | 0.35 |
| Tricolor shiner | 12 | - | 1.00 | 1.00 | 1.00 | 0.68 | 0.27 | 0.27 | 0.26 |
| Coosa chub | 14 | - | 1.00 | 1.00 | 1.00 | 0.33 | 0.47 | 0.26 | 0.30 |
| Riffle minnow | 17 | - | 1.00 | 0.30 | 0.20 | 1.00 | 0.20 | 0.28 | 0.26 |
| **Average for minnows** | **-** | **-** | **0.84** | **0.82** | **0.64** | **0.75** | **0.49** | **0.29** | **0.29** |
| Speckled madtom | 13 | - | 1.00 | 0.41 | 1.00 | 1.00 | 0.68 | 0.24 | 0.27 |
| Coosa madtom | 12 | 0.94 | 1.00 | 0.99 | 0.25 | 0.97 | 0.98 | 0.98 | 0.95 |
| **Average for madtoms** | **-** | **0.94** | **1.00** | **0.70** | **0.63** | **0.99** | **0.83** | **0.61** | **0.61** |
| Amber darter | 26 | 1.00 | 1.00 | 0.54 | 1.00 | 0.24 | 0.24 | 0.42 | 0.44 |
| Bronze darter | 9 | - | 1.00 | 1.00 | 0.66 | 1.00 | 0.88 | 0.26 | 0.22 |
| Rock darter | 17 | - | 1.00 | 1.00 | 0.34 | 0.93 | 0.37 | 0.62 | 0.31 |
| Speckled darter | 20 | - | 0.27 | 0.90 | 0.23 | 0.30 | 0.86 | 1.00 | 0.72 |
| **Average for darters** | **-** | **1.00** | **0.82** | **0.86** | **0.56** | **0.62** | **0.59** | **0.58** | **0.42** |
| **Average across species** | **-** | **0.97** | **0.86** | **0.81** | **0.60** | **0.75** | **0.60** | **0.47** | **0.41** |

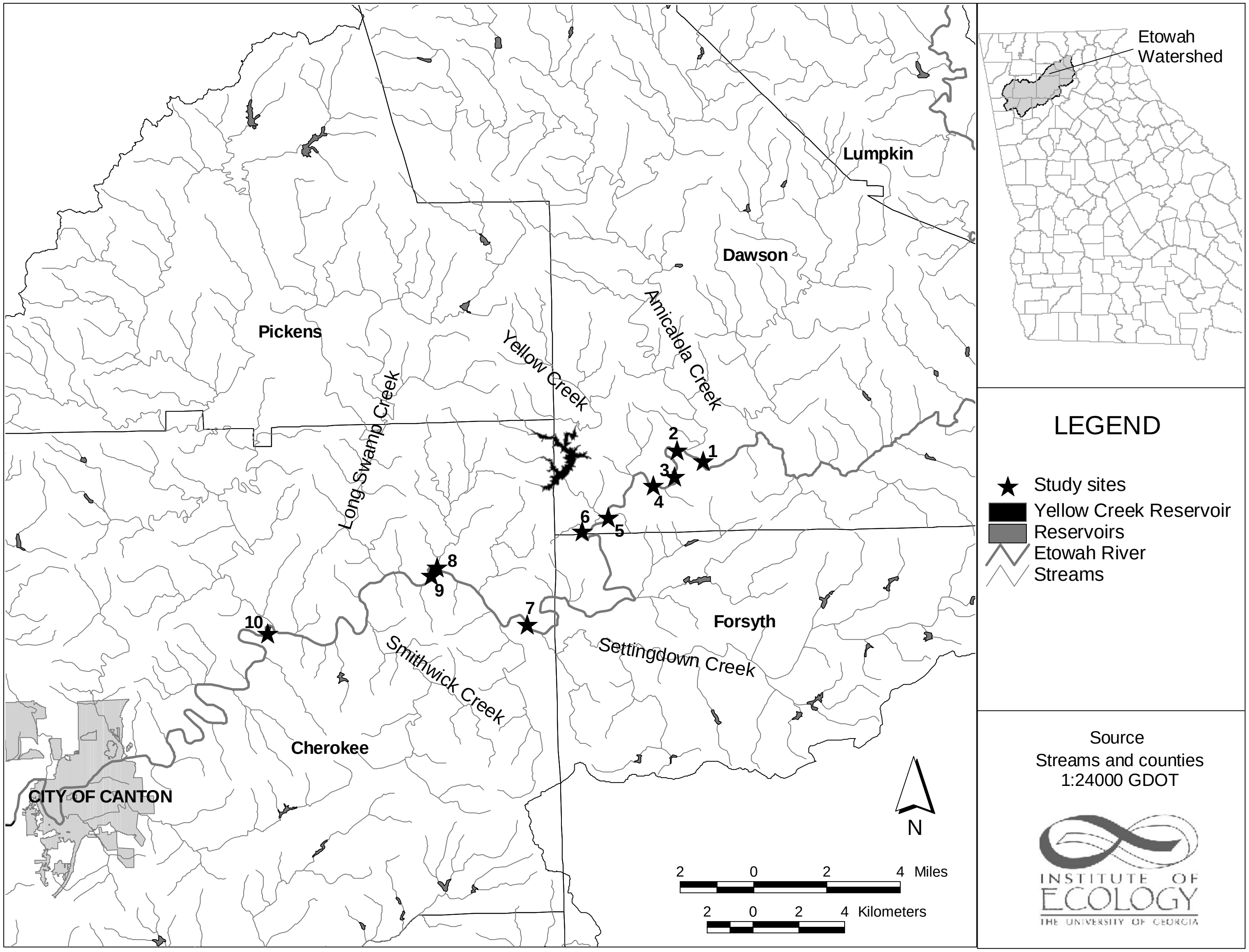


Figure 1. Location of Yellow Creek Reservoir and ten study shoals in the Etowah Watershed, Georgia.

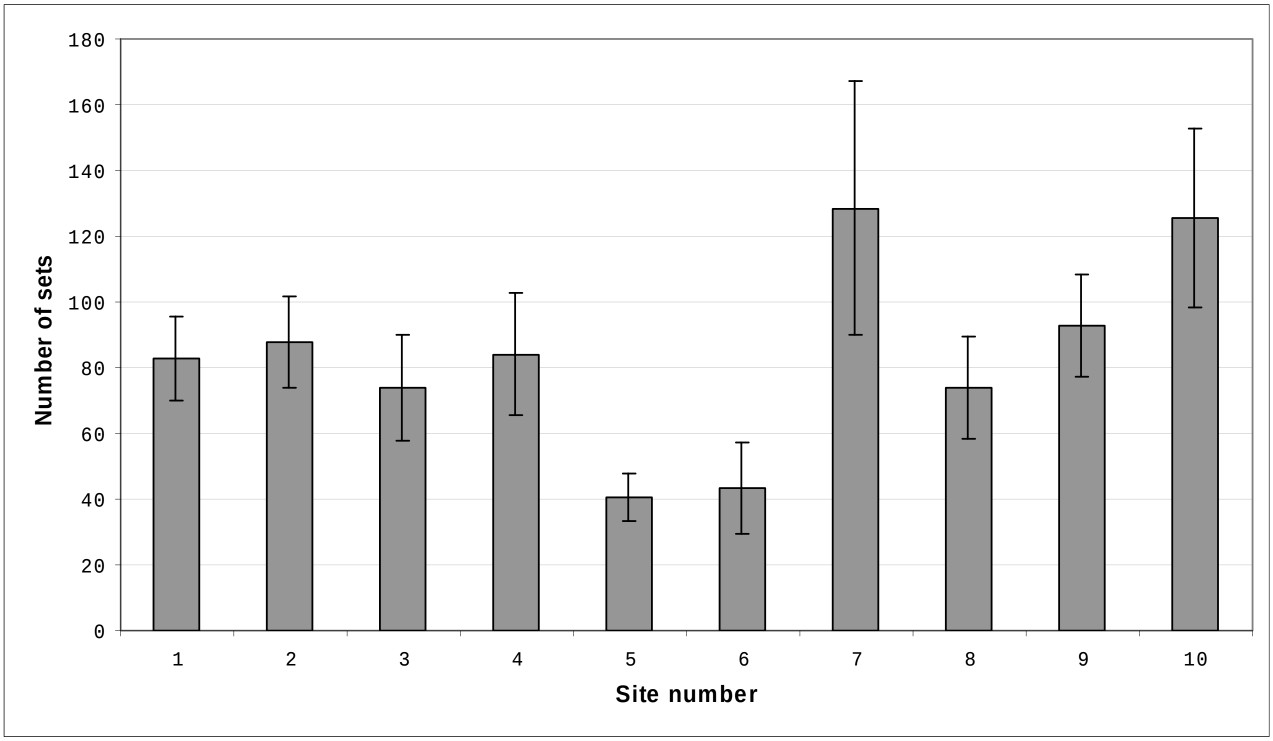


Figure 2. Average number of sets at each site with standard deviation.

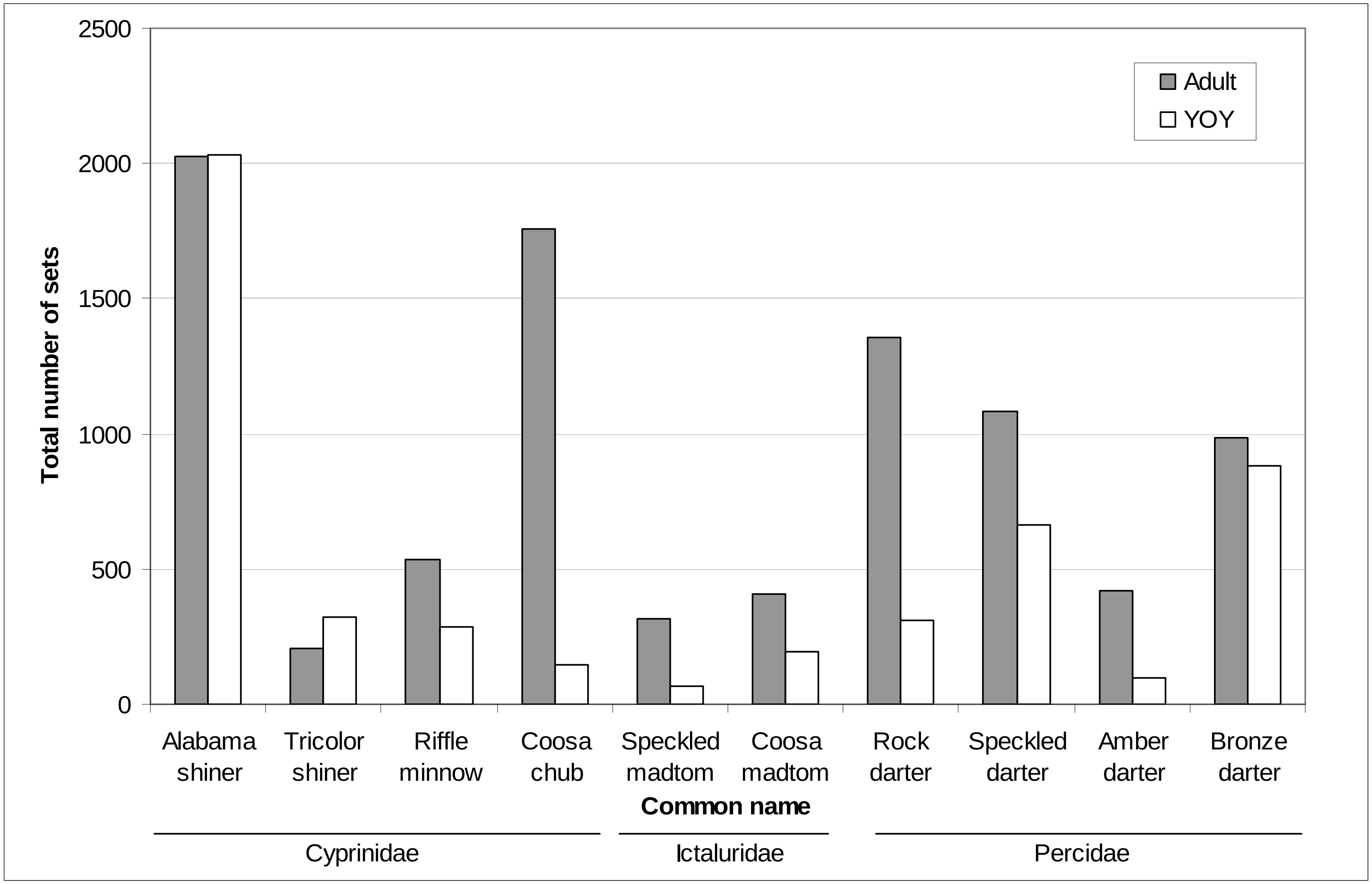


Figure 3. Total number of sets in which each species occurred. Adults and young-of-year are shown separately.

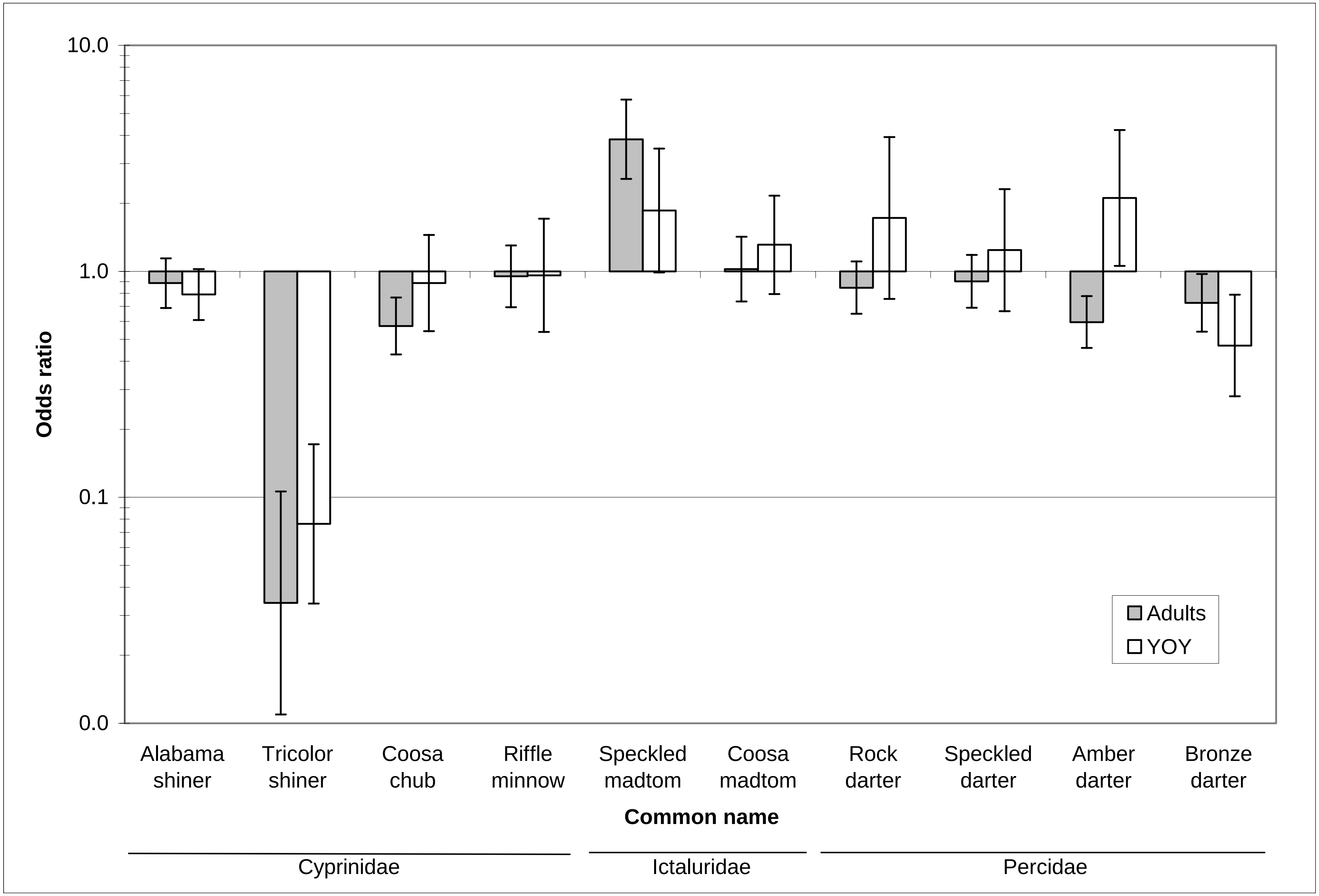


Figure 4. Average effect of downstream group on adults and young-of-year. Model-weighted average odds ratio indicating the effect of shoal position in the downstream group of five sites on the probability of occurrence of adult and YOY individuals in a set with 90% unconditional confidence intervals.

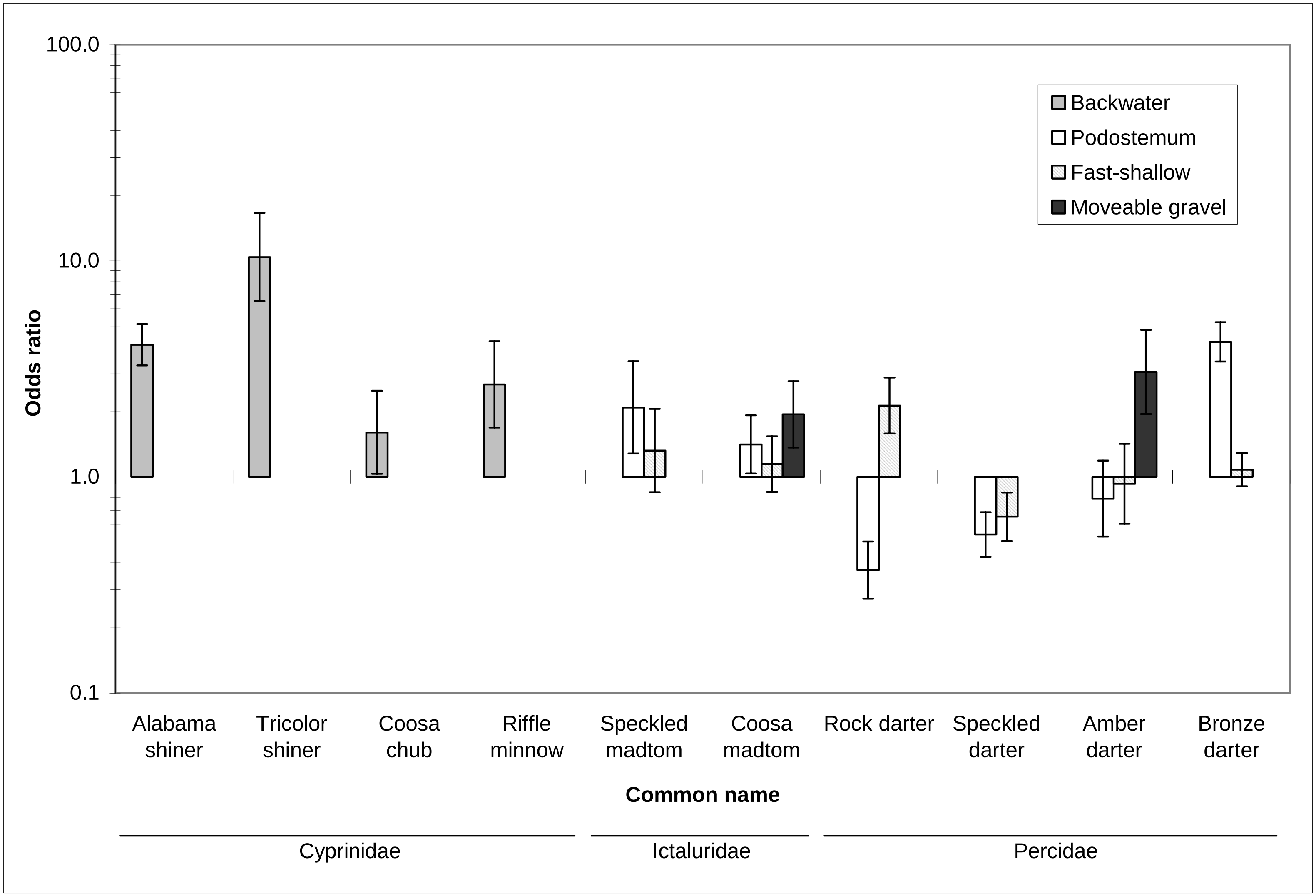


Figure 5. Average effect of microhabitat features on occurrence of young-of-year. Model-weighted average odds ratio indicating the effect of presence of backwater habitat (minnows), *Podostemum* and fast-shallow habitat (madtoms and darters), and moveable gravel (Coosa madtom and amber darter only) on the probability of occurrence of YOY individuals in a set with 90% unconditional confidence intervals.

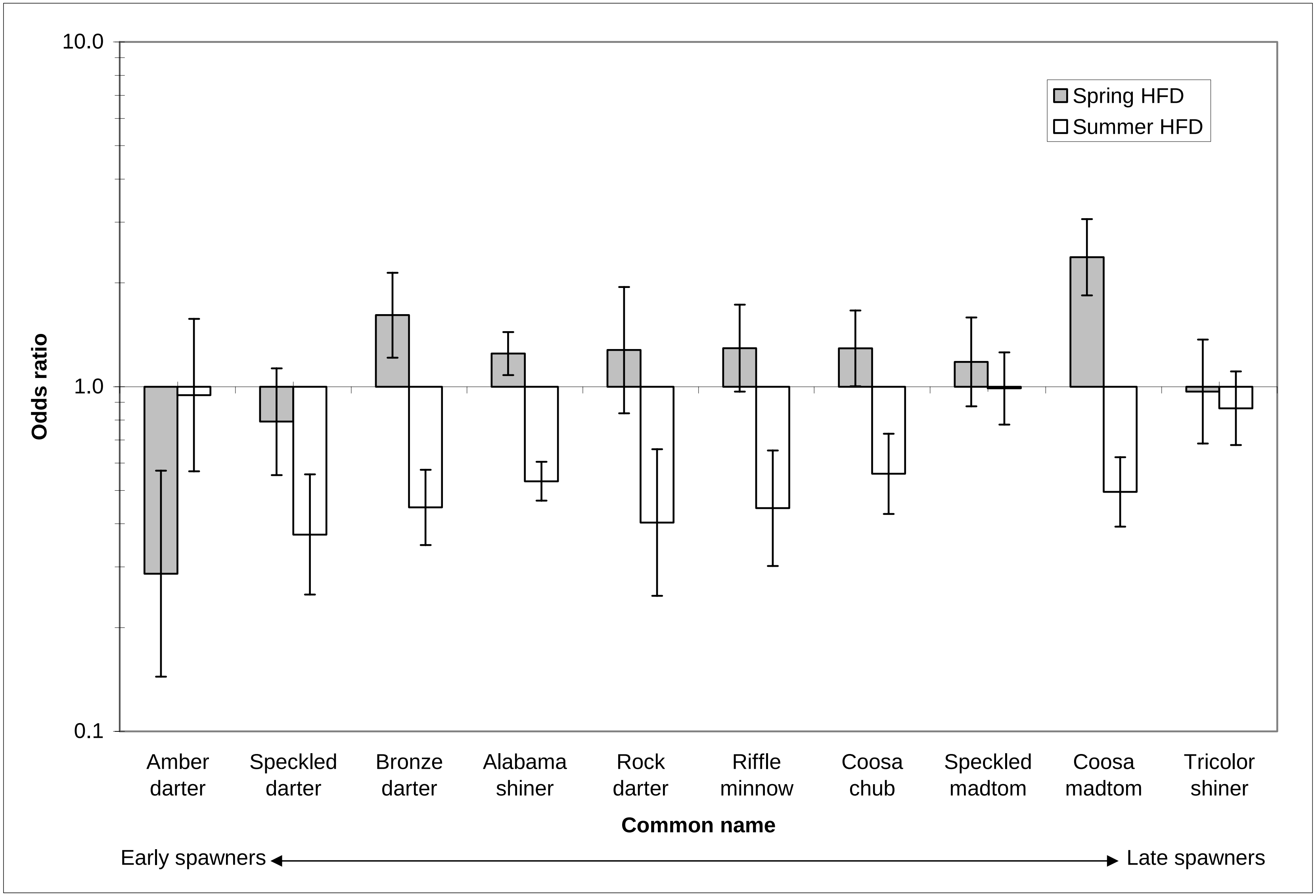


Figure 6. Average effect of increasing days of high flow on the occurrence of young-of-year. Model-weighted average odds ratios are scaled to indicate the effect of an increase of seven days of spring or summer high flow on the probability of occurrence of YOY individuals in a set, with 90% unconditional confidence intervals.

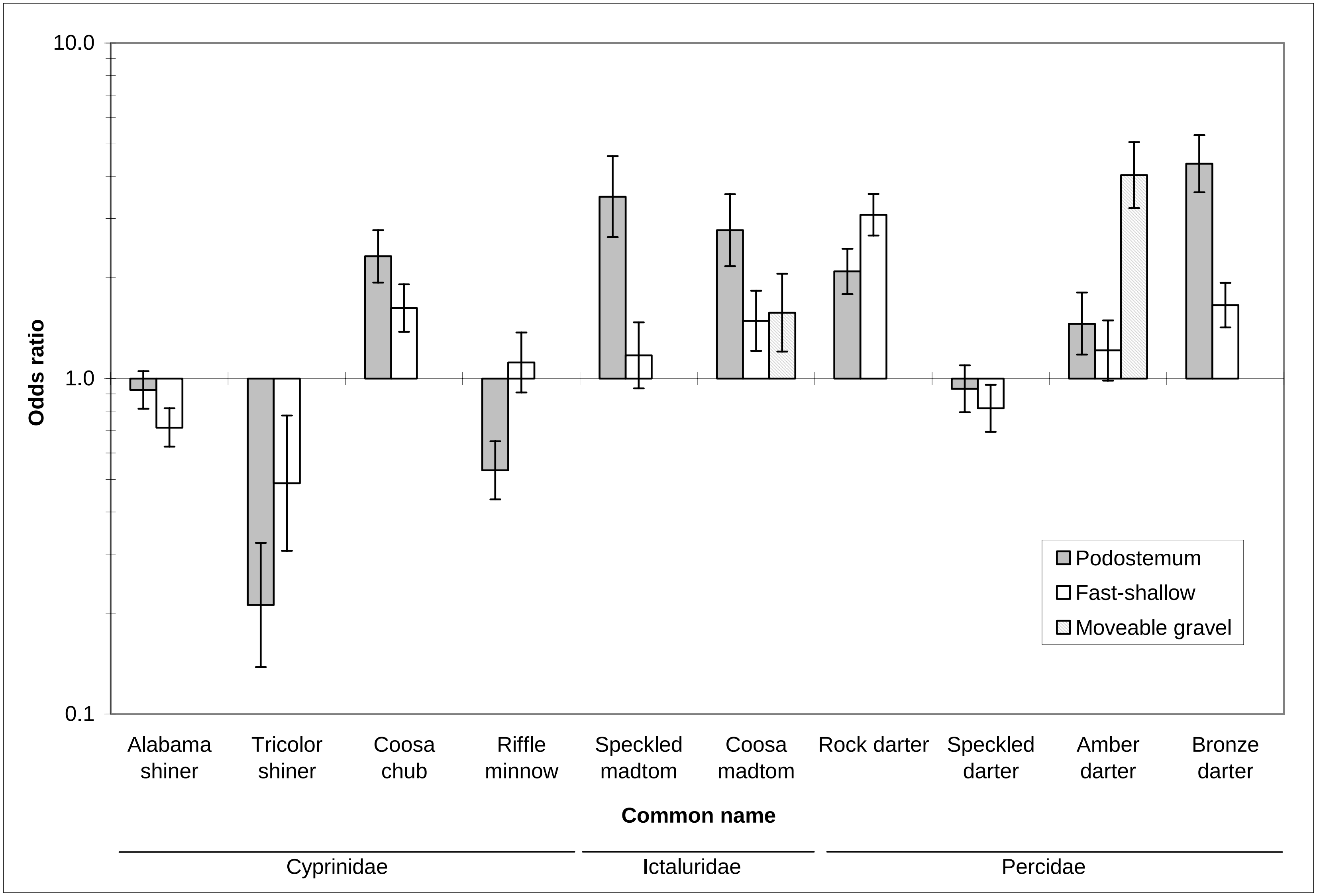


Figure 7. Average effect of microhabitat features on occurrence on adults. Model-weighted average odds ratio indicating the effect of presence of *Podostemum*, fast-shallow habitat and moveable gravel (Coosa madtom and amber darter only) on the probability of occurrence of adult individuals in a set, with 90% unconditional confidence intervals.

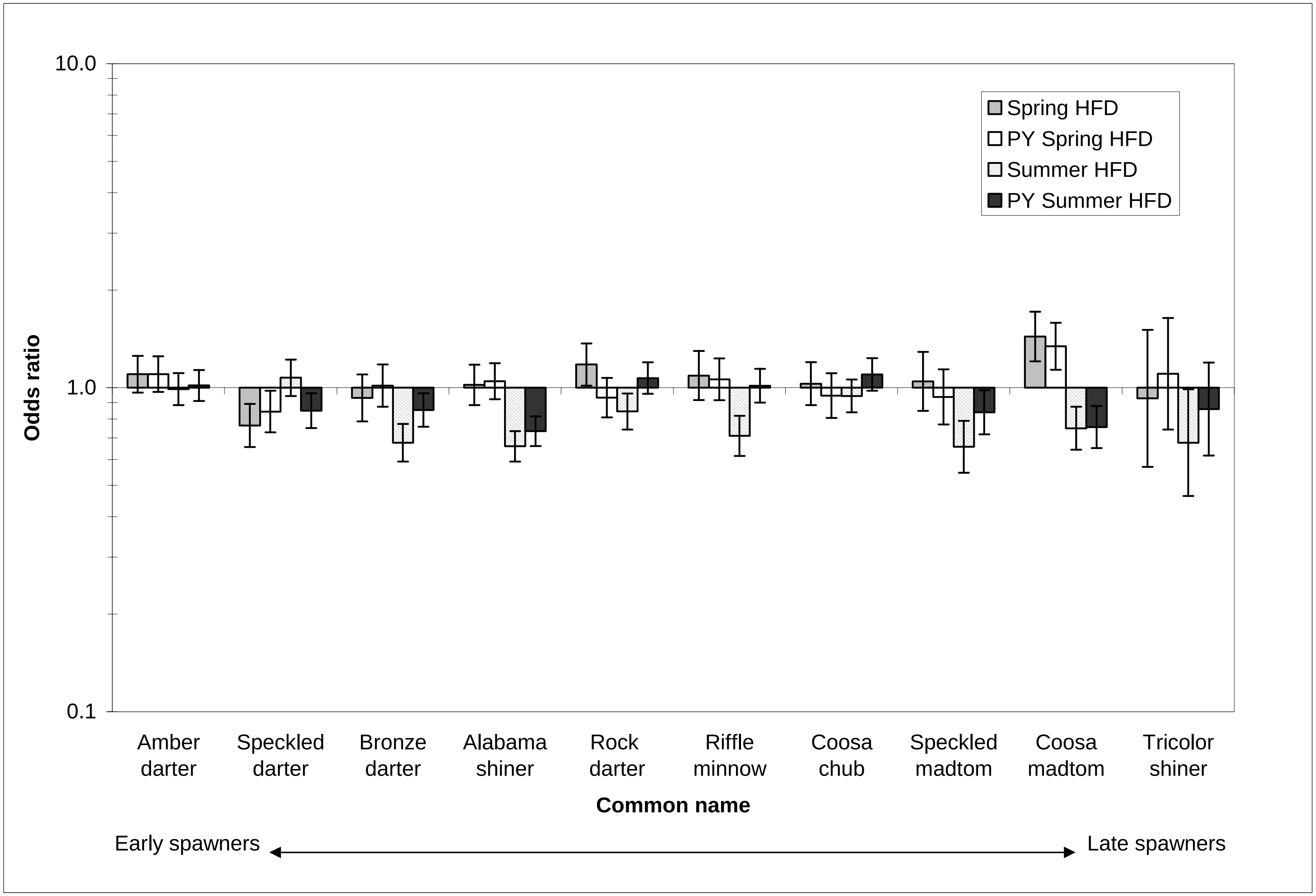


Figure 8. Average effect of increasing days of high flow on the occurrence of adults. Model-weighted average odds ratio are scaled to indicate the effect of an increase of seven days of spring or summer high flow on the probability of occurrence of adult individuals in a set, with 90% unconditional confidence intervals.

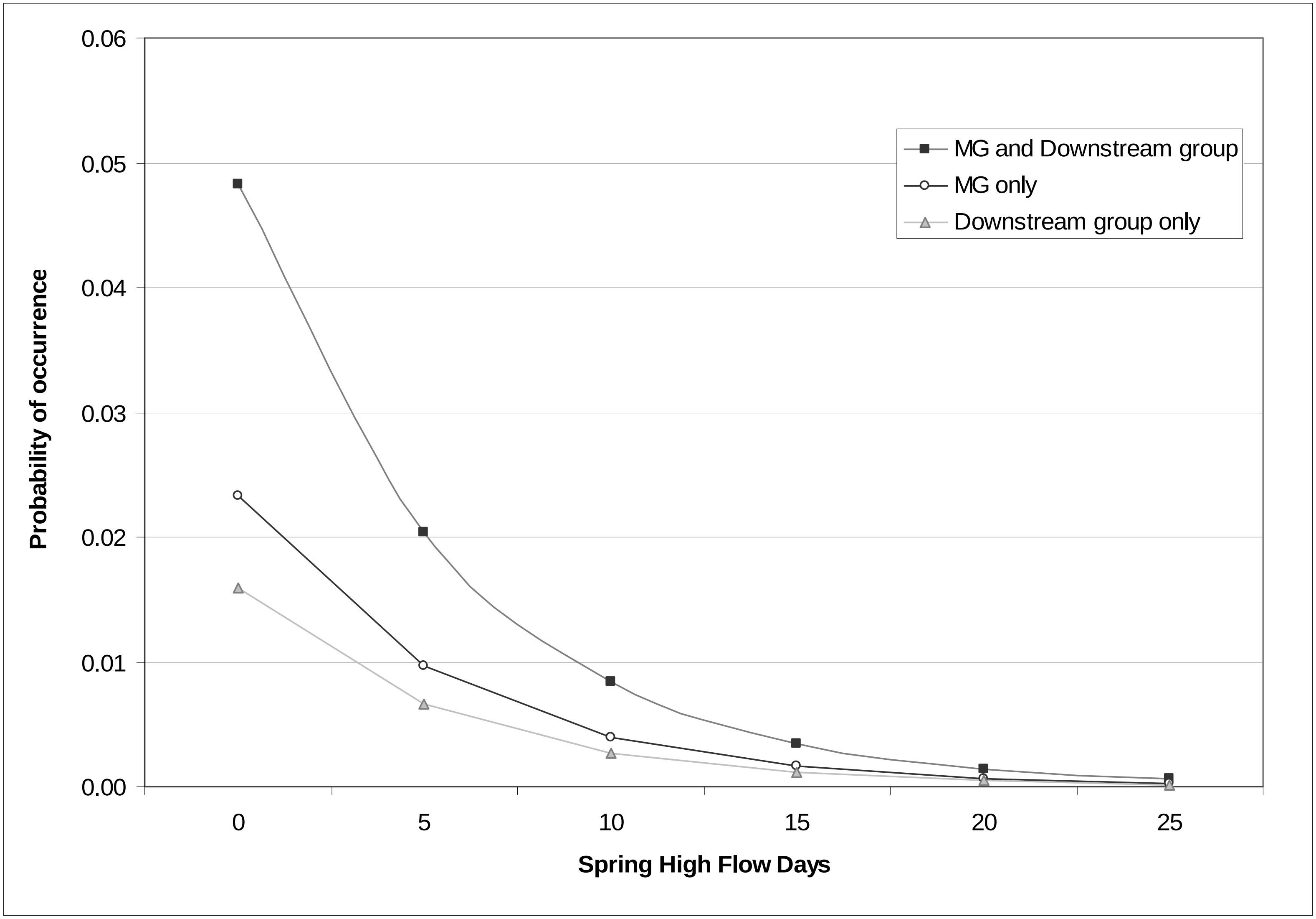


Figure 9. Probability of occurrence of YOY amber darters as spring HFD increases. Using the estimates and parameters in the top model, three different scenarios are shown over a range increasing spring HFD: moveable gravel present, position at the downstream group of five sites, and the combination of both those conditions. The range of spring HFD shown is similar to that seen during the study.