DOI: 10.1007/s00267-005-0169-3

Fish Assemblage Responses to Water Withdrawals and Water Supply Reservoirs in Piedmont Streams

MARY C. FREEMAN*
US Geological Survey
Patuxent Wildlife Research Center
University of Georgia
Athens, Georgia 30602, USA

PAULA A. MARCINEK
Institute of Ecology
University of Georgia
Athens, Georgia 30602, USA

ABSTRACT / Understanding effects of flow alteration on stream biota is essential to developing ecologically sustainable water supply strategies. We evaluated effects of altering flows via surface water withdrawals and instream reservoirs on stream fish assemblages, and compared effects with other hypothesized drivers of species richness and assemblage composition. We sampled fishes during three years in 28 streams used for municipal water supply in the Piedmont region of Georgia, U.S.A. Study sites had permitted average withdrawal rates that ranged from < 0.05 to > 13 times the stream's seven-day, ten-year recurrence low flow (7Q10), and were located directly downstream either from a water supply reservoir or from a withdrawal taken from an unimpounded stream. Ordination analysis of catch data showed a shift in assemblage composition at reservoir sites corresponding to dominance by habitat generalist species. Richness of fluvial specialists averaged about 3 fewer species downstream from reservoirs, and also declined as permitted withdrawal rate increased above about 0.5 to one 7Q10-equivalent of water. Reservoir presence and withdrawal rate, along with drainage area, accounted for 70% of the among-site variance in fluvial specialist richness and were better predictor variables than percent of the catchment in urban land use or average streambed sediment size. Increasing withdrawal rate also increased the odds that a site's Index of Biotic Integrity score fell below a regulatory threshold indicating biological impairment. Estimates of reservoir and withdrawal effects on stream biota could be used in predictive landscape models to support adaptive water supply planning intended to meet societal needs while conserving biological resources.

The ecological effects of meeting the water demands of an expanding human population are of concern worldwide (Postel 2000; Jackson and others 2001). Water withdrawals and diversions used to supply municipalities, industries, and agricultural irrigation have the potential to degrade aquatic habitats to the point that these systems fail to support native biota or to supply other ecosystem services (Moyle and Leidy 1992; Baron and others 2002; Naiman and others 2002). Prominent examples include conflicts between offstream water users and instream flow needs to sustain imperiled species (Collares-Pereira and others 2000; Cooperman and Markle 2003; Ward and Booker 2003), and collapse of fisheries and productivity in flow-deprived ecosystems (Postel 1996, 2000). Even in regions where water historically has been considered an abundant resource, such as eastern North America, rapidly growing populations are placing increasing demands on productive freshwater systems that support unique biodiversity.

The challenges of meeting growing demands for water supply while protecting aquatic ecosystems are exemplified in portions of the southeastern United States. One such area is the southern Piedmont, situated between the Appalachian Mountains and the Coastal Plain, which has experienced some of the highest rates of population growth in the United States in recent decades (Conroy and others 2003; Walters and others 2005). Population growth and urbanization are encroaching on aquatic habitats that support high levels of aquatic biodiversity and endemism, as well as supporting imperiled species (Abell and others 2000; Warren and others 2000). Threats to native biodiversity caused by altered runoff and pollution from urbanizing areas are likely to be compounded by water supply development, largely dependent on surface water in the Piedmont, unless specific management actions are taken to safeguard vulnerable streams. Regulators in the region are attempting to define instream flow

KEY WORDS: Stream fish; Species richness; Flow depletion; Hydrologic alteration; Water supply planning

Published online April 21, 2006.

*Author to whom correspondence should be addressed; *email:* mary_freeman@usgs.gov

© 2006 Springer Science+Business Media, Inc.

needs to protect flowing-water ecosystems, while accommodating societal needs for water.

Management of surface waters tapped for water supply has focused on protecting minimum flow levels, although ecologists have stressed the importance of flows across the range of the natural hydrograph for maintaining structure and function of aquatic ecosystems (Poff and others 1997; Richter and others 1997; Silk and others 2000; Bunn and Arthington 2002). Recent efforts to improve river management have involved developing ecological flow requirements intended to sustain floodplain and in-channel habitats, and recognize flow seasonality and inter-annual variation as drivers of biological communities (Postel and Richter 2003). The holistic approach to defining needs for lotic ecosystems has also shifted the management question from "how much flow must be provided to meet ecosystem needs?" to that of "how much can flow regimes be altered without incurring undesirable ecosystem change?" (Silk and others 2000; Bunn and Arthington 2002). To develop ecologically sustainable water supply policies, regulators will need clear information linking withdrawal levels to effects on aquatic ecosystems.

Previous studies of flow regulation effects on fish assemblages have indicated greater detriment to fluvial specialists, i.e., species that require flowing-water habitats for at least a portion of their life-cycle (Kinsolving and Bain 1993; Travnichek and others 1995) or rheophilic species (Copp 1990), in comparison with habitat generalist species, which are able to maintain populations in lotic and lentic systems. A recent study of fishes in a flow-depleted river in the northeastern United States similarly has revealed a shift in species composition toward habitat generalists and a loss of fluvial specialists (Armstrong and others 2001). Quantifying the responses of differing faunal groups to flow alteration may provide important information to resource managers attempting to balance water use with conserving biota. Additionally, regulatory agencies are often interested in the status of biological communities relative to reference or unimpaired conditions (Barbour and others 1999), in which case effects of water supply development on an assessment score such as the Index of Biotic Integrity (IBI) would be useful.

Our purpose was to improve understanding of the biological effects of water withdrawal by quantifying variation in fish assemblages across streams that are differentially used for municipal water supply. Streams used for water supply vary with respect to permitted withdrawal rate relative to the size of the stream. Withdrawals also vary as to whether they are made directly from an unimpounded stream or from an instream reservoir. Reservoirs, by trapping and storing water during periods of higher runoff, potentially alter downstream flows over a broader range of the flow regime than direct withdrawals. Thus, we investigated the effects of increasing the relative withdrawal rate and the use of water-supply reservoirs on stream fish assemblages. We specifically examined effects on richness of fluvial specialist (FS) and habitat generalist (HG) fishes, and compared the influences of withdrawal rate and reservoir presence with effects of three site-level variables chosen to represent influences of natural (drainage area, bed sediment size) and anthropogenic (amount of urban land use) factors on fish assemblages. We also asked whether sample-specific instream habitat conditions improved site-level models for predicting species richness. To analyze assemblages relative to reference conditions, we used multivariate ordination to analyze assemblage similarity between our samples and samples taken in Piedmont reference streams, and also evaluated IBI scores for our samples in relation to a regulatory threshold used to indicate biological impairment. We used results to estimate quantitative effects of increasing water allocations and using instream reservoirs on stream fish assemblages, and considered how these estimates could be used to incorporate biodiversity conservation in water supply planning.

Methods

Study Site Selection

To hold other landscape influences more constant, we restricted the study to one physiographic area, the lower portion of the Piedmont physiographic region of Georgia (Figure 1). We used a GIS database of 53 permitted water withdrawals, obtained from the Georgia Department of Natural Resources, Environmental Protection Division (GDNR, EPD), to identify potential study sites within 6 river systems (Savannah, Ogeechee, Oconee, Ocmulgee, Flint, and Chattahoochee). We selected 27 study sites in 2000 that represented all of the wadeable streams with apparently active withdrawals and drainage areas exceeding about 12 km^2 (corresponding to the smallest reference site sampled in 2000 by the GDNR Stream Survey Team). In addition to sites located in non-wadeable streams, sites that were dry (2), affected by ongoing construction or pump-storage operations (2), or that were not accessible (2) were not included in the study. Of these 27 sites, 13 were situated downstream from direct water withdrawals ("intakes") and 14 were located downstream from water supply reservoirs ("reservoirs"; Appendix 1). We

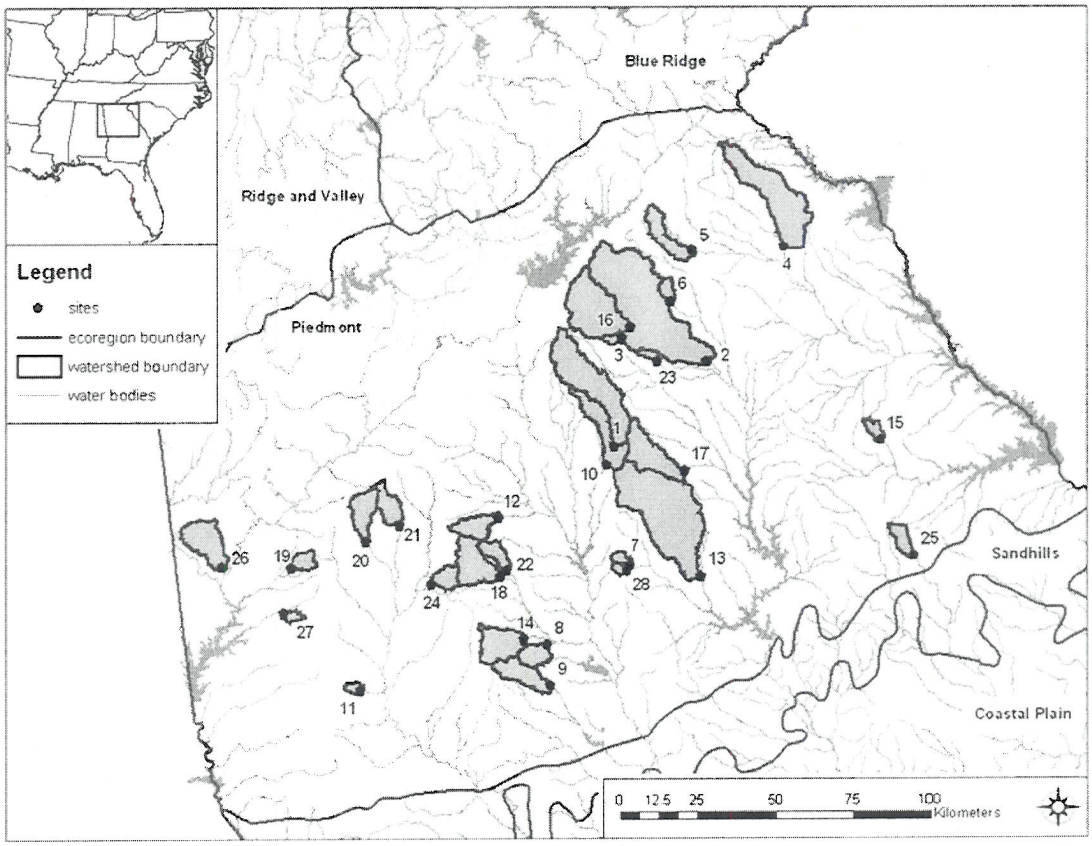

Figure 1. Watershed boundaries for 28 municipal water supply withdrawals in the Piedmont ecoregion, and adjacent ecoregion boundaries. Numbers correspond to sites listed in Appendix 1.

repeated sampling in two subsequent years, 2001 and 2003, to assess effects over a range of instream habitat conditions. For the 2001 field season, we added one intake site that was dry during 2000 and eliminated one intake site that became non-wadeable. During 2003, which had substantially higher rainfall than in 2000 and 2001, we were able to sample 20 (12 reservoir sites and eight intakes) of the 28 sites sampled in the previous years; the remaining eight sites were not sampled because they became non-wadeable under the higher flow conditions.

The GDNR sampled streams chosen as Piedmont stream reference sites (i.e., for bioassessment purposes) in 2000 and 2001 and made those data available for comparison to our study sites. Reference sites were chosen by GDNR on the basis of appearing relatively unimpaired and supporting relatively intact fish assemblages, and were located within the lower Piedmont in five of the six river systems containing study sites. None of the sites were directly downstream from withdrawals or reservoirs. Seven Piedmont reference sites were sampled in 2000, ranging from 12.3 to 690 km^2 in drainage area. These seven and two additional sites (9.7 and 20 km^2) were sampled in 2001. The GDNR did not sample Piedmont reference sites in 2003.

Sampling Procedures

We sampled withdrawal sites between June and September in each study year; reference sites were sampled during September and October in 2000 and 2001. The June through October timeframe represented a period of relative assemblage stability (Matthews 1990; Peterson and Rabeni 1995) occurring after the spring period of spawning migrations by some species, and was within the sampling period (April through October) used by GDNR to assess integrity of stream fish assemblages. We sampled fishes following protocols developed by GDNR (GDNR 2000). Reach length approximated 35 times mean wetted-channel width (estimated from width measurements at five randomly chosen locations for each 100 m length included) to a maximum of 500 m. We sampled fishes from the downstream to upstream boundaries of the

sample reach using one or two backpack electrofishers, or a barge-mounted boat electrofisher (if mean stream width exceeded about 8 m and the stream was deep throughout), dip nets, and seines. Captured fishes were transferred to buckets and coolers; fish to be measured and released were kept in aerated, frequently exchanged water. Fish that were preserved were first anesthetized with tricaine methanesulfonate (MS-222) and subsequently transferred to 10% formalin. All fish were identified to species and measured (total length) either in the field or laboratory. We also recorded incidences of individuals with evident disease, eroded fins, lesions, and tumors, and with "black spot" (trematode cysts).

We measured stream discharge, water temperature, and turbidity on each sampling date. Turbidity was measured in nephelometric turbidity units (NTU) with a Hach® Model 2100P turbidity meter. In 2000 and 2001, we also measured dissolved oxygen (DO) concentration at the upstream end of each sample reach with a Hydrolab® multiprobe. We estimated stream discharge near the upstream end of the site using a Marsh-McBirney Flo-Mate® electromagnetic current velocity meter and top-setting wading rod. Discharge was based on depth and velocity measured every 0.5 m along a tape measure stretched from bank to bank, or at intervals sufficient to give at least 20 measurements across the stream.

Habitat data were collected during low flow conditions, usually immediately following fish collections. The length of each pool, riffle, and run in the sample reach was measured and recorded in sequence by type. We randomly selected three to five locations for cross-section measurements from the total length of each habitat type. At each cross-section, we recorded depth, velocity, and dominant bed sediment size [recorded in *phi* intervals (Gordon and others 1992)] at channel edges and at three equally spaced positions across the channel (0.25, 0.5, and 0.75 times wetted width). Depth, velocity, and bed sediment averages for each site were computed as means of pool, run, and riffle measurements, weighted by the proportion of the site in each habitat type. In 2003, dominant bed sediment size was recorded longitudinally along the mid-channel at intervals equal to 0.5 times average wetted-channel width to give a more complete profile of sediment variation.

Analyses

Site Characteristics. We summarized average stream flow, depth, velocity, and water quality measurements to compare flow and habitat conditions among years and between intake and reservoir sites. Land use in the catchment upstream from each site was estimated using a statewide land cover map based on 1998 *Landsat* Thematic Mapper imagery, with 30-m resolution (produced by the Natural Resources Spatial Analysis Laboratory, University of Georgia, in 2001). We examined three land use categories: urban (low- and high-intensity), forest (including deciduous, evergreen, and mixed forest), and agriculture (pasture and row crop). We estimated mean bed sediment size at sites by averaging the mean values computed for each year the site was sampled.

To facilitate among-site comparison of potential withdrawal rate relative to stream size, we computed a "withdrawal index" (WI) for each site as the maximum permitted monthly average withdrawal rate (in million gallons per day, mgd) divided by the estimated seven-day, ten-year recurrence low flow (7Q10) at the withdrawal site (also expressed in mgd). The WI thus represented the fraction or multiple of the 7Q10 flow permitted for withdrawal on a monthly average basis. The 7Q10 flow is commonly used by regulatory agencies to set wastewater discharge criteria, and has also been used to set minimum flow requirements. We used 7Q10 flows to standardize permitted withdrawal rates across sites because 7Q10 estimates could be obtained from EPD files or estimated from low-flow profile data (Carter and others 1986, 1988a,b). Other flow statistics that could also be used to standardize withdrawal rates, such as average annual flow, were not available because 27 of the 28 sites lacked stream gages. This also precluded quantifying actual hydrologic patterns or flow alteration. To examine actual water withdrawal in relation to WI, we used the maximum monthly withdrawal rate reported for 25 sites during the 12-month period prior to our fish samples in 2000 and 2001, divided by 7Q10 for the site. Monthly withdrawal data were provided by EPD or by permit holders. Because we observed strong relations between WI and water use (results reported below), and because water use varied at many sites across months and water use data were not available for all sites and months, we used WI as our measure of potential withdrawal effects in all analyses.

Fish Assemblage Patterns. We used the catch data across sites and years in an ordination analysis to examine the relative similarity of fish assemblage data in our samples to those from the GDNR Piedmont reference sites. We employed nonmetric multidimensional scaling (NMDS), using Bray-Curtis dissimilarity, to ordinate our study-site samples ($n = 74$) and Piedmont reference site samples ($n = 16$). NMDS provided graphic representation of the relative similarity among samples based on taxa abundances (Field and others

1982; Clarke 1993; McCune and Grace 2002). For each sample, we applied a fourth-root transformation to abundance data in order to dampen the influence of common taxa (Clarke 1993), retaining for analyses all taxa that occurred in at least six samples overall and that had ranges encompassing all sample locations. To meet the latter criterion, we combined abundances of some congeneric species with ranges restricted to a subset of the sampled river systems (Appendix 2). We used a total of 34 taxonomic entities (24 species and 10 multispecies genera) in NMDS analysis. Analyses were accomplished with PC-ORD (McCune and Mefford 1999), using a step-down procedure (from 6- to 1-dimensions) to find the most appropriate solution, with 200 iterations, 10 runs with the real data, 20 runs with randomized data, and stability criterion set to 0.0001 (McCune and Grace 2002). Because of reviewer concerns that the PC-ORD solution might be far from the minimum stress solution, we also conducted NMDS ordination using the function isoMDS, package vegan, in the R programming environment (Oksanen and others 2005), using Bray-Curtis dissimilarity and the same number of dimensions (3) as in the final solution from PC-ORD. We used product-moment correlation coefficients between taxa abundances and ordination axes, and graphical representation, to examine patterns of assemblage differences among sites.

Water Withdrawal and Reservoir Effects on Species Richness. We used the limiting form of the jackknife estimator for model M_h (Burnham and Overton 1979; Williams and others 2002) to estimate richness of FS and HG species in each sample, given the observed numbers of species and numbers of species in each sample represented by 1, 2, 3, 4, or 5 individuals. We used the program SPECRICH, available at http://www.mbr-pwrc.usgs.gov/software.html. The purpose of using the jackknife estimator for richness rather than actual sample counts of species was to reduce bias resulting from incomplete species detection and among-species differences in detectability.

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate the relative effects of WI and upstream presence of a reservoir on fish species richness. Our approach was to construct a set of alternative linear regression models that, first, would allow us to compare the effects of WI and reservoir presence with each other and with other site-level variables hypothesized to influence species richness. Secondly, we wished to evaluate effects of among-year differences in instream habitat on species richness. Our data set comprised 72 observations (one to three observations at 27 sites; see Results). To avoid model over-fitting, we restricted models to a maximum of 7 parameters (i.e., to keep the ratio of observations to parameters to about 10 to 1; Burnham and Anderson 2002). All regression models included a term for random variation among sites to account for unmeasured site-specific influences on the repeated observations (Snijders and Bosker 1999) in addition to an intercept and within-site residual error term. Thus, we included a maximum of four explanatory variables in regression models to limit the total number of model parameters to seven.

We considered the effects of three site-level variables in addition to WI and reservoir presence on species richness for FS and HG fishes. First, we included drainage area in all models because fish species richness generally increases as a function of stream size (Matthews 1998). Given that our sites spanned two orders of magnitude in drainage area, we did not believe that any credible explanatory model could ignore drainage area as a predictor variable. We also hypothesized that the average size of the stream bed sediments would influence species richness of FS and HG fishes, based on observations in upper Piedmont streams of a shift in fish assemblage structure from dominance by fluvial specialists in steeper, rockier streams to habitat generalists in lower gradient streams with finer bed sediments (Walters and others 2003b). Finally, we hypothesized that the level of urbanization upstream from the study sites could depress species richness, at least of FS species, as observed in other Piedmont streams (Weaver and Garman 1994; Walters and others 2003a; Roy and others 2005). Therefore, we evaluated 13 models with drainage area and combinations of WI (ln transformed), reservoir presence, mean *phi*, and percent urban land use upstream from the site (arcsine transformed). We also evaluated whether adding terms indicating basin identity, presence or absence of a minimum flow requirement, and an interaction between WI and reservoir presence improved the best-fit site-level model predicting species richness. Our purpose was to construct a small set of preselected candidate models (Burnham and Anderson 2002) intended specifically to compare effects of WI and reservoir presence with variables representing natural and land use influences, while also testing for the potential influences of differences attributable to basins, minimum flow requirements, and the possibility of a reservoir-withdrawal level interaction. Basin identity was coded as Apalachicola (i.e., Chattahoochee and Flint river systems), Altamaha/Ogeechee (i.e., Ocmulgee, Oconee, and Ogeechee river systems), or Savannah following Warren and others (2000).

We used estimates of mean depth and mean velocity measured for each yearly sample to evaluate the relative importance of hydraulic habitat conditions on species richness. We compared linear regression models with mean depth and mean velocity in addition to drainage area alone and in combination with WI and reservoir presence. Because of missing measurements, we used reduced data sets to compare the predictive ability of depth and velocity with that of turbidity and water temperature (data for 71 samples) and DO (data for 49 samples). Velocity, turbidity, and DO data were ln transformed to reduce departures from normality.

Models were compared on the basis of differences in Akaike's Information Criterion values, corrected for small sample size (AIC_c; Burnham and Anderson 2002). AIC provides an estimate of the expected, relative distance between a fitted model and the unknown mechanism(s) that generated the data, so that the best-supported model among a set of plausible models is indicated by the lowest AIC (Burnham and Anderson 2002). The approach thus allows selection of the simplest, best-fitting model(s) given the observed data, while avoiding the problems of multiple hypothesis testing and arbitrary probability levels associated with stepwise variable selection. An information-theoretic approach also allows one to make inferences (in this case, regarding WI and reservoir effects on species richness) based on multiple models that share relatively strong support, thereby incorporating uncertainty in model selection. To this end, we used Akaike weights (ω_i), which vary from 0 to 1 with the best-fitting model having the highest weight, to evaluate relative support for each model. Summing weights across the models that included each variable provided an estimate of relative variable importance. We also used weights to estimate model-averaged effect sizes of WI and reservoir presence on species richness, with 90% confidence intervals (CIs) based on unconditional standard errors (Burnham and Anderson 2002). All models were fit in SAS version 8.01 (SAS Institute, Cary, NC, USA) using PROC MIXED and specifying maximum likelihood estimation to derive AIC values, or restricted maximum likelihood to estimate among-site and residual variance components (Snijders and Bosker 1999). Unconditional models (i.e., with no explanatory variables) were fit to estimate total variances attributable to among-site and residual components, and to provide a basis for computing how much variance in each component was accounted for by explanatory variables.

Water Withdrawal and Reservoir Effects on Probability of Site Impairment. We computed IBI values for each sample using the GDNR protocol to evaluate evidence that WI or presence of an upstream reservoir contributed to sites qualifying as "impaired." Under the GDNR protocol, IBI values are computed as sums of scores of 1, 3, or 5 for 12 metrics that reflect aspects of species richness and composition, trophic composition, and fish abundance and condition (GDNR 2000). Sites scoring lower than 34 are assigned to classes of "poor" or "very poor" and are classified by the State as biologically impaired for purposes of water quality assessment under section 305(b) of the Clean Water Act. We thus analyzed effects of WI and reservoirs on probability of impairment because of the regulatory relevance of the question, and because IBI calculations are widely used to assess biological aspects of stream quality (Karr and Chu 2000). We note, however, that IBI estimates may be biased by uncontrollable variation in capture efficiency among sites (e.g., resulting from habitat differences; J. T. Peterson, USGS, Athens GA, personal communication). Additionally, our methods differed somewhat from those employed by the GDNR survey team. Specifically, whereas the GDNR team frequently used multiple electrofishers moving upstream in parallel and closely followed by dip-netters, we more frequently sampled by shocking downstream into a seine set in flowing-water habitats, and we combined electrofishing and dip-netting with seine hauls in slack water. We have not estimated capture efficiency for either protocol or as a function of site characteristics, and therefore we interpret results based on IBI values cautiously.

We used logistic regression to compare the effects of (1) WI and reservoir presence compared to other site variables (drainage area, mean bed sediment size, and percent urban land use) and (2) hydraulic habitat conditions (mean depth and velocity) on probability that a site scored as "impaired" in a given sample. Our model set included: all five site variables; four variables (omitting either WI or reservoir presence); three variables (omitting both WI and reservoir presence), and WI and reservoir presence alone and in combination with each of the other site variables and each other (16 models total). We also tested whether the presence or absence of a minimum flow requirement or an interaction between WI and reservoir presence improved the best-fit site-level model. We did not constrain models to include drainage area or test for an effect of basin identity because IBI computations explicitly account for these variables. Finally, we tested whether adding mean depth and velocity improved fit of the highest-ranked site-level models. Logistic regression models were fit in SAS using PROC GENMOD and specifying repeated measurements at sites to account for clustered data (Allison 1991). As above, models

Table 1. Habitat conditions at intake and reservoir sites in each year, showing means (standard error, range)

Variable	Withdrawal type	Year		
		2000	2001	2003
Flow, discharge/7Q10	Intake	0.62 (0.20, 0 – 2.31)	3.22 (0.97, 0 – 14.0)	7.41 (2.52, 1.15 – 20.8)
	Reservoir	0.62 (0.16, 0 – 1.62)	3.92 (0.86, 0.03 – 12.1)	9.30 (1.68, 0.85 – 21.7)
Depth, m	Intake	0.28 (0.04, 0.10 – 0.51)	0.42 (0.04, 0.16 – 0.60)	0.36 (0.04, 0.23 – 0.55)
	Reservoir	0.28 (0.03, 0.06 – 0.49)	0.34 (0.04, 0.10 – 0.52)	0.35 (0.04, 0.16 – 0.55)
Velocity, m/s	Intake	0.07 (0.025, 0 – 0.29)	0.15 (0.021, 0.03 – 0.30)	0.17 (0.05, 0.07 – 0.44)
	Reservoir	0.04 (0.012, 0 – 0.13)	0.09 (0.019, 0.02 – 0.24)	0.17 (0.03, 0.03 – 0.40)
Temperature, °C	Intake	25.5 (0.86, 21.8 – 33)	24.7 (0.54, 21.2 – 27.3)	23.8 (1.0, 20 – 28)
	Reservoir	26.6 (0.62, 22.9 – 29.3)	26.2 (0.63, 21.3 – 29.9)	27.4 (0.8, 23 – 32)
Turbidity, NTU	Intake	32.0 (8.0, 6.5 – 94.6)	17.7 (2.6, 5.5 – 41.5)	19.1 (3.6, 8.2 – 39)
	Reservoir	33.3 (12.8, 2.6 – 151)	13.2 (3.4, 3.7 – 54.4)	11.4 (1.6, 4.8 – 21.8)
Dissolved oxygen, mg/L	Intake	5.4 (0.39, 1.8 – 6.7)	7.1 (0.26,4.7 – 8.5)	Not measured
	Reservoir	4.5 (0.45, 1.5 – 6.7)	6.7 (0.31, 4 – 8)	Not measured

were compared on the basis of AIC_c values and Akaike weights, which we also used to derive model-averaged estimates of effect sizes.

Results

Site Characteristics

Permitted water withdrawal levels ranged from 1.5 to 45 million liters per day (0.4 to 12 mgd) across the 28 study sites (Appendix 1). WI values ranged from 0 (where withdrawals were discontinued) to 13.33 across sites and were negatively correlated with drainage area ($r = -0.43$, $n = 27$). Actual water withdrawal amounts during the 12 months preceding 2000 and 2001 samples varied substantially among sites and among months at a given site. The maximum monthly withdrawal reported during a year ranged from 0.02 to 13.5 times 7Q10, and was strongly correlated with WI in 2000 ($r = 0.97$, $n = 25$) and 2001 ($r = 0.90$, $n = 24$).

Reservoir sites had a smaller average drainage area, 54 km^2, compared to 270 km^2 at intake sites, and a larger average WI (2.90 compared to 1.50 at intake sites). Reservoir and intake sites were similar in other characteristics. Catchment land use upstream from intake and reservoir sites was predominantly forest (means = 57% and 59%, respectively), followed by agriculture (means = 21% and 20%, respectively) and urban (means = 4.7% and 3.5%, respectively). Average dominant bed sediment size ranged from small cobble to sand (*phi* = −7 to 1) at all except for two sites that were dominated by bedrock. The 11 sites with the smallest average bed sediment sizes (*phi* = −1 to 1) were nearly evenly divided between intake and reservoir sites (Appendix 1).

Stream flow, depths and velocities during sampling periods corresponded to drought conditions during 2000 and 2001, and to elevated flows during 2003, and were similar between intake and reservoir sites in all years (Table 1). Temperature ranges were similar among years, although during the wetter conditions of 2003, streams below intakes averaged 3.6°C cooler than those below reservoirs. Dissolved oxygen levels were lowest in 2000 (Table 1), when we recorded levels less than 5 mg/L at seven reservoir and four intake sites. One reservoir and one intake site had a DO level <5 mg/L in 2001. Turbidity varied widely across sites, from <5 to >150 NTU in 2000, with lower values in subsequent years (Table 1).

Fish Assemblage Patterns

The NMDS ordinations produced by PC-ORD and R were strongly similar, with stress values of 14.43 and 14.37, respectively, for a three-dimensional solution. We have used the PC-ORD results to illustrate among-site differences. In this ordination, axes 2 and 3 cumulatively represented 76% (33 and 43%, respectively) of the variance in the original among-sample distance matrix. Axis 1 represented less (8%) of the among-sample variance; therefore, we used scores on axes 2 and 3 to illustrate assemblage similarity among samples. The ordination showed a shift in fish assemblage structure at reservoir sites away from reference sites (Figure 2), corresponding to dominance by habitat generalist taxa in reservoir site samples. Reservoir sites mostly scored relatively high on axis 2 and low on axis 3, and displayed almost no overlap with reference sites, which scored oppositely. Intake samples overlapped with reference and reservoir samples, but mostly scored higher on axis 3 than did reservoir sites. Higher sample scores on axis 2 corresponded to higher abundances of primarily HG taxa (Table 2), specifically several sunfish species (genus *Lepomis*), largemouth

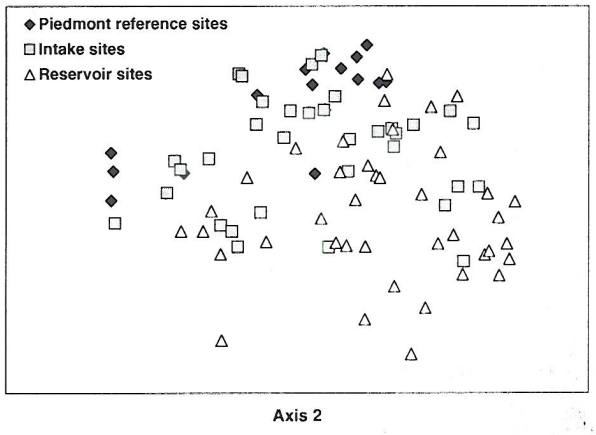

Figure 2. NMDS ordination of fish sample data from 2000, 2001, and 2003 at intake, reservoir, and Piedmont reference sites, illustrating relative similarities among sites based on assemblage composition.

bass *Micropterus salmoides*, and crappie (genus *Pomoxis*). Conversely, higher scores on axis 3 corresponded to higher abundances of FS taxa, especially insectivorous cyprinids ("shiners" *Cyprinella* spp., spottail shiner *Notropis hudsonius*), benthic invertivores (madtom catfishes *Noturus* spp., blackbanded darter *Percina nigrofasciata*), catostomids ("jumprocks" *Scartomyzon* spp., "redhorses" *Moxostoma* spp.), snail bullhead (*Ameiurus brunneus*), and black basses other than largemouth bass (*Micropterus* spp., Table 2). One HG species, redbreast sunfish *Lepomis auritus*, also had a relatively strong positive correlation with axis 3 (Table 2).

Table 2. Correlations between transformed taxa abundances and sample scores on NMDS axes 2 and 3

Species or taxonomic group	Category	Axis 2	Axis 3
Lepomis macrochirus	HG	0.68	0.00
Micropterus salmoides	HG	0.59	0.05
Lepomis microlophus	HG	0.56	0.18
Lepomis gulosus	HG	0.55	0.00
Pomoxis spp.	HG	0.51	0.29
Lepomis punctatus	HG	0.41	0.24
Notropis spp.	FS	0.41	0.28
Dorosoma cepedianum	HG	0.27	0.28
Gambusia spp.	HG	0.26	−0.28
Minytrema melanops	FS	0.21	0.32
Percina nigrofasciata	FS	0.14	0.80
Ictalurus punctatus	HG	0.14	0.47
Perca flavescens	HG	0.14	0.39
Cyprinus carpio	HG	0.14	0.32
Lepomis cyanellus	HG	0.10	0.44
Lepomis auritus	HG	0.07	0.69
Cyprinella spp.	FS	0.05	0.84
Moxostoma spp.	FS	0.03	0.73
Noturus spp.	FS	0.03	0.63
Notropis hudsonius	FS	−0.01	0.70
Ameiurus brunneus	FS	−0.16	0.79
Micropterus spp.	FS	−0.28	0.60
Scartomyzon spp.	FS	−0.31	0.70
Etheostoma spp.	FS	−0.35.	0.37
Hybopsis spp.	FS	−0.38	0.50
Nocomis leptocephalus	FS	−0.59	0.40
Notropis lutipinnis	FS	−0.65	0.17

Note: Taxa are listed in descending order by score on axis 2, and are categorized as habitat generalists (HG) or fluvial specialists (FS). Seven HG taxa for which correlation coefficients were ≤ 0.2 are not listed: *Anguilla rostrata, Esox niger, E. americanus, Notemigonus crysoleucas, Erimyzon oblongus, Ameiurus* spp., and *A. natalis*.

Species Richness Variation

We collected a total of 47 FS species, all of which were native to one or more of the sampled river systems; we collected a total of 39 HG species, of which six were not native to any of the sampled river systems. We based all FS and HG richness estimates on 1st-order jackknife calculations, using the number of species observed and the number represented by a single individual. The 1st-order estimate provided the best fit to our data in 85% of the samples, and higher-order estimates had substantially larger standard errors and generally were inconsistent at a site across years.

Estimated richness of FS fishes varied from 0 to 24 species across study sites and years, and was, on average, lowest at reservoir sites and highest at reference sites (Figure 3A). Overall, 75.6% of the variance in FS richness at reservoir and intake sites was attributable to differences among sites (i.e., among-site variance = 20.30; residual = 6.57). Estimated FS richness increased with drainage area (Figure 4A). Estimates of HG richness varied from 2 to 20 species across sites, were similar between intake and reservoir sites, and were similar to estimates at reference sites in 2001 (Figure 3B). Contrary to our expectations, HG richness did not increase with drainage area (Figure 4B); overall, 26.8% of the variance in HG richness was attributable to differences among sites (i.e., among-site variance = 5.00; residual = 13.68).

Water Withdrawal and Reservoir Effects on Species Richness

The most strongly supported linear regression models of fluvial specialist richness incorporated drainage area, WI, and reservoir presence (Table 3). Support for including any of the other site level variables (% urban, mean *phi*, basin identity, or occurrence of a minimum flow requirement) was relatively weak; e.g., AIC_c differences between the best site-level model (using DA, WI, and reservoir presence) and models with other site-level variables ranged from 2.3 to 9.6 (Table 3). Drainage area, WI, and reservoir presence,

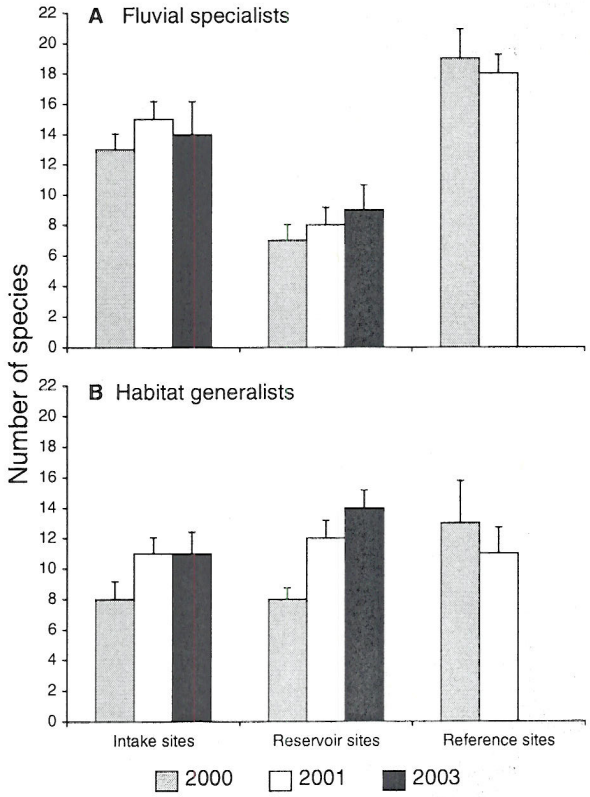

Figure 3. Mean estimated richness for fluvial specialist (**A**) and habitat generalist (**B**) fishes at intake, reservoir, and Piedmont reference sites in 2000, 2001, and 2003. Error bars indicate one standard error.

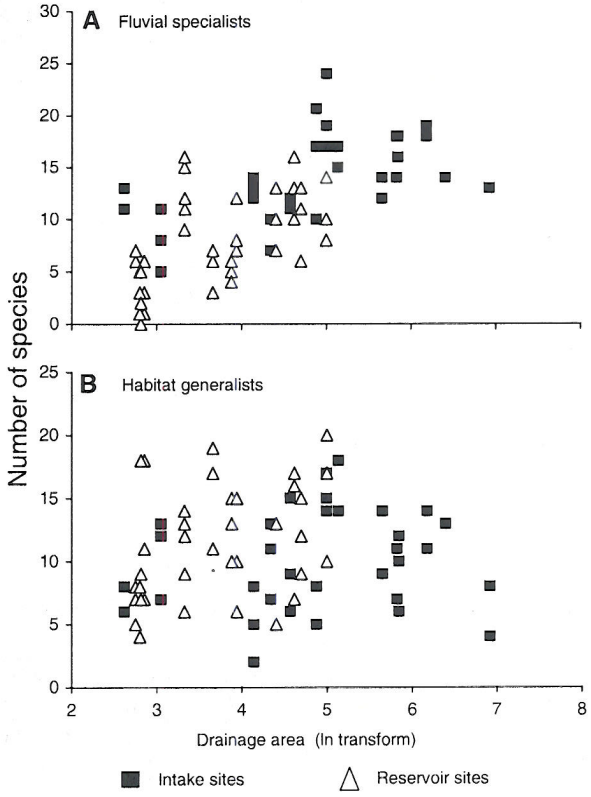

Figure 4. Richness estimates for fluvial specialist (**A**) and habitat generalist (**B**) fishes plotted in relation to drainage area at intake and reservoir sites, data for all years.

together, accounted for 70.3% of the among-site variation in FS richness estimates (i.e., among-site variation declined from 20.30 to 6.02). FS richness declined with increasing WI and with reservoir presence (Figure 5A). Summed weights for the 14 models with reservoir presence was 0.81 compared to 0.56 for the 14 models that included WI, indicating greater support for the influence of reservoir presence on FS richness. Incorporating average water velocity and, to a lesser degree, average depth improved model fit for FS richness (Table 3), and accounted for 18.8 and 9.1% of residual variance, respectively. FS richness increased with increasing velocity and depth. Tests with reduced data sets showed that velocity was substantially more predictive of FS richness than turbidity or water temperature (n = 71, AIC_c differences from velocity model = 8.1 and 11.2, respectively), or DO (n = 49, AIC_c difference from velocity model = 4.8).

None of the tested models provided a good fit to HG richness estimates, which displayed no relation to WI or reservoir presence (Figure 5B). Including six site-level variables (drainage area, WI, reservoir presence, % urban, mean *phi*, basin identity) accounted for only 18.9% of the total variance in HG richness estimates. The best-supported model included depth alone and accounted for 8.4% of total variance.

Model-averaged effect sizes show a decrease in FS richness of about 1.7 species for a unit increase in ln-transformed WI values (mean = −1.69, 90% CI = −0.34 to −3.04). This equates to a loss of about one species as permitted withdrawal increases from 0 to 0.8 × 7Q10, and loss of an additional three species as WI increases to 12 × 7Q10. Sites below reservoirs are predicted to have an average of about three fewer FS species (mean = −3.26, 90% CI = −1.09 to −5.42) compared with sites below intakes. The large confidence intervals for these estimates reflect variation in the data and uncertainty associated with model selection.

Water Withdrawal and Reservoir Effects on Site Impairment

Twelve (86%) of the reservoir sites and seven (50%) of the intake sites scored as impaired in at least one year, although fewer sites (four reservoir and two

Table 3. Alternative linear regression models of fluvial specialist richness listed in order from best- to least-supported

Site variables	Habitat variables	ΔAIC_c	ω_i
DA, WI, Reservoir	**Velocity**	**0**	**0.39**
DA, Reservoir	**Velocity**	**1.2**	**0.21**
DA, Reservoir	**Depth, Velocity**	**1.8**	**0.16**
DA, WI	**Velocity**	**3.0**	**0.09**
DA,WI	**Depth, Velocity**	**4.3**	**0.05**
DA	Velocity	4.9	0.03
DA, WI, Reservoir	Depth	5.7	0.02
DA	Depth, Velocity	6.2	0.02
DA, Reservoir	Depth	6.9	0.01
DA, WI	Depth	9.1	0.00
DA, WI, Reservoir		9.5	0.00
DA, WI, Reservoir, WI*Reservoir		11	0.00
DA	Depth	11.2	0.00
DA, Reservoir		11.4	0.00
DA, WI, Reservoir, Minimum Q		11.8	0.00
DA, WI, Reservoir, Mean *phi*		11.9	0.00
DA, WI		12.0	0.00
DA, WI, Reservoir, % Urban		12.0	0.00
DA, WI, Reservoir, Basin		12.4	0.00
DA, Reservoir, % Urban		12.8	0.00
DA, Reservoir, Mean *phi*		13.8	0.00
DA, WI, % Urban		14.1	0.00
DA, WI, Mean *phi*		14.4	0.00
DA		14.9	0.00
DA, % Urban		16.7	0.00
DA, Mean *phi*		17	0.00
DA, Mean *phi*, % Urban		19.1	0.00

Note: Results show variables included, differences in AIC_c from the best-fit model, and model weights (ω_i). Results shown in bold are for models used to derive model-averaged effect sizes. DA = in-transformed drainage area; WI = in-transformed withdrawal index; Reservoir = reservoir presence; % Urban = arcsine-transformed percent urban land use; Velocity = in-transformed average velocity.

intake) scored as impaired in all years sampled. The best-supported logistic regression models for probability of a sample at a site scoring as impaired incorporated WI, drainage area, average velocity, and, with lesser support, average depth (Table 4). In contrast to the models for FS richness, adding reservoir presence to the model was not as strongly supported (e.g., 2.2 difference in AIC_c values for site-level models with WI and reservoir presence versus WI alone, Table 4). The odds of scoring as impaired increased by about 300% with a unit increase in ln-transformed WI value (model-averaged odds ratio = 4.07; 90% CI = 0.95 to 17.43), or as WI increased from 0 to about 2 × 7Q10. However, the large 90% confidence interval for the odds ratio encompassed no effect and indicated substantial uncertainty in the predictions.

Discussion

The results of this study have allowed us to estimate the effects of increasing the allowable rate of water withdrawal from streams, and of using instream reservoirs, on composition of downstream fish assemblages. In the wadeable, lower Piedmont streams included in our study, increasing the potential for water withdrawal and use of an instream reservoir were associated with a loss of native fish species that are dependent on flowing-water habitats. Vulnerable species included a variety of minnows (Cyprinidae), redhorse and jumprock suckers (Catostomidae), darters (Percidae), and catfishes (Ictaluridae), as well as stream-dwelling basses (Centrarchidae). Models using drainage area, WI, and reservoir presence to predict fluvial specialist richness were better supported by our data than models using drainage area alone or in combination with any of the other site-level variables tested. Models were improved by including sample-specific average water velocity, indicating the influence of velocity on site habitability by fluvial specialist fishes.

Our results are consistent with the hypothesis that altering flow regimes will affect stream biota in relation to the degree of alteration (Poff and others 1997; Bunn and Arthington 2002). Raising the permitted water withdrawal rate potentially increases the proportion of flow removed across the hydrograph, reducing seasonal and interannual variability in baseflow

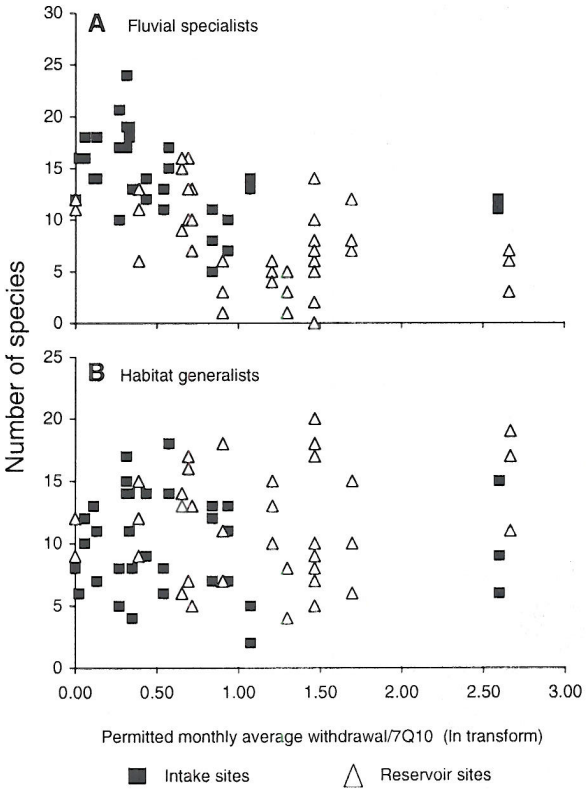

Figure 5. Richness estimates for fluvial specialist (**A**) and habitat generalist (**B**) fishes plotted in relation to withdrawal index at intake and reservoir sites, data for all years.

conditions. Creating water storage with instream reservoirs further increases the capacity for altering flows. Reservoirs use runoff to refill depleted storage, thereby diminishing high flows (e.g., during wetter seasons or years). The effect on downstream fishes may be expected to vary as a function of reservoir volume relative to inflow and rate of water withdrawal. However, despite likely variation in reservoir operations, we observed a general effect on downstream richness of fluvial specialist species. In contrast, habitat generalist species displayed no association with either the rate of permitted water withdrawal or upstream reservoir presence.

Reservoirs can also influence downstream water quality, depending on temperature and dissolved oxygen conditions within the reservoir and from what reservoir stratum water is released downstream. The water supply reservoirs in our study primarily release surface water. Surface releases can send warm water downstream during summer, whereas hypolimnetic releases may be cooler and low in dissolved oxygen (Baxter 1977; Collier and others 1996). Our data show higher average water temperatures downstream from reservoirs than from intakes, whereas we have observed instances of low dissolved oxygen below intakes as well as reservoirs. Elevated water temperatures would be expected to be more detrimental to fluvial specialists adapted to forested streams than to pond- and lake-adapted habitat generalists (Scott and Helfman 2001). Thus, increasing downstream water temperatures may be a mechanism by which water-supply reservoirs can cause a shift in fish assemblages. Reservoirs may also trap sediments, resulting in lower downstream turbidities (Collier and others 1996), although our turbidity measurements below intakes and reservoirs are variable with broadly overlapping ranges. We also have not observed large average differences between intake and reservoir sites in mean depth, mean water velocity, or relative flows. These comparisons are based on measurements made on a few days during low-flow periods; continuous data would provide better information on the occurrence of periodically stressful instream conditions. However, the similarities in observed conditions during low flows below intakes and reservoirs supports the hypothesis that the apparent reduction in habitat suitability for fluvial specialists downstream from reservoirs is not solely a function of altered water quality or low-flow habitat, but also results from alteration in flow regimes.

Our estimates of effect sizes of withdrawals and reservoirs on fluvial specialist fishes reflect considerable uncertainty, resulting in part from the broad array of factors that may influence stream fish assemblages. Present and past land use, geomorphology and instream habitat structure, pollutants, species interactions, and stochastic variation may all influence the composition of local fish assemblages. Moreover, each stream reach is part of a landscape in which phenomena operating at larger temporal and spatial scales, notably geomorphic processes and animal movements, likely influence local populations (Fausch and others 2002). Given the large number of factors potentially affecting local stream assemblages, it is not surprising that only a portion of the variance in assemblage characteristics can be accounted for by models based on drainage area and permitted water supply rates or use of an upstream reservoir for supply. For example, isolation by reservoirs (upstream and downstream) as well as close proximity to downstream urban areas and point-source discharges are likely to diminish local species assemblages, whereas connections with nearby tributary systems having intact faunal communities are likely to augment local species richness, independently of flow alteration effects. The observation that water supply

Table 4. Alternative logistic regression models for probability of a stream sample scoring as impaired, listed in order from best- to least-supported

Site variables	Habitat variables	ΔAIC_c	ω_i
WI	**Velocity**	**0**	**0.51**
DA, WI	**Velocity**	**1.6**	**0.23**
WI	**Depth, Velocity**	**2.1**	**0.18**
DA, WI	**Depth, Velocity**	**3.9**	**0.07**
WI		12.0	0.00
DA, WI		12.4	0.00
WI	Depth	13.3	0.00
WI, WI*Reservoir		13.7	0.00
WI, Minimum Q		13.8	0.00
WI, Mean *phi*		14.2	0.00
WI, % Urban		14.2	0.00
WI, Reservoir		14.2	0.00
DA, WI	Depth	14.4	0.00
DA, WI, Reservoir		14.5	0.00
WI, Reservoir, Mean *phi*		16.4	0.00
WI, Reservoir, % Urban		16.4	0.00
DA, WI, Mean *phi*, % Urban		16.8	0.00
DA, Mean *phi*, % Urban		19.0	0.00
DA, WI, Reservoir, Mean *phi*, % Urban		19.1	0.00
DA, Reservoir		20.1	0.00
DA, Reservoir, Mean *phi*, % Urban		21.2	0.00
Reservoir		22.7	0.00
Reservoir, % Urban		22.8	0.00
Reservoir, Mean *phi*		24.5	0.00

Note: Results show the variables included, differences in AIC_c from the best-fit model, and model weights (ω_i). Results shown in bold are for models used to derive model-averaged effect sizes. DA = in-transformed drainage area; WI = in-transformed withdrawal index; Reservoir = reservoir presence; % Urban = arcsine transformed percent urban land use; Velocity = in-transformed average velocity.

variables do improve predictive models for richness of fluvial-dependent species (or probability that a site scores as impaired) implies that decisions concerning how to supply water for offstream uses will have measurable consequences for biotic integrity, even though other landscape factors may add to or modify those effects.

Model selection uncertainty and sampling error also contributed to uncertainty in estimated effects of water supply variables on stream fishes. For example, models predicting FS richness as functions of drainage area and reservoir presence were weighted almost as highly as the best-supported model, which also included relative rate of permitted water withdrawal. We could not entirely separate the effects of reservoirs from withdrawals in this study because higher withdrawal rates tended to be associated with reservoirs (although not absolutely, as one of the highest relative withdrawals was at a stream intake). Model averaging increased estimated standard errors, but allowed us to estimate effects of withdrawals and reservoirs while incorporating alternative hypotheses (e.g., that either or both factors were responsible for decreased FS richness).

Management Implications

Understanding potential effects of alternatives for landscape development on native biological communities is fundamental to making informed management decisions. This study has provided information on relations between increasing the allocation of water for offstream use, and of supplying water through creation of instream reservoirs, on species richness of native fishes in Piedmont streams. Across our study streams, water supply variables appear more predictive of species richness than catchment urbanization or average bed sediment size, although the effects are not precisely known. How could decision makers best use this information? Specifically, questions are posed such as: What minimum flow levels will protect aquatic ecosystems? What levels of withdrawal are compatible with maintaining integrity of aquatic ecosystems? And, given options such as building large, regional supply reservoirs versus using multiple smaller reservoirs or withdrawals from unimpounded streams, which provide the best balance of maximizing water supply and conserving ecosystem integrity?

The question of protective minimum flow levels remains unanswered, except to note that there is no evidence that providing for a minimum flow of 7Q10 protects stream fish assemblages, either from our data or more generally (Stalnaker and others 1995). Higher minimum flow provisions may mitigate some effects of withdrawals and reservoirs, but only if periodic low-flow depletion is the primary pathway by which hydrologic alteration influences stream biota. If biotic integrity is diminished by flow reduction during periods of normally higher base flows, then requiring a protected minimum flow level will be insufficient to protect stream ecosystem integrity (Poff and others 1997; Richter and others 1997).

The results of this study support two hypotheses that could be applied, tested, and refined through the process of developing water supply in the rapidly growing regions of the eastern United States. Our results indicate that (1) increasing permitted water withdrawal levels is likely to result in local loss of stream fish species, specifically fluvial-dependent species, and (2) construction of instream water supply reservoirs is similarly likely to result in reduced richness of fluvial-dependent species. Based on our data, streams in the lower Piedmont may begin to experience species losses if permitted withdrawal exceeds about 0.5 to one 7Q10-equivalent of water. Additional research to broaden the geographic scope and size of the data set could improve our ability to predict effects of water withdrawal and use of reservoirs on stream fishes. However, given the ecological complexity of stream systems, i.e., structural uncertainty (Williams and others 1996), and the difficulties in precisely quantifying the richness and abundance of many stream species (i.e., partial observability), there likely always will be considerable uncertainty when predicting the effects of any given withdrawal or reservoir on stream biota.

Taking an adaptive management approach (Walters 1986) to future water supply development could allow communities to meet their water needs while working with managers and regulators to conserve the biological diversity native to a region's streams. Conroy and others (2003) argue that, given uncertainty and the high ecological stakes of current development trajectories in areas such as the southern Piedmont, management should be based on adaptive decision making utilizing predictive models that relate policy decisions to integrity of stream ecosystems at varying scales. Estimates such as generated in this study could be useful in beginning this process. For example, in the Piedmont region of Georgia, managers could use our results to hypothesize that withdrawals exceeding a given rate are likely to result in species losses, and that supplying water by way of multiple, dispersed withdrawals capped below that level will have fewer effects than concentrating supply at large withdrawals or instream reservoirs. Decision makers could identify streams that appear "over-allocated" with respect to supporting native fishes, and test and refine this hypothesis, as well as identifying areas within basins where further allocation is likely to lead to faunal decline. Decision makers could also evaluate alternative supply scenarios with respect to predicted biological effects given this hypothesis, preferably in the context of a predictive model incorporating other influences such as changing land use. Decisions regarding individual projects will be influenced by multiple factors, including the presence of rare or imperiled stream biota (e.g., species protected under the Endangered Species Act or Georgia's Endangered Wildlife Act) and economic considerations, but whatever decisions are made, one could predict effects on biological integrity in the affected stream systems. Importantly, monitoring stream biota before and after implementation of new withdrawals could then test those predictions, with the results used to improve our understanding of relations between withdrawals, water supply reservoirs, land use change, and stream biota. Applied at a regional scale, water supply development could be planned to avoid excessive depletion and fragmentation in stream systems critical for supporting unique faunal assemblages. This approach would differ from that currently taken by shifting the emphasis from minimum flow policy and provisions, to the adaptive development of water supply strategies that conserve biological resources.

Acknowledgments

We appreciate field assistance provided by John Seginak, USGS, and the following students and technicians from the University of Georgia: Richard Weyers, Shane Hawthorne, Peter Esselman, Jesslyn Shields, Patricia Rodriguez, Sandra Helms, Leif Stephens, Judith Barkstedt, Clay Brady, Erica Curry, Megan Hagler, Sarah McClurg, Casey Storey, Dean Sedgewick, John Knight, and Allison Roy. Bud Freeman (UGA) and John Biagi and Patti Lanford (GDNR) provided logistic support and data for reference sites. This research was funded through the USGS State Partnership Program and by additional funding supplied by the GA Department of Natural Resources to the University of Georgia. The manuscript was substantially improved by comments from Jonathan Kennen, Mike Harris, Brett Albanese, Lance Williams, and three anonymous reviewers.

Appendix 1. Withdrawal site characteristics and years sampled

Site name	Site number	Withdrawal type	Drainage area, km^2	Max monthly withdrawal, mgd	Withdrawal index	Mean *phi*	% Urban	Minimum flow requirement	Year(s) sampled
Alcovy R. Social Circle	1	Intake	338.50	1.00	0.14	−0.46	11	1.8*7Q10	2000, 2001
Middle Oconee River	2	Intake	1010.70	12.00	0.42	−3.84	6	None	2000, 2001
Cedar Creek	3	Reservoir	15.70	1.00	3.33	−6.50	10	None	2000, 2001, 2003
North Fork Broad River	4	Intake	344.70	0.40	0.02[a]	−1.12	2	None	2000, 2001, 2003
Grove River	5	Reservoir	101.30	4.20	1.00	−0.23	1	None	2000, 2001, 2003
Curry Creek	6	Reservoir	27.90	1.75	0.92	−1.83	4	None	2000, 2001, 2003
Lowery Branch	7	Intake	21.10	0.50	1.32	−0.15	1	None	2000, 2001, 2003
Rocky Creek	8	Intake	62.70	1.50	1.92[b]	−7.22	1	None	2000, 2001, 2003
Tobesofkee Creek	9	Reservoir	109.80	1.00	0.48	−1.96	1	7Q10	2000, 2001, 2003
Alcovy R. Covington	10	Intake	481.50	4.00	0.39	−0.50	9	None	2000, 2001
Pound Creek	11	Reservoir	17.40	0.50	1.47	0.33	0	None	2000, 2001, 2003
Walnut Creek	12	Reservoir	81.80	2.40	1.04	−4.08	6	7Q10	2000, 2001, 2003
Little River	13	Intake	599.80	1.00	0.12	−8.88	1	None	2000
Little Towaliga River	14	Intake	131.10	1.00	0.31	−0.73	1	7Q10	2000, 2001, 2003
Beaverdam Creek	15	Reservoir	28.00	1.80	0.00[c]	−2.43	0	None	2000, 2001
Mulberry River	16	Intake	284.30	4.10	0.54	−0.62	7	7Q10	2000, 2001
Hard Labor Creek	17	Intake	169.50	1.50	0.77	−0.31	2	7Q10	2000, 2001
Towaliga River	18	Reservoir	148.20	11.00	3.33	−3.12	2	7Q10	2000, 2001, 2003
Brown/Sandy Creek	19	Reservoir	38.90	8.00	13.33	−0.94	9	7Q10	2000, 2001, 2003
Line Creek	20	Intake	96.70	12.00	12.38	−4.45	12	2.1*7Q10	2000, 2001, 2003
Whitewater Creek	21	Intake	76.80	3.00	1.55	−0.14	11	7Q10	2000, 2001, 2003
Indian Creek	22	Reservoir	51.50	8.00	4.44	−4.60	4	7Q10	2000, 2001, 2003
Barber Creek	23	Reservoir	16.50	0.80	2.67	−2.67	3	None	2000, 2001, 2003
Heads Creek	24	Reservoir	51.80	12.00	—[d]	−0.33	8	None	2000, 2001
Rocky Comfort Creek	25	Reservoir	48.50	0.75	2.34	0.66	0	None	2000, 2001, 2003
Centralhatchee Creek	26	Intake	148.00	3.10	0.37	−1.47	1	7Q10	2000, 2001, 2003
Blue Creek	27	Reservoir	16.70	1.00	3.33	−2.75	1	7Q10	2000, 2001, 2003
Pope's Branch	28	Intake	13.70	0.50	0.72	−1.42	1	None	2001, 2003

[a]The withdrawal index for site 4 increased to 0.06 in 2001.

[b]The withdrawal index for site 8 changed to 0 in 2003.

[c]Withdrawals were discontinued at site 15 prior to 2000.

[d]Site 24 was used to store water pumped from the Flint River, and WI was not estimated. Data for Site 24 were omitted from all models.

Note: Site numbers correspond to Figure 1; maximum monthly withdrawal is the permitted rate and withdrawal index = permitted withdrawal rate/7Q10.

Appendix 2. Taxa comprising multiple species for use in NMDS analysis

Taxon name	Species included
Cyprinella spp.	*Cyprinella callisema, C. callitaenia, C. nivea, C. venusta, C. xaenura*
Hybopsis spp.	*Hybopsis rubrifrons, H.* sp. cf. *H. winchelli*
Notropis spp.	*Notropis cummingsae, N. hypsilepis, N. longirostris, N. petersoni, N. texanus*
Scartomyzon spp.	*Scartomyzon brasseus, S. lachneri, S. rupiscartes*
Moxostoma spp.	*Moxostoma collapsum, M. robusturn, M.* sp. cf. *M. poecilurum*
Noturus spp.	*Noturus gyrinus, N. insignis, N. leptacanthus*
Ameiurus spp.	*Ameiurus catus, A. melas, A. nebulosus*
Gambusia spp.	*Gambusia affinis, G. holbrooki*
Pomoxis spp.	*P. annularis, P. nigromaculatus*
Micropterus spp.	*Micropterus cataractae, M. coosae,* M *punctulatus*
Etheostoma spp.	*Etheostoma inscriptum, E. fusiforme, E. hopkinsi, E. olmstedi, E. swaini*

Literature Cited

Abell, R. A., D. M. Olson, E. Dinerstein, P. T. Hurley, J. T. Diggs, W. Eichbaum, S. Walters, W. Wettengel, T. Allnutt, C. Loucks, and P. Hedao. 2000. Freshwater ecoregions of North America: a conservation assessment. World Wildlife Fund, Washington, DC, 319 pp.

Allison, P. D. 1991. Logistic regression using the SAS system: theory and application. SAS Institute Inc., Cary, North Carolina, 288 pp.

Armstrong, D. S., T. A. Richards, and G. W. Parker. 2001. Assessment of habitat, fish communities and streamflow requirements for habitat protection, Ipswich River, Massachusetts, 1998–99. US Geological Survey Water Resources Investigations Report 01–4161.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, 2nd ed. EPA 841-B-99-002. Office of Water, U. S. Environmental Protection Agency, Washington, DC.

Baron, J. S., N. L. Poff, P. L. Angermeier, C. N. Dahm, P. H. Gleick, N. G. Hairston Jr., 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.

Baxter, R. M. 1977. Environmental effects of dams and impoundments. *Annual Review of Ecology and Systematics* 8:255–283.

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.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, 488 pp.

Burnham, K. P., and W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60:927–936.

Carter R. F., E. H. Hopkins, H. A. Perlman. 1986. Low-flow profiles of the upper Ocmulgee and Flint rivers in Georgia. US Geological Survey Water Resources Investigations Report 86–4176.

Carter, R. F., E. H. Hopkins, and H. A. Perlman. 1988a. Low-flow profiles of the upper Savannah and Ogeechee rivers and tributaries in Georgia. US Geological Survey Water Resources Investigations Report 88–4047.

Carter, R. F., E. H. Hopkins, and H. A. Perlman. 1988b. Low-flow profiles of the upper Oconee River and tributaries in Georgia. US Geological Survey Water Resources Investigations Report 88–4048.

Clarke, K. R. 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18:117–143.

Collares-Pereira, M. J., I. G. Cowx, F. Ribeiro, J. A. Rodrigues, and L. Rodago. 2000. Threats imposed by water resource development schemes on the conservation of endangered fish species in the Guadiana River Basin in Portugal. *Fisheries Management and Ecology* 7:167–178.

Collier, M., R. H. Webb, and J. C. Schmidt. 1996. Dams and rivers: primer on the downstream effects of dams. USGS Circular 1126. US Geological Survey, Tuscon, Arizona.

Conroy, M. J., C. R. Allen, J. T. Peterson, L. J. Pritchard, and C. T. Moore. 2003. Landscape change in the southern Piedmont: challenges, solutions, and uncertainty across scales. *Conservation Ecology* 8:3. [online]URL:http//www.consecol.org/vol8/iss2/art3.

Cooperman, M. S., and D. F. Markle. 2003. The Endangered Species Act and the National Research Council's interim judgment in Klamath Basin. *Fisheries* 28:10–19.

Copp, G. H. 1990. Effect of regulation on 0+ fish recruitment in the Great Ouse, a lowland river. *Regulated Rivers: Research and Management* 5:251–263.

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.

Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for analyzing multispecies distribution patterns. *Marine Ecology Progress Series* 8:37–52.

GDNR (Georgia Department of Natural Resources). 2000. Standard operating procedures for conducting biomonitoring on fish communities in the Piedmont ecoregion of Georgia. Georgia Department of Natural Resources, Wildlife Resources Division, Fisheries Section, Social Circle, Georgia.

Gordon, N. D., T. F. McMahon, and B. L. Finlayson. 1992. Stream hydrology: an introduction for ecologists. John Wiley & Sons, Chichester, 526 pp.

Jackson, R. B., S. R. Carpenter, C. N. Dahm, D. M. McKnight, R. J. Naiman, S. L. Postel, and S. W. Running. 2001. Water in a changing world. *Ecological Applications* 11:1027–1045.

Karr, J. R., and E. W. Chu. 2000. Sustaining living rivers. *Hydrobiologia* 422/423:1–14.

Kinsolving, A. D., and M. B. Bain. 1993. Fish assemblage recovery along a riverine disturbance gradient. *Ecological Applications* 3:531–544.

Matthews, W. J. 1990. Spatial and temporal variation in fishes of riffle habitats: a comparison of analytical approaches for the Roanoke River. *American Midland Naturalist* 124:31–45.

Matthews, W. J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York, 756 pp.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, Version 4.25. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, 300 pp.

Moyle, P. B., and R. A. Leidy. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. Pages 127–169 *in* P. L. Fielder and S. K. Jain (eds.), Conservation biology: The theory and practice of nature conservation, preservation, and management. Chapman and Hall, New York.

Naiman, R. J., S. E. Bunn, C. Nilsson, G. E. Petts, G. Pinay, and L. C. Thompson. 2002. Legitimizing fluvial ecosystems as users of water: an overview. *Environmental Management* 30:455–467.

Oksanen, J., R. Kindt, and R. B. O'Hara. 2005. Vegan: Community Ecology Package. Available from http://cc.oulu.fi/~jarioksa/.

Peterson, J. T., and C. F. Rabeni. 1995. Optimizing sampling effort for sampling warmwater stream fish for communities. *North America Journal of Fisheries Management* 15:528–541.

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. 1996. Dividing the waters: food security, ecosystem health, and the new politics of scarcity. Worldwatch Paper 132. Worldwatch Institute, Washington, DC, 76 pp.

Postel, S., and B. Richter. 2003. Rivers for life: managing water for people and nature. Island Press, Washington, DC, 253 pp.

Postel, S. L. 2000. Entering an era of water scarcity: the challenges ahead. *Ecological Applications* 10:941–948.

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.

Scott, M. C., and G. S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries* 26:6–15.

Silk, N., J. McDonald, and R. Wigington. 2000. Turning instream flow water rights upside down. *Rivers* 7:298–313.

Snijders, T. A. B., and R. J. Bosker. 1999. Multilevel analysis: an introduction to basic and advanced multilevel modeling. Sage Publications, London, 266 pp.

Stalnaker, C., B. L. Lamb, J. Henrickson, K. Bovee, and J. Bartholow. 1995. The Instream Flow Incremental Methodology, a primer for IFIM. Biological Report 29. US National Biological Service, Washington, DC.

Travnichek, V. H., M. B. Bain, and M. J. Maceina. 1995. Recovery of a warmwater fish assemblage after initiation of a minimum-flow release downstream from a hydroelectric dam. *Transactions of the American Fisheries Society* 124:836–844.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan, New York, 374 pp.

Walters, D. M., D. S. Leigh, and A. B. Bearden. 2003a. Urbanization, sedimentation, and homogenization of fishes 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, U.S.A. *Freshwater Biology* 48:1950–1970.

Walters, D. M., M. C. Freeman, D. S. Leigh, B. J. Freeman, and C. M. Pringle. 2005. Urbanization effects on fishes and habitat quality in a southern Piedmont river basin. Pages 69–85 *in* L. R. Brown, R. H. Gray, R. M. Hughes and M. R. Meador (eds.), Effects of urbanization on stream ecosystems. American Fisheries Society Symposium 47, Bethesda, Maryland.

Ward, F. A., and J. F. Booker. 2003. Economic costs and benefits of instream flow protection for endangered species in an international basin. *Journal of the American Water Resources Association* 39:427–440.

Warren, M. L., Jr., B. M. Burr, S. J. Walsh, H. L. Bart Jr., 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. *Fisheries* 25(10):7–29.

Weaver, L. A., and G. C. Garman. 1994. Urbanization of a watershed and historical changes in a stream fish assemblage. *Transactions of the American Fisheries Society* 123:162–172.

Williams, B. K., F. A. Johnson, and K. Wilkins. 1996. Uncertainty and the adaptive management of waterfowl harvests. *Journal of Wildlife Management* 60:223–232.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, 817 pp.