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POPULATION MODELS FOR STREAM FISH RESPONSE TO HABITAT AND HYDROLOGIC ALTERATION: THE CVI WATERSHED TOOL

by

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Notice

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Foreword

Streams and rivers provide important ecological services, including habitat for fishes and other organisms, and drinking water supplies, yet these ecosystems are among the most impaired across the country. Management for these ecosystems involves the assessment of probable causes of impairments and management alternatives, as well as the forecasting of future condition in a scientifically defensible fashion to more effectively protect and restore valued ecosystems. Communities, watershed groups and states require decision support tools for managing the quality of aquatic systems. Community-based environmental management is a long-term goal of the Agency, and providing the methods/tools and technical transfer mechanisms to achieve this goal are critical to the role of ORD. Effective client collaborations are the most efficient means to achieve this.

This report is the result of a collaboration with the Canaan Valley Institute (CVI) in which a decision analysis toolkit was produced in order to support management of fisheries in the Mid-Atlantic Highlands. Although there are many ecological endpoints that are important indicators of the condition of aquatic communities and their associated watersheds, *fish health* is arguably one of the most important, since fishability is a principal designated use for surface waters under the Clean Water Act. The approach used here can be applied to aid CVI and other agencies in the management of aquatic resources in the Mid-Atlantic Highlands, and may serve as a model for management tools for aquatic systems in other regions.

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Abstract

The Canaan Valley Institute (CVI) is dedicated to addressing the environmental problems in the Mid-Atlantic Highlands (MAH). Their goal is to develop and implement solutions to restore damaged areas and protect aquatic systems. In most wadeable streams of the Mid-Atlantic Highlands region of the eastern United States, habitat alteration resulting from agriculture and development is the primary stressor for fish communities. Sedimentation is the primary source of habitat degradation in Highlands streams, and productive, sustainable fisheries, i.e., trophy trout streams, are the valued aquatic endpoints. Planned restoration activities in the region include riparian zone restoration and stream channel design to mitigate near stream inputs and stabilize streambanks. Natural Stream Channel Design (NSCD) is also being investigated by CVI for further optimization of instream habitats for fish communities. Models that predict the responses of fish populations and communities to key habitat characteristics are necessary for CVI's watershed management goals, both for determining where to restore and how, as well as evaluating the most probable outcome of various alternatives. The USEPA National Exposure Research Laboratory (NERL) has developed a suite of modeling tools to be used for this purpose. The CVI Watershed Health Assessment Tool Investigating Fisheries, WHAT IF, contains four components: 1) a Hydrology Tool for predicting hydrologic characteristics of new streams of interest; 2) a Clustering Tool for assigning the most probable fish assemblages to unsampled Mid-Atlantic Highlands streams, 3) a Habitat Suitability Calculator, which evaluates habitat suitability of streams to support fish species and families, and 4) the Bioaccumulation and Aquatic System Simulator (BASS) model, a generalized aquatic ecosystem model that simulates fish community dynamics with time, which permits the evaluation of comparative risk regarding instream restoration combined with fisheries management. The USEPA Environmental Monitoring and Assessment Program (EMAP) surface water dataset (available online, two index periods in the 1990's) is the basis of the habitat associations derived for fish species and communities. Additionally, a tutorial is provided for the user to examine existing scenarios for fish stocking, harvest and restoration combined. Stakeholders interact with the software interface to frame the problem by: selecting valued endpoints of concern and analytical methods, accessing data and models to establish the causal relationships between stream habitat characteristics and changes in endpoint status/trend, and performing multiple model executions and visualizations of projected outcomes to span the range of various management scenarios that might be taken so that associated costs and benefits can be evaluated.

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List of Acronyms

BASS	**B**ioaccumulation and **A**quatic **S**ystem **S**imulator
BMP	**B**est **M**anagement **P**ractice
CVI	**C**anaan **V**alley **I**nstitute
EMAP	**E**nvironmental **M**onitoring and **A**ssessment **P**rogram
EPA	**E**stimated **P**rediction **A**ccuracy
ERD	**E**cosystems **R**esearch **D**ivision
GIS	**G**eographic **I**nformation **S**ystems
GUI	**G**raphical **U**ser **I**nterface
HSI	**H**abitat **S**uitability **I**ndex
IBI	**I**ndex of **B**iological **I**ntegrity
MAH	**M**id-**A**tlantic **H**ighlands
NERL	**N**ational **E**xposure **R**esearch **L**aboratory
USEPA	**U.S**. **E**nvironmental **P**rotection **A**gency
USGS	**U.S. G**eological **S**urvey

1. Introduction

Scientists recognize that fish assemblages in developed watersheds are affected primarily by nonpoint source anthropogenic stressors that result from land use development, in particular alteration of physical habitat (Williams et al. 1989, Richter et al. 1997, Wilcove et al. 1998). Over half of the streams in the Mid-Atlantic Highlands (MAH) have fish communities that are in fair or poor condition, and the USEPA concluded that physical habitat alteration represents the greatest potential stressor across this region (USEPA 2000). Habitat alteration can occur both in terms of habitat quantity and quality. Loss or destruction of habitat quantity reduces the total amount of habitat available to aquatic species, and can isolate patches of suitable habitat within a stream, which reduces species' survival and alters natural fish movement and migration patterns (Reeves et al. 1995). Loss of habitat quantity is often associated with significant hydrologic alterations, such as impoundments (Yeager 1993), whereas loss of habitat quality can be due to factors such as landscape development and alteration of flow patterns on the landscape.

The mission of the Canaan Valley Institute (CVI) is to address the environmental problems in the Mid-Atlantic Highlands through a program of environmental stewardship that considers and integrates natural, economic, and human concerns in the management of natural resources (CVI 2002). Their goal is to develop and implement solutions to restore damaged areas and protect aquatic systems. To achieve this goal, they require sound science that combines theory, detailed knowledge, monitoring and modeling (CVI 2002). Toward this goal, CVI developed its own geographic information system (GIS)-based management tool, Landscape Analyst, based on the proprietary ArcView GIS (ESRI, Redlands, CA), for estimating land use change impacts on water quantity and quality (http://www.canaanvi.org/). However, the adoption and widespread application of the tool has been less than anticipated. In order to access Landscape Analyst, users must posses the required GIS software and utilities and be familiar with GIS software and its operation. Complexity in the software user interface, as well as the supporting science modules, is a barrier to widespread adoption of the tools. Refining the aquatic assessment needs further, CVI posed these questions on behalf of regional stakeholders: What conditions will sustain aquatic endpoints in the long-term? Can we evaluate restoration techniques like natural stream channel design (NSCD) and agriculture and forestry stream best management practices (BMPs) for their effectiveness in improving aquatic endpoints? Can we create "what if" scenarios and evaluate management actions based on the response of aquatic endpoints?

In support of CVI, the USEPA National Exposure Laboratory's Ecosystem Research Division (ERD) has conducted research to develop watershed modeling tools for CVI and their stakeholders in the Mid-Atlantic Highlands. Specifically, models have been developed that support the information required to conduct aquatic ecosystem assessments, including:

- the assignment of instream hydrological habitat quantities for ungauged/unmeasured streams of interest: stream flow, depth, width and temperature (Hydro Tool)

- the assignment of the most probable fish communities for unsampled streams (Clustering Tool)

- the evaluation of the physical habitat variables that affect suitability for fish species and families/guilds to further refine the fish community assignment and address restoration and BMP actions for selected species (Habitat Suitability Calculator)

- the evaluation of expected trophic dynamics of the dominant fish species under various fisheries management and restoration actions for cumulative/comparative risk assessment 3,5 or 10 years in the future (BASS bioaccumulation and population dynamics model).

The result is a suite of tools for regional application to wadeable Mid-Atlantic Highlands streams, the Canaan Valley Institute – Watershed Health Assessment Tools Investigating Fisheries, CVI–WHAT IF. WHAT IF is entirely open source and does not require proprietary software. It is not GIS-based, nor does it contain models difficult to apply for all but expert users. Models are complementary in the information provided and are designed to be efficient and problem focused. For example, WHAT IF incorporates statistical hydrology in the toolset rather than a watershed hydrology model. Models that require a high degree of input data processing and model setup put undue burden on novice users (Doherty and Johnston 2003). A fitted parameter model such as the Hydrologic System Program Fortran (HSPF), though widely used, is complex and calibration intensive and does not match the aquatic assessment needs for evaluating outcomes of near and instream restorations. Similarly, models with a large degree of overhead in their use, including sediment hydrodynamic models, are unsuitable for the majority of CVI stakeholders and are not straightforward in application.

WHAT IF consists of models of varying complexity, suited to the problem needs of the client rather than imposing a ‘one model fits all needs’ restriction. In this manner, the toolset is question driven as opposed to model-focused. WHAT IF is stream-based, permitting users to evaluate streams of interest for outcomes of management approaches and specific restoration actions. Habitat quality and aquatic ecosystem response models have been linked to a regional hydrologic model that simulates habitat characteristics (e.g., water depth, current velocity and water temperature) that determine the survival, reproduction, and recruitment of fish and aquatic invertebrates. To facilitate the use and application of these models, graphical user interfaces (GUI), supporting databases, and libraries of management scenarios were developed. The Canaan Valley Institute (CVI) software/toolset is a stream-based decision support tool that is object-oriented in design and easily maintained. Ultimately, what has been developed using available data collected by the USEPA Environmental Monitoring and Assessment Program (EMAP) is a framework based on the biogeography of fish suitable for applying all models for regional assessments of important fish health issues in the Mid-Atlantic Highlands. It is set in the form of a series of questions for the user (**Figure 1.1**).

The EMAP surface water dataset (http://www.epa.gov/nheerl/arm/) is a stratified random sampling design and contains over 300 sites and 600 samples (multiple site visits) used in the final research product. Fish count data were pre-processed by conversion to biomass for both clustering and habitat suitability analyses, using a utility associated with the BASS model. In this manner, actual communities were derived from the base data, so that conclusions could be made with respect to biomass per unit area and ultimately the carrying capacity of impaired versus restored streams. The EMAP dataset represents two index periods (1993-1995 and 1997-1998) and habitat associations are statistically valid within the region of the Mid-Atlantic Highlands, which includes portions of Pennsylvania, Maryland, West Virginia and Virginia. Watershed characteristics, in stream and near stream habitat quantitative data, are used in addition to fish, benthic insect, and periphyton data (i.e., attached algae). Field data were collected from late Spring to late Summer and span a range of stream sizes and watershed areas throughout the Highlands.

The overall flow of information between the various models is as follows. The Hydrology Tool supplies stream conditions for sites in the software archive, as well as a means of calculating conditions (mean monthly flow, depth and water temperature) for new streams of interest. The Clustering Tool provides a means of assigning the most probable fish community to a stream based on combinations of remotely sensed and field collection data. This tool also permits a user to perform simple screening level assessments of habitat changes (water flow, temperature and percent fines) and the probable changes in the assigned stream community. After identifying a stream of interest and assigning a fish community, the Habitat Suitability Calculator is used to evaluate that stream's potential to support members of the potential community, on a fish-by-fish basis. Habitat features of interest are those that relate to key aspects of fish life history requirements: water velocity, water depth, stream bottom composition (substrate) and amount of refugia (cover, riparian vegetation, etc.). The BMP tool that is part of the Suitability Calculator provides a means of translating habitat changes (i.e., restoration actions under consideration) into suitability scores for each fish in the community. BASS is a generalized aquatic ecosystem simulator capable of treating a variety of managed freshwater ecosystems and accepts the assigned fish community as an initial condition, as well as any habitat multipliers investigated using the BMP tool. Stream depth and temperature information is also passed from the Hydrology Tool to BASS. With these tools, environmental managers are better able to characterize and quantify relationships between stressors and stream responses for valued ecological resources in a manner that supports diagnosis of current condition and assists in management activities.

Figure 1.1 Questions to guide the user through the CVI tool.

Hydro

What is the average flow depth, streamflow, and water temperature in my stream?

Clustering

What fishes might I have in my stream?

How might species composition change with changes in watershed and stream characteristics?

Habitat Suitability

How suitable is my stream for specific fish species?

How might suitability be improved for these species?

BASS

How does average length weight and other attributes of fish populations and communities change through time when BMPs are applied?

How does the proportion of trophy-sized trout change with various stocking programs?

Tutorial: Review Expected Community Dynamics

How do trout respond to riparian zone restoration?

How do trout respond to stocking?

How do trout respond to a combination of riparian restoration and stocking?

2. Hydro Tool: Predicting Mean Depth, Width, and Streamflow for Small Streams

2.1. Introduction

Instream physical habitat characteristics, such as water depth, temperature, and mean flow velocity, are important to the growth and survival of fish species at different life stages. The ecologically-focused average annual discharge is highly correlated with drainage area. In addition, bankfull discharge and average annual discharge are also highly correlated with each other. Both are important data for resource managers and planners who would like to know the maximum flow frequency that fills and forms the channel shape (bankfull) and the average discharge available to sustain fish and aquatic habitats throughout the year. In this work, a regional regression method is developed for the determination of mean water depth and mean flow velocity variables.

2.2. What is the average flow depth, streamflow, and water temperature in my stream?

The regional regression method is based on the quantification of relationships between drainage area and stream hydraulic characteristics. To enhance the predictive potential of the regression equations and to reduce the percentage of the variability not explained by the model, we developed separate regression for each physiographic province. The Mid-Atlantic region consists of four physiographic provinces: Appalachian Plateau, Blue Ridge, Ridge and Valley, and Piedmont. We combined the Ridge and Valley and Blue Ridge Physiographic Provinces as one and developed a total of three sets of regression equations.

In each physiographic province, about 25 streams with variable drainage areas were selected. The criteria used to select the study watersheds were based on watershed area, land use type, and availability of over 10 years of observed streamflow data. All selected watersheds had a drainage area ranging between 2 to about 400 square miles. All selected watersheds had high percent of forest cover and agricultural land use and a low percent of impervious surface cover. Only watersheds with USGS gaging stations were

Table 2.1 Regional regression equations for the three physiographic provinces of the Mid-Atlantic region. All length units are in feet; flow is cubic feet/sec; flow area is in square feet; drainage area is in square miles.

Regression Model Summary Statistics							
Model	R^2	N	Coefficients	Value	Standard Error	Lower 95% CB	Upper 95% CB
Appalachian Plateau Physiographic Province							
$Q = aDA^b$	0.96	25	a	3.41	0.78	1.83	4.97
			b	0.85	0.04	0.76	0.94
$W = aQ^b$	0.81	25	a	6.09	1.72	2.54	9.66
			b	0.47	0.05	0.37	0.58
$A = aQ^b$	0.86	25	a	3.16	1.13	0.81	5.51
			b	0.67	0.06	0.54	0.80
$D= aQ^b$	0.84	19	a	0.33	0.05	0.22	0.44
			b	0.27	0.03	0.21	0.34
Ridge and Valley Physiographic Province							
$Q = aDA^b$	0.95	25	a	2.98	0.87	1.17	4.78
			b	0.82	0.05	0.71	0.94
$W = aQ^b$	0.86	25	a	3.82	1.30	1.13	6.51
			b	0.58	0.06	0.45	0.72
$A = aQ^b$	0.91	25	a	1.12	0.51	0.07	2.20
			b	0.89	0.08	0.72	1.06
$D= aQ^b$	0.88	19	a	0.31	0.05	0.21	0.42
			b	0.3	0.03	0.23	0.36
Piedmont Physiographic Province							
$Q = aDA^b$	0.98	25	a	1.35	0.23	0.87	1.84
			b	0.99	0.03	0.92	1.06
$W = aQ^b$	0.90	19	a	7.39	1.32	4.65	10.3
			b	0.47	0.04	0.39	0.54
$A = aQ^b$	0.91	19	a	3.67	1.01	1.57	5.76
			b	0.65	0.05	0.54	0.76
$D= aQ^b$	0.86	19	a	0.40	0.04	0.30	0.48
			b	0.23	0.02	0.18	0.28

selected for the development of regional regression equations. For each gaging station, the mean annual streamflow was determined from the historical streamflow data. Hydraulic channel geometry data such as width, depth, velocity, and cross-sectional area plus flow velocity that correspond to the mean streamflow were determined from USGS stream measurement data. Using regression analysis, we developed quantitative relationships between the drainage area of a watershed and its mean stream hydraulic properties such as mean streamflow rate, mean flow depth, mean flow width, and mean cross-sectional flow area. Regression equations for the three physiographic province groups are shown in **Table 2.1**. These regional regression equations can be used to estimate mean streamflow rate, mean depth, mean width, and mean cross-section area for small streams located in ungaged watersheds.

Our study is ecologically-oriented, and its focus is to determine micro-habitat variables needed as input variables into ecological endpoint models such as the Bioaccumulation in Aquatic Systems Simulator (BASS) Model. For this reason, the **Table 2.1** regression equations have been incorporated into the CVI Watershed Tool to automatically provide input for various components of the tool. The interface for the Hydro Tool is shown in **Figure 2.1**. This tool calculates the annual mean watershed hydraulic parameter values using regional regression equations, but also uses a ratio approach to estimate monthly values based on the predicted annual mean as well.

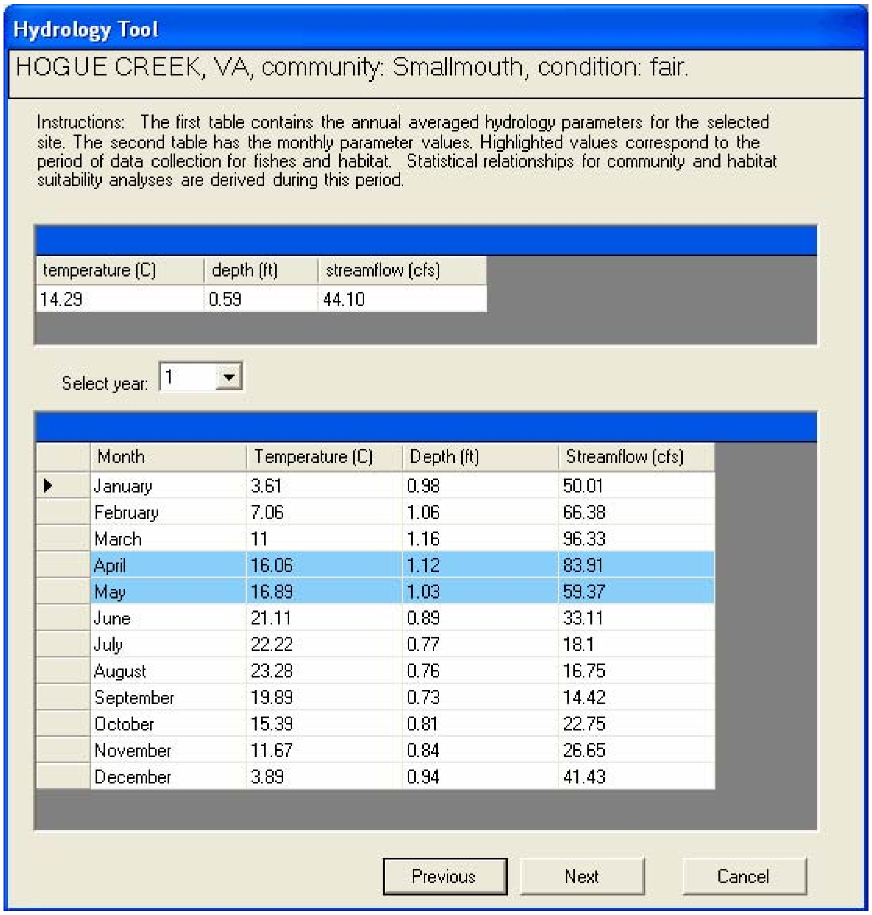
2.2.1. A ratio approach for estimating mean monthly streamflow

The ratio approach is based on the assumption that, within a relatively large watershed, normalized mean streamflow remains nearly constant across all sub-watersheds of the large watershed. Based on this assumption, normalized streamflow can be transferred from a nearby gaged watershed to an ungaged subwatershed of interest within the large watershed. One requirement is that the gaged watershed must have larger drainage area than the ungaged watershed. In general, it is desirable to select a gaged watershed from downstream of the ungaged watershed. Note that this approach uses both drainage area and mean streamflow normalization as basis for transfer of streamflow data from a gaged watershed to an unaged watershed. This approach serves two purposes. First, it addresses the limitations of the regional regression equations that are based on the assumption that all watersheds within a physiographic province can be represented by a single regression equation. The use of the ratio approach to transfer a streamflow data from a nearby gaged station therefore adjusts the prediction of the regional equations to address the variability in streamflow within each physiographic province. Second, the ratio approach is a transfer method that does not use precipitation as a predictor variable but rather uses streamflow to transfer streamflow data from a gaged watershed to an ungaged watershed. The ratio approach can be written as:

$$Q_y = [A_{y}(Q_x/A_x) + Q_{ar}(Q_x/Q_{mean})]/2 \tag{2-1}$$

where Q_y is the monthly streamflow from the unaged watershed; A_y is the drainage area of the ungaged watershed; Q_x is the monthly streamflow of the gaged watershed; Q_x is the monthly streamflow of the gaged watershed; Q_{ar} is the mean annual streamflow determined by the regional regression method; and Q_{mean} is mean annual streamflow of the gaged watershed determined from the long-term monthly streamflow data.

Figure 2.1 Hydro Tool Interface for Hogue Creek, VA



HOGUE CREEK, VA, community: Smallmouth, condition: fair.

Instructions: The first table contains the annual averaged hydrology parameters for the selected site. The second table has the monthly parameter values. Highlighted values correspond to the period of data collection for fishes and habitat. Statistical relationships for community and habitat suitability analyses are derived during this period.

temperature (C)	depth (ft)	streamflow (cfs)
14.29	0.59	44.10

Select year: 1

	Month	Temperature (C)	Depth (ft)	Streamflow (cfs)
▶	January	3.61	0.98	50.01
	February	7.06	1.06	66.38
	March	11	1.16	96.33
	April	16.06	1.12	83.91
	May	16.89	1.03	59.37
	June	21.11	0.89	33.11
	July	22.22	0.77	18.1
	August	23.28	0.76	16.75
	September	19.89	0.73	14.42
	October	15.39	0.81	22.75
	November	11.67	0.84	26.65
	December	3.89	0.94	41.43

2.2.2. Stream Temperature Predictions

In this study, relationships between air and water temperature developed by Stefan and Preudhomme

(1993) were used to estimate stream water temperature from daily air temperature measured from a nearby weather station. The results of their study concluded that stream water temperatures follow closely with air temperature with some lag that varies with time scale, i.e., hours or days and with increasing stream depth. Small shallow rivers had smaller temperature deviations than large, deep rivers. Their regression equation is written as:

$$T_w = 5 + 0.75 * T_a \tag{2-2}$$

where T_w is stream water temperature and T_a is air temperature in degree Celsius.

Webb et al. (2003) also studied the water-air temperature relationships and its moderation by streamflow. They found that the relationships are stronger and more sensitive to flows below the median flow and that water temperature is inversely related to streamflow for all time scales and drainage areas. They concluded that streamflow had greater impact on stream temperature variations at short time scales and in larger watersheds.

The procedure followed to determine water temperature was to identify the nearest weather station for each stream and then use the relationships given in Equation **(2-2)** to estimate stream water temperature from air temperature. In watersheds with no nearby weather stations or in some cases where significant elevation differences exist between the stream location and weather station location, development of elevation-latitude-time of the year and air temperature relationships may be needed.

3. Clustering Tool: Predicting Fish Assemblages in the Mid-Atlantic Highlands

3.1. Background

To predict fish community response to various proposed environmental restoration actions in the MAH Region using an empirical approach, one must first have information on fish abundance and diversity. We used data collected by the USEPA EMAP program to identify the fundamental fish assemblages in wadeable streams of the Mid-Atlantic Highlands Region. EMAP staff, working with personnel from the US Fish and Wildlife Service, as well as state and contract personnel, set out to assess the physical, chemical, and biological condition of MAH streams (USEPA 2000). Given that there are approximately 80,000 total stream miles in the MAH, it was not possible to sample each one. Instead, a spatially-constrained, randomized statistical design was developed to choose a subset of 1st through 3rd order wadeable streams where data collection would occur. The EMAP objective was to provide unbiased estimates of stream condition throughout the MAH, quantify the proportion of stream miles that are biologically degraded or impaired, and examine the relative importance of various stressors on stream fish communities in the region.

To gather data on the fish species present in the sampled streams, the EMAP team used backpack electroshocking as their primary method of collection. At each sampling location, they performed three passes over a reach length approximately 40 times the mean wetted channel width at the midpoint of the reach, with a minimum distance of 150 m. This insured sampling was performed across a range of habitats at each site (runs, riffles, rapids, and pools). The abundance and diversity of fish species were recorded at each site. Habitat measurements were also taken at many of these sites (e.g., stream flow, dissolved oxygen, temperature, sediment levels, riparian cover) as well as watershed characteristics (e.g., total watershed area and percents of agriculture, forest, and disturbed land areas in the watershed). Our focus in developing this model was on smaller, wadeable streams, so we only analyzed data from those EMAP sites that were less than 20 meters in width. Fish densities recorded by EMAP personnel at nearly 80% of streams over this size were less than 100 fish per hectare. For streams under 20 meters in width, this low fish density was seen at 3% of sites. This discrepancy in fish densities between small and large streams likely stems from bias in the sampling technique (backpack electroshocking); capture efficiency declines appreciably in larger lotic systems (Reynolds 1996). Due to the inherent bias of the sampling techniques that were used, these EMAP data can be used to estimate relative abundance of fishes within and between sites, but should not be used to estimate absolute fish abundances at the sampled sites.

Numerous researchers have used multivariate statistical approaches to find patterns in fish assemblage data using a variety of sorting criteria, amongst them taxonomic, geographic, limnologic, and physiographic. Angermeier and Winston (1999) used several multivariate techniques to examine fish communities in Virginia streams at several spatial scales. They also examined relationships between community composition and landscape variables, such as stream order, channel slope, and elevation. They found that ecological and taxonomic characterizations of community composition produced similar results. Madejczyk et al. (1998) used cluster analysis to investigate electrofishing data and related the presence and absence of various species to artificial and natural habitats along the shoreline of the upper Mississippi River. Saiki and Martin (2001) used Ward's minimum variance method of cluster analysis to find two dominant fish communities in Abbotts Lagoon in Point Reyes National Seashore. Their analysis was based on data from gill nets and minnow traps. Kendrick and Francis (2002) used both Ward's cluster analysis and Canonical Correspondence Analysis to analyze the species assemblages of the Hauraki Gulf, New Zealand. They worked with trawl data, and found four dominant fish assemblages, with an additional four species showing no relation to these groups. They caution that year-to-year variation in fish abundance can greatly affect any assemblage analysis. Mathews and Robinson (1988) identified five faunal regions within Arkansas and related these regions to geography, meteorology, and physical variables. Wilkinson and Edds (2001) performed a space-constrained cluster analysis, along with a principal coordinates analysis, to conclude that three distinct fish fauna existed in the Spring River basin, and that these communities were related to differences in geographic and habitat differences between the Ozark Highlands, Central Plains, and mainstream regions of the basin. The spatial and temporal patterns of distribution and abundance of a tropical fish community were investigated via cluster analyses by Ornellas and Coutinho (1998). Their findings indicated the fish community was greatly influenced by the aquatic macrophyte beds which determined the availability of space and habitats. Ansari et al. (1995) looked at data from trawl hauls on the structure and seasonal variation of fish species at Goa on the West Coast of India. Their cluster analysis showed a strong seasonal component in the determination of species groupings. Fish communities in freshwater lakes from watersheds near Lake Ontario were identified using cluster analysis by Kelso and Johnson (1991).

McCormick et al. (2000) used a subset of the MAH dataset we analyzed. They performed a cluster analysis on the fish collection data to arrive at primary fish assemblages for the region. Along with this analysis, they also investigated whether or not fish assemblages could be defined based on spatial data, such as ecoregions and catchments, as well as stream order. Their analyses were based on count data, and they concluded that any historic fine-scale structures of Highland fish assemblages have been overridden by intricate zoogeographic patterns and many years of human disturbance. We have chosen a different route, opting to analyze relative fish biomass rather than abundance. Because biomass is always conserved while numbers of individuals are not, the former is seen as a more robust indicator of ecological importance within fish communities (Diana 1995). In addition, there is the necessity of having biomass measures for creating the input files that will drive our BASS modeling effort.

3.2. What fishes might I have in my stream?

3.2.1. Methods

A software tool was developed using the EMAP stream sampling data from the MAH and incorporated into WHAT-IF. This statistical model predicts a stream's fish assemblage using stream and watershed characteristics. Step one in the tool development was a k-means cluster analysis (Fisher 1958) that grouped streams with similar dominant fish species. The data matrix input into SAS for analysis consisted of 562 rows, one per sampled site, and 105 columns (representing the various fish species sampled across all sites). For each site, the relative biomass of the three most abundant species was recorded in the appropriate columns; the procedure used to estimate species biomasses from EMAP's reported count/density data is outlined in Appendix A. Species of lesser abundance at each site were not considered because our goal was to identify the dominant species/assemblages of the MAH. Other statistical techniques would need to be applied to this dataset if the focus were on prediction of the presence of rare species in a given stream. By examination of the results of the SAS clustering output, we found further justification for using only the three most abundant species to represent each site, i.e., the presence of subdominant species could warp the clustering results. We observed that observations/ clusters could be grouped with other observations/clusters if the two shared a number of subdominant species, despite the fact that they did not share the same dominant, or even secondary, species. This result was dissatisfying, and so we choose to cluster based only on the three most dominant species present at each site.

Clustering techniques typically define each cluster by a multidimensional mean, or centroid. In our case, this centroid was the vector of biomass values for every species in the cluster. During each iteration of the process, observations (streams) were added to the cluster with the nearest centroid. However, we specified that an observation had to be within 48 units of Euclidean distance of a cluster centroid to be permitted to join that cluster. This distance was based on the EMAP data, which showed on average that the dominant species at a site accounted for 55% of total fish biomass, while the second most abundant species on average accounted for 21% of fish biomass at the site. If two sites had a reversal of their dominant and secondary species, but shared the same third-most abundant species, the Euclidean distance between these sites would be $\sqrt{2\times(55-21)^2} \approx \mathbf{48}$. In essence, we designated that a reversal of the dominant and secondary species was a highly significant change and should be used as a threshold of difference between sites. After any observation was added to a cluster, that cluster centroid was recalculated. The process was terminated only after all observations ceased to change their cluster membership from iteration to iteration. Clusters with less than 11 members (2% of the total sample size of 562 streams) were deleted at the end of any iteration step, meaning any observations in these clusters had to be reassigned in the next iteration. These smaller clusters were judged not to be representative of dominant fish assemblages in the MAH.

The first step in the k-means clustering analysis is selection of sites to serve as “seeds” that define the initial clusters at the start of iteration 1. This selection of initial seeds influences the end results of the analysis. Due to the subjectivity of this process, we choose to adopt a random initial seed selection, within the constraint that any new seed had to be at least 48 units of Euclidean distance from any existing seed. We set the maximum number of initial seeds to 25, which was roughly equivalent to the total number of different species that were dominant at more than one site in the EMAP dataset. Because initial seed selection was random, results of the cluster analysis varied from run to run. We arrived at the final results by running the clustering algorithm hundreds of times (each time with a different set of initial seeds), then choosing the run with the “best” combination of three outputs:

1) Cubic Clustering Criterion (CCC Sarle 1983) - a measure of the variation in the dataset explained by the clusters

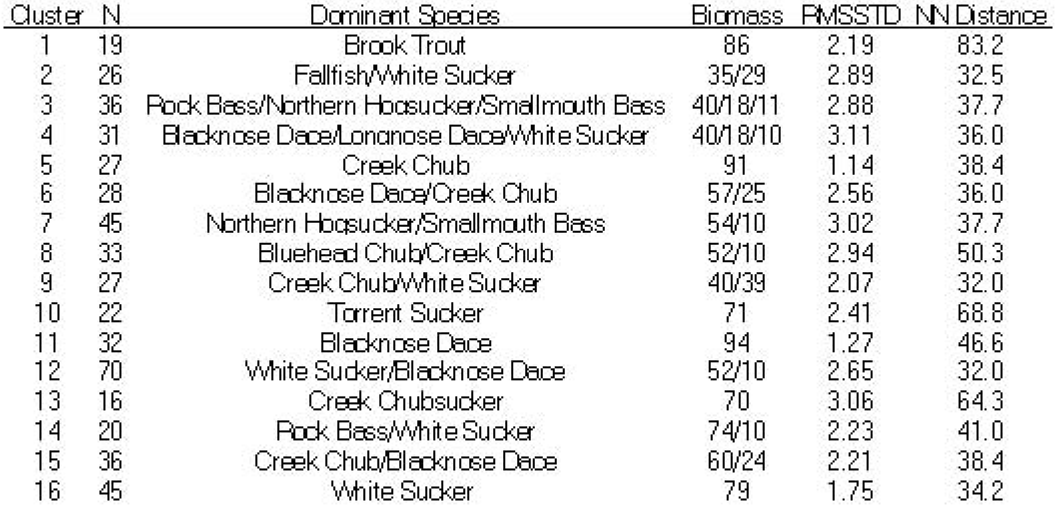
2) Nearest Neighbor distances - the distance between each cluster centroid and the nearest cluster’s centroid. Runs with the very highest CCC values tend to have larger numbers of clusters, but the fish

assemblages of some of the resulting clusters can be very similar. This result would hinder a subsequent discriminant analysis. The analyst should thus decide on a minimum tolerable nearest neighbor distance between the final clusters. After examining many pairs of nearest neighbor clusters, we concluded that a distance of approximately 30 Euclidean units was appropriate for this data set.

3) Root Mean Square Standard Deviation (RMSSTD) - the variability within each cluster. Taking the average RMSSTD value across all clusters is an indication of how well-defined the clusters are.

After generating approximately 1000 simulations, we saved the output from the runs with the top 5 CCC values. We then looked at the nearest neighbor distances and the average RMSSTD values for these five runs. As our designated "winner," we chose the run with the third largest CCC value. This run had good separation between the final clusters, with no nearest neighbor distance below 30 Euclidean units, and it had the second-lowest average RMSSTD value. The run with the highest CCC value also had the lowest average RMSSTD value, but it had three pairs of clusters with nearest neighbor distances below 30 Euclidean units, one of which was below 20 Euclidean units.

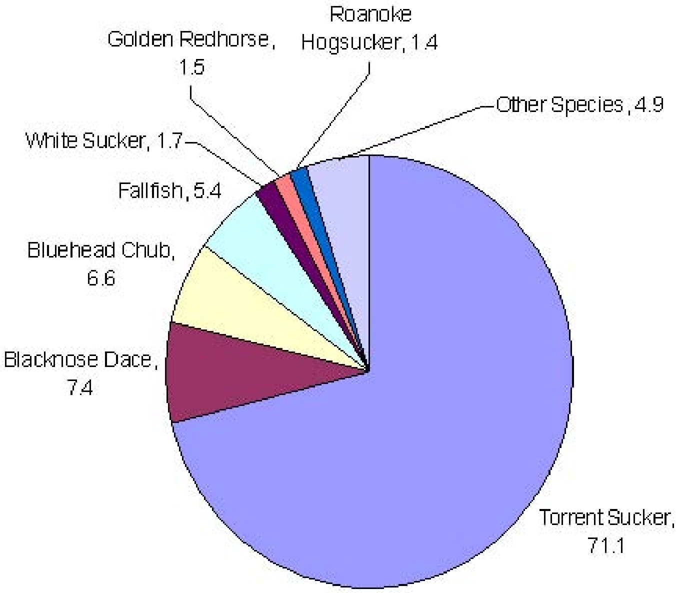
Table 3.1 Fundamental fish assemblages of the Mid-Atlantic Highlands. Species representing more than 10% of the assemblage biomass are listed in the cluster name.



Cluster	N	Dominant Species	Biomass	RMSSTD	NN Distance
1	19	Brook Trout	86	2.19	83.2
2	26	Fallfish/White Sucker	35/29	2.89	32.5
3	36	Rock Bass/Northern Hogsucker/Smallmouth Bass	40/18/11	2.88	37.7
4	31	Blacknose Dace/Longnose Dace/White Sucker	40/18/10	3.11	36.0
5	27	Creek Chub	91	1.14	38.4
6	28	Blacknose Dace/Creek Chub	57/25	2.56	36.0
7	45	Northern Hogsucker/Smallmouth Bass	54/10	3.02	37.7
8	33	Bluehead Chub/Creek Chub	52/10	2.94	50.3
9	27	Creek Chub/White Sucker	40/39	2.07	32.0
10	22	Torrent Sucker	71	2.41	68.8
11	32	Blacknose Dace	94	1.27	46.6
12	70	White Sucker/Blacknose Dace	52/10	2.65	32.0
13	16	Creek Chubsucker	70	3.06	64.3
14	20	Rock Bass/White Sucker	74/10	2.23	41.0
15	36	Creek Chub/Blacknose Dace	60/24	2.21	38.4
16	45	White Sucker	79	1.75	34.2

Our chosen run produced 16 clusters (**Table 3.1**). High cluster variability (as indicated by larger RMSSTD values for Clusters 4, 7, and 13) is an indication that the assemblage is less well-defined, i.e., there are a large number of species associated with the cluster and differences in species-specific biomass from stream to stream. This also means that one's success in predicting the precise species composition of any one stream within these highly-variable clusters is lessened. It is important to note that the species listed in **Table 3.1** are not the only species found in their respective clusters. For instance, the primary members of Cluster 16 (according to percent of total assemblage biomass) are shown in **Figure 3.1**. We note that the assemblage of fishes defined by one of these clusters is not identical to the fish community found in any one stream in the set, but instead provides a pool of species that could be found in streams of this type. For example, Cluster 8 is defined by a set of 20 species, but an actual stream from this group might only have a subset of six to ten species from the total species pool. The fish community of Stream A could consist of bluehead chub, creek chub, redbreast sunfish, northern hogsucker, and green sunfish, while the community of stream B is bluehead chub, green sunfish, rock bass, redbreast sunfish, and blacknose dace. These two streams belong to the same cluster and have three species in common, but they do not have identical fish communities.

Figure 3.1 Primary members of Cluster 10, according to percent of total assemblage biomass.



Discriminant Analysis

Step two in the tool development process was a discriminant analysis that produced a system of equations to predict a stream's fish assemblage based on characteristics of that stream and its watershed. Some of the characteristics used in the analysis can be quantified by simply looking at maps or using available databases, while other data must be collected at actual stream sites or calculated via regression equations in the Hydrology Tool. Below is a list of variables of each type that we included.

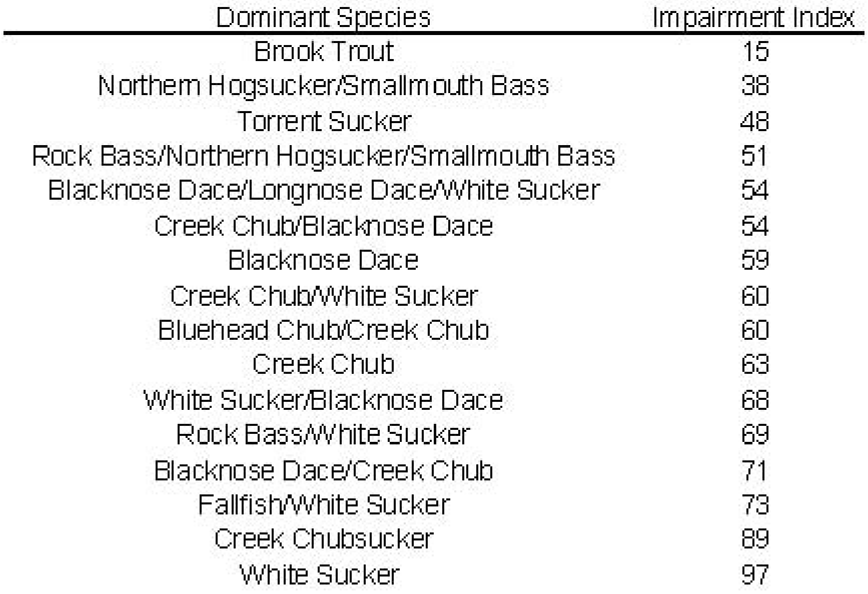
Remotely-Sensed
Latitude
Longitude
Watershed Area (ha)
% Agricultural Area in Watershed
% Urban Area in Watershed
% Forested Area in Watershed
Stream Slope
Mean Stream Elevation (m)
Annual Mean Precipitation (m)
Watershed Road Density (m per ha)
Watershed Population Density (people per km^2)

Measured On-Site/Determined via Regression
Mean Stream Depth (cm)
Mean Stream Width (m)
Mean Stream Flow (cfs)
Dissolved Oxygen in Stream (mg per liter)
Stream Temperature (degrees C)
% of Stream Bank with Riparian Cover
% of Stream Bottom Covered in Fine Sediments

To begin, the correlation matrix of all predictors was examined, and for predictor pairs with a correlation above 0.75, the most easily interpretable and understandable member the pair was retained for analysis. Then, using the clusters from **Table 3.1** as the response variable, all remaining predictors were added to form the full model (Minitab software was used to perform the analysis). At that point, one by one, the least useful predictors, in terms of their effect on predictive success probabilities, were dropped from the model, i.e., a backwards-selection methodology was used. The process of deleting predictors was stopped when the predictive success probability dropped by more than 5% after removing a predictor from the model. The final model contained the following predictors: latitude, longitude, stream elevation, stream slope, % disturbed area in the watershed, stream width, mean thalweg depth, stream flow, temperature, dissolved oxygen, % of the stream bed covered in fine sediment.

Basic summary statistics were also used to examine the clusters of **Table 3.1**. **Table 3.2** gives the assemblages sorted by an Impairment Index that was calculated as the sum of four parameters: % Agricultural Landuse, % Urban Landuse, % Fine Sediments, and (100 - % Riparian Zone). Watersheds with sizeable disturbed areas will typically experience more soil erosion and have higher in-stream sedimentation than streams in heavily forested watersheds. Species tolerant of sediments, such as white sucker and creek chubsucker are more prevalent in agricultural watersheds, whereas intolerant species, such as the brook trout and northern hogsucker, are found in primarily undisturbed, forested watersheds.

Table 3.2 Relating the impairment index to fish communities in MAH streams.



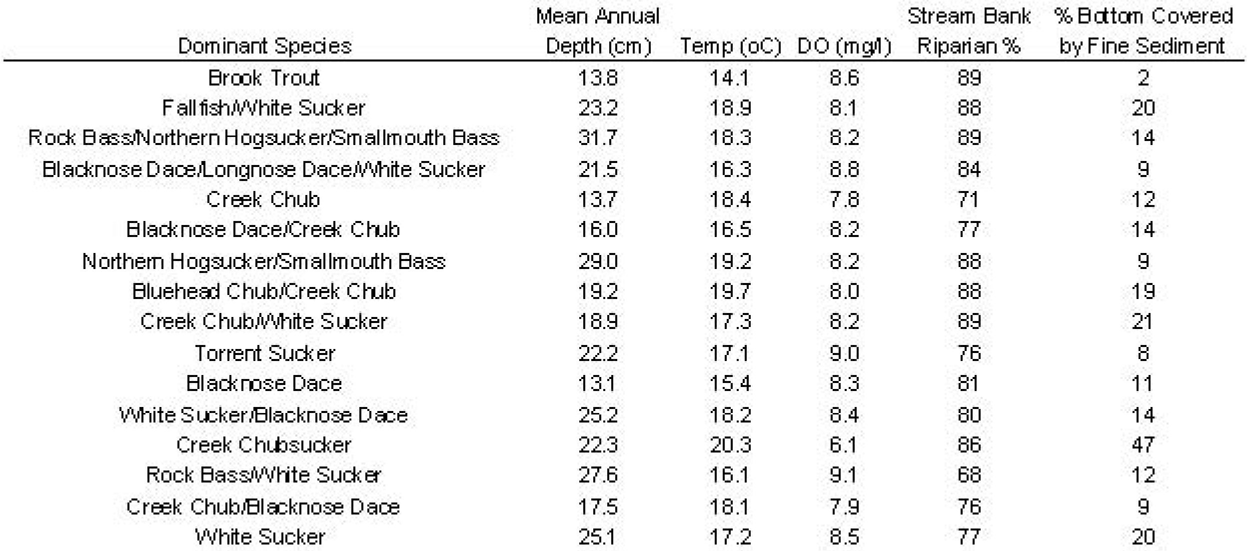
Dominant Species	Impairment Index
Brook Trout	15
Northern Hogsucker/Smallmouth Bass	38
Torrent Sucker	48
Rock Bass/Northern Hogsucker/Smallmouth Bass	51
Blacknose Dace/Longnose Dace/White Sucker	54
Creek Chub/Blacknose Dace	54
Blacknose Dace	59
Creek Chub/White Sucker	60
Bluehead Chub/Creek Chub	60
Creek Chub	63
White Sucker/Blacknose Dace	68
Rock Bass/White Sucker	69
Blacknose Dace/Creek Chub	71
Fallfish/White Sucker	73
Creek Chubsucker	89
White Sucker	97

Table 3.3 summarizes the averages of measured on-site variables for each cluster in **Table 3.1**. This information quickly indicates the type of stream each assemblage would likely inhabit. For example, a brook trout dominated assemblage would most likely be found in a small, cool, well-oxygenated stream with little sediment and extensive riparian buffer.

3.2.2. Discriminatory Power

Using the 16 functions (one for each cluster) output by the discriminant analysis, we could predict the correct stream cluster for streams in our dataset with approximately 41% accuracy. Given that there were 16 total clusters included, the random chance of picking the correct stream cluster would only be about 6% (1/16). The power of prediction was thus increased by nearly seven times by using the stream and watershed characteristics. In addition, the correct stream cluster was predicted to be one of the three most likely outcomes (as opposed to the more rigorous case discussed above) for 70% of the stream sites. Randomly, given three choices, one would only have a 3 in 16 chance of picking the correct cluster (19%).

Table 3.3 Relating stream characteristics to fish communities in MAH streams.



Dominant Species	Mean Annual Depth (cm)	Temp (oC)	DO (mg/l)	Stream Bank Riparian %	% Bottom Covered by Fine Sediment
Brook Trout	13.8	14.1	8.6	89	2
Fallfish/White Sucker	23.2	18.9	8.1	88	20
Rock Bass/Northern Hogsucker/Smallmouth Bass	31.7	18.3	8.2	89	14
Blacknose Dace/Longnose Dace/White Sucker	21.5	16.3	8.8	84	9
Creek Chub	13.7	18.4	7.8	71	12
Blacknose Dace/Creek Chub	16.0	16.5	8.2	77	14
Northern Hogsucker/Smallmouth Bass	29.0	19.2	8.2	88	9
Bluehead Chub/Creek Chub	19.2	19.7	8.0	88	19
Creek Chub/White Sucker	18.9	17.3	8.2	89	21
Torrent Sucker	22.2	17.1	9.0	76	8
Blacknose Dace	13.1	15.4	8.3	81	11
White Sucker/Blacknose Dace	25.2	18.2	8.4	80	14
Creek Chubsucker	22.3	20.3	6.1	86	47
Rock Bass/White Sucker	27.6	16.1	9.1	68	12
Creek Chub/Blacknose Dace	17.5	18.1	7.9	76	9
White Sucker	25.1	17.2	8.5	77	20

3.2.3. Use of the Cluster/Discriminant Fish Assemblage Tool

1) At the model execution screen (see Figure 3.2), input the stream and watershed characteristics for the stream of interest, then click the “Calculate” button.

The “Estimated Prediction Accuracy” (EPA) that appears indicates the overall success rate for predicting a stream’s actual cluster using our EMAP dataset. A successful prediction was defined to be when the stream’s actual cluster was one of the 3 most likely assemblages predicted by the model.

Above the species list of each assemblage is the Relative Score for that assemblage. As opposed to the EPA, the Relative Score of the assemblages *will* change as a user changes parameter values. This numerical score gives an indication of the relative likelihood of each predicted assemblage. The Relative Scores are calculated by dividing the discriminant score for each assemblage by the largest discriminant score (i.e., the discriminant score for the most likely assemblage). These scores are scaled so that the most likely assemblage always receives a Relative Score of 1.0 and the least likely assemblage receives a Relative Score of 0.0. If the second and third most likely assemblages have Relative Scores near 1.0, that should lead the user to conclude that any of the three could easily be correct. However, if the second and/or third most probable assemblages have Relative Scores much less than the most probable assemblage, then the user would have confidence that the most probable assemblage is much more likely to be correct.

2) For the predicted assemblages, note the actual species and the relative dominance of each within the assemblage. The % of total fish biomass for each species is given in parentheses. If you see Bluehead Chub (33.3) in one of the assemblages, it means the biomass of Bluehead Chub on average comprises 33.3% of the total fish biomass in streams from this cluster.

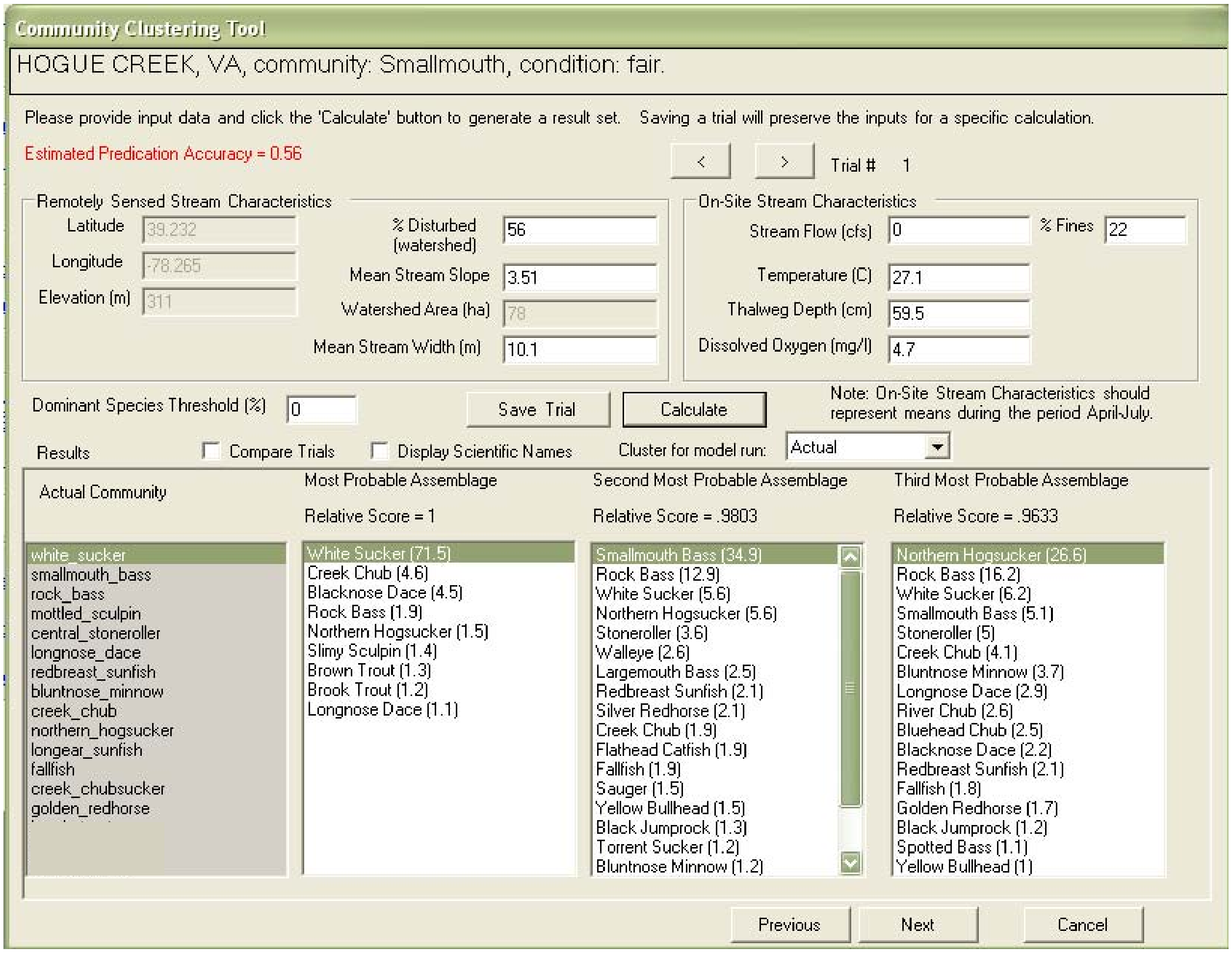
3) If examining the influence of stream restoration/degradation is desired, change the characteristics of the stream in accordance with the predicted outcomes of best management practices, stream restoration efforts, or environmental degradation and rerun the analysis. This could include reducing/increasing the % forested area in the watershed, or the values of stream slope and/or mean depth. After the desired changes are made, recalculate the most probable fish assemblages and note differences.

If changing the stream and watershed characteristics produced a new set of most probable fish communities, note that the time scale over which the fish assemblage could be expected to change cannot be predicted. This process could take months, years, or decades, depending on how different the new communities are from the originals, whether or not species would be stocked into the stream, and rates of natural immigration from other locations. If the species of the assemblage were not predicted to change, but only the relative dominance of species within the assemblage, the change process would likely be faster. If an assemblage of entirely new species were predicted, one could expect this process to be relatively much slower.

3.3. Intended Audience

We envision this tool being used by a wide diversity of stakeholders, from private landowners and public interest groups to municipal planners and developers to environmental management professionals. One goal would be to predict fish communities in streams for which basic watershed and stream characteristics are known, when actual sampling of the stream is cost prohibitive. Users could also investigate potential impacts of hypothesized environmental restoration/degradation scenarios by altering stream and watershed characteristics, then noting subsequent changes in the predicted fish community. For researchers, this tool's basic fish community information can be passed to more complex, mechanistic fish community models that can examine the effects of specific stressors on stream fish communities.

Figure 3.2 Software tool for predicting stream fish assemblages based on stream and watershed characteristics.



HOGUE CREEK, VA, community: Smallmouth, condition: fair.

Please provide input data and click the 'Calculate' button to generate a result set. Saving a trial will preserve the inputs for a specific calculation.

Estimated Predication Accuracy = 0.56

Trial # 1

Remotely Sensed Stream Characteristics

Latitude: 39.232
Longitude: -78.265
Elevation (m): 311
% Disturbed (watershed): 56
Mean Stream Slope: 3.51
Watershed Area (ha): 78
Mean Stream Width (m): 10.1

On-Site Stream Characteristics

Stream Flow (cfs): 0
% Fines: 22
Temperature (C): 27.1
Thalweg Depth (cm): 59.5
Dissolved Oxygen (mg/l): 4.7

Dominant Species Threshold (%): 0

Note: On-Site Stream Characteristics should represent means during the period April-July.

Results

☐ Compare Trials
☐ Display Scientific Names

Cluster for model run: Actual

Actual Community

white_sucker
smallmouth_bass
rock_bass
mottled_sculpin
central_stoneroller
longnose_dace
redbreast_sunfish
bluntnose_minnow
creek_chub
northern_hogsucker
longear_sunfish
fallfish
creek_chubsucker
golden_redhorse

Most Probable Assemblage

Relative Score = 1

White Sucker (71.5)
Creek Chub (4.6)
Blacknose Dace (4.5)
Rock Bass (1.9)
Northern Hogsucker (1.5)
Slimy Sculpin (1.4)
Brown Trout (1.3)
Brook Trout (1.2)
Longnose Dace (1.1)

Second Most Probable Assemblage

Relative Score = .9803

Smallmouth Bass (34.9)
Rock Bass (12.9)
White Sucker (5.6)
Northern Hogsucker (5.6)
Stoneroller (3.6)
Walleye (2.6)
Largemouth Bass (2.5)
Redbreast Sunfish (2.1)
Silver Redhorse (2.1)
Creek Chub (1.9)
Flathead Catfish (1.9)
Fallfish (1.9)
Sauger (1.5)
Yellow Bullhead (1.5)
Black Jumprock (1.3)
Torrent Sucker (1.2)
Bluntnose Minnow (1.2)

Third Most Probable Assemblage

Relative Score = .9633

Northern Hogsucker (26.6)
Rock Bass (16.2)
White Sucker (6.2)
Smallmouth Bass (5.1)
Stoneroller (5)
Creek Chub (4.1)
Bluntnose Minnow (3.7)
Longnose Dace (2.9)
River Chub (2.6)
Bluehead Chub (2.5)
Blacknose Dace (2.2)
Redbreast Sunfish (2.1)
Fallfish (1.8)
Golden Redhorse (1.7)
Black Jumprock (1.2)
Spotted Bass (1.1)
Yellow Bullhead (1)

4. Habitat Suitability Tool

4.1. Introduction to habitat suitability assessment

The suitability of instream physical habitat for particular fish species has been assessed using a variety of quantitative methods. One of the earliest approaches to assess habitat suitability was through the use of habitat suitability index (HSI) models. These index models are composite scores of the suitability of multiple habitat variables. For each of the habitat variables, suitability ranges from 0 (unsuitable) to 1 (fully supporting of the species). These models are based on the assumption that there is a positive relationship between the suitability index and habitat carrying capacity (USFWS 1981). A similar approach is the development of guild-based habitat suitability criteria, which have been used to represent species groups, or guilds, that utilize similar habitats in similar manners (Leonard and Orth 1988, Aadland 1993, Vadas and Orth 2001). In a recent review of predictive habitat distribution models, Guisan and Zimmermann (2000) reported that multiple regression models are a very popular approach to predict habitat distribution, and that neural networks, ordination and classification, and Bayesian methods are also used. All of these techniques have successfully been applied to stream fish (Lefwich et al. 1997, Mastrorillo et al. 1997, Rieman et al. 2001). Here, multiple logistic regression was used to develop quantitative relationships between instream habitat variables and the presence or absence of selected fish species. Although we initially considered an HSI approach, few species known from the MAH had developed HSIs (McCormick et al. 2001). While other techniques, in particular neural networks, may give higher correct percentages, logistic regressions perform reasonably well in comparison (Olden and Jackson 2002) and may be easier to interpret.

In general, studies relating stream fish occurrence and habitat quality have found that such relationships exist at multiple scales, including reach, watershed, and landscape scale (Angermeier et al. 2002 , and references therein). In this analysis, only reach-scale habitat variables were used as predictors, because recent analyses of fish data in this region showed that little differences in fish communities occurred across regional-scale variables of physiographic provinces, drainage basins, and other geographic features (McCormick et al. 2000, McCormick et al. 2001). Local-scale habitat variables that are most often included in habitat suitability studies are instream cover, substrate, and physical characteristics (e.g., Edwards et al. 1983, Freeman et al. 1997, Barbour et al. 1999). For example, Lefwich et al. (1997)

found that the presence of a darter species in Virginia could be predicted by multiple logistic regression models that included elevation, depth, width, and substrate particle size. Wilson and Belk (2001) found that the occurrence of the leatherside chub in the Great Basin of the western United States was related to water velocity, water depth, and substrate composition. Guay et al. (2000) used a logistic model that included water depth, current speed, and substrate composition to predict the distribution of Atlantic salmon in a Quebec river. Habitat variables such as these were chosen for this analysis.

4.2. How suitable is my stream for specific fish species?

4.2.1. Methodology

The fish and habitat data used in this analysis were produced by the USEPA EMAP program for MAH surface waters during 1993-6 (http://www.epa.gov/emap/html/dataI/surfwatr/data/ma9396.html). A description of the methods and quality assessment of the EMAP habitat data is given in Kauffman et al. (1999). Samples outside of the MAH were excluded from the dataset using a Geographic Information Systems (GIS) approach: a GIS coverage of the boundary of the MAH region was overlaid on a map of the sites, and only sites that fell within those boundaries were selected for use in the analysis.

Fish species were either assessed individually or in groups. The decision was made based on McCormick et al. (2000), who identified dominant species for the MAH. All dominant species mentioned by McCormick et al. (2000) were assessed individually; in general these were the most common species in the dataset. Rarer species were grouped taxonomically, generally following the metrics developed by McCormick et al.(2001). Grouping of species facilitates analysis because many of the species were rare, and sufficient occurrences are needed to develop a robust model (Harrell 2001).

We used the set of samples from the habitat dataset for which fish collection data were also available. In order to improve normality, percentage variables were arcsine-squareroot transformed, width and depth variables were square-root transformed, and slope was log-transformed (Zar 1974). Boxplots were used to identify extreme outliers (>3 interquartile ranges away from either the sample 25th or 75th percentiles) (SAS 1989); samples with extreme outliers were deleted. Pearson correlation coefficients were calculated among the variables, and only those that were correlated at $|r|<0.80$ were retained for analysis, in order to reduce multicollinearity (Glantz and Slinker 1990). For each pair, one of the two variables was selected for use in the analysis based on a preliminary examination of their explanatory power in the logistic regression models (Jongman et al. 1995). Samples with missing data were deleted. This resulted in a final data set of 337 samples (**Figure 4.1**) and twenty habitat variables (**Table 4.1**).

Equations to predict the presence of multiple fish species/groups in the MAH from instream habitat data were developed using multiple logistic regression analysis with backward stepwise selection in SAS (SAS 1989). Logistic regression is a statistical technique to predict or model a categorical response variable from one or more continuous explanatory variables. The categorical response variable of fish presence-absence was used because it is more robust to sampling biases than measures of densities (Green 1979). The default of binary logit model with Fisher's scoring for the optimization technique was used (SAS 1989). A significance value of 0.05 was used for retaining habitat variables into the model.

Table 4.1 Instream habitat measures that were selected from the EMAP dataset as possible explanatory variables for the presence of fish species in the Mid-Atlantic Highlands region.

Variable	EMAP Code	Habitat measure (units)	Mean	S.D.	Min	Max
Boulder	XFC_RCK	Boulder/rock ledge cover (%)	18.3	19.9	0	87.5
Coarse_gravel	PCT_BIGR	Coarse gravel substrate (>16 mm) (%)	62.76	25.38	0	100
Cobble	PCT_CB	Cobble substrate (64-240 mm) (%)	26.5	19.2	0	100
Depth	XDEPTH	Mean thalweg depth (cm)	34.09	19.07	3.77	98.59
Fine_gravel	PCT_GF	Gravel substrate (2-16mm) (%)	9.7	9.9	0	54.6
Fine_sediments	PCT_FN	Fine sediment, i.e., silt/clay/muck (%)	12.8	15.4	0	100
Glide	PCT_GL	Glide habitat (%)	36.3	24.7	0	100
Overhanging	XFC_OHV	Overhanging vegetation cover (%)	11.9	13.1	0	79.3
Pool	PCT_POOL	Pool habitat (%)	14.5	19.3	0	99
Riffle	PCT_RI	Riffle habitat (%)	42.3	23.3	0	100
Rip_ground	XG	Riparian vegetation (ground layer) (%)	56.0	24.4	20	100
Rip_layers	XPCMG	Riparian vegetation (3 layers) (%)	80.3	26.4	0	100
Sand	PCT_SA	Sand substrate(0.6-2mm) (%)	13.0	16.1	0	87.3
SD_depth	SDDEPTH	Standard deviation of depth (cm)	15.9	9.3	2.4	65.7
Slope	XSLOPE	Water surface gradient over reach (%)	1.58	1.72	0.055	11.25
Slow	PCT_SLOW	Slow-water habitat (% glide and pool)	50.8	25.9	0	100
Temp	TEMP_FLD	Temperature (C)	17.8	4.4	7.8	30.1
Undercut	XFC_UCB	Undercut bank cover (%)	4.9	6.5	0	41.8
Width	XWIDTH	Mean wetted width (m)	8.40	8.75	0.43	51.75
Woody	XFC_LWD	Large woody debris cover (%)	3.5	5.2	0	38.2

The outputs of each logistic regression model included habitat variables retained in the model, maximum likelihood estimates and significance values for the coefficients, a test of the significance of the residuals, and goodness-of-fit statistics for the overall model. Goodness of fit statistics included the Hosmer and Lemeshow test, for which a low significance value indicates a poorly fit model (Hosmer and Lemeshow 2000), and the percent of samples correctly classified. This percentage was derived via leave-one-out cross-validation, that is, each sample was sequentially left out, model parameters were reestimated, and the predicted probability of presence (the species/group was assumed to be present at a predicted probability of $p \geq 0.5$) was compared to the observation for that sample. The probability of occurrence (p) of each species at a particular site was calculated by the logit equation

$$p = \frac{1}{1 + \exp(-r)} \quad \textbf{(4-1)}$$

where r denotes the species fitted logistic regression equation, i.e.,

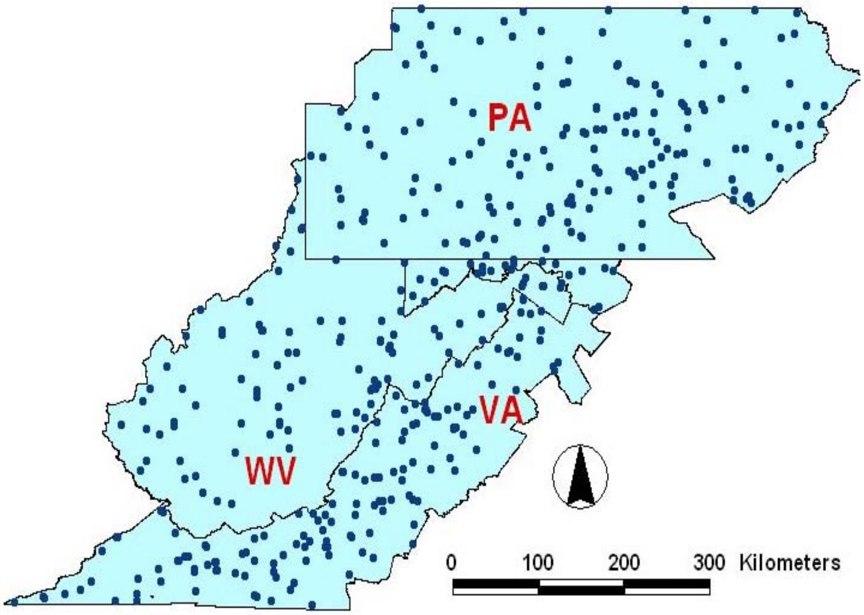
$$r = l_0 + \sum_{i=1}^{n} l_i X_i \quad \textbf{(4-2)}$$

See SAS (1989). Assuming that the probability of a species occurrence at a site is representative of that site's habitat suitability for that fish species, the aforementioned equations and fitted regressions were then used to develop an interactive computer tool for analyzing stream habitat suitability for eighteen fish species and higher taxonomic groups.

4.2.2. Results and Discussion

Wald chi-square results indicated that all of the overall logistic regression models to estimate the probability of presence of MAH stream fish species/groups were significant ($p<0.05$) (**Table 4.2**). Hosmer and Lemeshow tests and residuals tests were nonsignificant ($p>0.05$) for all models except for suckers ($p=0.0023$). Our results for the percent correctly predicted are in the range of 65-81%, and half of the models are >75%, which has been suggested as acceptable model performance for managers and researchers (Hurley 1986). Moderate to high values occurred for both sensitivity (the ability to predict an occurrence correctly) and specificity (the ability to predict an absence correctly) (**Table 4.2**). High values for both sensitivity and specificity are desirable. Low sensitivity, which occurs for more rare species, implies that it will be more difficult to predict the occurrence of organisms whose conservation may be most critical (Olden and Jackson 2002). Sensitivity can be increased by lowering the threshold at which presence is assumed (Fielding 2002), which may be desirable for certain applications, such as the identification of sites for species relocation.

Figure 4.1 Location of sample sites within the Mid-Atlantic Highlands region.



These results indicate that instream physical habitat does have significant relationships with the presence of fish species in MAH streams, although there may be other factors influencing the presence of fishes, including population dynamics, species interactions, historical factors, barriers to movement, and spatial autocorrelation. Species interactions, including predation, can affect presence/absence. However, the majority of the sites were relatively small and predation is of less importance in smaller streams (Grossman et al. 1998). Barriers to movement can cause species absence even when suitable habitat exists, and this may be more significant for poor dispersers (Angermeier et al. 2002). Although spatial autocorrelation, that is, patchiness due to factors other than habitat characteristics, can influence models (Guisan and Zimmermann 2000), McCormick et al. (2000) concluded that large-scale patchiness was not a factor in explaining fish species occurrences. Finally, there may be imperfect detection of presence in the streams due to sampling inefficiencies(MacKenzie et al. 2004). Logistic regression models are limited in that they assume a linear response of the fishes to habitat variables; this is possibly a limiting assumption, since nonlinear responses also occur. Because of these considerations, the models should be used cautiously, and not considered to be absolute predictors of presence/absence. However, they can be a useful way to conduct assessment of stream ecosystems (Oberdorff et al. 2001).

Table 4.2 Results from logistic regression models of presence of Mid-Atlantic Highlands stream fish species/groups. Results include the number of occurrences in the data set (N) and goodness-of-fit statistics for overall logistic regression models: the Wald Chi-square value and its significance (P), and the percentage of correct classifications determined using cross-validation (a higher value indicates greater predictive ability).

Species/ group name	Species within group	N	Wald Chi-square [df]	P	% correct	Sensitivity	Specificity
black bass	*Micropterus sp.*	103	73.52 [5]	<0.0001	81.3	59.2	91.0
blacknose dace	*Rhinichthys atratulus*	242	45.39 [5]	<0.0001	76.3	93.4	32.6
brook trout	*Salvelinus fontinalis*	76	45.70 [4]	<0.0001	80.1	26.3	95.8
brown trout	*Salmo trutta*	92	32.05 [6]	<0.0001	71.2	14.1	93.1
catfish	*Ameiurus sp., Ictalurus sp., Noturus sp., Pylodictus sp.*	96	59.33 [4]	<0.0001	76.3	42.7	89.6
chub	*Nocomis sp., Semotilus, sp., Exoglossum sp.*	272	47.79 [4]	<0.0001	83.4	96.7	27.7
creek chub	*Semotilus atromaculatus*	200	56.03 [5]	<0.0001	70.0	80.5	54.7
dace	*Margariscus sp., Phoxinus sp.*	81	40.61[4]	<0.0001	76.3	9.9	97.3
darters	*Etheostoma sp., Percina sp.*	227	71.09 [7]	<0.0001	78.9	89.4	57.3
longnose dace	*Rhinichthys cataractae*	137	62.80 [10]	<0.0001	70.9	57.7	80.0
northern hogsucker	*Hypentelium nigricans*	125	77.98[5]	<0.0001	81.4	71.2	88.2
rock bass	*Ambloplites rupestris*	110	67.95 [5]	<0.0001	76.6	52.7	88.1
sculpin	*Cottus sp.*	161	36.57 [4]	<0.0001	65.3	59.0	71.0
shiners	*Notropis sp.*	100	70.56 [5]	<0.0001	81.0	57.0	91.1
stoneroller	*Campostoma anomalum*	160	59.15 [7]	<0.0001	68.8	63.8	73.4
suckers	*Hypentileum sp., Moxostoma sp.*	152	76.73 [6]	<0.0001	81.6	78.3	84.3
sunfish	*Lepomis sp.*	154	72.30 [9]	<0.0001	70.9	64.9	76.0
white sucker	*Catostomus commersoni*	186	60.48 [6]	<0.0001	73.3	81.2	63.6

Although different fish species/groups responded to different habitat variables, over half the species/groups analyzed responded to stream temperature, slope, and/or width (**Table 4.3**). Twelve species/groups demonstrated significant responses to stream slope. All of these species/groups (i.e., black bass, brown trout, central stoneroller, chubs, creek chubs, darters, longnose dace, northern hogsuckers, rock bass, sculpins, suckers, and white suckers) responded negatively to this variable. This finding is likely due to the fact that this region is mountainous and steep mountain streams provide flashy, unstable habitats. Eleven species/groups demonstrated significant responses to stream width. Whereas seven species/groups (i.e., black bass, central stonerollers, darters, northern hogsuckers, rock bass, shiners, and suckers) responded positively to this variable, four species/groups (i.e., blacknose dace, creek chubs, daces, and white suckers) responded negatively. Eleven species/groups also demonstrated significant responses to stream temperature. Whereas eight species/groups (i.e., black bass, catfish, central stonerollers, chubs, creek chubs, northern hogsucker, suckers, and sunfish) responded positively to this variable, three species/groups (i.e., brook trout, brown trout, and sculpins) responded negatively.

A third half or more of the species/groups analyzed responded to stream depth, large gravel cover, and riparian cover (**Table 4.3**). Six species/groups responded significantly to stream depth. Whereas creek chubs displayed a negative respond to this variable, the remaining species (i.e., catfish, daces, longnose dace, sunfish, and white suckers) responded positively to increasing stream depth. Vadas and Orth (2001) found that depth was the most important factor in habitat selection for seven fish guilds in the Roanoake River drainage in Virginia. Central stonerollers, chubs, longnose dace, and white suckers responded positively to the presence of large gravel stream bottoms whereas rock bass, shiners, and suckers responded negatively to this variable. Eight species/groups showed significant positive responses to increasing riparian cover metrics. In particular, blacknose dace, brown trout, catfish, darters, longnose dace, and shiners responded to riparian ground cover, and darters, suckers, and sunfish responded to either overhanging or multilayer riparian vegetation.

Fishes responded to the cover metrics, and the response was generally positive, although some fish species showed a negative relationship with undercut bank cover. This is surprising, since fishes can use undercut bank habitat as cover and refuge. However, undercut banks can also occur as a result of landuse development and physical habitat alteration and these stressors can have a negative effect on fish species in streams. Large gravel and sand substrate species responded to multiple larger substrates, which provide for cover and reproduction; a mix of substrates may be most favorable. Many fish species/groups responded positively to riparian vegetation, which slows water flow, traps sediment and other pollutants, and stabilizes streambanks.

Fish species/groups responded individually to habitat variables, so management activities that alter these variables will favor different species in different ways (e.g., slow water habitat). However, most fish species/groups are predicted to benefit from the maintenance of flow volume, large gravel substrate, and riparian vegetation.

Table 4.3 Parameter estimates and odds ratios from logistic regression models of presence of Mid-Atlantic Highlands stream fish species/groups.

Species Group	Variable	Coefficient	P-value	Species Group	Variable	Coefficient	P-value
black bass	Intercept	-7.13	<0.0001	central stoneroller	Intercept	-4.10	<0.0001
	Cobble	2.00	0.0082		Coarse_gravel	1.96	0.0003
	Sand	2.50	0.0007		Glide	1.13	0.0472
	Slope	-3.17	0.0024		Pool	1.57	0.0034
	Temp	0.13	0.0005		Slope	-2.79	0.0008
	Width	1.12	<0.0001		Temp	0.07	0.0393
blacknose dace	Intercept	1.50	0.0074		Width	0.41	0.0040
	Glide	4.97	0.0016	chub	Intercept	-3.03	0.0042
	Pool	4.10	0.0021		Coarse_gravel	2.39	0.0007
	Rip_ground	1.69	0.0012		Sand	1.73	0.0387
	Slow	-6.24	0.0002		Slope	-4.33	<0.0001
	Width	-0.47	<0.0001		Temp	0.21	<0.0001
brook trout	Intercept	0.98	0.1565	creek chub	Intercept	2.20	0.0121
	Boulder	1.62	0.0033		Depth	-0.50	0.0036
	Glide	-1.33	0.0135		SD_depth	0.56	0.0048
	Temp	-0.15	<0.0001		Slope	-4.02	<0.0001
	Woody	2.35	0.0370		Temp	0.10	0.0016
brown trout	Intercept	-2.74	0.0097		Width	-0.57	0.0017
	Cobble	2.62	<0.0001	daces	Intercept	-0.27	0.6237
	Fine_gravel	2.07	0.0163		Depth	0.74	<0.0001
	Rip_ground	1.10	0.0371		SD_depth	-0.5	0.0271
	SD_depth	0.34	0.0126		Width	-1.13	<0.0001
	Slope	-2.49	0.0030		Woody	-3.01	0.0124
	Temp	-0.10	0.0040	darters	Intercept	-3.38	0.0012
catfish	Intercept	-8.45	<0.0001		Boulder	-1.9	0.0052
	Depth	0.67	<0.0001		Rip_ground	2.00	0.0007
	Rip_ground	1.40	0.0083		Rip_layers	0.99	0.0157
	Slow	-1.34	0.0127		Sand	1.69	0.0157
	Temp	0.19	<0.0001		Slope	-2.23	0.0152
					Width	1.19	<0.0001
					Woody	-3.55	0.0049

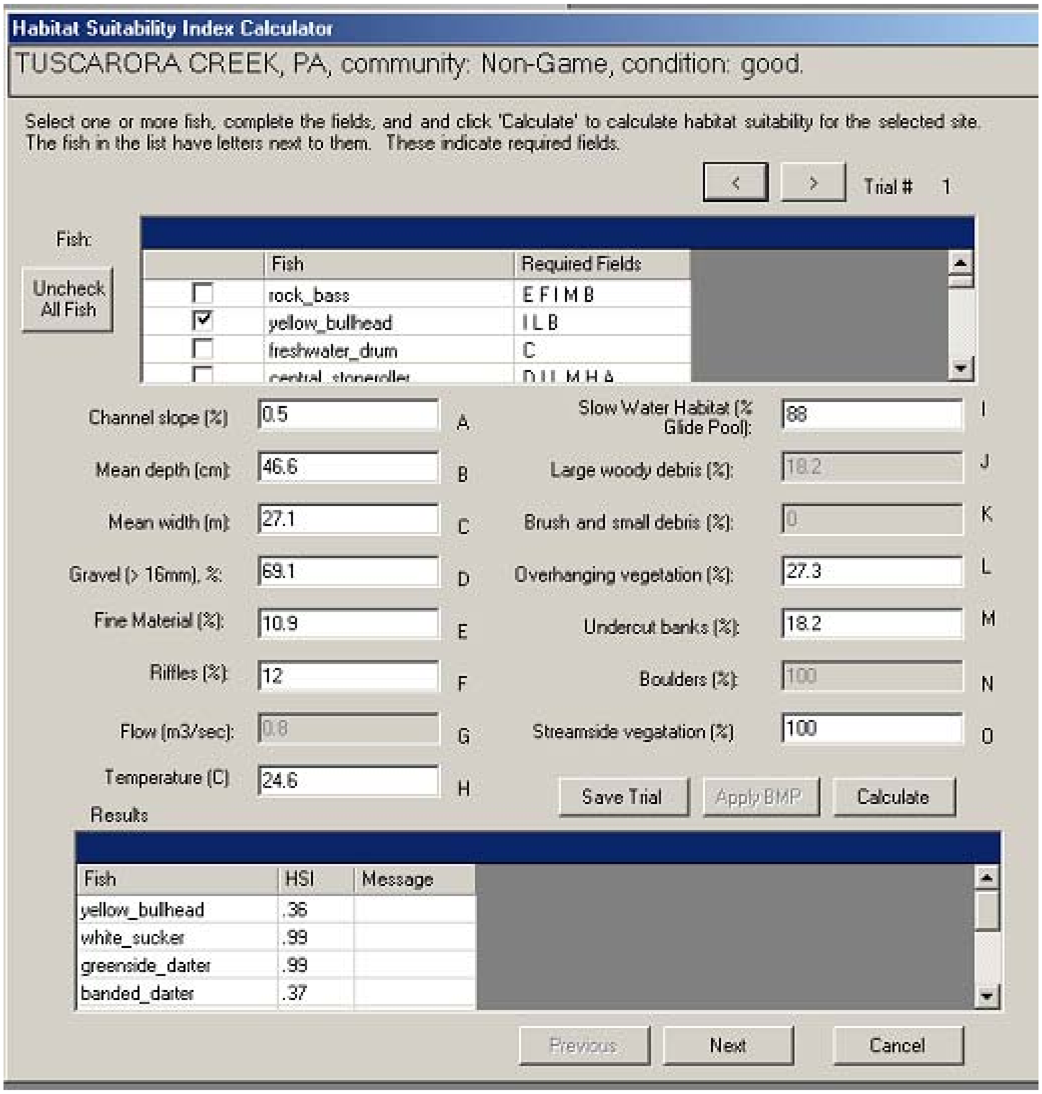
4.2.3. Interactive Tool

The predictive habitat models developed here have been incorporated into an interactive software tool that outputs changes in the probability of occurrence for these fish species under various habitat management scenarios (**Figure 4.2**). The interface provides a list of the fish species from which the user can select one or more by checking the associated checkboxes; habitat variables needed to predict the suitability for selected fish species are highlighted and variables not needed are grayed-out. The tool allows the user to vary the instream habitat parameters within their specified ranges. The user can then recalculate the habitat suitability scores as a separate trial. If the user specifies a value that is out of range, an error message is generated in the message field that indicates the accepted range.

Table 4.3 Continued.

Species Group	Variable	Coefficient	P-value	Species Group	Variable	Coefficient	P-value
longnose dace	Intercept	-8.02	<0.0001	suckers	Intercept	-5.26	<0.0001
	Coarse_gravel	3.14	0.0001		Coarse_gravel	-1.78	0.0162
	Depth	0.51	<0.0001		Cobble	2.06	0.0058
	Fine_gravel	2.11	0.0315		Overhanging	1.95	0.0149
	Fine_sediments	1.67	0.0457		Sand	2.99	<0.0001
	Glide	5.00	0.0143		Slope	-3.16	0.0011
	Pool	2.99	0.0463		Slow	-1.27	0.0473
	Rip_ground	1.57	0.0036		Temp	0.11	0.0042
	Slope	-2.53	0.0060		Width	1.29	<0.0001
	Slow	-6.65	0.0024	sunfish	Intercept	-10.58	<0.0001
northern hogsucker	Intercept	-6.43	<0.0001		Coarse_gravel	2.50	0.0260
	Cobble	2.39	0.0018		Depth	0.20	0.0447
	Sand	3.09	<0.0001		Fine_sediments	3.36	0.0015
	Slope	-5.32	<0.0001		Glide	-1.79	0.0186
	Temp	0.13	0.0003		Rip_layers	0.76	0.0352
	Width	1.09	<0.0001		Sand	3.04	0.0043
rock bass	Intercept	-3.90	<0.0001		Slow	3.49	<0.0001
	Slope	-2.99	0.0023		Temp	0.14	0.0002
	Slow	1.70	0.0019	white sucker	Intercept	-4.96	0.0011
	Width	0.98	<0.0001		Coarse_gravel	3.84	0.0006
sculpin	Intercept	3.70	<0.0001		Depth	0.47	0.0010
	Fine_sediments	-2.11	0.0001		Fine_sediments	3.05	0.0027
	Sand	-2.23	<0.0001		Sand	2.48	0.0154
	Slope	-2.15	0.0011		Slope	-4.59	<0.0001
	Temp	-0.10	0.0004		Width	-0.42	0.0185
shiners	Intercept	-4.64	<0.0001				
	Coarse_gravel	-1.92	0.0008				
	Cobble	1.48	0.0224				
	Rip_ground	1.89	0.0003				
	Sand	2.78	<0.0001				
	SD_depth	0.37	0.0327				
	Width	0.57	0.0015				

Figure 4.2 Interface for the Habitat Suitability Tool in the CVI Watershed.



TUSCARORA CREEK, PA, community: Non-Game, condition: good.

Select one or more fish, complete the fields, and and click 'Calculate' to calculate habitat suitability for the selected site. The fish in the list have letters next to them. These indicate required fields.

Trial # 1

Fish:

	Fish	Required Fields
☐	rock_bass	E F I M B
☑	yellow_bullhead	I L B
☐	freshwater_drum	C
☐	central_stoneroller	D I L M H A

Channel slope (%) 0.5 A
Mean depth (cm): 46.6 B
Mean width (m): 27.1 C
Gravel (> 16mm), %: 69.1 D
Fine Material (%): 10.9 E
Riffles (%): 12 F
Flow (m3/sec): 0.8 G
Temperature (C) 24.6 H
Slow Water Habitat (% Glide Pool): 88 I
Large woody debris (%): 18.2 J
Brush and small debris (%): 0 K
Overhanging vegetation (%): 27.3 L
Undercut banks (%): 18.2 M
Boulders (%): 100 N
Streamside vegatation (%) 100 O

Results

Fish	HSI	Message
yellow_bullhead	.36	
white_sucker	.99	
greenside_darter	.99	
banded_darter	.37	

How might suitability be improved for these species?

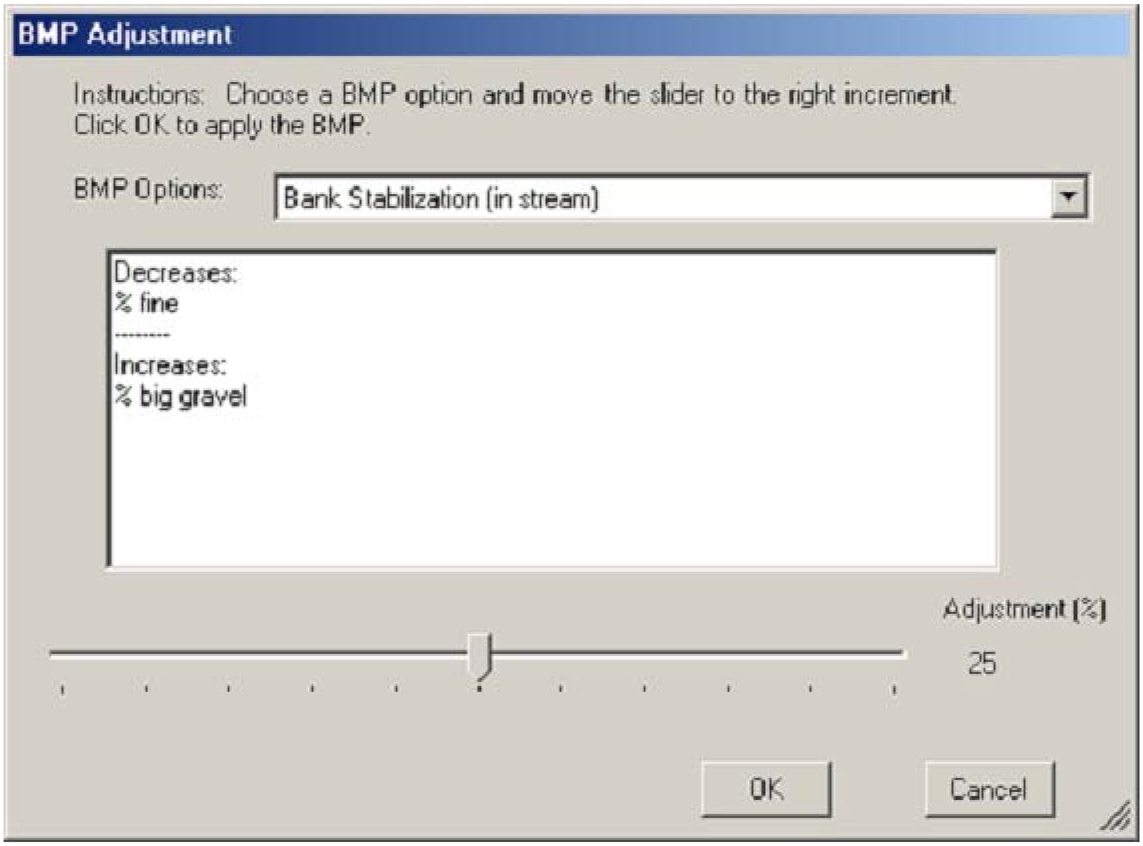
The Habitat Suitability tool allows the user to examine how habitat suitability for particular species or groups of fish changes in response to changing habitat characteristics, that is, the user can alter any of the input habitat variables and recalculate the score. The models will be most reliable for smaller levels of change and with reasonable combinations of variables. Additionally, three scenarios for Best Management Practices (BMPs), based on best professional judgement and information from the literature (e.g., Rosgen 1996), are provided as options to be applied at a particular stream site (**Figure 4.3**, **Table 4.4**). The user can select the level of percent change that occurs in the scenario. The results should be interpreted in a comparative fashion: higher values for the probability of occurrence indicate a higher likely suitability for that species.

Table 4.4 Scenarios of Best Management Practices (BMPs) provided within the CVI Habitat Suitability tool.

BMP scenario	Increases	Decreases
Riparian Zone Restoration	Large woody debris Small woody debris Overhanging vegetation	Temperature
Bank stabilization (instream)	Percent coarse gravel	Percent fine sediment
Natural stream channel design	Percent riffle Width	Percent glides and all pool types

Models that predict the presence of stream fish species based on habitat characteristics can be useful in watershed management: they allow managers and researchers to understand the link between physical habitat alteration and fish community condition. Such models can be used to assess the effectiveness of management actions. For example, management actions that may be undertaken in the MAH to improve physical habitat for stream fish include protecting existing riparian vegetation, restoring stream bank vegetation, and restoring streams to more natural flow regimes (USEPA 2000). The models can also be used to aid in species conservation (Angermeier et al. 2002). For example, the models can inform management about which habitat factors should be considered in conservation and restoration activities for particular species. Most often endangered species are endangered due to habitat loss. By focusing on conservation of specific habitats and habitat characteristics favored by species at risk, such species can be helped before they become endangered. We anticipate that the Habitat Suitability approach will also be useful as a tool for optimization of restoration efforts in subwatersheds. A next step would be to couple these results with economic analyses, specifically to relate cost estimates to BMP activities and associated ecological benefits, in order to assess trade-offs in management and restoration (Holmes et al. 2004). Such analyses can lead to more comprehensive planning and decision-making for watersheds.

Figure 4.3 Interface for Best Management Practice (BMP) scenarios in the CVI Habitat Suitability Tool.



Instructions: Choose a BMP option and move the slider to the right increment.
Click OK to apply the BMP.

BMP Options: Bank Stabilization (in stream)

Decreases:
% fine

Increases:
% big gravel

Adjustment (%) 25

5. BASS: a Simulation Model for Fisheries Management

5.1. Using Simulation Models for Fisheries Management

Some of the most important assessment questions related to fisheries management in the MAH can be summarize as follows:

- How will the destruction of riparian buffers impact the expected body sizes and population abundances of recreationally important fish species such as trout and smallmouth bass?
- How will the destruction of riparian buffers impact the expected body sizes and population abundances of non-game fish species such as darters, suckers, and other fish of special concern?
- How will the restoration of riparian buffers improve the expected body size and population abundances of recreationally important fish species such as trout and smallmouth bass?
- How will the restoration of riparian buffers improve the expected body sizes and population abundances of non-game fish species such as darters, suckers, and other fish of special concern?
- How can trout stocking programs be managed to provide anglers with abundant catches of moderately sized fish for consumption, as well as sufficient numbers of trophy size fish?
- How can trout stocking programs be managed to minimize the almost unavoidable negative impacts on native non-game fish species due to competition and predation?

Process-based models that describe

- the expected growth and trophic dynamics,
- the spawning and recruitment patterns, and the effects that
- the interactions of physical habitat and water quality have on the feeding, metabolism, reproduction, survival, and dispersal

of the community's dominant fish species are perhaps the most obvious tools that fisheries managers need to address these and other related issues.

Although several excellent fish bioenergetic models were available that could be used to analyze the above assessment questions, the **B**ioaccumulation and **A**quatic **S**ystem **S**imulator (BASS) was chosen for this purpose in the CVI Watershed Toolkit. BASS is a general and extremely flexible Fortran 95 model that simulates not only fish chemical bioaccumulation but also individual and population growth dynamics of age-structured fish communities using a temporal and spatial resolution of a day and a hectare, respectively. Because a species' age class can be specified as either a month or a year, users can readily simulate small, short-lived species, such as daces and minnows, along with larger, long-lived species such, as suckers, bass, perch, sunfishes, and trout. The community's food web is specified by defining one or more foraging classes for each fish species based on either body weight, body length, or age. The dietary composition of each of these foraging classes is then specified as a combination of benthos, incidental terrestrial insects, periphyton, phytoplankton, zooplankton, and/or other fish species, including its own.

Although BASS was originally developed to simulate the bioaccumulation of chemical pollutants within a community or ecosystem context, it is also suited for simulating population and community dynamics of fish assemblages that are exposed to a wide variety of nonchemical stressors. In particular, BASS can be easily setup to simulate the population and community dynamics of fish assemblages that are subjected to altered thermal regimes associated with riparian and hydrological alterations. BASS can also be used to simulate the population and community dynamics of fish assemblages that are subjected to introductions of exotic species or stockings of recreational sport fishes.

Notable capabilities of BASS include:

- there are no restrictions to the number of chemicals that can be simulated;

- there are no restrictions to the number of fish species that can be simulated;
- there are no restrictions to the number of cohorts that fish species can have; and
- there are no restrictions to the number of feeding/foraging classes that fish species can have.

Model output includes:

- summaries of all model input parameters and simulation controls;
- tabulated annual summaries of the bioenergetics of individual fish by species and age class;
- tabulated annual summaries of the chemical bioaccumulation within individual fish by species and age class;
- tabulated annual summaries of the community level consumption, production, and mortality of each fish species by age class; and
- plotted annual dynamics of model variables, as requested by the user, as a function of fish species age or size classes.

5.2. Model Description

To understand how BASS can be used to address the assessment questions formulated previously, it is useful to review BASS' basic model structure that solves the following system of differential equations for each "year" class or cohort of fish:

$$\frac{dB}{dt} = J_g + J_i - J_m \qquad \textbf{(5-1)}$$

$$\frac{dW_d}{dt} = F - E - R - EX - SDA \qquad \textbf{(5-2)}$$

$$\frac{dN}{dt} = - EM - NM - PM \qquad \textbf{(5-3)}$$

In these equations, B and W_d denote the chemical contaminant body burden (μg / fish) and dry body weight (g[DW] / fish) of the average individual within the cohort, respectively, and N denotes the cohort's population density (fish / ha). In Equation **(5-1)** J_g and J_i denote the net chemical exchange across a fish's gills from the water and across its intestine from food, respectively, and J_m denotes the chemical's biotransformation or metabolism. In Equation **(5-2)** F, E, R, EX, and SDA denote the fish's feeding, egestion, routine respiration, excretion, and specific dynamic action (i.e., the additional respiratory expenditure in excess of R required to assimilate food), respectively. Although many physiologically based models for fish growth are formulated in terms of energy content and fluxes (e.g., kcal / fish and kcal / day), formulating a physiologically based growth model in terms of dry weight is fundamentally identical to the former, since the energy densities of fish depend on their dry weight (Kushlan et al. 1986, Hartman and Brandt 1995). Finally, in Equation **(5-3)** EM, NM and PM denote the cohort's emigration (i.e., dispersal), non-predatory, and predatory mortality, respectively. Although immigration can be a significant process in determining population sizes, this process is not presently modeled in BASS. Because cohort recruitment and fishery stockings are treated as boundary conditions, the right-hand side of Equation **(5-3)** does not require a term to address these processes. Though it may not be immediately apparent from the symbols and notation used, these equations are tightly coupled to one another. For example, the cohort's realized feeding depends on the availability (i.e., density and biomass) of suitable prey. The fish's predatory mortality, in turn, is determined by the individual feeding levels and population densities of its predators. Finally, the fish's dietary exposure to organic and metallic chemical pollutants is determined by its rate of feeding and the levels of those contaminants in its prey.

Appendix B summaries how BASS models the mass fluxes in the above system of equations. However, due to the focus of the assessment questions above, this discussion is restricted to only the cohort's growth and population Equations **(5-2)** and **(5-3)**. Readers interested in BASS's bioaccumulation algorithms should see Barber (2001).

5.3. Developing Case Studies to Evaluate Mid-Atlantic Fisheries

In order to develop initial fishery management and riparian alteration assessment scenarios for the MAH, 18 EMAP surface water stream sites were chosen as case studies. These streams were selected such that two streams are representative of typical trout, smallmouth, and non-game dominated communities within each of the states of Pennsylvania, West Virginia, and Virginia. For each of the nine community type × state combinations, one stream was selected that had excellent or minimally disturbed riparian vegetation, and one stream was selected that had poor or disturbed riparian vegetation. See **Table 5.1**.

Habitat suitability scores developed in Section **4.2** (i.e., Equations **(4-1)** and **(4-2)** and **Table 4.3**) were used as habitat suitability multipliers on each species non-predatory mortality and dispersal within these streams as discussed in Appendix B (see Section **B.5** Equation **(B-38)**). After simulating the nominal community dynamics of the 18 case study streams, the expected effects of riparian destruction or restoration were investigated by recalculating each species habitat suitability multiplier assuming a 25% decrease or increase in the streams' associated riparian ground cover and multilayer vegetation.

Table 5.1 EMAP fish sites selected as fisheries and riparian alteration case studies.

Stream, state	EMAP id	Community	Impactedness
Powdermill Run, PA	pa531s_1993.1	trout	marginal
Falling Spring, PA	par01s_1993.1	trout	moderate
North River, VA	maia97-132_1997.1	trout	marginal
Beaver Creek, VA	va806s_1994.1	trout	moderate
Little Black Fork, WV	wv774s_1994.1	trout	marginal
South Br Wolf Run, WV	wv773s_1994.1	trout	moderate
Allegheny Creek, PA	maia97-101_1997.1	smallmouth	marginal
Little Tenmile Creek, PA	maia97-028_1997.1	smallmouth	moderate
Calfpasture River, VA	va754s_1994.1	smallmouth	marginal
Hogue Creek, VA	maia97-052_1997.1	smallmouth	moderate
Clifford Hollow, WV	wv750s_1997.0	smallmouth	marginal
Dillons Run, WV	wvr03s_1993.1	smallmouth	moderate
Kettle Creek, PA	maia97-081_1997.1	non-game/northern hogsucker	marginal
Bell Run, PA	pa523s_1994.1	non-game/northern hogsucker	moderate
Dunnavant Creek, VA	maia97-137_1997.1	non-game/bluehead chub	marginal
Flat Creek, VA	maia98-115_1998.0	non-game/bluehead chub	moderate
Brake Run, WV	maia97-019_1997.1	non-game/blacknose dace	marginal
Tuscarora Creek, WV	wvr01s_1993.1	non-game/blacknose dace	moderate

Because trout stocking is one of the most important and widespread fisheries management practices in the region, a default stocking scenario was developed for application to each of the 18 streams. This stocking scenario assumes that brook, rainbow, and brown trout are stocked at the rates of 200, 100, and 50 fish/ha, respectively, once a month from February through May. Whereas the stocking length of brook and rainbow trout was assumed to be approximately 7 inches, brown trout were assumed to be 12 inches. Annual fishing mortality (i.e., harvest) for each trout species was set at 90%.

5.3.1. Developing Initial Conditions

The species compositions of the 18 case study stream communities were assigned to be the most abundant species in terms of calculated biomass (g[FW]/m^2) such that the relative biomasses of the selected species summed to least 95%. This selection criteria resulted in an average number of species per stream equal to 5.8.

Species biomasses and initial cohort densities were calculated from EMAP fish data by first converting the reported species counts into species densities (fish/m^2) using the reported stream segment length and mean width. Total species densities were then converted into a vector of cohort densities using the self-thinning algorithm described in Appendix A. Initial live body weights of each cohort were than estimated using the growth rates summarized in **Table A.2**. Finally, the product of each cohort's estimated body weight and density were summed to estimate the species total biomass. When growth data were unavailable for a given species, a default growth rate was assigned based on the species' genus. See **Table 5.2**.

Macroinvertebrates biomasses were also estimated from EMAP surface water data. In particular reported taxa densities were converted into biomasses using the conversion factor summarized in **Table 5.3**.

5.3.2. Parameterization of BASS Physiological and Ecological Processes

A Fortran 95 fish community program was developed to generate BASS input files automatically while estimating the species biomasses and cohort densities described in Section **5.3.1**. Data required to define diets and to assign reproductive parameters were taken from Carlander (1969, 1977, 1997), Jenkins and Burkhead (1994), and Etnier and Starnes (1993). All fish species were assumed to feed on the generalized prey categories of benthos, periphyton/attached algae, zooplankton/drifting invertebrates, and fish in direct proportion to the biomasses of these prey as summarized by afore mentioned authorities. For example, species that generally feed on benthic invertebrates and periphyton were assumed to have feeding electivities for benthos and periphyton equal to zero. Similarly, species that generally feed on benthic invertebrates and fish were assigned feeding electivities equal to zero for benthos and all fish species within the stream of interest. See appendix Section **B.3** for details. Maximum daily consumption of all species was modeled using BASS's linear feeding model (see Appendix B Equation **(B-18)**) and the growth data and default parameterization assignments summarized in **Table A.2** and **Table 5.2**. Family-specific respiratory parameters (see Appendix B Equations **(B-23)** and **(B-24)**) were estimated for all species from the OXYREF database (Thurston and Gehrke 1993) that can be downloaded from the USEPA Center for Exposure Assessment Modeling web site at **http://www.epa.gov/ceampubl/oxyref.htm**. All other physiological and ecological parameters were assigned as interspecies means of data summarized in Barber (2004b).

Table 5.2 Summary of default species assignments for parameterizing BASS for MAH genera.

Default species	Genus
Alosa pseudoharengus	*Alosa, Dorosoma*
Ameiurus nebulosus	*Ameiurus, Ictalurus*
Etheostoma spp	*Ammocrypta, Crystallaria*
Catostomus commersoni	*Catostomus*
Cottus cognatus	*Cottus*
Etheostoma spp	*Etheostoma, Psychromaster, Litocara, Allohistrium, Nanostoma, Doration, Boleosoma, Ioa, Vallantia, Nothonotus, Fuscatelum, Belophlox, Ozarka, Oligocephalus, Catonotus*
Erimyzon spp	*Erimyzon*
Hypentelium nigricans	*Hypentelium*
Lampetra spp	*Lampetra, Ichthyomyzon*
Lepisosteus osseus	*Lepisosteus*
Lepomis macrochirus	*Lepomis*
Morone chrysops	*Morone*
Moxostoma spp	*Moxostoma*
Semotilus atromaculatus	*Exoglossum, Nocomis, Semotilus*
Notropis spp	*Cyprinella,uxilus, Lythrurus, Notropis, Phoxinus, Margariscus, Clinostomus*
Noturus miurus	*Noturus*
Pimephales spp	*Pimephales*
Percina spp	*Percina, Hadropterus, Swania, Alvordius, Ericosma, Odontopholis, Cottogaster, Imostoma*
Rhinichthys spp	*Rhinichthys, Erimystax, Hybopsis, Phenacobius*

Table 5.3 Summary of conversion factors for EMAP macroinvertebrate data.

Group	Average Weight (mg dry weight)
Diptera	0.02944
Ephemeroptera	0.34833
Megaloptera	3.94963
Plecoptera	0.12037
Trichoptera	0.57713
Other Insect (primarily Coleoptera and Odonata)	0.14265
Oligochaetes (Annelida and Nemotoda)	0.08900
Non-Insect (Amphipods, Cladocerans, Cyclopoids, Isopods, Ostracods, Hydracarina, Harpacticoids)	0.18492

5.4. Community Responses to Riparian Alteration and Fisheries Management

As an illustration of the use of the BASS CVI Watershed Tool, this section summaries the predicted community structure during the fifth year of a riparian alteration or fisheries management program for the following streams:

Bell Run, PA	Non-Game/ white sucker
Flat Creek, VA	Non-Game/ bluehead chub
Tuscarora Creek, WV	Non-Game/ blacknose dace

5.4.1. Responses of Non-game Streams to Riparian Restoration

Table 5.4 summarizes the predicted year 5 mean annual biomasses, community trophic flows, and average interspecies HSIs for Bell Run, Flat Creek, and Tuscarora Creek with and without 25% riparian restoration.

The total year 5 fish biomasses predicted for Bell Run, Flat Creek, and Tuscarora Creek without riparian alteration or trout stocking are 47.5, 86.7, and 2.88 kg[FW]/ha, respectively. These estimated biomasses are reasonably consistent with results of Randall et al. (1995) who reported average total fish biomasses for lakes and rivers as 83.8 and 146.1 kg[FW]/ha, respectively. The total year 5 fish densities predicted for Bell Run, Flat Creek, and Tuscarora Creek under status quo conditions are 3130, 10900, and 2002 fish/ha, respectively. The mean interspecies HSIs for Bell Run, Flat Creek, and Tuscarora Creek are 0.757, 0.605, and 0.468, respectively.

Whereas the proportion of stream reach possessing a three-layer riparian cover varies from zero to 0.64 for Bell Run, Flat Creek, and Tuscarora Creek, the proportion of stream reach having riparian ground cover varies from 0.35 to 0.87. When the proportions of riparian ground cover and three-layer riparian cover are increased by 25%, the mean interspecies HSIs for Bell Run, Flat Creek, and Tuscarora Creek increase to 0.797, 0.634, and 0.542, respectively. In other words, mean HSI scores increase by 5 to 15 %. These restoration HSIs, however, do not include potential changes in fine sediments or water temperatures that would be expected with increasing riparian vegetation cover (see for example Daniels and Gilliam 1996, Blann et al. 2002). These restoration HSIs also do not consider the expected increases to large and small instream woody debris (see **Table 4.4**). Although the total year 5 fish biomasses predicted for Bell Run and Flat Creek after riparian restoration are essentially unchanged, the total year 5 fish biomass for Tuscarora Creek increases by 31% to 3.77 kg[FW]/ha. Similar trends are also predicted for the total year 5 fish densities of these streams. These results are consistent with the fact that the HSIs for the community dominants of Bell Run and Flat Creek (i.e., white suckers and bluehead chubs) are independent of riparian cover metrics while the HSI for the community dominant of Tuscarora Creek (i.e., blacknose dace) responds positively to increasing riparian ground cover (see **Table 4.3**).

The preceding analysis should only be considered only as the immediate benefits of riparian restoration. Evaluation of the longer term benefits requires good empirical or process-based models for stream temperature dynamics, fine sediment transport, and allochthonous inputs of woody debris and terrestrial invertebrates. These models are planned for development during the next phase of the CVI-WHAT IF software program.

5.4.2. Responses of Non-game Streams to Trout Stocking

Table 5.4 also summarizes the predicted year 5 mean annual biomasses, community trophic flows, and average interspecies HSIs for Bell Run, Flat Creek, and Tuscarora Creek with and without trout stocking as outlined in Section **5.3**.

The mean interspecies HSIs for Bell Run, Flat Creek, and Tuscarora Creek with trout stocking are 0.652, 0.508, and 0.340, respectively. The decrease in mean interspecies HSIs with respect to these streams' unstocked condition simply reflects low HSI scores for brook, brown, and rainbow trout in these streams.

The total year 5 fish biomasses predicted for Bell Run, Flat Creek, and Tuscarora Creek with trout stocking are 37.3, 37.9, and 8.88 kg[FW]/ha, respectively. These values correspond to 22 and 56 percent reductions for Bell Run and Flat Creek, respectively, and a 308 percent increase for Tuscarora Creek. The total year 5 fish densities predicted for Bell Run, Flat Creek, and Tuscarora Creek with trout stocking are 1403, 3301, and 330 fish/ha, respectively. The total year 5 non-game fish biomasses of Bell Run, Flat Creek, and Tuscarora Creek are predicted to be 22.3, 31.3, and 0.004 kg[FW]/ha, respectively. These values represent 53.1, 63.9, and 99.9 percent reductions in the native or resident fishes of these streams. These reductions are the direct consequence of trophic competition with trout for drifting and benthic macroinvertebrates and of predation by trout and are consistent with field studies that have evaluated the impacts of game fish stocking to native/resident fish populations (see for example Garman and Nielsen 1982, Fisher Huckins et al. 2000, Vander Zanden et al. 2004, Weidel et al. in review). Negus (1995) predicted similar results and trends using the Wisconsin Bioenergetics Model (Hewett and Johnson 1992, Hanson et al. 1997) for salmonid stocking programs in Minnesota waters of Lake Superior. In a related application, Irwin et al. (2003) used the Wisconsin Bioenergetics Model to evaluate how largemouth bass might to used to control gizzard shad introductions to small impoundments.

In Bell Run the mean annual biomass of benthic macroinvertebrates for both the stocked and unstocked trout scenarios is 9.52 kg[DW]/ha since this resource is modeled as a system forcing function. The total annual consumption of benthic macroinvertebrates by all fish species for the stocked and unstocked scenarios is 35.1 and 15.1 kg[DW]/ha/yr, respectively. The increased consumption of benthic macroinvertebrates by stocked trout has the greatest impact on resident non-ominivorous species such as northern hogsucker, rock bass, and common shiner. Ominivorous species (i.e., white suckers, stonerollers, river chubs, creek chubs, bluntnose minnows, and blacknose dace) are less impacted since these fish can augment the lost of benthic macroinvertebrate prey with periphyton. For example, the per capita total annual consumption of periphyton by non-game fish species for stocked and unstocked scenarios is 0.0216 and 0.0485 kg[DW]/fish/yr, respectively.

Piscivory in Bell Run significantly increases with trout stocking. Total annual piscivory for the unstocked

Bell Run scenario is predicted to be only 0.0713 kg[DW]/ha/yr. However, trout stocking increases Bell Run's total annual piscivory by an order of magnitude to 0.977 kg[DW]/ha/yr. Although this increased piscivory is still small with respect to the total food consumption of Bell Run fish species (i.e., approximately 1%), it has significant impacts on the ultimate population numbers of non-game species since most of the predicted piscivory occurs on small and young-of-year fish. For example, total annual predatory mortality in Bell Run increases from 301 to 5037 fish/ha/yr with trout stocking. The mean annual biomass and population density of white sucker, which is the community dominant with and without stocking, decreases from 31.6 kg[FW]/ha and 726 fish/ha to 17.7 kg[FW]/ha and 436 fish/ha.

The trends predicted for Bell Run are repeated for Flat Creek in which bluehead chub is the community dominant. In this case, the mean annual biomass and population density of bluehead chub decreases from 76.7 kg[FW]/ha and 10340 fish/ha to 23.4 kg[FW]/ha and 2839 fish/ha. The per capita annual consumption of periphyton by non-game species increases from 0.00263 kg[DW]/fish/yr for the status quo scenario to 0.0032 kg[DW]/fish/yr for the trout stocking scenario. The order of magnitude difference in the per capita periphyton consumption rates between Bell Run and Flat Creek is directly related their estimated benthic macroinvertebrate to periphyton biomass ratios that equal 0.133 and 4.0, respectively. See **Table 5.4** for further details.

Unlike Bell Run and Flat Creek trout stocking is predicted to completely displace the resident fishes in Tuscarora Creek. The mean annual biomasses of resident fish and benthic macroinvertebrates in this stream without trout stocking are only 0.663 and 10.0 kg[DW]/ha, respectively. On the other hand, the total predicted annual consumption of fish and marcroinvertebrates by brook, brown, and rainbow trout under the assumed stocking schedule is 19.3 kg[DW]/ha/yr. Thus, while Tuscarora Creek could maintain a mixed trout fishery, it would do so at the expense of virtually all of its native fish fauna. If a trout fishery was still desired, it would be advisable to the limit stockings to brook trout, which are less piscivorous than brown or rainbow trout, and consider stocking rates even lower than those assumed in this analysis.

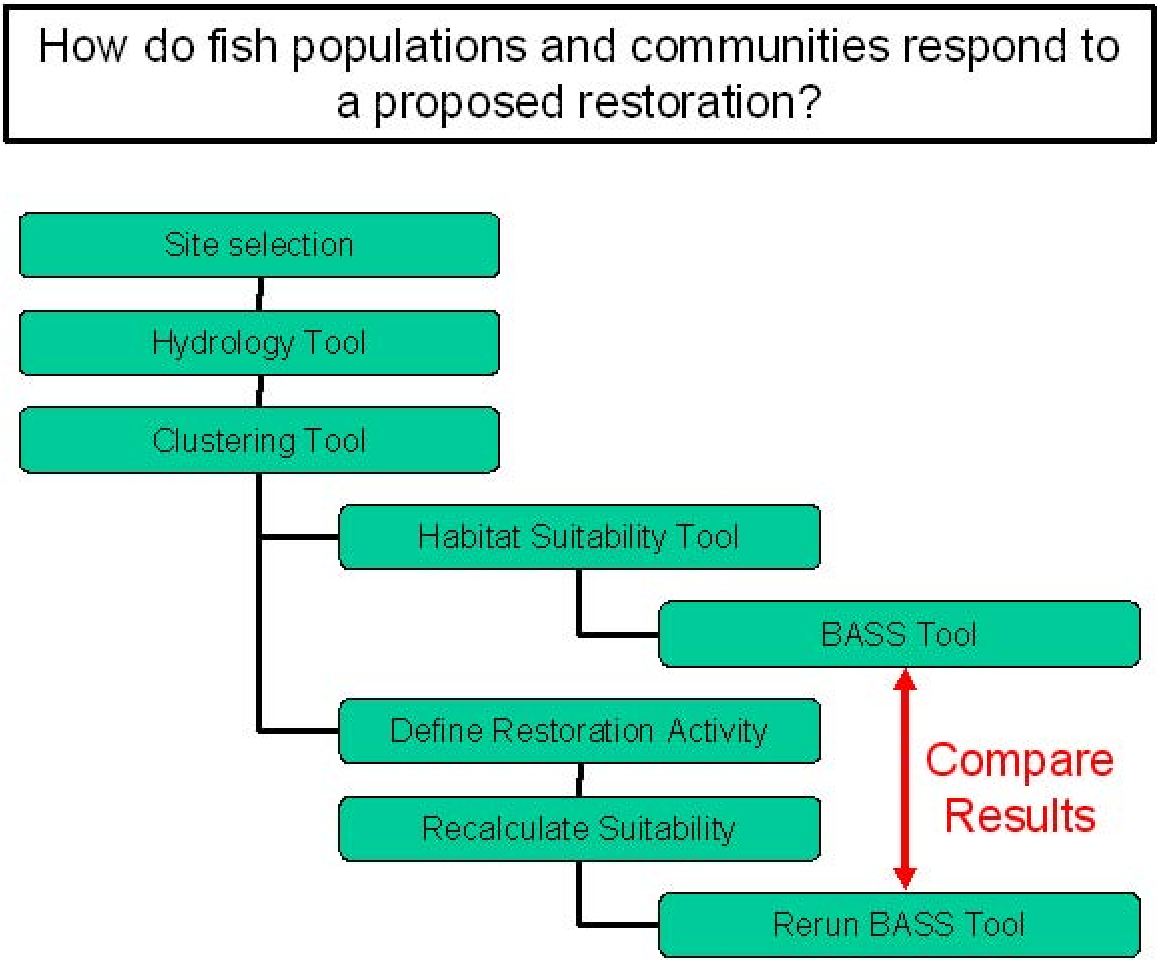
Table 5.4 Summary of annual mean biomasses and fluxes predicted by BASS for Bell Run PA, Flat Creek VA, and Tuscarora Creek WV for status quo conditions, with a 25% restoration of riparian canopy and ground cover, and with trout stocking.

Community Variable : Condition	Bell Run	Flat Creek	Tuscarora Creek
average HSI : status quo	0.7568	0.6049	0.4675
average HSI : restoration	0.7913	0.6344	0.5428
average HSI : stocking	0.6524	0.5075	0.3400
total fish biomass kg(FW)/ha : status quo	47.54	86.68	2.884
total fish biomass kg(FW)/ha : restoration	47.82	86.50	3.767
total fish biomass kg(FW)/ha : stocking	37.31	37.92	8.881
total non-game fish biomass kg(FW)/ha : stocking	22.25	31.30	0.004
total fish density fish/ha : status quo	3130	10900	2002
total fish density fish/ha : restoration	3331	10960	2896
total fish density fish/ha : stocking	1403	3301	330
total non-game fish density fish/ha : stocking	626	3048	2.82
consumption of macroinvertebrates kg(DW)/ha/yr : status quo	15.14	118.8	0.440
consumption of macroinvertebrates kg(DW)/ha/yr : restoration	15.27	118.4	0.655
consumption of macroinvertebrates kg(DW)/ha/yr : stocking	35.09	54.49	18.62
consumption of periphyton kg(DW)/ha/yr : status quo	67.68	28.72	5.589
consumption of periphyton kg(DW)/ha/yr : restoration	67.92	28.57	6.579
consumption of periphyton kg(DW)/ha/yr : stocking	30.38	9.814	0.00792
predatory mortality kg(DW)/ha/yr : status quo	0.0713	0.286	<0.001
predatory mortality kg(DW)/ha/yr : restoration	0.0784	0.338	<0.001
predatory mortality kg(DW)/ha/yr : stocking	0.977	1.416	0.076
predatory mortality fish/ha/yr : status quo	301	1081	<1
predatory mortality fish/ha/yr : restoration	332	1311	<1
predatory mortality fish/ha/yr : stocking	5037	5405	1066

6. Example Application of the CVI Watershed Toolkit

The tools within the CVI Watershed Toolkit can be used either independently or together to analyze expected responses of fish populations and communities to proposed stream restoration and/or fisheries management. **Figure 6.1** illustrates how CVI-WHAT IF tools can work together to evaluate a proposed BMP for riparian stream restoration.

Figure 6.1 The use of the WHAT-IF tool to address a more complex management question for a particular stream site.



To illustrate this process, we will now show how a riparian restoration analysis could be conducted for Hogue Creek, Frederick County, VA which is an impacted smallmouth bass stream. For this example, we assume that Hogue Creek's riparian ground cover and canopy cover are increased by 25% of their current values. We also assume that this riparian restoration results in a 25% decrease of the creek's current percent bottom coverage by fine sediments. The creek's restored stream bottom is then assumed to be replaced with 50% sands (0.06-2 mm), 25% fine gravel (2-16 mm), 12.5% coarse gravel (16-64 mm), and 12.5% cobble (64-250 mm).

The first step in an integrated analysis of Hogue Creek riparian restoration is the estimation of the creek's expected mean annual streamflow, depth, and water temperatures. Using the Hydro Tool, these parameters are estimated to be 44.10 cfs, 0.59 ft, and 14.29 Celsius, respectively. See **Figure 2.1**.

Hogue Creek's mean annual streamflow, depth, and width can now be ported to the Clustering Tool where these parameters are augmented with user-specified or CVI-WHAT IF database landscape variables (i.e., site longitude and latitude, percent agriculture, percent stream slope, etc.) to predict the stream's expected fish assemblage. See **Figure 3.2**. If the stream of interest is actually contained in the CVI-WHAT IF database, as is Hogue Creek, the stream's predicted fish assemblages can be considered as other fish communities that might exist at stream reaches other than the one contained in the CVI database. Users can now port the stream's actual or predicted/alterative fish assemblage to either the Habitat Suitability Tool or the BASS-Clustering Interface Tool.

When the user's ultimate goal is to run a BASS simulation analysis for a predicted/alternative fish assemblage, the BASS-Clustering Interface Tool is used to translate knowledge of the stream's cluster membership into a realized stream community and to assign initial conditions to that community. Two methods are available to accomplish this task. The first of these is the *nearest-neighbor* option. This option presents the user a list of all database streams that are members of the stream's predicted cluster. This list is arranged in ascending order of the Euclidean distance from the stream of concern. The user then selects any member of this list as a surrogate for the stream of interest. BASS data files for the selected stream are then loaded into the user's active project. The second method is the *ranked relative biomass* option. When choosing this option, the user constructs a fish community for the stream of interest by selecting fish species from a series of lists. The i-th list in this series identifies those species that are the i-th most abundant species (based on relative biomass) in one or more streams of the predicted cluster. Generally the number of species lists presented to the user will vary from cluster to cluster, dependent on the number species needed to account for 95% of the biomass of streams within the cluster. The BASS-Clustering Interface Tool then constructs initial conditions for the stream of interest assuming that the stream's total fish biomass equals the mean total fish biomass of the predicted cluster' streams. Additionally, the rank ordered relative biomasses of the stream of interest are assigned as the means of the ranked ordered relative biomasses of streams within the predicted cluster. These rank ordered relative biomasses generally will not be identical to the relative biomasses displayed by the Clustering Tool itself. See Section 3.2.1 and the discussion concerning **Table 3.1** and **Figure 3.1**. for details.

The Habitat Suitability Tool is now used to calculate habitat suitability scores for each species within the selected fish assemblage. Although the resulting habitat suitability scores can be ported directly to the user's BASS project as habitat multipliers on species non-predatory mortality and dispersal, they can also be used to corroborate or to redefine the stream's species composition predicted by the Clustering Tool. Whereas the Clustering Tool essentially predicts a collection of species that is likely to occur in streams possessing similar landscape features, scores predicted by the Habitat Suitability Tool are actually probabilities of species occurrences at a stream based instream habitat features. Consequently, although the Clustering Tool may predict that species A is a resident of the stream of interest (based on landscape features), the Habitat Suitability Tool could predict (based on instream features) such a low probability of occurrence for species A that a user might want to exclude species A from any further consideration. Habitat suitability scores predicted for Hogue Creek before and after the riparian restoration scenario outlined above are presented in **Table 6.1**. According to **Table 6.1**, HSI scores for all of the species under the status quo scenario are >0.5, which is the generally-accepted criterion for occurrence, so the results of the HSI are consistent with the observed community at the site. Under the restoration scenario, the interspecies mean increased from 0.7689 to 0.8240. This analysis demonstrates how a restoration can be expected to improve overall species habitat and fish community condition.

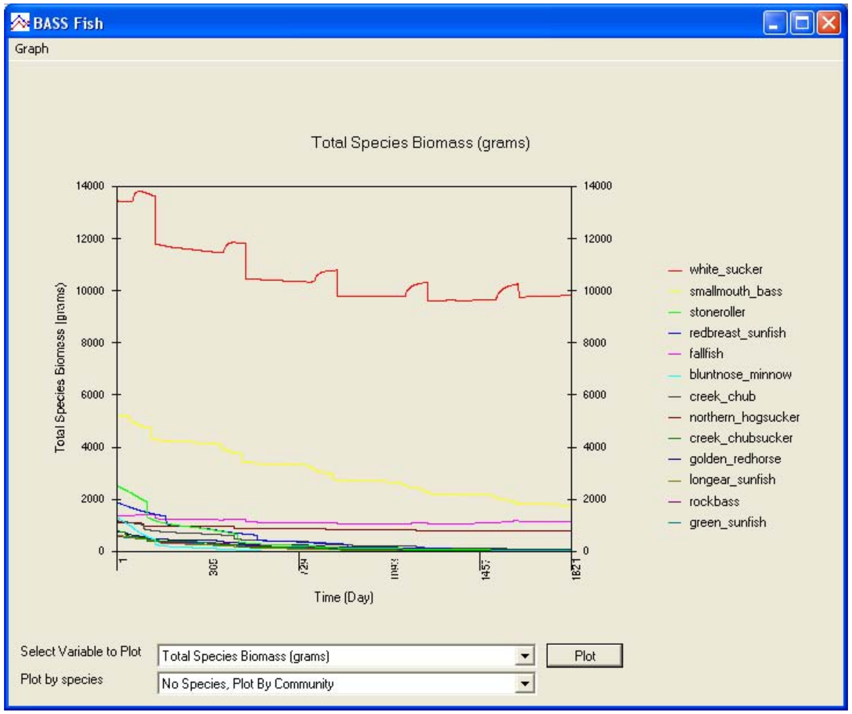
Having estimated the stream's hydrological features, community structure, and habitat relationships, the BASS fish community model can now be run to simulate Hogue Creek's responses to the proposed riparian restoration scenario. **Figure 6.2** and **Figure 6.3** display the predicted 5 year biomass dynamics of Hogue Creek fishes with and without riparian restoration. The total year 5 fish biomasses predicted for Hogue Creek with and without riparian restoration are 14.1 and 17.1 kg[FW]/ha, respectively. Thus, for

Hogue Creek a 25% increase of riparian covers is expected to increase total fish biomass by 21.2%. The stream's average annual fish density, however, is predicted to remain essentially unchanged. In particular, the total year 5 fish densities predicted for Hogue Creek before and after riparian restoration are 422 and 437 fish/ha, respectively.

Table 6.1 Status quo and restoration HSI for Hogue Creek, VA

Species	status quo HSI	restoration HSI
white sucker	0.8800	0.9022
smallmouth bass	0.7110	0.7906
stoneroller	0.8342	0.8363
redbreast sunfish	0.8766	0.9232
fallfish	0.9869	0.9903
bluntnose minnow	0.5150	0.6827
creek chub	0.8739	0.8739
northern hogsucker	0.8241	0.8883
creek chubsucker	0.5406	0.6589
golden redhorse	0.5406	0.6589
longear sunfish	0.8766	0.9232
rockbass	0.6597	0.6597
green sunfish	0.8766	0.9232
interspecies mean	0.7689	0.8240

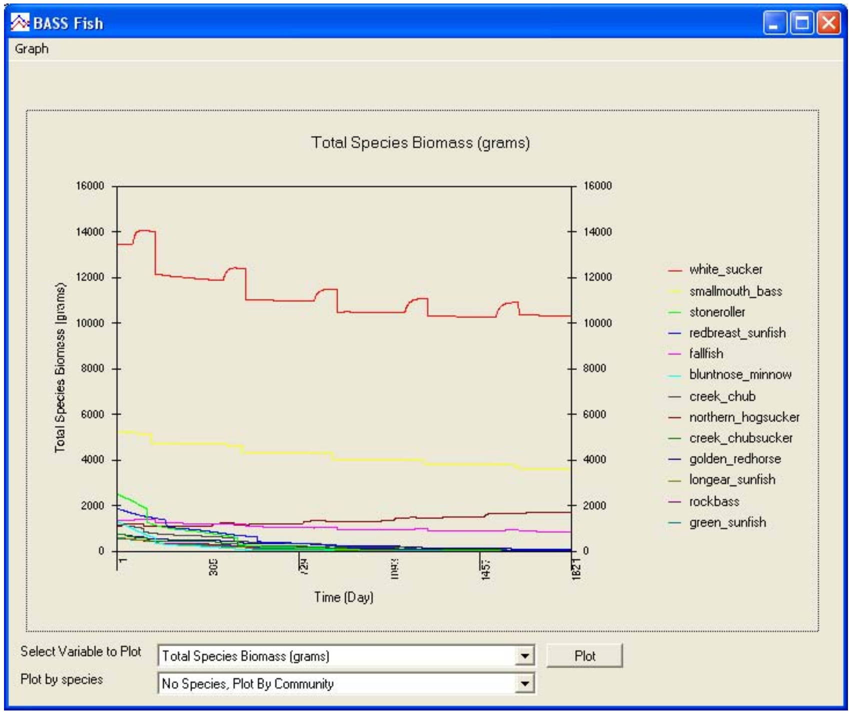
Figure 6.2 Predicted biomass dynamics of Hogue Creek, VA before riparian restoration



Select Variable to Plot: Total Species Biomass (grams)

Plot by species: No Species, Plot By Community

Figure 6.3 Predicted biomass dynamics for Hogue Creek, VA after riparian restoration



Select Variable to Plot: Total Species Biomass (grams)

Plot by species: No Species, Plot By Community

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Appendix A. Clustering Methods and Algorithms

A.1. Density-to-Biomass Conversion Algorithm

Although EMAP, like most fish surveys or monitoring programs, reported only species counts from which fish densities (fish/ha) can be straightforwardly estimated, fish standing stocks (kg/ha) are also important indicators of the condition of fish assemblages as a whole. Fortunately, fish biomasses can be estimated from observed densities if one makes certain simplifying assumptions concerning the recruitment, mortality, and average body growth dynamics of the species of interest. These assumptions include:

> 1) a species' observed density is functionally dependent on its mean body weight, and similarly the density of each cohort is dependent on its mean body weight;
>
> 2) the mean body weights of a species and of its cohorts is determined primarily by the species physiological growth rather than by size specific predation, environmentally induced mortality, or dispersal; and
>
> 3) the recruitment strength for each cohort or year class within the observed population density has been relatively constant or has been fluctuating around the long term average for the species.

Using these assumptions, a density-to-biomass conversion algorithm can be developed using the general empirical observation that population densities of most vertebrates can be adequately characterized by the self-thinning power function relationship

$$N = a W^{-b} \qquad \textbf{(A-1)}$$

where N and W denote the density (inds/area) and the mean body weight, respectively, of a population of interest. Importantly, the population of interst can be either a collection of species (e.g., a guild or higher taxonomic grouping), a single species, or the individual cohorts of a species. For fish populations, the self-thinning exponent b generally varies from 0.75 to 1.5 (Boudreau and Dickie 1989, Grant and Kramer 1990, Gordoa and Duarte 1992, Elliott 1993, Bohlin et al. 1994, Randall et al. 1995, Dunham and

Vinyard 1997, Grant et al. 1998, Dunham et al. 2000, Keeley 2003). Larger exponents ranging from 1.5 to 3.0, however, have also been reported (Steingrímsson and Grant 1999).

If Equation **(A-1)** is differentiated with respect to time, it immediately follows that

$$\frac{dN}{dt} = -\frac{baW^{-b}}{W}\frac{dW}{dt} = -b\gamma N = -\mu N \qquad \textbf{(A-2)}$$

where $\gamma = W^{-1}\,dW/dt$ is the specific growth rate for individuals within the population; and $\mu = b\gamma$ is the population's lumped rate of mortality and dispersal. Readers should consult Peterson and Wroblewski (1984), McGurk (1993, 1999), and Lorenzen (1996) for detailed discussions of the theoretical foundations and implications of Equation **(A-2)**. Also see Section **D.4** herein. Equation **(A-2)**, however, is also equivalent to

$$\frac{dN}{N} = -b\,\frac{dW}{W} \qquad \textbf{(A-3)}$$

which can be reintegrated to obtain the following reformulation of Equation **(A-1)**

$$\begin{aligned} \ln\frac{N(t)}{N(t_0)} &= -b\,\ln\left(\frac{W(t)}{W(t_0)}\right) \\ N(t) &= N(t_0)\,\exp\left[-b\,\ln\left(\frac{W(t)}{W(t_0)}\right)\right] \end{aligned} \qquad \textbf{(A-4)}$$

A species total population density can now be formulated by applying Equation **(A-4)** to each of its cohorts, i.e.,

$$\begin{aligned} N(t) &= \sum N_i(t) \\ N(t) &= \sum N_i(t-a_i)\,\exp\left\{-b\,\ln\left[\frac{W_i(t)}{W_i(t-a_i)}\right]\right\} \end{aligned} \qquad \textbf{(A-5)}$$

where N_i, W_i, and a_i denote the density, average body weight, and age, respectively, of the i-th cohort. If each cohort is assumed to be recruited into the population with the same initial body weight (W_0) and population density (N_0), the preceding equation can be simplified to

$$N(t) = N_0 \sum \exp\left\{ - b \ln \left[\frac{W_i(t)}{W_0} \right] \right\} \tag{A-6}$$

If the growth rate trajectories of each cohort have also remained relatively constant, it also follows that

$$N(t) = N_0 \sum \exp\left\{ - b \ln \left[\frac{W_i(a_i)}{W_0} \right] \right\} \tag{A-7}$$

From this equation it should be reasonably clear that given the species current population density (N) and a reasonable model for the species body growth, one can straightforwardly calculate the species' apparent long term year-class strength N_0. Having done so, the species' total biomass can then be estimated by

$$B = \sum W_i(a_i)\, N_i(t) = N_0 \sum W_i(a_i) \exp\left\{ - b \ln \left[\frac{W_i(a_i)}{W_0} \right] \right\} \tag{A-8}$$

Selecting an appropriate growth model to parameterize Equation **(A-8)**, like most model selections, is not a trivial concern since over the past 50 years at least four different models (i.e., von Bertalanffy, Richards, Gompertz, and Parker-Larkin models) have become standard tools for characterizing the growth of fishes. See Ricker (1979) for a detailed discussion of these models and other less commonly used models.

According to the von Bertalanffy model, a fish's growth rate is the simple mass balance of anabolic processes that are directly proportional to the fish's surface area and of catabolic processes that are directly proportional to the fish's body weight. Assuming isometric growth (i.e., $W = \lambda L^3$), the fish's growth dynamics is therefore governed by the following differential equation

$$\frac{dW}{dt} = \phi \, W^{2/3} - \rho \, W \qquad \textbf{(A-9)}$$

where ϕ is the fish's rate of feeding and assimilation; and ρ is the fish's total metabolic rate. In terms of body length, this model is also equivalent to

$$\frac{dL}{dt} = \frac{\rho}{3} \, (L_{\max} - L) \qquad \textbf{(A-10)}$$

where L is the fish's body length; and $L_{max} = \phi \, / \, (\rho \, \lambda^{1/3})$ is the fish's "maximum" body length that is obtained by setting Equation **(A-9)** to zero. For further discussion, see Parker and Larkin (1959) and Paloheimo and Dickie (1965).

The Richard's model (Richards 1959) is a generalization of the von Bertalanffy model that relaxes the assumption of isometric growth and strict proportionality between a fish's feeding/assimilatory processes and its absorptive surface areas. In this model, the fish's feeding is simply assumed to be a power functions of its body weight. The fish's growth is then described by the differential equation

$$\frac{dW}{dt} = \phi_1 \, W^{\phi_2} - \rho \, W \qquad \textbf{(A-11)}$$

Although both the von Bertalanffy and the Richards models appear to have a strong physiological foundation, a more critical inspection of the parameters of these models cast doubts on such assertions. One particular point of contention is the assumption that a fish's metabolism (i.e., respiration and excretion) is directly proportional to its body weight. Although this assumption is certainly satisfied or closely approximated for some fish species, most fish species have metabolic demands that are best described as power functions of their body weights. Consequently, from a purely physiologically-based perspective a much better anabolic-catabolic process model for fish growth would be

$$\frac{dW}{dt} = \phi_1 \, W^{\phi_2} - \rho_1 \, W^{\rho_2} \qquad \textbf{(A-12)}$$

See Paloheimo and Dickie (1965). Unlike the von Bertalanffy and Richards models, however, this model generally does not have a closed analytical solution. Furthermore, when this model is fit to observed data, there is no a priori guarantee that the fitted exponents will actually match expected physiological exponents unless the analysis is suitably constrained.

In light of these criticisms, simpler empirical growth models may be more than adequate for most applications. Two such models that have proved useful in this regard are the Gompertz and Parker-Larkin models. Both of these models are intended to describe the growth of fishes that decreases with the age or size of the individual. Whereas the Gompertz model describes fish growth by

$$\frac{dW}{dt} = \epsilon_1 \exp(-\epsilon_2 t)\ W \qquad \textbf{(A-13)}$$

the Parker-Larkin model (1959) assumes that

$$\frac{dW}{dt} = \alpha\ W^{\beta} \qquad \textbf{(A-14)}$$

where the exponent β is generally less than 1.

Although each of the aforementioned models can describe very different growth trajectories, much of the discussion surrounding their use has focused on whether the models predict asymptotically zero or indeterminate growth (Parker and Larkin 1959, Paloheimo and Dickie 1965, Knight 1968, Schnute 1981). Although growth rates of individual fish almost always decrease with increasing age or body size, Knight (1968) argued that the traditional notion of asymptotically zero growth is seldom, if ever, supported by studies that have focused on actual growth increments rather than on size at age. Because the Parker-Larkin model is the only model outlined above that assumes that the growth of fish is fundamentally indeterminate, this model has conceptual advantages over the von Bertalanffy, Richards, and Gompertz models. The Parker-Larkin model also does not rely on the a priori assumption that the respiration of fishes is generally a linear function of their body weight as does the von Bertalanffy and Richards models.

Estimation of Fish Growth Rates

Wherever possible expected growth rates for MAH fish species were estimated using data summarized by Carlander(1969, 1977, 1997). The Carlander data summaries, however, were also supplemented with the data sources summarized in **Table A.1**. Reported body lengths at age were converted to live body weights using applicable weight-length regressions. Estimated live body weights were then fit to the analytical solution Parker-Larkin growth model, i.e.,

$$W(t) = \left[W(t_0)^{1-\beta} + \alpha\,(1-\beta)\,(t - t_0) \right]^{1/(1-\beta)} \qquad \textbf{(A-15)}$$

using the NL2SOLV non-linear regression and optimization software. However, because Equation **(A-15)** is discontinuous at β=1, the growth parameters α and β for each species were actually obtained by fitting calculated body weights to the equivalent expression

$$W(t) = \left[W(t_0)^{\exp(-b)} + \alpha\,\exp(-b)\,(t - t_0) \right]^{\exp(b)} \qquad \textbf{(A-16)}$$

where exp (-*b*) = (1 - β). Results of these regressions are summarized in **Table A.2**.

Table A.1 Data sources for supplementing Carlander (1969, 1977, 1997)

Species	Data source
Aphredoderus sayanus	Shepherd and Huish (1978)
Aplodinotus_grunniens	Dreves et al. (1996), Nelson (1974), Priegel (1969), Purkett (1957), Swedberg (1968), Wrenn (1968)
Carpiodes carpio	Morris (1965), Nelson (1974), Purkett (1957)
Carpiodes cyprinus	Woodward and Wissing (1976)
Etheostoma blennioides	Wolfe et al. (1978)
Moxostoma anisurum	Hackney et al. (1970)
Moxostoma duquesnei	Bowman (1970)
Notropis hudsonius	McCann (1959), Smith and Kraemer (1964)
Noturus spp	Burr and Mayden (1982), Mayden and Walsh (1984)
Percopsis omiscomaycus	House and Wells (1973), Pereira and LaBar (1983)
Percopsis transmontana	Gray and Dauble (1979)
Rhinichthys atratulus	Reed and Moulton (1973)
Rhinichthys cataractae	Reed and Moulton (1973), Reed (1959), Kuehn (1949)
Semotilus corporalis	Reed (1971)

Table A.2 Summary of growth data used for biomass estimation of MAH fish species

Species	max cohorts	g(fw) range	daily growth rate	g(fw) - length regression
Alosa pseudoharengus	5	10<W[g]<131	0.0165*W[g]$^{-0.618}$	0.514E-05*TL[mm]$^{3.064}$
Alosa sapidissima	8	73<W[g]<2132	0.3516*W[g]$^{-0.907}$	0.279E-04*TL[mm]$^{2.801}$
Ambloplites rupestris	12	3<W[g]<355	0.0259*W[g]$^{-0.687}$	0.149E-04*TL[mm]$^{3.074}$
Ameiurus catus	14	12<W[g]<2283	0.0025*W[g]$^{-0.160}$	0.141E-05*TL[mm]$^{3.395}$
Ameiurus melas	6	35<W[g]<750	0.0314*W[g]$^{-0.495}$	0.106E-04*TL[mm]$^{3.085}$
Ameiurus natalis	5	18<W[g]<986	0.0506*W[g]$^{-0.567}$	0.423E-05*TL[mm]$^{3.232}$
Ameiurus nebulosus	5	17<W[g]<519	0.0126*W[g]$^{-0.359}$	0.839E-05*TL[mm]$^{3.105}$
Aphredoderus sayanus	3	3<W[g]<7	0.0049*W[g]$^{-0.989}$	0.376E-04*TL[mm]$^{2.768}$
Aplodinotus_grunniens	16	14<W[g]<6174	0.0166*W[g]$^{-0.423}$	0.693E-05*TL[mm]$^{3.090}$
Campostoma anomalum	4	8<W[g]<62	0.0061*W[g]$^{-0.456}$	0.191E-03*TL[mm]$^{2.390}$
Carpiodes carpio	14	3<W[g]<2587	0.0606*W[g]$^{-0.647}$	0.330E-05*TL[mm]$^{3.248}$
Carpiodes velifer	8	10<W[g]<921	0.3676*W[g]$^{-1.002}$	0.887E-04*TL[mm]$^{2.808}$
Catostomus commersoni	7	17<W[g]<960	0.0734*W[g]$^{-0.686}$	0.176E-04*TL[mm]$^{2.940}$
Centrarchus macropterus	7	4<W[g]<95	0.0214*W[g]$^{-0.803}$	0.550E-03*TL[mm]$^{2.325}$
Coregonus alpenae	9	21<W[g]<642	0.0257*W[g]$^{-0.627}$	0.568E-05*TL[mm]$^{3.061}$
Coregonus artedii	10	13<W[g]<466	0.0171*W[g]$^{-0.593}$	0.497E-05*TL[mm]$^{3.073}$
Coregonus clupeaformis	17	17<W[g]<2760	0.1185*W[g]$^{-0.782}$	0.154E-05*TL[mm]$^{3.289}$
Coregonus hoyi	9	5<W[g]<165	0.0203*W[g]$^{-0.760}$	0.127E-04*SL[mm]$^{3.010}$
Coregonus kiyi	8	13<W[g]<157	0.3299*W[g]$^{-1.398}$	0.384E-05*TL[mm]$^{3.122}$
Coregonus sardinella	10	8<W[g]<383	0.0032*W[g]$^{-0.282}$	0.515E-05*FL[mm]$^{3.129}$
Cycleptus elongatus	6	18<W[g]<1645	0.0806*W[g]$^{-0.615}$	0.269E-05*TL[mm]$^{3.170}$
Cyprinus carpio	10	539<W[g]<29040	0.0210*W[g]$^{-0.326}$	0.230E-04*TL[mm]$^{3.194}$
Dorosoma cepedianum	9	17<W[g]<201	0.3686*W[g]$^{-1.307}$	0.423E-05*TL[mm]$^{2.941}$
Erimyzon oblongus	6	25<W[g]<1133	0.2569*W[g]$^{-0.878}$	0.574E-05*TL[mm]$^{3.189}$
Erimyzon spp	6	13<W[g]<633	0.0669*W[g]$^{-0.702}$	0.574E-05*TL[mm]$^{3.189}$
Erimyzon sucetta	6	5<W[g]<383	0.1069*W[g]$^{-0.863}$	0.574E-05*TL[mm]$^{3.189}$
Esox americanus	4	19<W[g]<112	0.0017*W[g]$^{-0.042}$	0.588E-05*TL[mm]$^{2.979}$
Esox lucius	24	81<W[g]<12335	0.0988*W[g]$^{-0.638}$	0.428E-05*TL[mm]$^{3.059}$
Esox masquinongy	19	63<W[g]<22537	0.7863*W[g]$^{-0.823}$	0.774E-06*TL[mm]$^{3.317}$
Esox niger	8	51<W[g]<1543	0.0567*W[g]$^{-0.630}$	0.323E-05*TL[mm]$^{3.098}$
Etheostoma blennioides	5	2<W[g]<6	0.0030*W[g]$^{-0.801}$	0.647E-05*TL[mm]$^{3.120}$
Etheostoma spp	4	1<W[g]<4	0.0016*W[g]$^{-0.421}$	0.281E-04*TL[mm]$^{3.120}$
Etheostoma zonale	4	1<W[g]<2	0.0012*W[g]$^{-0.794}$	0.458E-05*TL[mm]$^{3.193}$
Gila atraria	10	3<W[g]<275	0.0385*W[g]$^{-0.783}$	0.933E-04*SL[mm]$^{2.738}$
Hiodon alosoides	9	20<W[g]<942	0.1824*W[g]$^{-0.920}$	0.135E-04*TL[mm]$^{2.971}$
Hiodon tergisus	7	14<W[g]<384	0.7033*W[g]$^{-1.277}$	0.234E-05*TL[mm]$^{3.270}$
Hypentelium nigricans	9	9<W[g]<743	0.3453*W[g]$^{-0.979}$	0.437E-05*TL[mm]$^{3.164}$
Ictalurus furcatus	11	32<W[g]<24023	0.0508*W[g]$^{-0.440}$	0.128E-05*TL[mm]$^{3.370}$
Ictalurus punctatus	14	11<W[g]<9249	0.0146*W[g]$^{-0.346}$	0.187E-05*TL[mm]$^{3.348}$
Ictiobus bubalus	14	32<W[g]<6497	0.0023*W[g]$^{-0.132}$	0.504E-05*TL[mm]$^{3.208}$
Ictiobus cyprinellus	12	77<W[g]<13878	0.0420*W[g]$^{-0.491}$	0.853E-05*TL[mm]$^{3.118}$
Ictiobus niger	8	63<W[g]<3293	0.0523*W[g]$^{-0.522}$	0.891E-05*TL[mm]$^{3.093}$
Lampetra spp	6	0<W[g]<2	0.0016*W[g]$^{-0.347}$	0.154E-05*TL[mm]$^{3.025}$
Lepisosteus osseus	22	383<W[g]<7561	0.3423*W[g]$^{-0.890}$	0.155E-06*TL[mm]$^{3.449}$
Lepomis auritus	6	6<W[g]<132	0.0137*W[g]$^{-0.579}$	0.176E-04*TL[mm]$^{2.997}$
Lepomis cyanellus	6	6<W[g]<158	0.0184*W[g]$^{-0.575}$	0.122E-04*TL[mm]$^{3.101}$
Lepomis gibbosus	9	3<W[g]<204	0.0149*W[g]$^{-0.573}$	0.774E-05*TL[mm]$^{3.211}$
Lepomis gulosus	7	7<W[g]<444	0.0174*W[g]$^{-0.527}$	0.661E-05*TL[mm]$^{3.241}$
Lepomis humilis	3	1<W[g]<10	0.0091*W[g]$^{-0.800}$	0.284E-05*TL[mm]$^{3.271}$
Lepomis macrochirus	8	5<W[g]<195	0.0171*W[g]$^{-0.590}$	0.787E-05*TL[mm]$^{3.173}$

Table A.1 Continued

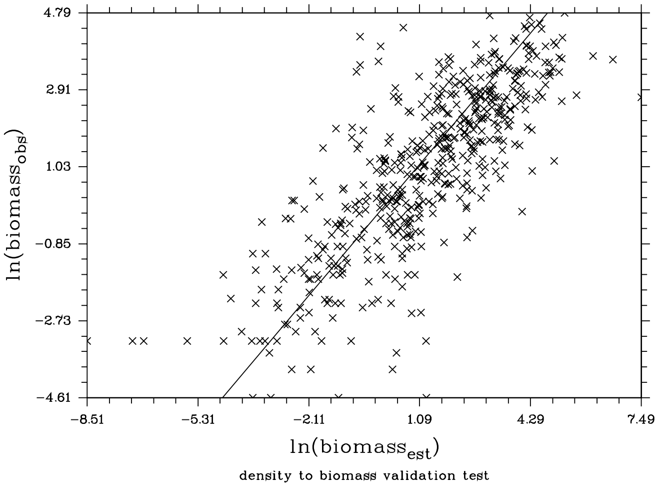
Species	max cohorts	g(fw) range	daily growth rate	g(fw) - length regression
Lepomis megalotis	7	3<W[g]<63	0.0141*W[g]$^{-0.719}$	0.912E-05*TL[mm]$^{3.160}$
Lepomis microlophus	7	15<W[g]<375	0.0424*W[g]$^{-0.708}$	0.344E-05*TL[mm]$^{3.333}$
Micropterus coosae	10	2<W[g]<213	0.0167*W[g]$^{-0.654}$	0.661E-05*TL[mm]$^{3.120}$
Micropterus dolomieu	12	13<W[g]<1361	0.0888*W[g]$^{-0.701}$	0.469E-05*TL[mm]$^{3.200}$
Micropterus punctulatus	7	20<W[g]<1352	0.0537*W[g]$^{-0.598}$	0.406E-05*TL[mm]$^{3.215}$
Micropterus salmoides	11	33<W[g]<2537	0.1088*W[g]$^{-0.698}$	0.678E-05*TL[mm]$^{3.127}$
Minytrema melanops	6	23<W[g]<1045	0.2076*W[g]$^{-0.827}$	0.537E-05*TL[mm]$^{3.168}$
Morone americana	10	26<W[g]<509	0.0200*W[g]$^{-0.587}$	0.755E-05*TL[mm]$^{3.136}$
Morone chrysops	9	64<W[g]<1089	0.6429*W[g]$^{-1.032}$	0.859E-05*TL[mm]$^{3.081}$
Morone mississippiensis	7	8<W[g]<180	0.0784*W[g]$^{-0.915}$	0.721E-05*TL[mm]$^{3.133}$
Morone saxatilis	14	110<W[g]<14645	0.1581*W[g]$^{-0.623}$	0.119E-04*TL[mm]$^{3.007}$
Moxostoma anisurum	9	55<W[g]<1874	0.6701*W[g]$^{-0.987}$	0.356E-04*TL[mm]$^{2.778}$
Moxostoma carinatum	12	7<W[g]<2070	0.0755*W[g]$^{-0.668}$	0.168E-04*TL[mm]$^{2.914}$
Moxostoma duquesnei	10	8<W[g]<339	0.0648*W[g]$^{-0.859}$	0.257E-04*SL[mm]$^{2.950}$
Moxostoma erthrurum	8	18<W[g]<2298	0.0297*W[g]$^{-0.494}$	0.170E-04*TL[mm]$^{2.908}$
Moxostoma macrolepidotum	9	10<W[g]<2039	0.0158*W[g]$^{-0.394}$	0.144E-04*TL[mm]$^{2.962}$
Moxostoma spp	12	13<W[g]<2012	0.0337*W[g]$^{-0.541}$	0.170E-04*TL[mm]$^{2.908}$
Nocomis spp	4	5<W[g]<81	0.0113*W[g]$^{-0.524}$	0.537E-05*TL[mm]$^{3.170}$
Notemigonus crysoleucas	8	6<W[g]<87	0.1788*W[g]$^{-1.361}$	0.237E-05*TL[mm]$^{3.294}$
Notropis cornutus	5	2<W[g]<47	0.0050*W[g]$^{-0.291}$	0.275E-05*TL[mm]$^{3.290}$
Notropis hudsonius	4	2<W[g]<11	0.0243*W[g]$^{-1.554}$	0.903E-05*TL[mm]$^{2.989}$
Notropis spp	5	1<W[g]<25	0.0022*W[g]$^{-0.121}$	0.610E-05*TL[mm]$^{3.040}$
Noturus flavus	9	5<W[g]<209	0.0160*W[g]$^{-0.714}$	0.375E-04*SL[mm]$^{2.841}$
Noturus spp	36	0<W[g]<6	0.0056*W[g]$^{-1.133}$	0.132E-04*SL[mm]$^{3.070}$
Oncorhynchus aguabonita	5	2<W[g]<310	0.1083*W[g]$^{-0.858}$	0.170E-04*FL[mm]$^{3.000}$
Oncorhynchus clarki	7	5<W[g]<1023	0.0084*W[g]$^{-0.309}$	0.389E-05*TL[mm]$^{3.033}$
Oncorhynchus mykiss	7	56<W[g]<2582	0.0111*W[g]$^{-0.282}$	0.712E-05*TL[mm]$^{3.053}$
Osmerus mordax	7	1<W[g]<120	0.0011*W[g]$^{0.000}$	0.530E-05*TL[mm]$^{2.952}$
Perca flavescens	11	7<W[g]<485	0.0387*W[g]$^{-0.730}$	0.411E-05*TL[mm]$^{3.230}$
Percina spp	4	2<W[g]<12	0.0038*W[g]$^{-0.425}$	0.412E-05*TL[mm]$^{3.235}$
Percopsis omiscomaycus	8	1<W[g]<30	0.0137*W[g]$^{-1.127}$	0.842E-05*TL[mm]$^{3.008}$
Percopsis transmontana	6	2<W[g]<13	0.0082*W[g]$^{-1.079}$	0.237E-04*FL[mm]$^{2.910}$
Pimephales spp	3	13<W[g]<77	0.0097*W[g]$^{-0.433}$	0.498E-04*TL[mm]$^{3.228}$
Polyodon spathula	7	67<W[g]<5657	0.0561*W[g]$^{-0.487}$	0.328E-06*TL[mm]$^{3.350}$
Pomoxis annularis	8	7<W[g]<671	0.0328*W[g]$^{-0.574}$	0.150E-05*TL[mm]$^{3.384}$
Pomoxis nigromaculatus	9	10<W[g]<539	0.0300*W[g]$^{-0.578}$	0.571E-05*TL[mm]$^{3.180}$
Prosopium cylindraceum	12	45<W[g]<4217	0.1895*W[g]$^{-0.726}$	0.103E-04*TL[mm]$^{3.259}$
Prosopium williamsoni	9	14<W[g]<629	0.0326*W[g]$^{-0.643}$	0.618E-05*TL[mm]$^{3.085}$
Rhinichthys atratulus	4	5<W[g]<30	0.0034*W[g]$^{-0.261}$	0.126E-03*TL[mm]$^{2.965}$
Rhinichthys cataractae	6	1<W[g]<14	0.0032*W[g]$^{-0.531}$	0.179E-03*TL[mm]$^{2.394}$
Rhinichthys spp	5	7<W[g]<81	0.0073*W[g]$^{-0.445}$	0.540E-04*TL[mm]$^{3.090}$
Salmo trutta	8	117<W[g]<28084	0.0304*W[g]$^{-0.344}$	0.185E-04*TL[mm]$^{3.030}$
Salvelinus fontinalis	7	13<W[g]<825	0.0196*W[g]$^{-0.455}$	0.148E-04*TL[mm]$^{2.928}$
Salvelinus namaycush	16	19<W[g]<9267	0.0364*W[g]$^{-0.504}$	0.228E-05*TL[mm]$^{3.222}$
Semotilus atromaculatus	7	3<W[g]<102	0.0194*W[g]$^{-0.774}$	0.142E-04*TL[mm]$^{2.925}$
Semotilus corporalis	10	1<W[g]<994	0.0167*W[g]$^{-0.485}$	0.103E-04*TL[mm]$^{2.998}$
Stizostedion canadense	11	138<W[g]<4304	0.2183*W[g]$^{-0.709}$	0.587E-04*TL[mm]$^{2.870}$
Stizostedion vitreum	15	34<W[g]<6838	0.0193*W[g]$^{-0.449}$	0.352E-05*TL[mm]$^{3.180}$
Thymallus arcticus	11	17<W[g]<873	0.1598*W[g]$^{-0.928}$	0.299E-04*TL[mm]$^{2.768}$

To validate the density-to-biomass conversion procedure outlined above, a database of studies that have reported measured fish densities and associated fish biomasses was compiled from the literature (Quinn 1988, Reed and Rabeni 1989, Ensign et al. 1990, Buynak et al. 1991, Flick and Webster 1992, Bettoli et al. 1993, Waters et al. 1993, Maceina et al. 1995, Mueller 1996, Allen et al. 1998, Radwell 2000, Dettmers et al. 2001, Pierce et al. 2001, Habera et al. 2004). Reported fish densities were converted into estimated biomasses assuming evenly spaced self-thinning exponents *b* ranging from -0.5 to -1.0 at 0.025 increments. Reduced major axis (RMA) regressions were then calculated for each assumed self-thinning exponent. The self-thinning exponent that minimized the intercurve area between the calculated RMA regression line and the identity relationship was *b*=-0.800. This regression was

$$\begin{aligned} \ln B_{obs} &= 0.846 \ln B_{est} - 0.147 \quad (n = 499;\ r^2 = 0.662) \\ B_{obs} &= 0.712\ B_{est}^{0.846} \end{aligned} \qquad \textbf{(A-17)}$$

Figure A.1 displays the data for the regression **(A-17)** and the identity relationship $B_{obs} = B_{est}$.

Figure A.1 Plot of observed versus predicted biomasses. Indicated line represents the identity relationship of observed biomass equals predicted biomass.



Appendix B. BASS Bioenergetic and Population Dynamics Algorithms

B.1. Modeling Temperature Effects on Individual Growth

Because one of the principal consequences of riparian destruction/restoration on stream fishes centers on their bioenergetic responses to altered stream temperatures, it is instructive to outline the temperature response algorithm that BASS uses to predict fish feeding, metabolism, and growth before actually describing how these processes are represented in BASS.

Although the temperature dependence of physiological processes are often described using an exponential response equation, e.g.,

$$r_1 = r_0 \exp[\epsilon(T_1 - T_0)] \qquad \textbf{(B-1)}$$

where r_0 and r_1 are the reaction rates of the process at temperatures T_0 and T_1, respectively, such descriptions are generally valid only with a range of the organism's thermal tolerance. In most cases, the process's reaction rate increases exponentially with increasing temperature up to a temperature T_1 after which it decreases. Moreover, in most cases the temperature at which a process's rate is maximal is very close to the organism's upper thermal tolerance limit. To address this problem, Thornton and Lessem (1978) developed a logistic multiplier to more realistically describe the temperature dependence of a wide variety of physiological processes. Although this algorithm has been used successfully in a variety of fish bioenergetic models, BASS uses an exponential-type formulation that is assumed to respond hyperbolically to increasing temperature.

Let P denote the rate of a physiological process and T_1 denote the temperature at which the rate is at its maximum value. If this process generally exhibits an exponential response to temperature changes well below T_1, then Equation **(B-1)** can be used to describe this process for T and $T_0 << T_1$, i.e.,

$$P = P_0 \exp[\beta(T - T_0)] \qquad \textbf{(B-2)}$$

$$\frac{dP}{dT} = \beta P \qquad \textbf{(B-3)}$$

where P_0 is the process's rate at the low-end reference temperature T_0. To incorporate the adverse effects of high temperatures on this process, the right hand side of Equation **(B-3)** can be multiplied by a hyperbolic temperature term that approaches unity as temperature decreases well below T_1, equals zero at T_1, and becomes increasingly negative as temperatures approach the fish's upper thermal tolerance limit $T_L = T_2$. Modifying Equation **(B-3)** in this fashion yields

$$\frac{dP}{dT} = \beta P \left(\frac{T - T_1}{T - T_2} \right) \qquad \textbf{(B-4)}$$

whose solution is

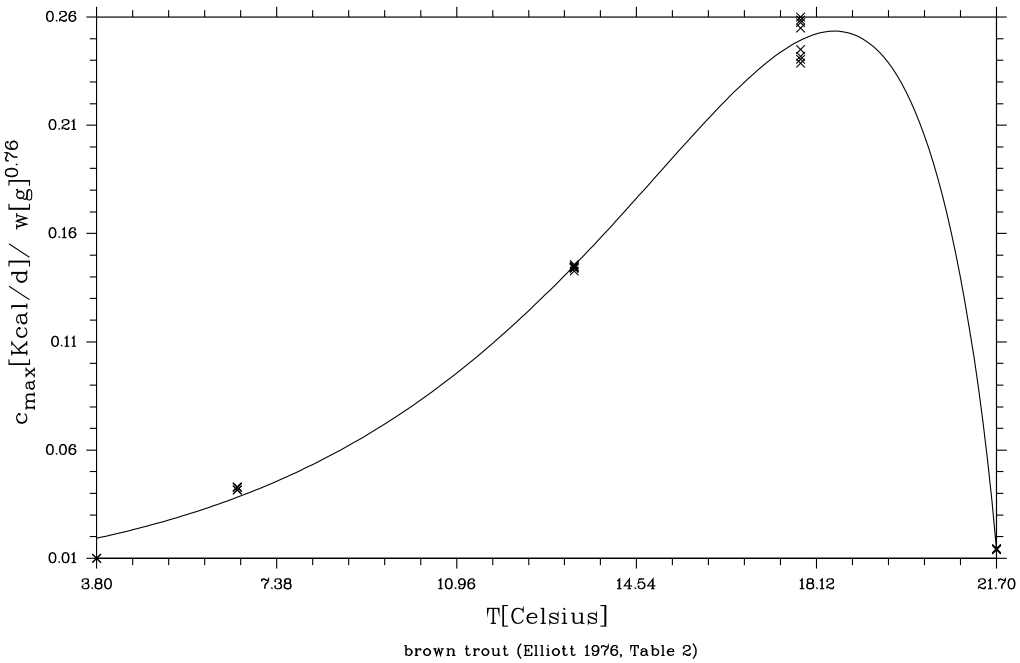
$$P = P_0 \exp[\beta (T - T_0)] \left(\frac{T_2 - T}{T_2 - T_0} \right)^{\beta (T_2 - T_1)} \qquad \textbf{(B-5)}$$

If one assumes, without loss of generality, that $T_0 = 0$, the preceding equation can be simplified to

$$P = P_0 \exp(\beta T) \left(1 - \frac{T}{T_2} \right)^{\beta (T_2 - T_1)} \qquad \textbf{(B-6)}$$

Figure B.1 displays the utility of this equation for describing the temperature dependence of the maximum feeding rate of brown trout (*Salmo trutta*) as reported by Elliott (1976b). Although rate equations of this form apparently have not been used to describe physiological responses of fish, results summarized by Barber (2004a) clearly demonstrate their applicability for doing so. For other applications of this model see Lassiter and Kearns (1974), Lassiter (1975), and Swartzman and Bentley (1979).

Figure B.1 Maximum daily ingestion of brown trout (*Salmo trutta*) as a function of temperature. Data from Elliott (1976b).



brown trout (Elliott 1976, Table 2)

B.2. Modeling Growth of Fish

As already mentioned, BASS simulates fish growth in terms of a dry weight mass balance of feeding, egestion, respiration, and excretion. However, because BASS' bioaccumulation algorithms are necessarily formulated in terms of the fish's live weight, and because many of BASS' basic physiological parameters are generally determined with respect to the fish's live weight, BASS also calculates a fish's wet weight (W_f) from its simulated dry weight using the following relationships:

$$W_f = W_a + W_d = W_a + W_l + W_o \qquad \textbf{(B-7)}$$

$$P_l = \lambda_1 W_f^{\lambda_2} \qquad \textbf{(B-8)}$$

$$P_a = \alpha_0 - \alpha_1 P_l \qquad \textbf{(B-9)}$$

$$P_0 = 1 - P_a - P_l \tag{B-10}$$

where W_a, W_d, W_l, and W_o denote the fish's aqueous, dry, lipid, and non-lipid organic weights, respectively; and P_a, P_l, and P_o are the corresponding wet weight proportions of these components. Whereas Equations **(B-7)** and **(B-10)** follow directly from mass conservation, Equations **(B-8)** and **(B-9)** are purely statistical in nature. Although Equation **(B-8)** is assumed because simple power functions of this form generally describe a wide variety of morphometric relationships for most organisms, Equation **(B-9)** is based on the results of numerous field and laboratory studies (Eschmeyer and Phillips 1965, Brett et al. 1969, Groves 1970, Elliott 1976a, Staples and Nomura 1976, Craig 1977, Shubina and Rychagova 1981, Beamish and Legrow 1983, Weatherley and Gill 1983, Flath and Diana 1985, Lowe et al. 1985, Kunisaki et al. 1986, Morishita et al. 1987).

BASS calculates a fish's realized feeding by first estimating its maximum *ad libitum* consumption and then adjusting this potential by the availability of appropriate prey as described in the next section. Because a wide variety of models and methods have been used to describe maximum feeding of fish, BASS is coded to allow a user the option of using any one of four different models to simulate the feeding of any particular age / size class of fish. The first formulation that can be used is a temperature-dependent power function

$$F_{\max} = f_1 W_f^{f_2} \exp(\beta T) \left(1 - \frac{T}{T_2} \right)^{\beta (T_2 - T_1)} \tag{B-11}$$

where f_1, f_2, β, T_1, and T_2 are empirical constants specific to the fish's feeding.

A commonly used alternative to the preceding allometric model is the Rashevsky-Holling model that is defined by the equations:

$$\begin{aligned} F_{\max} &= \phi (G_{\max} - G) \\ \frac{dG}{dt} &= F_{\max} - A - E \end{aligned} \tag{B-12}$$

where ϕ is the fish's *ad libitum* feeding rate (day^{-1}); G_{max} is the maximum amount of food (g[DW]) that the fish's stomach / gut can hold; G is the actual amount of food (g[DW]) present in the gut; and A denotes the rate of food assimilation by the fish (Rashevsky 1959, Holling 1966). The ad libitum feeding rate ϕ can be estimated using the following equations

$$F(t) = \int_0^t \phi \left[G_{\max} - F(\tau) \right] d\tau \qquad \textbf{(B-13)}$$

$$\frac{dF(t)}{dt} = \phi \left[G_{\max} - F(t) \right] \qquad \textbf{(B-14)}$$

$$-\phi t = \ln \left[1 - \frac{F(t)}{G_{\max}} \right] \qquad \textbf{(B-15)}$$

where $F(t)$ denotes the total amount of food consumed during the interval $(0, t]$ (also see Dunbrack 1988).

For planktivores BASS can also estimate a fish's maximum ingestion rate using the clearance volume model

$$F_{\max} = \Psi Q_{cl} \qquad \textbf{(B-16)}$$

where Ψ is the plankton standing stock (g[DW] / L); and Q_{cl} is the planktivore's clearance volume (L / day) that is assumed to be given by

$$Q_{cl} = q_1 W_f^{q_2} \exp(\beta T) \left(1 - \frac{T}{T_2} \right)^{\beta (T_2 - T_1)} \qquad \textbf{(B-17)}$$

where q_1, q_2, β, T_1, and T_2 are empirical constants specific to the fish's filtering rate.

The fourth and final option is based on knowing the fish's projected growth and routine respiratory demands. In particular, because assimilation, egestion, specific dynamic action, and excretion can be calculated as linear functions of feeding and routine respiration as discussed subsequently, it is then a straightforward matter to calculate a fish's expected ingestion given its projected growth and respiration. When a user elects this feeding option, BASS assumes that the fish's specific growth rate $\gamma = W_f^{-1}\, dW_f/dt$ (day^{-1}) is given by

$$\gamma = g_1\, W_f^{g_2} \exp(\beta\, T) \left(1 - \frac{T}{T_2} \right)^{\beta (T_2 - T_1)} \tag{B-18}$$

where g_1, g_2, β, T_1, and T_2 are empirical constants specific to the fish's growth rate.

When BASS estimates a fish's feeding rate using Equations **(B-11)**, **(B-16)**, or **(B-18)** , the fish's assimilation and egestion are estimated as simple fractions of its realized ingestion F, i.e.,

$$A = \alpha_f F \tag{B-19}$$

$$E = (1 - \alpha_f) F \tag{B-20}$$

where α_f is the fish's net assimilation efficiency that is a weighted average of the fish's assimilation efficiencies for invertebrate, piscine, and vegetative prey. However, when the Rashevsky-Holling feeding model is used, BASS calculates these fluxes by substituting F with a function that describes the fish's pattern of intestinal evacuation. The general form of this function is assumed to be

$$EV = e_1\, G^{e_2} \exp(\beta\, T) \left(1 - \frac{T}{T_2} \right)^{\beta (T_2 - T_1)} \tag{B-21}$$

where e_1, e_2, β, T_1, and T_2 are empirical constants specific to the fish's gastric evacuation.

The numerical value of this function's exponent, e_2, depends both on characteristics of the food item being consumed and on the mechanisms that presumably control gastro-intestinal motility and digestion (Jobling 1981, 1986, 1987). For example, when gut clearance is controlled by intestinal peristalsis, e_2 should approximately equal ½ since peristalsis is stimulated by circumferential pressure exerted by the intestinal contents which, in turn, is proportional to the square root of its mass. On the other hand, when surface area controls the rate of digestion, e_2 should be approximately either ⅔ or unity. If the fish consumes a small number of large-sized prey (e.g., a piscivore), $e_2 = ⅔$ may be the appropriate surface area model. On the other hand, if the fish consumes a large number of smaller, relatively uniform-sized prey (e.g., a planktivore or drift feeder), $e_2 = 1$ is more appropriate since total surface area and total volume of prey become almost directly proportional to one another.

A fish's specific dynamic action, i.e., the respiratory expenditure associated with the digestion and assimilation of food, is modeled as a constant fraction of the fish's assimilation. In particular,

$$SDA = \sigma A \tag{B-22}$$

where σ is generally on the order of 0.15 to 0.20 (Ware 1975, Tandler and Beamish 1981, Beamish and MacMahon 1988).

BASS assumes that body weight losses via metabolism are due entirely to the respiration of carbon dioxide and the excretion of ammonia. Respiratory losses R are calculated from a fish's routine oxygen consumption, R_{O2} (g(O_2) / day) using respiratory quotients RQ (L [CO_2] respired) / L [O_2] consumed) as follows

$$\begin{aligned} R = {} & \frac{12\, g\ C}{mole\ CO_2} \bullet \frac{mole\ CO_2}{22.4\, L\ CO_2} \bullet RQ \\ & \bullet \frac{22.4\, L\ O_2}{mole\ O_2} \bullet \frac{mole\ O_2}{32\, g\ O_2} \bullet R_{O2} = \frac{12}{32} \bullet RQ \bullet R_{O2} \end{aligned} \tag{B-23}$$

BASS calculates a fish's routine oxygen consumption as a constant multiple of its basal or standard oxygen consumption (Ware 1975) that is specified using the temperature-dependent power function

$$R_{O2} = b_1\, W_f^{b_2} \exp(\beta\, T) \left(1 - \frac{T}{T_2} \right)^{\beta (T_2 - T_1)} \tag{B-24}$$

where b_1, b_2, β, T_1, and T_2 are empirical constants specific to the fish's oxygen consumption. Although ammonia excretion could be modeled using an analogous function (Paulson 1980, du Preez and Cockroft 1988a, b), BASS formulates this flux as a constant fraction of the fish's total respiration assuming that fish maintain a constant nitrogen / carbon ratio NC (g[N] / g[C]). Thus, BASS estimates a fish's excretory loss in body weight as

$$EX = \epsilon NC \left(R + SDA \right) \tag{B-25}$$

where $\epsilon = 17 / 14$ is the ratio of the molecular weight of ammonia to that of nitrogen.

B.3. Modeling Trophic Interactions and Predatory Mortalities

BASS is designed to simulate aquatic food webs in which each age class of a species can feed upon other fish species, benthos, incidental terrestrial insects, periphyton / attached algae, phytoplankton, and zooplankton. The realized feeding of any given age class of fish is determined by the estimated maximum feeding rate of individuals within the cohort, the cohort's population size, and the biomass of prey that is available to the cohort; the later quantity being the sum of the current biomass of potential prey minus the biomass of potential prey that is expected to be consumed by other fish cohorts that are more efficient foragers / competitors. BASS ranks the competitive abilities of different cohorts using the following assumptions:

ASSUMPTION 1. The competitive abilities and efficiencies of benthivores and piscivores are positively correlated with their body sizes (Garman and Nielsen 1982, East and Magnan 1991). Two general empirical trends support this assumption. The first of these is the trend for the reactive distances, swimming speeds, and territory sizes of fish to be positively correlated with their body size (Minor and Crossman 1978, Breck and Gitter 1983, Wanzenböck and Schiemer 1989, Grant and Kramer 1990, Miller et al. 1992, Keeley and Grant 1995, Minns 1995). Given two differently sized predators of the same potential prey, these trends would suggest that the larger predator is more likely to encounter that prey than is the smaller. Having encountered the prey, the other general trend for prey handling times to be inversely correlated with body size (Werner 1974, Miller et al. 1992) suggests that the larger predator could dispatch the prey and resume its foraging more quickly than the smaller predator.

ASSUMPTION 2. Unlike benthivores and piscivores, the competitive abilities and efficiencies of planktivores are inversely related to their body size due to their relative morphologies (Lammens et al. 1985, Johnson and Vinyard 1987, Wu and Culver 1992, Persson and Hansson 1999). Consequently, "large" planktivores only have access to the leftovers of "small" planktivores.

BASS calculates the relative frequencies $\{...,d_i,...\}$ of the different prey consumed by each cohort using dietary electivities, i.e.,

$$e_i = \frac{d_i - f_i}{d_i + f_i} \tag{B-26}$$

where f_i is the relative availability of the *i*-th prey with respect to all other prey consumed by the cohort. One can easily verify that the range of dietary electivities is $-1 < e_i < 1$. One can also verify that if the fish does not eat a potential food item *i* that $e_i = -1$. Similar, if the fish consumes a potential prey item *i* in direct proportion to the prey's relative abundance, then $e_i = 0$. BASS actually allows users to specify a fish's diet as either a set of fixed dietary frequencies $\{...,\bar{d}_i,...\}$, a set of electivities $\{...,\bar{e}_i,...\}$, or a combination of fixed frequencies and electivities $\{...,\bar{d}_i,...,\bar{e}_j,...\}$. To calculate a cohort's realized dietary composition, however, BASS converts all user supplied fixed dietary frequencies into their equivalent electivities using the current simulated relative abundances $\{...,f_i,...\}$ of the cohort's prey. These electivities are then combined with any user specified electivities to form a set of unadjusted electivities $\{...,\hat{e}_i,...\}$ that is subsequently converted into a consistent set of realized electivities $\{...,e_i,...\}$. Using these realized electivities, BASS then calculates the cohort's realized dietary frequencies using

$$d_i = \left(\frac{1 + e_i}{1 - e_i}\right) f_i \tag{B-27}$$

The important step in this computational process is the conversion of the unadjusted electivities into a set of realized electivities. Readers interested in the details of this process should consult Barber (2001, 2004a).

Because numerous studies have shown that there is generally a strong positive correlation between the body sizes of piscivorous fish and the forage fish that they consume (Parsons 1971, Lewis et al. 1974, Timmons et al. 1980, Gillen et al. 1981, Knight et al. 1984, Moore et al. 1985, Stiefvater and Malvestuto 1985, Storck 1986, Jude et al. 1987, Johnson et al. 1988, Yang and Livingston 1988, Brodeur 1991, Elrod and O'Gorman 1991, Hambright 1991, Juanes et al. 1993, Mattingly and Butler 1994, Hale 1996, Madenjian et al. 1998, Margenau et al. 1998, Mittelbach and Persson 1998, Bozek et al. 1999), when BASS uses the above procedure to calculate piscivorous interactions, only a specific size range of forage fish are assumed to be available to a piscivorous cohort. To determine this size range, BASS first assumes that the mode of the body lengths of forage fish ingested by a piscivore is given by

$$L_{mode} = \begin{cases} \lambda_1 + \lambda_2 L_{predator} \\ \lambda_1 + \lambda_2 \exp\left(\lambda_3 L_{predator}\right) \end{cases} \qquad \textbf{(B-28)}$$

where λ_1, λ_2, and λ_3 are empirical constants specific to the mode of the predator's ingestable prey length. Using this relationship, BASS then assumes that the minimum length of prey consumed by the piscivore is given by

$$L_{\min} = 0.5\, L_{mode} \qquad \textbf{(B-29)}$$

As like the mode, the maximum length of prey consumed by the piscivore is assumed to be given by an equation of the form

$$L_{\max} = \begin{cases} \lambda_1 + \lambda_2 L_{predator} \\ \lambda_1 + \lambda_2 \exp\left(\lambda_3 L_{predator}\right) \end{cases} \qquad \textbf{(B-30)}$$

where λ_1, λ_2, and λ_3 are again empirical constants specific to the predator's maximum ingestable prey length. All relative frequencies d_i of forage fish in the diet of a piscivorous cohort are then calculated relative to sum of forage fish biomasses whose body lengths are both greater than $L_{\min}$ and less than $L_{\max}$ minus the biomass of those prey sizes that are predicted to be consumed by more efficient piscivorous cohorts (see Assumption 1).

When two or more cohorts of a forage species i can be consumed by a piscivore, the relative frequencies of those cohorts s_{ij} in the piscivore's diet are calculated assuming that prey sizes follow a simple triangular distribution defined by Equations **(B-28) - (B-30)**. For example, let L_{i1} and L_{i2} denote the body lengths of two age classes of species that are prey for the cohort. If P_{ij} denotes the triangular distribution function

$$P_{ij} = \begin{cases} \dfrac{2\ (L_{ij} - L_{\min})}{(L_{\max} - L_{\min})\ (L_{mode} - L_{\min})} & for \quad L_{ij} < L_{mode} \\ \dfrac{2\ (L_{\max} - L_{ij})}{(L_{\max} - L_{\min})\ (L_{\max} - L_{mode})} & for \quad L_{ij} > L_{mode} \end{cases} \qquad \textbf{(B-31)}$$

the relative frequencies of these two age classes in the cohort's diet are calculated to be $s_{i1} = d_i\,[P_{i1}/(P_{i1} + P_{i2})]$ and $s_{i2} = d_i\,[P_{i2}/(P_{i1} + P_{i2})]$. If only one age class of a forage species is vulnerable to the cohort, then $s_{ij} = d_i$.

If during the calculation of the dietary frequencies of a piscivorous cohort BASS predicts that the cohort's available prey is insufficient to satisfy its desired level of feeding, BASS reassigns the cohort's unadjusted electivities $\{...,\hat{e}_i,...\}$ in a manner to simulate prey switching. These reassignments are based on the following assumption:

ASSUMPTION 3. When forage fish become limiting, piscivores switch to benthic macroinvertebrates or incidental terrestrial insects as alternative prey. However, piscivores that must switch to benthos or that routinely consume benthos in addition to fish, are less efficient benthivores than are obligate benthivores (Hanson and Leggett 1986, Lacasse and Magnan 1992, Bergman and Greenberg 1994). Consequently, only the leftovers of non-piscivorous benthivores are available to benthic feeding piscivores. If such resources are still insufficient to satisfy the piscivores' metabolic demands, piscivores are assumed to then switch to planktivory (Werner and Gilliam 1984, Magnan 1988, Bergman and Greenberg 1994). In this case, piscivores have access only to the leftovers of non-piscivorous planktivores. Using this assumption, BASS first assigns the cohort's electivity for benthos to 0 regardless of its previous value. BASS also reassigns any other electivity which does not equal -1, to 0.

If benthos become limiting for benthivores, or if plankton becomes limiting for planktivores, BASS assumes that benthivores can shift their diets to include plankton and terrestrial insects and that planktivores can shift their diets to include benthos and terrestrial insects. See, for example, Ingram and Ziebell (1983)

After BASS has calculated a cohort's dietary composition, it then assigns its realized feeding rate adjusted for prey availability as

$$F = \max\left(F_{\max},\ N^{-1} \sum_{e_j \neq -1} AB_j \right) \tag{B-32}$$

where F_{max} is the cohort's maximum or desired individual ingestion, N is the cohort's population size, and AB_j is the biomass of prey j that is available to that cohort. Using its predicted dietary compositions and realized feeding rates, BASS then calculates the predatory mortalities for each cohort and non-fish biotic resource.

B.4. Modeling Dispersal, Non-Predatory Mortalities, and Recruitment

The algorithm that BASS employs to simulate a species' dispersal and non-predatory mortality is based on the general empirical observation that population densities of most vertebrates can be adequately characterized by the self-thinning power function relationship

$$N = a\,W^{-b} \tag{B-33}$$

where N is the species' density (fish / area) and W is the species' mean body weight (Damuth 1981, Peters and Raelson 1984, Juanes 1986, Robinson and Redford 1986, Dickie et al. 1987, Boudreau and Dickie 1989, Gordoa and Duarte 1992, Randall et al. 1995, Dunham and Vinyard 1997, Steingrímsson and Grant 1999, Dunham et al. 2000). For fish species, the body weight exponent b generally varies from 0.75 to 1.5(Boudreau and Dickie 1989, Grant and Kramer 1990, Gordoa and Duarte 1992, Elliott 1993, Bohlin et al. 1994, Randall et al. 1995, Dunham and Vinyard 1997, Grant et al. 1998, Dunham et al. 2000, Knouft 2002, Keeley 2003). Larger exponents ranging from 1.5 to 3.0, however, have also been reported (Steingrímsson and Grant 1999). If Equation **(B-33)** is differentiated with respect to time, it immediately follows that a species' population dynamics can be modeled using the time varying linear differential equation

$$\frac{dN}{dt} = \frac{-a\,b\,W^{-b}}{W}\frac{dW}{dt} = -\,b\,\gamma\,N \tag{B-34}$$

where γ is the species' specific growth rate. Consequently, $b\gamma$ corresponds to the cohort's total mortality rate. Readers interested in detailed discussions concerning the underlying process-based interpretation and general applicability of this result should consult Peterson and Wroblewski (1984), McGurk (1993, 1999), and Lorenzen (1996).

Because Equations **(B-33)** and **(B-34)** encompass the species predatory mortality, non-predatory mortality, and dispersal, and because BASS explicitly models the cohort's predatory mortality, BASS assumes that the cohort's rate of non-predatory mortality and dispersal is simply a fraction δ of $b\gamma$. In particular,

$$EM + NM = \delta\,b\,\gamma\,N \tag{B-35}$$

If community population dynamics are strongly dominated by predation, the fraction δ will be "small" (e.g., $\delta < 0.5$) for forage fishes and "large" (e.g., $\delta > 0.5$) for predatory species. However, if community population dynamics are dominated by dispersal mechanisms related to competition for food, space, or other limiting community resource, the fraction δ will be large for both forage and predatory species alike.

BASS estimates a species' recruitment by assuming that each species turns over a fixed percentage of its potential spawning biomass into new young-of-year (YOY). This percentage is referred to as the species' reproductive biomass investment (rbi). The species' spawning biomass is defined to be the total biomass of all cohorts whose body lengths are greater than or equal to a specified minimum value (tl_r0) marking the species' sexual maturation. When reproduction is simulated, the body weight of each sexually mature cohort is decreased by its rbi and the total number of YOY that are recruited into the population as a new cohort is estimated by simply dividing the species' spawned biomass by the species' characteristic YOY body weight. Although this formulation does not address the myriad of factors known to influence population recruitment, it is logically consistent with the spawners abundance model for fish recruitment. See Myers and Barrowman (1996) and Myers (1997).

B.5. Modeling Habitat Effects

Although BASS does not explicitly model physical habitat features of the fish community of concern, it does allow users to specify habitat suitability multipliers on the feeding, reproduction / recruitment, and dispersal / non-predatory mortality for any or all species. Because these multipliers are assumed to be analogous to subcomponents of habitat suitability indices, they are assumed to take values from 0 to 1. If these multipliers are not specified by the user, BASS assigns them the default value of 1.

When feeding habitat multipliers are specified, BASS uses the specified parameters as simple linear multipliers on the fish's maximum rate of ingestion, i.e.,

$$F_{\max,\ habitat} = HSI_{feeding}\, F_{\max} \qquad \textbf{(B-36)}$$

The resulting adjusted maximum feeding rate ($F_{\max,\ habitat}$) then replaces $F_{\max}$ in Equation **(B-32)**. These multipliers are assumed to modify the fish's ability to perceive or to intercept prey either by effecting the fish's reactive distance etc. or by providing modified refuges for its potential prey. Habitat interactions that actually change the abundance of potential prey should not be specified as feeding habitat multipliers since these interactions are automatically addressed by the algorithms outlined in Section **B.3**.

Like the aforementioned feeding habitat multipliers, BASS uses any specified recruitment habitat multipliers as simple linear multipliers on the number of young-of-year that is recruited into the species population, i.e.,

$$N_{0,\ habitat} = HSI_{recruitment}\, N_0 \qquad \textbf{(B-37)}$$

These multipliers can represent either the availability of suitable spawning sites or the ability of the otherwise successful spawns to result in the expected numbers of young-of-year as discussed in Section **B.3**.

Finally, when habitat multipliers are specified for dispersal / non-predatory mortality, the specified values are assumed to act as hyperbolic multipliers as follows:

$$(EM + NM)_{habitat} = \left(\frac{\delta\, b\, \gamma}{HSI_{survival}} \right) N \qquad \textbf{(B-38)}$$

See Equation **(B-35)**. Thus, as habitat suitability decreases dispersal and non-predatory mortality increases and vicea versa.

Because constructing or estimating the aforementioned habitat suitability multipliers in a general or standard way is not a trivial issue, BASS relegates their construction to the user. Nevertheless there are several obvious starting points that users might consider when simulating habitat effects using BASS. Turbidity, for example, is known the effect the foraging abilities of both prey and predatory fishes, and one could readily use results of published studies (e.g. Vandenbyllaardt et al. 1991, Barrett 1992, Gregory 1993, Gregory and Northcote 1993, Miner and Stein 1996, Reid et al. 1999, Vogel and Beauchamp 1999, Bonner and Wilde 2002, Sweka and Hartman 2003) to estimate feeding multipliers for Equation **(B-36)** as power functions or polynominals of turbidity. Field-based HSI's are often estimated by logistic regression of presence-absence data without specifying the underlying mechanisms that actually determine habitat suitability for a species. Such HSI's could be used as habitat multipliers for a species' recruitment (Equation **(B-37)**) or persistence/survival (Equation **(B-38)**) or depending on the user's own interpretation of what the indices most likely represent.

B.6. Modeling Non-fish Compartments

BASS assumes that the non-fish components of a community of concern can be treated as 4 lumped compartments, i.e., benthos, periphyton/attached algae, phytoplankton, and zooplankton. These compartments can be treated either as community forcing functions or as bona fide state variables. In the later case, the required compartmental dynamics are simulated using the simple mass balance model

$$\frac{dY}{dt} = IP - R - \hat{F} - M \qquad \textbf{(B-39)}$$

where Y is the compartment's biomass ($g[\mathrm{DW}] / m^2$) ; and the fluxes IP, R, $\hat{F}$, and M, all in units of ($g[\mathrm{DW}] \cdot day^{-1} \cdot m^{-2}$) , denote the compartment's ingestion or photosynthesis, respiration, predatory mortality due to fish consumption, and other mortality and dispersal, respectively.

BASS formulates expressions for a compartment's ingestion, photosynthesis and respiration, by first formulating these processes for the individuals that comprise the compartment. In particular, BASS assumes that the ingestion, photosynthesis, and respiration by individuals within the aforementioned compartments can be adequately described by temperature dependent power functions of the form

$$P = \alpha W_d^{\beta} \exp(\gamma T) \left(1 - \frac{T}{T_2} \right)^{\gamma (T_2 - T_1)} \tag{B-40}$$

where W_d denotes the individual's gram-dry weight. Compartmental expressions for ingestion, photosynthesis, and respiration are then obtained by simply multiplying these individual-based power functions by the estimated numbers of individuals within the compartment.

For example, consider the following formulation of benthos consumption. If $\bar{W}_d$ denotes the average dry weight of individuals comprising the benthos compartment, it then follows that the expected density of individuals within the benthos compartment is simply

$$N = \frac{Y}{\bar{W}_d} \tag{B-41}$$

If the individual ingestion of benthic invertebrates is now given by the simplified power function

$$C = \alpha \bar{W}_d^{\beta} \exp(\gamma T) \tag{B-42}$$

it also follows that the compartmental consumption of the benthos is given by

$$\begin{aligned} IP = C\,N &= [\alpha \bar{W}_d^{\beta} \exp(\gamma T)] \frac{Y}{\bar{W}_d} \\ &= [\alpha \bar{W}_d^{\beta - 1} \exp(\gamma T)]\, Y \end{aligned} \tag{B-43}$$

Formulating compartmental ingestion, photosynthesis, and respiration by this method not only leads to an objective procedure to parameterize BASS, but also produces production estimates that are logically consistent with results reported by Plante and Downing (1989), Stockwell and Johannsson (1997), and Kuns and Sprules (2000).

Although BASS does not simulate the average individual body sizes of benthos, periphyton/attached algae, phytoplankton, and zooplankton, users can specify these parameters as functions of time.