Correspondence Between Environmental Gradients and the Assemblage Structure of Littoral Fishes in the Tidal Portion of Three Virginia Coastal Plain Rivers

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Master of Science

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by

C. Michael Wagner

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

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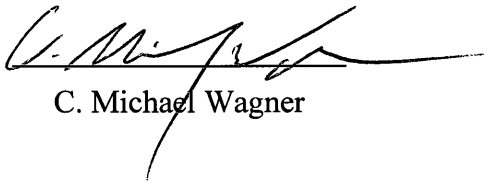

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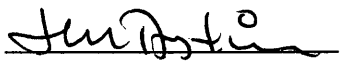

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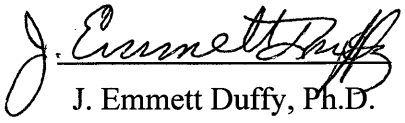

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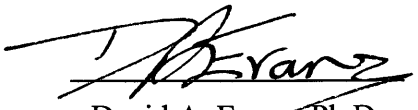

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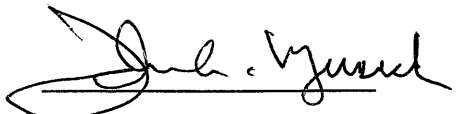

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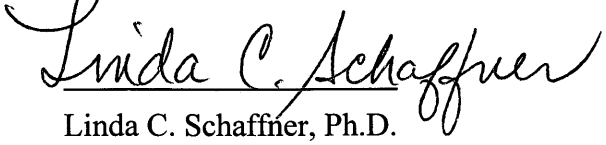

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ABSTRACT

The general distributional patterns of fishes associated with the Chesapeake Bay system have been addressed numerous times over the past century. These accounts are largely focussed on the mainstem of the Bay, and often offer little more than annotated species lists for the low salinity and tidal freshwater reaches of the major southern tributaries. This study focusses on the region of the lower Bay associated with the freshwater interface and provides details on the distribution and abundance of several littoral fish species with respect to large-scale environmental gradients. Littoral fishes were collected bi-weekly during a ten week period from July to mid-September from the major tributaries of lower Chesapeake Bay during the period 1990-1994 as part of a bay-wide effort to monitor the abundance of juvenile striped bass.

Littoral fishes were ordered along a large-scale spatial gradient between tidal freshwater and mesohaline river reaches during summer, when relatively stable hydrological conditions create a well-defined salinity gradient. This longitudinal coenocline was similar to patterns observed in other temperate and tropical zone coastal faunas, and is characterized by a series of species supplements and replacements in successive downstream locations. Fish assemblages generally grade smoothly into each other with one notable exception; the freshwater interface is a boundary with a markedly increased rate of species turnover due a peak in physiological stress associated with 0-2 ppt salinity. Large-scale zonation in the river systems corresponded to three basic habitat types: permanent tidal freshwater, the freshwater interface (lower tidal freshwater and oligohaline areas which straddle the interface) and the mesohaline mid-estuary. Though many of the species responsible for these patterns undergo large interannual fluctuations in abundance, the spatial assemblage structure during summer appears stable from year to year.

Dominant species were widely dispersed within each of the three ecoregions and few species were characteristic of only one aquatic habitat type. Two types of fishes dominated the littoral zone: juveniles of large migratory species and adults of small residents. Large-scale distribution of these fishes along the river axis corresponded with salinity (and its correlates) up to the interface, and with structural attributes of the habitat (nearshore sediment grain size, presence of SAV's) in the permanent tidal freshwater river reaches. Overall, patterns of species composition and richness in the saline portion of the study area agree well with earlier models of physico-chemical factors in structuring temperate estuarine faunas. A coenocline along the salinity gradient was evident, and exhibited: (1) intergrading, but distinct, fish assemblages; (2) a species minimum near 8-10 ppt as predicted by Remane (1934); and, (3) a peak in the rate of species turnover near the incipient stress point. The permanent tidal freshwater reaches were more riverine in character, and were typified by speciose and relatively stable assemblages dominated by resident second division freshwater fishes and the juveniles of several diadromous species. Although the resident fauna are certainly derivative of more upland, non-tidal streams, the open connection to the estuary and the free-flow of individual fishes across the interface, suggest tidal freshwater is best viewed as the upper end of the estuary.

Correspondence Between Environmental Gradients and the Assemblage Structure of Littoral Fishes in the Tidal Portion of Three Virginia Coastal Plain Rivers

INTRODUCTION

The goals of community ecology are to record the patterns of species associations which occur in nature, elucidate the causal processes underlying these patterns, and, as much as possible, to seek general explanations (Wiens 1984). During the early decades of modern American ecology most biologists took for granted the hypothesis of Frederic Clements that natural communities were well-defined units which were fundamental structures in nature and which contacted one another along narrow boundaries called 'ecotones' (Macintosh 1985, 1995). The natural community was likened to an individual 'super-organism'; a discrete functional assemblage of interrelated and interdependent parts (Tansley 1935; Clements 1936). In three elaborations of his 'individualistic concept', H.A. Gleason (1917, 1926, 1939) offered an opposing view predicated on the Gaussian distribution of species along gradients of variation in the environment and diverse probabilities of recruitment of new individuals. Gleason's (1926) version of the individualistic concept of community structure has since been recognized as one of the 'classic papers in the foundation of ecology' (Real & Brown 1991) and has provided the theoretical foundation for the empirical study of species distributions along natural gradients in habitat condition (the 'coenocline' from Whittaker 1967).

Spatial variation in the abundance of a species, and hence its apparent importance within an assemblage, has therefore been attributed to spatial variation in the environmental factors which affect it. Such factors include resource availability, climatic variables and other forces which comprise a complex hierarchy of physical and biotic environmental components that impinge (or promote) a species' reproduction and

survival. Consequently, explaining spatial variation in the abundance of species is scale dependent (May 1974; Steele 1989; Wiens 1989), and studies of the relationships between fishes and habitat variables offer no exceptions to this rule (Rahel *et al.* 1984; Livingston 1987; Dunham & Vinyard 1997). Since the mid-1980's, developments in ecologically sound multivariate techniques for gradient analysis (e.g., canonical correspondence analysis and non-metric multidimensional scaling) have intensified the interest in quantitative studies of the large-scale structure and diversity of finfish communities along complex riverine gradients (e.g., Matthews & Robison 1988; Townsend & Peirson 1988; Ibarra & Stewart 1989; Edds 1993). However, few studies have explicitly addressed the longitudinal patterns of assemblages in low salinity habitats adjacent to and crossing the freshwater interface of estuarine ecosystems (Odum 1988; Peterson & Ross 1991; Winemiller & Leslie 1992).

Longitudinal changes in assemblage structure within temperate non-tidal streams and rivers have been generally attributed to one of two processes: biotic zonation or continual addition of species downstream (Rahel & Hubert 1991). Biotic zonation refers to relatively distinct assemblages which arise in flowing waters as a consequence of local discontinuities in stream geomorphology or temperature. Early descriptions of these zones were articulated by European workers, who named the zones after locally dominant species (see Hawkes 1975), and similar patterns have been reported elsewhere (Balon & Stewart 1983; Moyle & Herbold 1987). In contrast to the advocates of zonation, many North American workers have viewed changes in assemblage structure as indicative of increasing community complexity through the sequential downstream addition of species

(Sheldon 1968; Jenkins & Freeman 1972; Evans & Noble 1979). The gradual downstream accumulation of species has been attributed to increases in habitat stability (Schlosser 1987) and diversity (Gorman & Karr 1978; Schlosser 1982). An alternate explanation maintains that upstream sites are more prone to periodic environmental disturbances where only a few, hardy species with rapid recolonization abilities will persist, while relatively stable downstream environs may support a broader assemblage of species (Horwitz 1978; Matthews & Styron 1981). However, recent data suggests that periods of environmental stress (e.g., drought) may actually promote the upstream colonization of species otherwise physically ill-equipped for the upstream migration (Grossman *et al.* in press).

Similarly, longitudinal patterns in estuarine fish assemblage structure have also been attributed to individual population responses to environmental gradients. Physiochemical factors appear to govern broad spatial distributions within the estuary, while species interactions (competition and predation) probably only fine tune spatial distributions on a smaller scale (Ross & Epperly 1985; Day *et al.* 1989; Menge & Olsen 1990). Historically, the most accepted of these factors for estuaries located along the western mid-Atlantic coast has been salinity (McHugh 1967). Distributions of estuarine macroinvertebrates and fishes have been shown to directly follow primary salinity gradients in the form of well-defined coenoclines (Boesch 1977; Weinstein *et al.* 1980). Other factors which have been implicated in governing the broad spatial distribution of estuarine fishes include temperature (Joseph 1973; Yáñez-Arancibia *et al.* 1982), turbidity (Blaber & Blaber 1980; Yáñez-Arancibia *et al.* 1985), calm water (Blaber &

Whitfield 1977), food availability (May 1974; Houde 1978; Lasker 1975; Whitfield 1980; Livingston 1982; Yáñez-Arancibia *et al.* 1986), predation pressure (Blaber & Blaber 1980) and distance from the estuary mouth (Loneragan *et al.* 1986).

Sandwiched between the well-studied environments of non-tidal streams and polyhaline estuaries are the realms of tidal freshwater and the low salinity upper estuary. The relative importance of environmental gradients to assemblage structure has yet to be fully evaluated for these aquatic systems. Although generally less studied (Moyle & Cech 1988; Peterson & Ross 1991), some studies in Gulf of Mexico (Rounsefell 1964; Felley 1987; Hastings *et al.* 1987; Peterson & Ross 1991) and western mid-Atlantic (Rogers *et al.* 1984; Odum *et al.* 1984; Odum 1988) estuaries have been focussed on the differences between tidal freshwater and estuarine fish assemblages. In general, the assemblages fish species present in the littoral zones of these aquatic systems are dominated by two groups of small individuals which occupy the shallows as a refugium from predators: (1) juveniles of larger migratory species (e.g., striped bass, Atlantic croaker); and, (2) adults of small resident species (e.g., cyprinnid minnows, killifishes).

The assemblage of fishes in tidal freshwater is markedly different from those associated with oligohaline and mesohaline estuarine waters (Rozas & Odum 1987b; Odum *et al.* 1984; Odum 1988; Rakocinski *et al.* 1992). Odum *et al.* (1987) compared published data from 13 tidal freshwater marsh systems from the western mid-Atlantic coast between the Hudson River, NY and the Altamaha River, GA. They described assemblages which, of the numerically dominant species, were comprised of 60% freshwater species, 20% anadromous species, 13% estuarine species and 7% marine

species. Though geographically very close to tidal freshwater, the oligohaline fish assemblages were dominated by estuarine and marine forms. Odum (1988) later concluded that marine and brackish water species were better equipped to exploit the low salinity conditions of the oliogohaline waters than the almost totally freshwater conditions of tidal freshwater. Conversely, freshwater species were less able to penetrate very far into the higher salinity waters. These observations are consistent with Deaton and Greenburg's (1986) conclusions that severe changes in ionic ratios occur in the range of 0-2 ppt and limit the distribution of freshwater species. Remane (1934) first described this phenomena, a species minimum occurring near oligohaline salinities, and it has been hypothesized as a general feature of strong gradient estuaries and other brackish systems such as the Baltic Sea.

Many of the previous works describing estuarine and tidal freshwater fish assemblages have focussed on the temporal changes in assemblage structure which accompany seasonal shifts in the estuarine environment and are the dominant influence on community structure during the late winter and spring months (Rakocinski *et al.* 1992). In contrast, spatial patterns seem most prevalent during the summer when salinity and water temperatures are relatively stable. Largely because of the need to spread limited sampling resources over the course of a year, intensive spatial studies are relatively rare. Fortunately, the annual juvenile striped bass seine survey conducted by the Virginia Institute of Marine Science (VIMS) occurs entirely in late summer and spans across the freshwater interface in three sub-estuaries of the lower Chesapeake Bay.

If environmental gradients are biologically meaningful to patterns of species

distributions near the freshwater interface, then a model of longitudinal assemblage structure that accounts for Gaussian responses to important gradients should help us to understand the dynamics of these species assemblages. A multivariate extension of the Gaussian model, correspondence analysis (CA), is appropriate for examining correlations between complex environmental gradients and changes in assemblage structure where patterns may be complex (Minchen 1987a; Palmer 1993). I applied CA-based techniques to investigate patterns of species association and longitudinal zonation of littoral fishes along the tidal freshwater to mesohaline gradient in the three sub-estuaries to the lower Chesapeake Bay (James, York and Rappahannock River systems). Specifically, the following questions are addressed:

(1) What are the primary components of the littoral fish faunas in the Rappahannock, York and James River systems below the fall line?

(2) What changes are evident in littoral beach fish assemblages along a longitudinal gradient from permanent tidal freshwater to mesohaline environments?

(3) How are patterns in fish assemblage structure related to large-scale and/or local environmental gradients?

(4) How do these changes in fish assemblage structure relate to general theories of riverine and estuarine community organization?

METHODS AND MATERIALS

Data Collection

The landscape of eastern Virginia is dominated by three major drainage basins which flow into the lower Chesapeake Bay: the James, York and Rappahannock Rivers. The tidal freshwater to mesohaline portions of these rivers have been sampled by beach seine annually since 1980 as part of the ongoing bay-wide summer juvenile striped bass monitoring program (Austin *et al.* 1996). This study utilized data collected during the five-year period 1990-1994.

Field sampling was conducted during five approximately bi-weekly rounds from July to mid-September at eighteen index and twenty-two auxiliary stations during daylight hours at or near low tide. The 40 sampling stations are shown in Figure 1. Twelve stations are located in the Rappahannock River and thirteen are along the James River (including two stations in the lower Chickahominy River which are not included in this analysis). Fifteen stations are located in the York River system: three in the mainstem York, six in the Mattaponi and six in the Pamunkey. Two replicate seine hauls are made at each index station, and one seine haul is made at each auxiliary station during each round. When two hauls were made, a period of at least 30 minutes was allowed between hauls. During this period, fishes captured in the first haul were retained in water filled buckets. All fishes were identified to species level, measured to fork-length and released upon completion of the station. Species of questionable field identification were returned to the lab and identified through the use of dichotomous keys (primarily Hildebrand & Schroeder 1972 and Jones *et al.* 1978).

Samples were collected with a 100' (30.5 m) long, 4' (1.22 m) deep, 1/4" (6.4 mm) bar mesh bagless minnow seine. The seine is set by hand with one end fixed on the beach and the other fully extended, perpendicular to the shoreline (or until a depth of approximately 4' was encountered). The seine is swept with the current and covers an area of approximately 730 m^2 (i.e., an approximately quarter-circle area with radius 100'). At stations where depth or current prevent full deployment, the distance from shore of the set is recorded. All sample abundances were standardized to a swept area of 1000 m^2 prior to classification and ordination analyses. No standardization was performed for species diversity calculations.

At each station the following environmental variables were measured using a Hydrolab Reporter® water quality instrument; temperature (°C), salinity (ppt), dissolved oxygen (mg ℓ^{-1}) and pH. Sampling time, tidal stage and general weather and hydrographic conditions were recorded at the time of each haul. In addition, sediment grain size was measured during the summer of 1997. I used a modified Wentworth scale to classify the dominant substrate type (Table 1). Conversations with survey personnel have confirmed that no significant change in dominant bottom type has occurred since the 1990-1994 period. Channel width (m; mean lower water), shoal width (m; measured as distance to the 6' depth contour at mean lower water) and distance to the bay mouth (nautical mile) were also included as covariables. Channel measurements were taken from U.S. Geological Survey 7.5' quadrangle maps.

Data Set Limitations

Beach seines are both species- and size-selective, and it was impossible to adjust for this type of selectivity without knowing the specific behavior of most species or the true age/size structure of the populations. However, the primary objective of this study is to identify the longitudinal distribution of abundance, not its absolute value. Fortunately, the family of correspondence analysis techniques utilized in this study are not reliant on a 'true' estimate of abundance. Rather, the analysis requires information on the presence/absence of a species, and its abundance distribution in the data set (i.e., location of the abundance peak).

As the statutory emphasis for this monitoring program is the generation of an index of relative abundance for juvenile striped bass, non-index stations are occasionally missed due to weather, boat failure, etc. To reduce the effect of unequal sample sizes between stations, any station which did not have at least 3 of the 5 collections within a year was eliminated.

Wilson and Weisberg (1993) analyzed data from ongoing beach seine monitoring programs for striped bass in the upper Chesapeake Bay, the Hudson River, and the Delaware River, to assess the effects of replicate hauls on index values. They concluded multiple hauls were inadvisable for two reasons: 1) repeated samples within a short time period are not true replicates; and, 2) when the upper Chesapeake Bay index was recalculated using data from the first haul only, there was a higher level of agreement with a commercial fishery data set. Therefore, to make index and non-index stations more comparable, data from the second tow taken at index stations were discarded.

Multivariate Analysis of Community Structure

The large, sparse arrays of species counts arising from field community studies commonly do not lend themselves to standard statistical tests based on multivariate normality (Coull 1985; Field *et al.* 1987). Instead, a valid and often more revealing approach uses informal display methods, such as numerical classification and ordination, based on a biologically appropriate definition of similarity between samples (Digby & Kempton 1987). Walker *et al.* (1979) have summarized three general alternative approaches to the analysis of such survey data:

(1) a search for patterns among the biological variables with an attempt to interpret these in terms of the available environmental data (indirect gradient analysis);

(2) a search for patterns of relationship between the biotic and environmental data simultaneously (direct gradient analysis); and,

(3) a search for patterns among the physical variables followed by a search for related patterns in the biotic data.

Walker *et al.* (1979) chose the third approach which may be suitable when one knows in advance which physical variables are likely to be dominant, and data are available (e.g., pollution effect surveys). Similarly, the second approach is powerful when the important environmental covariates are known (or strongly suspected), measured synoptically, and extraneous environmental factors are not included. However, as a general approach to the analysis of biological survey data, where synoptic environmental data may be sparse, the first approach often proves most effective. That is, we analyze the biotic data first, 'letting the species tell their story' (Day *et al.* 1971) and once groups of biotically similar

samples or stations have been recognized, the environmental variables may be tested for statistical differences. This strategy keeps separate the analyses of biotic and environmental data, avoiding the influence of any previous assumptions about spatio-temporal relationships between the species and their habitats, and minimizing the danger of circular argument in seeking to deduce relationships (Field *et al.* 1982).

Separate analyses were performed for each major river system (Rappahannock, York, Pamumkey, Mattaponi and James Rivers). Stations in the lower York were used with both Pamunkey and Mattaponi stations in separate analyses. Species which occurred with a frequency of <3% of the stations (within each river system) were not included in the gradient analysis. My specific approach had four major components which are expanded upon in the following sections:

(1) Stations and species were classified via two-way indicator species analysis, a polythetic divisive classification technique based on the correspondence analysis algorithm.

(2) Stations and species were ordinated via detrended correspondence analysis. Clusters determined in step 1 were superimposed on the station map. Species scores were used to determine whether: (a) distinct species assemblages (co-occurrences) are present; or, (b) species appear independently sorted in physical space.

(3) The statistical association of the station groups and species distributions to synoptic environmental data was examined by use of detrended canonical correspondence analysis.

(4) Longitudinal species diversity, evenness and richness were investigated across sites via standard indices (Shannon-Wiener Diversity, Pielou's Evenness) and rarefaction analysis.

Numerical Classification -- Numerical classification encompasses several techniques which attempt to order entities (samples or stations) into groups based upon the relationship of their attributes (species) according to mathematical criteria. Traditionally, studies of fish communities have relied on cluster analysis to identify groups of stations and/or species, usually using an agglomerative algorithm. However, as correspondence analysis techniques comprise the core evaluation of the data, Two-Way Indicator Species Analysis (Hill 1979), implemented by the computer program TWINSPAN, was considered best suited to the main objectives of this work.

In TWINSPAN, the data are first ordinated by correspondence analysis (CA). Those species that emphasize the CA axis extremes are then used to polarize the samples, and the samples are divided into two clusters by breaking the primary ordination axis near its middle. The sample division is refined by a reclassification using those species which best indicate the extremes (or poles) of the ordination axis. The division process is then repeated on the two sample clusters to give four clusters, and so on. The method '...

constructs a classification of the samples, and then uses this classification to obtain a classification of the species according to their ecological preferences. The two classifications are then used together to obtain an ordered two-way table that expresses the species synecological relations as succinctly as possible' (Hill 1979). The primary outputs of TWINSPAN are hierarchical classifications of stations and species, which may be represented as dendrograms, and a sorted community table in which stations and species are arranged along the major synthetic gradients extracted from the data. Abundance values are not used directly but are converted to a scale based on lower class limits (set at 0, 0.1, 1, 2, 5, 10, 20 and 50 individuals per 1000 m^2 swept area in this study to limit the influence of infrequent large catches of clupeomorph fishes).

Ordination -- Associations between stations and species were quantified via detrended correspondence analysis (DCA), a widely used nonlinear eigenvector ordination technique designed for use with large, multi-species data sets (Hill & Gauch 1980). The DCA algorithm can be expressed in terms of an eigenanalysis or as a 'reciprocal averaging' approach. It is referred to as reciprocal because site scores and species scores are calculated simultaneously. The reciprocal averaging procedure is computationally quite simple and the solution has several desirable mathematical properties:

(a) The first axis produces a map which incorporates the maximum correlation between site and species scores (Gauch 1982; Pielou 1984). Second and higher axes also have maximal site-species correlation subject to the constraint that axes

are orthogonal.

(b) Eigenvalues associated with each axis equal the correlation coefficient between species scores and site scores (Gauch 1982; Pielou 1984). Thus an eigenvalue close to 1 will represent a high degree of correspondence between species and sites, and an eigenvalue close to zero will indicated very little correspondence. If the fundamental model of species responses to environmental gradients is nonlinear and unimodal, as is generally accepted (Austin 1985; Minchen 1987*b*), then high eigenvalues are associated with long and strong environmental gradients (Gauch 1982).

The 'arch effect' was apparent in the species scores arising from the initial correspondence analysis suggesting the need for detrending (Gauch 1982). Detrending was accomplished by fitting a second-order polynomial equation to the relationship and subtracting its effect (ter Braak 1986). Detrending by second-order polynomials seems to avoid the destruction of ecologically meaningful information which may occur when detrending by segments, and is recommended for data sets where the arch is most likely due to a strong primary gradient (Jongman *et al.* 1995). The program CANOCO (vers. 3.12; ter Braak 1988, 1990) was used for all DCA analyses.

To aid in understanding patterns of species distribution, each species used in the ordinations was classified into one of six ecological affinity groups (modified from McHugh 1967):

(1) *Freshwater fishes* generally complete their entire life cycle in the upper estuary, spawn in freshwater (below 0.5 ppt), and have slight to moderate salinity tolerances. Records of most of these fishes in the middle and lower Bay are probably transient fish that have washed down from upstream environs.

(2) *Diadromous fishes* are found in the Bay in large numbers as they pass through on their way to fresh or salt water. Estuaries often serve as staging areas for anadromous fishes; for example, shad may remain in the estuary for several days or weeks before moving upstream. The upper portions of estuaries often serve as important nursery areas for the young of the year of many anadromous species (e.g., striped bass and American shad). The Chesapeake Bay houses a single catadromous species, the American eel (*Anguilla rostrata*).

(3) *Estuarine fishes* are those which usually occupy the estuary throughout their entire life cycle. They have wide salinity tolerances and the greatest spawning activity in the estuary. Often, adults of these species are small and numerous (e.g., bay anchovy, killifishes).

(4) *Estuarine-Marine fishes* are those that usually spend at least one stage of their life cycle in the estuary, typically using the Bay as a nursery for the young. They usually spawn in nearshore or offshore marine habitats and have wide salinity tolerances. Often these species are referred to as 'estuarine dependent' (e.g., spot,

Atlantic croaker).

(5) *Marine fishes* are commonly or infrequently observed in the lower and middle reaches of estuaries but do not depend upon them to complete their life cycle. They generally do not penetrate the Bay farther then the mouth of the Potomac River and are primarily distributed in the high salinity reaches near the bay mouth. They complete much of their life history in nearshore and offshore marine environments and can be important players in estuarine ecosystems, but they are more frequently important in the shallow-water marine environment (e.g., inshore lizardfish).

Linkage to Environmental Variables -- The statistical relationships between station groups, species scores and environmental variables were analyzed using detrended canonical correspondence analysis (DCCA), a nonlinear eigenvector ordination technique designed for the direct analysis of large, noisy ecological data sets with several environmental covariables (ter Braak 1986, 1988). The method operates on the species abundance and environmental data at the stations, and extracts from the environmental variables synthetic gradients (ordination axes) that maximize the niche separation among species (ter Braak & Verdonshot 1995). DCCA is an approximation to Gaussian regression under a certain set of simplifying assumptions, and is robust to violations of those assumptions (ter Braak & Prentice 1988; Palmer 1993). The program CANOCO (vers. 3.12; ter Braak 1988, 1990) was used for all DCCA analyses.

Significance tests for models relating assemblage structure to environmental variables were based on Monte Carlo permutation tests (10^3 permutations) for the sum of all eigenvalues. The significance of relationships between ordination axes and individual environmental variables was evaluated by *t*-tests for the inter-set correlations and the canonical coefficients (ter Braak 1988, 1990). The weighted average species scores were used in all DCCA ordination plots. Spearman rank correlation was used to ascertain the degree to which the linear combination (DCCA) and weighted average (DCA) station scores ordinations accounted for similar variation. A direct comparison of DCA and DCCA eigenvalues was used to indicate the importance of compositional gradients not accounted for by measured site variables (Allen & Peet 1990).

Estimation of Species Diversity Parameters -- The Shannon-Wiener Index (Shannon & Weaver 1963), coupled with a measure of evenness, provides a good evaluation of community diversity. Although this index has been challenged on theoretical grounds (Hurlbert 1971; Goodman 1975), it continues to be widely used as a method of inter-site comparison in ecological studies (Magurran 1988). The basic formula for the Shannon-Wiener Index (H') is given as:

$$H' = -\Sigma p_i \log p_i \qquad (2.1)$$

where p_i is the proportion of the community (abundance) belonging to the ith species. Pielou's Evenness (J') was used to assess the relative distribution of individuals amongst the species (Pielou 1966). This is derived by dividing the observed value of the Shannon-

Wiener Index by its theoretical maximum value:

$$J' = \frac{H(S)}{H(S)_{max}} \tag{2.2}$$

where $H(S)_{max} = \log S$ (S is the total number of species recorded).

Patterns in longitudinal numerical species richness (number of species per unit of abundance; Kempton 1979) were evaluated via rarefaction, a technique for calculating the expected number of species in each sample if all samples were of a standard size (Sanders 1968). Sander's formula, as modified by Hurlbert (1971), produces such an estimate:

$$E(S) = \sum [1 - [(\frac{N - N_i}{n}) / (\frac{N}{n})]] \tag{2.3}$$

where $E(S)$ is the expected number of species in the rarefied sample, n is the standardized sample size, N is the total number of individuals recorded in the sample to be rarified, and N_i is the number of individuals in the ith species in the sample to be rarified. A standard unit of 100 individuals was used in this analysis.

The program BIODIV (vers. 5.1) was used for all species diversity calculations (Baev & Penev 1995). Species diversity data were fit with a LOWESS line (LOcally WEighted Scatterplot Smoother). LOWESS calculates new smoothed y-values for each x-value and can help to explore the relationship between two variables without trying to fit a specific or predictive model.

Figure 1: Juvenile striped bass seine survey sampling locations. Numeric portion of station designations indicated river mile distances from the confluence with the Chesapeake Bay. * Chickahominy River stations were not included in the analysis.

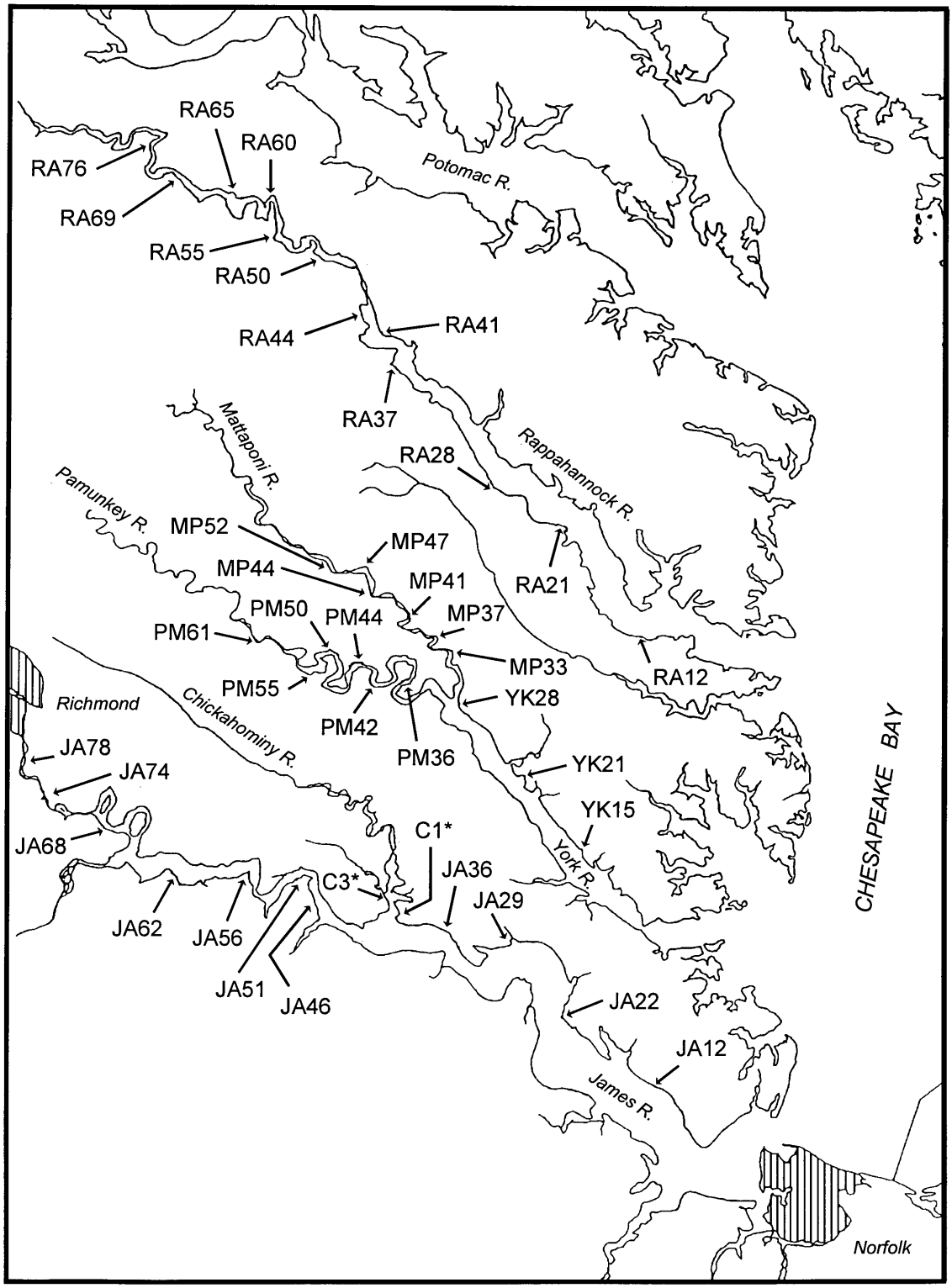

RA65
RA60
RA76
RA69
RA55
RA50
RA44
RA41
RA37
RA28
RA21
RA12
Potomac R.
Rappahannock R.
Mattaponi R.
Pamunkey R.
MP52
MP47
MP44
MP41
MP37
MP33
PM50
PM44
PM61
PM55
PM42
PM36
YK28
YK21
YK15
York R.
Richmond
Chickahominy R.
JA78
JA74
JA68
JA62
JA56
JA51
JA46
C3*
C1*
JA36
JA29
JA22
JA12
James R.
CHESAPEAKE BAY
Norfolk

Table 1: Nearshore substrate classification system.

Substrate Type	Size Class (mm)	Code
Silt - Fine Sand	< 0.25	1.0
Silt-Find Sand/Sand	mixed	1.5
Sand	0.25 - 2.0	2.0
Sand/Granule	mixed	2.5
Granule	2.0 - 4.0	3.0
Granule/Pebble	mixed	3.5
Pebble	4 - 64	4.0

RESULTS

General Attributes of the Fauna

During the period 1990-1994 a total of 90 species of fishes comprising 117,004 individuals (first tow only) were collected, of which 31 were represented by 10 or fewer individuals. The total number of taxa observed in all collections at a station varied from 20-35 species. The numerous rare species reflect the high species diversity of the Chesapeake Bay system relative to other temperate western Atlantic estuaries. The complete ichthyofauna of the Bay system (not including many tidal freshwater species) was recently estimated at over 260 species drawn from both tributaries and the mid-Atlantic bight (Murdy *et al.* 1997). In general, two types of fishes were captured by the beach seine: (1) juveniles of relatively large migratory species (e.g., Atlantic croaker, spot, striped bass); and, (2) adults of relatively small resident species (e.g., silversides, anchovies, minnows, etc.). Table 2 provides a general taxonomic summary for all species captured.

Clupeiform fishes were the most abundant and widely dispersed taxon with 9 species occurring in all three drainages and accounting for 29.1% of the total catch. Silversides (atherinidae) were also numerous (3 species, 15.8% of the individuals), with the Atlantic silverside (*Menidia menidia*) abundant in saltwater and the inland silverside (*Menidia beryllina*) abundant in freshwater. Juveniles of the moronid species white perch (*Morone americanus*) and striped bass (*Morone saxatilis*) were abundant near the freshwater interface, with 16.0% of the total individuals. Minnows and shiners (cyprinidae) were widely distributed in tidal freshwater with 9 species and 11.8% of the

individuals. Sunfishes and basses (centrarchidae) were also commonly encountered in upstream, permanent freshwater regions with 11 species collected. The sciaenidae represented 9 species and 7.4% of the individuals, with juveniles of the spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) abundant in oligo- and mesohaline waters.

The Atlantic menhaden (*Brevoortia tyrannus*, 14.2%), Atlantic silverside (*M. menidia*, 14.2%), white perch (*M. americana*, 10.6%), hogchoker (*Trinectes maculatus*, 9.6%) and spottail shiner (*Notropis hudsonius*, 8.3%) accounted for 56.9% of the total catch and generally present a longitudinal dominance series from mesohaline to tidal freshwater reaches of the estuary. Other species were common in particular habitats, and perhaps can be regarded as indicators of those habitats. For example, the yellow perch (*Perca flavescens*) and juvenile blue catfish (*Ictalurus furcatus*) were indicators of pebble substrate in the Rappahannock River, while the bluespotted sunfish (*Enneacanthus gloriosus*) was only captured in the Mattaponi River in association with submerged aquatic vegetation beds (SAVs).

These relationships and others are described in detail for each river system in the following sections. Appendix 1 contains a general guideline for interpreting the multivariate plots.

Table 2: Summary data and ecological affinity group classification for fish species captured by the VIMS juvenile striped bass seine survey during the period 1990-1994 (first tow only unless otherwise noted).

Order Family (no. of species) Species	Length Range (FL*, mm)	Total Caught (number, rank)	Drainage	Ecological Affinty Group
Myliobatiformes				
Dasyatidae (1)				
Dasyatis centroura	425	1 (64)	R	Marine-Occasional
Myliobatidae (1)				
Rhinoptera bonasus	1200	1 (64)	R	Estuarine-Marine
Lepisosteiformes				
Lepisosteidae (1)				
Lepisosteus osseus	206 - 490	9 (56)	R, Y	Freshwater
Elopiformes				
Elopidae (1)				
Elops saurus	216	1 (64)	J	Marine-Occasional
Anguilliformes				
Anguillidae (1)				
Anguilla rostrata	145 - 614	62 (42)	J, R, Y	Catadromous
Clupeiformes				
Engraulidae (2)				
Anchoa hepsetus	18 - 100	302 (28)	J, R, Y	Estuarine-Marine
Anchoa mitchelli	20 - 95	4,530 (9)	J, R, Y	Estuarine
Clupeidae (7)				
Alosa aestivalis	26 - 84	2,051 (13)	J, R, Y	Anadromous
Alosa pseudoharengus	42 - 92	93 (38)	J, R, Y	Anadromous
Alosa sapidissima	40 - 107	341 (26)	J, R, Y	Anadromous
Brevoortia tyrannus	32 - 196	16,564 (1)	J, R, Y	Estuarine-Marine
Dorosoma cepedianum	26 - 352	6,354 (7)	J, R, Y	Semi-Anadromous
Dorosoma petenense	13 - 176	3,573 (12)	J, R, Y	Semi-Anadromous
Opisthonema oglinum	50 - 126	265 (29)	J, R, Y	Marine-Frequent
Aulopiformes				
Synodontidae (1)				
Synodus foetens	53 - 225	143 (34)	J, R, Y	Marine-Frequent
Siluriformes				
Ictaluridae (6)				
Ameiurus catus	40 - 452	623 (21)	J, R, Y	Freshwater
Ictalurus furcatus	52 - 270	340 (27)	J, R	Freshwater
Ictalurus nebulosus	33 - 230	9 (56)	J, R, Y	Freshwater
Ictalurus punctatus	21 - 519	769 (20)	J, R, Y	Freshwater
Noturus gyrinnus	54	1 (64)	Y	Freshwater
Noturus insignis	75	1 (64)	Y	Freshwater

Order Family (no. of species) Species	Length Range (FL, mm)	Total Caught (number, rank)	Drainage	Ecological Affinty Group
Cypriniformes				
Catastomidae (3)				
Carpiodes cyprinnus	41 - 175	16 (51)	J	Freshwater
Erimyzon oblongus	172 - 173	2 (63)	Y	Freshwater
Moxostoma macrolepidotum	82 - 210	16 (51)	J,Y	Freshwater
Cyprinidae (9)				
Cyprinella analostana	33 - 105	1,882 (15)	J, R, Y	Freshwater
Cyprinnus carpio	70 - 694	16 (51)	J, R	Freshwater
Hybognathus regius	37 - 113	2,034 (14)	J, R, Y	Freshwater
Nocomis leptocephalus	55 - 176	8 (57)	J, Y	Freshwater
Notemigonus chrysoleucas	45 - 155	83 (39)	J, R, Y	Freshwater
Notropis cornutus	60	1 (64)	J	Freshwater
Notropis hudsonius	27 - 116	9,726 (5)	J, R, Y	Freshwater
Notropis spilopterus	58	1 (64)	R	Freshwater
Semotilus corporalis	62 - 65	3 (62)	R	Freshwater
Batrachoidiformes				
Batrachoididae (1)				
Opsanus tau	59 - 262	13 (53)	R, Y	Estuarine
Gobisociformes				
Gobisocidae (1)				
Gobiesox strumosus	34 - 58	9 (56)	J, R, Y	Estuarine
Beloniformes				
Belonidae				
Strongylura marina	75 - 240	77 (40)	J, R, Y	Estuarine-Marine
Cyprinodontiformes				
Cyprinodontidae (2)				
Cyprinodon variegatus	20 - 48	5 (60)	R, Y	Estuarine
Lucania parva	33	1 (64)	Y	Estuarine
Fundulidae (3)				
Fundulus diaphanus	22 - 117	1,210 (17)	J, R, Y	Freshwater
Fundulus heteroclitus	25 - 108	3,787 (10)	J, R, Y	Estuarine
Fundulus majalis	14 - 155	995 (18)	J, R, Y	Estuarine
Poecilidae (1)				
Gambusia affinis	23 - 47	35 (46)	R, Y	Freshwater
Atheriniformes				
Atherinidae (3)				
Membras martinica	38 - 100	195 (31)	J, R, Y	Estuarine
Menidia beryllina	25 - 100	1,700 (16)	J, R, Y	Freshwater
Menidia menidia	28 - 135	16,562 (2)	J, R, Y	Estuarine
Gasterosteiformes				
Syngnathidae (1)				
Syngnathus fuscus	45 - 160	12 (54)	R, Y	Estuarine

Order Family (no. of species) Species	Length Range (FL, mm)	Total Caught (number, rank)	Drainage	Ecological Affinty Group
Scorpaeniformes				
Triglidae				
Prionotus evolans	61 - 76	2 (63)	Y	Marine-Frequent
Prionotus tribulus	35 - 82	4 (61)	Y	Marine-Occasional
Perciformes		10 (55)	J, R, Y	Marine-Frequent
Stromateidae (1)				
Peprilus alepidotus	23 - 90	25 (50)	J, R, Y	Marine-Frequent
Carangidae (3)				
Caranx chrysos	36	1 (64)	J	Marine-Frequent
Caranx hippos	35 - 185	31 (47)	J, R, Y	Marine-Frequent
Trachinotus falcatus	40 - 52	3 (62)	J	Marine-Frequent
Scombridae (2)				
Scomber japonicus	80 - 106	7 (58)	Y	Marine-Occasional
Scomberomorous maculatus	73 - 150	26 (49)	J, R, Y	Marine-Frequent
Mugilidae (2)				
Mugil cephalus	33 - 400	615 (22)	J, R, Y	Estuarine-Marine
Mugil curema	38 - 200	846 (19)	J, R, Y	Estuarine-Marine
Sciaenidae (9)				
Bairdiella chrysoura	31 - 130	186 (32)	J, R, Y	Estuarine
Cynoscion nebulosus	30 - 156	28 (48)	R, Y	Estuarine-Marine
Cynoscion regalis	30 - 111	57 (44)	J, R, Y	Estuarine-Marine
Leiostomus xanthurus	36 - 236	4,650 (8)	J, R, Y	Estuarine-Marine
Micropogonias undulatus	22 - 263	3,609 (11)	J, R, Y	Estuarine-Marine
Mentichirrus americanus	39 - 150	140 (36)	J, R, Y	Marine-Frequent
Mentichirrus saxatilis	52 - 148	3 (62)	Y	Marine-Frequent
Orthopristus chrysoptera	60 - 72	5 (60)	R	Marine-Frequent
Sciaenops oscellatus	48 - 328	7 (58)	J, R, Y	Estuarine-Marine
Epphididae (1)				
Chaetodipterus faber	25 - 78	10 (55)	J, R, Y	Marine-Frequent
Pomatomidae (1)				
Pomatomus saltatrix	50 - 323	75 (41)	J, R, Y	Estuarine-Marine
Gobiidae (1)				
Gobisoma bosci	35	1 (64)	R	Estuarine
Moronidae (2)				
Morone americana	23 - 280	12,353 (3)	J, R, Y	Semi-Anadromous
Morone saxatilis	25 - 520	6,366 (6)	J, R, Y	Anadromous
Percidae (2)				
Etheostoma olmstedii	28 - 89	602 (23)	J, R, Y	Freshwater
Perca flavescens	42 - 267	541 (24)	J, R, Y	Freshwater
Gerreidae (1)				
Eucinostomus gula	59	1 (64)	J	Marine-Occasional
Sparidae (1)				
Stenotomus chrysops **	60 - 129	** **	J	Marine-Frequent

Order Family (no. of species) Species	Length Range (FL, mm)	Total Caught (number, rank)	Drainage	Ecological Affinty Group
Perciformes *cont'd*				
Centrarchidae (11)				
Centrarchus macropterus	47	1 (64)	J	Freshwater
Enneacanthus gloriosus	25 - 68	37 (45)	Y	Freshwater
Lepomis auritus	25 - 175	369 (25)	J, R, Y	Freshwater
Lepomis gibbosus	38 - 177	183 (33)	J, R, Y	Freshwater
Lepomis gulosus	78	1 (64)	R	Freshwater
Lepomis macrochirus	25 - 178	208 (30)	J, R, Y	Freshwater
Lepomis microlophus	71 - 204	14 (52)	J, R, Y	Freshwater
Lepomis punctatus	53	1 (64)	Y	Freshwater
Micropterus dolomieu	48 - 108	26 (49)	J, R, Y	Freshwater
Micropterus salmoides	45 - 315	142 (35)	J, R, Y	Freshwater
Pomoxis nigromaculatus	50 - 152	3 (62)	J, Y	Freshwater
Polynemidae (1)				
Polydactylus octonemus	105	1 (64)	J	Marine-Occasional
Tetraodontiformes				
Tetraodontidae (1)				
Sphoeroides maculatus	45 - 148	4 (61)	J, R, Y	Marine-Frequent
Pleuronectiformes				
Cynoglossidae (1)				
Symphurus plagiusa	40 - 132	101 (37)	J, R, Y	Estuarine
Achiridae (1)				
Trinectes maculatus	15 - 159	11,238 (4)	J, R, Y	Estuarine
Paralichthyidae (1)				
Paralichthys dentatus	46 - 455	59 (43)	J, R, Y	Estuarine-Marine

* All lengths are fork length; if the caudal fin is not forked, lengths are total length. Lengths for rajaform fishes are disk width.

** *Stenotomus chrysops* was only captured in a second tow and is included for informational purposes only.

Rappahannock River Community Patterns

A total of 67 species of fishes comprising 44,051 individuals were collected (first tow only), of which 21 were represented by 5 or fewer individuals, and 38 met the 3% capture frequency criterion for inclusion in the gradient analysis.

Spatial Assemblage Patterns (TWINSPAN & DCA) -- The first three levels of the TWINSPAN classification of all stations clearly reveals the longitudinal salinity gradient (Fig. 2), and suggests the presence of six intergrading assemblages of sandy beach fishes. The first dichotomy was very strong (eigenvalue 0.62) and separates primarily tidal freshwater stations (subset 0) from saline stations (subset 1). At the second division level, tidal freshwater stations (subset 0) were subdivided into pebble bottoms (Group 1) vs. sandy bottoms (subset 01). Subset 01 separated at the third division level into permanent tidal freshwater stations (Group 2) and those stations which are infrequently saline (i.e., average salinity < 1 ppt; Group 3). Saline stations (subset 1) separated at the second division level into oligohaline stations (Group 4) vs. mesohaline stations (subset 11). Subset 11 further separated at the third division level due primarily to the limited upstream penetration of a few polyhaline species (Groups 5 and 6). Further divisions of Groups 1-6 were not considered as they seemed mainly due to the presence of less common species and did not yield distinct groups within the DCA ordination space.

The DCA ordination of all stations is presented in Figure 3. Although the TWINSPAN groups are generally well defined, many stations in neighboring groups are

adjacent. Overall, the ordination represents a continuum of riverine beach assemblages. The largest separation occurs across the origin of axis 1 and corresponds to the faunal break associated with the freshwater interface. Station scores along the first axis were generally separated into four regions along the salinity gradient associated with permanent tidal freshwater (Groups 1-2), freshwater interface (Group 3), oligohaline (Group 4) and mesohaline salinities (Groups 5-6). The eigenvalue (0.61) of the first axis suggests the gradient represented by it is highly significant and by far the most important. The ecological distance of about 3.7 SD between the permanent tidal freshwater and mesohaline station groups indicates that the faunas at the extremities of the estuarine gradient were about 93% dissimilar. The second axis has a lower eigenvalue (0.13), is relatively short (1.64 SD; 41% dissimilar), and served primarily to separate permanent tidal freshwater stations according to nearshore substrate.

Figure 4 shows the DCA ordination of the 38 species from the Rappahannock River meeting the first tow 3% frequency criterion for retention. Species symbols correspond to the modified ecological affinity groups of McHugh (1967) as defined in the Methods and Materials section. The first DCA axis described a longitudinal gradient running from permanent tidal freshwater stations to less speciose oligohaline stations and finally into the mesohaline reach of the lower estuary. A large faunal break occurs across the origin of the first axis (1.6 SD) producing two groups of species: those with negative scores (primarily freshwater and diadromous species), and those with positive scores (estuarine and marine species).

Environmental Correlates (DCCA) -- A direct comparison of the distribution of constrained (DCCA) and unconstrained (DCA) station scores is given in Table 3. Spearman rank correlations indicate that the two ordination methods accounted for similar variation. Further support for this interpretation is indicated by similar gradient lengths and eigenvalues generated by the two methods. The lower correlation between the second axis of DCA and DCCA probably indicates the importance of unmeasured variables (or spatial scales), and may be complicated by the relatively large stochasticity in abundance and distribution patterns for estuarine vs. freshwater fish assemblages.

The overall ordination was significant ($p<0.001$) and the first two DCCA axes explained 78.8% of the total variance in species-environment relations (Tab. 4). Significant correlations and canonical coefficients of species scores on DCCA axis 1 with environmental factors indicated that this axis was positively correlated with salinity (0.91) and negatively correlated with fluvial distance to the bay mouth (-0.93). A strong and unsurprising negative correlation between these two variables was observed. However, station groups with similar salinities (Groups 1 & 2; Groups 5 & 6) are separated along the second DCA axis implicating salinity as the primary actor in the gradient represented by axis 1. Only nearshore substrate grain size was significant on the second DCCA axis (-0.67), and largely served to separate pebble from sandy nearshore substrates in the permanent tidal freshwater reach of the river. Correlations on the third and higher DCCA axes were not considered due to their low eigenvalues.

The arrangement of species scores on DCCA axes 1 and 2 strongly support the results derived from TWINSPAN/DCA (Fig. 5). The order of species along the first axis

corresponds well with the general salinity preferences and tolerances of McHugh's ecological affinity groups; with species scores well ordered from freshwater → estuarine → marine taxa. The large variation of freshwater resident species along axis 2 probably represents small-scale (i.e., 10's - 100's of meters) habitat preferences, particularly with respect to nearshore substrate. Other unmeasured variables which have been implicated in the distribution of freshwater stream fishes may also be important (e.g., current speed, turbidity and the presence of woody debris).

Species-Environment Associations -- Specific species associations with TWINSPAN station groups are catalogued below and are summarized in Table 5. Environmental values for TWINSPAN station groups are summarized in Table 6.

Permanent Tidal Freshwater (Pebble Bottom): This group included 9 stations and is derived entirely from samples taken in the permanent tidal freshwater reach of the river at stations RA-65 and RA-69 (TWINSPAN Group 1). These stations support primarily freshwater (24) and anadromous (5) species with a total of 4,128 individuals and 33 species collected. The spottail shiner (*Notropis hudsonius*; 27.3%), gizzard shad (*Dorosoma cepedianum*; 12.2%), juvenile white perch (*Morone americana*; 10.8%), inland silverside (*Menidia beryllina*; 9.8%), blue catfish (*Ictalurus furcatus*; 7.3%) and yellow perch (*Perca flavescens*; 6.4%) comprised 73.8% of all individuals captured at these sites. This group exhibits a relatively well-defined species composition: it contains many of the ubiquitous species found in the other permanent tidal freshwater stations, and several characteristic species with high densities and frequencies of occurrence (FOC). TWINSPAN identified the gizzard shad (FOC 74%), yellow perch (FOC 90%),

pumpkinseed (*Lepomis gibbosus*; FOC 51%) and the American eel (*Anguilla rostrata*; FOC 41%) as indicator species which served to separate these stations from other tidal freshwater stations (i.e., TWINSPAN Groups 2 and 3). The spottail shiner (FOC 97%) was numerically dominant and the most frequently occurring species. Other widely distributed tidal freshwater taxa consistently found at these sites included the juvenile white perch (FOC 90%) and the satinfin shiner (*Cyprinella analostana*; FOC 74%).

Juveniles of the anadromous shads and herrings (*Alosa aestivalis*, *Alosa pseudoharengus* and *Alosa sapidissima*) were also centered near the pebble substrate stations in permanent tidal freshwater. In Chesapeake Bay tributaries, juvenile alosids are distributed widely throughout the water column in tidal freshwater during the spring and early summer, but move upstream in late summer with the encroachment of salt water (Warinner *et al.* 1970; Loesch 1987). Therefore, this may represent a concentration of individuals above the influence of the salt wedge, and not necessarily a substrate choice.

Permanent Tidal Freshwater (Sandy Bottoms): This group included 11 stations (TWINSPAN Group 2), and supports primarily ubiquitous freshwater (24) and anadromous species (4) with a total of 5,213 individuals and 35 species collected. Juvenile white perch (*M. americana*; 36.8%), spottail shiner (*N. hudsonius*; 14.1%), juvenile striped bass (*M. saxatilis*; 10.8%), the eastern silvery minnow (*Hybognathus regius*; 7.6%), satinfin shiner (*C. analostana*; 7.6%), the banded killifish (*Fundulus diaphanus*; 7.1%) and the hogchoker (*T. maculatus*; 5.4%) comprised 89.4% of all individuals captured at these sites. Relatively high densities and FOC of the hogchoker (FOC 84%) and the banded killifish (FOC 73%) characterized this group in the

TWINSPAN analysis. The most frequently occurring species were juvenile white perch (FOC 93%), juvenile striped bass (FOC 91%) and the spottail shiner (FOC 89%).

Lower Tidal Freshwater (Sandy Bottoms): This group included 13 stations (TWINSPAN Group 3), and supports several freshwater (17), diadromous (5), estuarine (6) and estuarine-marine (7) species, with a total of 9,804 individuals and 37 species collected. Juvenile white perch (*M. americana*; 20.0%), juvenile striped bass (*M. saxatilis*; 16.9%), spottail shiner (*N. hudsonius*; 13.0%), juvenile alewife (*Alosa pseudoharengus* ; 11.6%), juvenile Atlantic menhaden (*Brevoortia tyrannus*; 8.3%), the inland silverside (*M. beryllina*; 3.8%) and the satinfin shiner (*C. analostana*; 3.3%) comprised 76.9% of the total catch. These stations were dominated by low salinity and freshwater/anadromous species, yet the TWINSPAN analysis identified juveniles of the higher salinity species Atlantic croaker (*Micropogonias undulatus*; FOC 40%) and spot (*Leiostomus xanthurus*; FOC 32%) as indicator species. The most frequently occurring species were juvenile white perch (FOC 95%), juvenile striped bass (FOC 94%), spottail shiner (FOC 94%) and the tessellated darter (*Etheostoma olmstedi*; FOC 81%).

Oligohaline: This group included 13 stations (TWINSPAN Group 4), and supports primarily estuarine (9) and estuarine-marine (9) species, although numerous freshwater (14) and diadromous (3) species occur in lower numbers. A total of 17,814 individuals and 40 species were collected. Juvenile Atlantic menhaden (*B. tyrannus*; 43.2%), the Atlantic silverside (*Menidia menidia*; 18.4%), juvenile white perch (*M. americana*; 9.8%), juvenile striped bass (*M. saxatilis*; 6.2%), the spot (*L. xanthurus*; 6.2%) and the mummichog (*Fundulus heteroclitus*; 3.8%) comprised 87.6% of all

individuals captured at these sites. Though estuarine and estuarine-marine species were numerically dominant, the TWINSPAN analysis identified the freshwater interface centered species juvenile white perch (FOC 89%) and channel catfish (*Ictalurus punctatus*; FOC 27%) as indicator species. The most frequently occurring species were juvenile white perch (FOC 89%), the spot (FOC 86%), the Atlantic silverside (FOC 83%) and juvenile striped bass (FOC 74%). Average salinity for the stations in this group was 3.75 ± 0.34 ppt.

Mesohaline I: This group included 9 stations (TWINSPAN Group 5), and supports primarily estuarine (13), estuarine-marine (12) and marine (5) species with a total of 15,443 individuals and 36 species collected. Juvenile Atlantic menhaden (*B. tyrannus*; 63.6%), the Atlantic silverside (*M. menidia*; 20.9%), the bay anchovy (*Anchoa mitchelli*; 6.4%) and the spot (*L. xanthurus*; 5.1%) comprised 96.0% of all individuals captured at these sites. High densities and FOC of the Atlantic silverside (FOC 98%) and bay anchovy (FOC 72%) distinguished this group in the TWINSPAN analysis. The spot (FOC 84%) was also a regular component of the fish assemblage. Average salinity for the stations in this group was 12.42 ± 0.43 ppt.

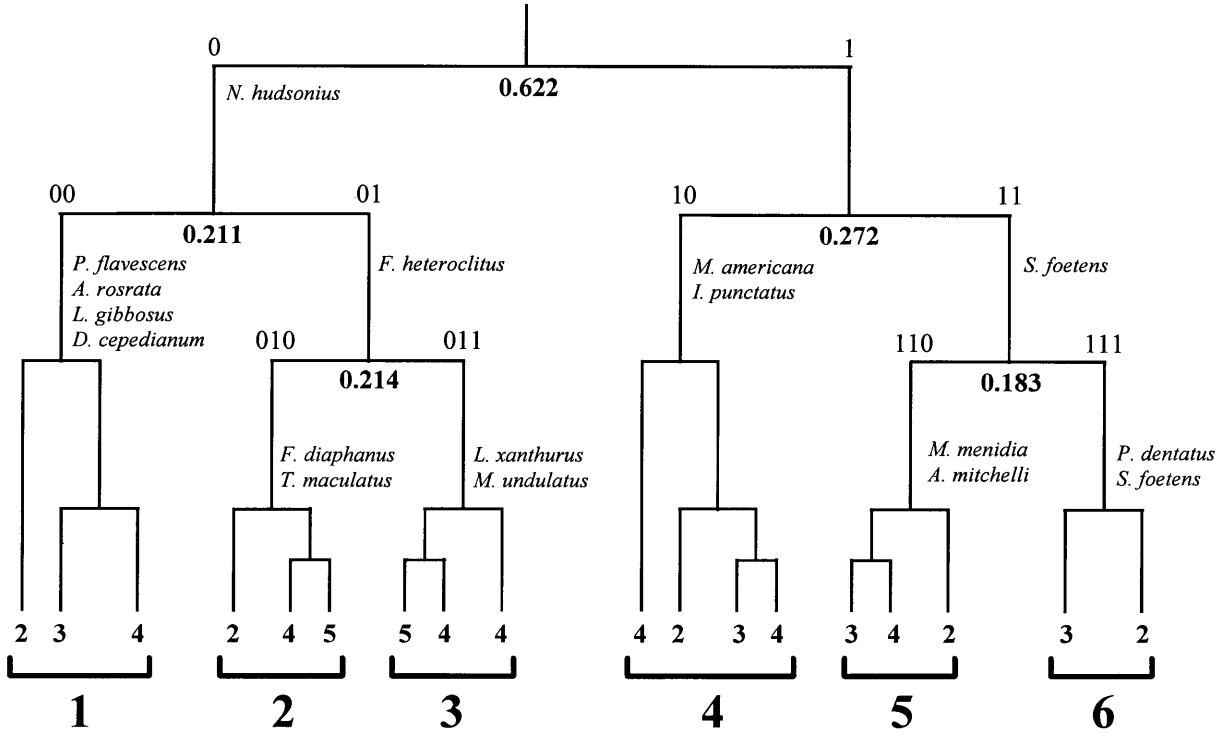
Mesohaline II: This group included 5 stations (TWINSPAN Group 6; all collections from RA-12), and supports primarily estuarine-marine (7), estuarine (9) and marine (7) species with a total of 2,557 individuals and 27 species collected. Juvenile Atlantic menhaden (*B. tyrannus*; 38.1%), the spot (*L. xanthurus*; 32.9%) and the Atlantic silverside (*M. menidia*; 13.6%) comprised 84.6% of all individuals captured at this site. Relatively high first tow densities and frequency of occurrence of the inshore lizardfish

(*Synodus foetens*; FOC 67%) and summer flounder (*Paralichthys dentatus*; FOC 33%) served to separate these stations from other mesohaline stations in the TWINSPAN analysis. The most frequently occurring species were the spot (FOC 96%) and Atlantic silverside (FOC 75%). Average salinity for the stations in this group was 14.42 ± 0.55 ppt.

Species Diversity -- Rarefied longitudinal species richness (alpha diversity) was generally lower in the saline portion of the river, and demonstrated a persistent minimum near RA-28 (Fig. 6b). A local minimum was also evident in the tidal freshwater portion near RA-60 which may be associated with a lower total sample area (i.e., the species-area effect; Fig. 7). Total species richness displayed similar patterns (Fig. 6a); although, the upstream increase was less pronounced. This may be partially due to the generally higher abundances of the dominant species in mesohaline vs. fresh waters. However, the removal of Atlantic menhaden (which represented 60% of the total catch in mesohaline waters) had no noticeable effect on the rarefaction curve. Species evenness and diversity displayed a similar trend of increasing values moving upstream (Figs. 8 & 9). Interannual variability in both evenness and diversity were noticeably less in the tidal freshwater areas (i.e., above RA-50) suggesting more stable and diverse assemblages above the influence of saline waters. Similarly, the highest compositional turnover (beta diversity) in the Rappahannock River was observed across the freshwater interface between sites RA-37 and RA-55; above and below these sites the rate of change was noticeably less (Fig. 10).

Figure 2: TWINSPAN classification of Rappahannock River stations. Indicator species for each division are shown in decreasing order of importance. Eigenvalues of major divisions are shown in bold under each division. Binary numbers above divisions denote major subsets. Smaller font numbers below final groups are the number of stations within that group. Larger font numbers below brackets are final TWINSPAN group labels. Station labels are rivermile-year.

Rappahannock River
(n=60)



1	2	3	4	5	6
RA65-90	RA55-94	RA44-90	RA28-94	RA28-90	RA12-90
RA65-92		RA44-93		RA28-91	RA12-91
RA65-93	RA60-90	RA44-94	RA37-90	RA28-92	RA12-92
RA65-94	RA60-91		RA37-91	RA28-93	RA12-93
	RA60-92	RA50-90	RA37-92		RA12-94
RA69-90	RA60-93	RA50-91	RA37-93	RA21-90	
RA69-91	RA60-94	RA50-92	RA37-94	RA21-91	
RA69-92		RA50-93		RA21-92	
RA69-93	RA76-90	RA50-94	RA41-90	RA21-93	
RA69-94	RA76-91		RA41-91	RA21-94	
	RA76-92	RA55-90	RA41-92		
	RA76-93	RA55-91	RA41-93		
	RA76-94	RA55-92	RA41-94		
		RA55-93			
			RA44-91		
			RA44-92		

Figure 3: Axes 1 and 2 of DCA ordination of Rappahannock River stations. Symbols correspond to TWINSPAN groups. Units are standard deviations in species turnover rate.

Rappahannock River Station Scores
(TWINSPAN Groups)

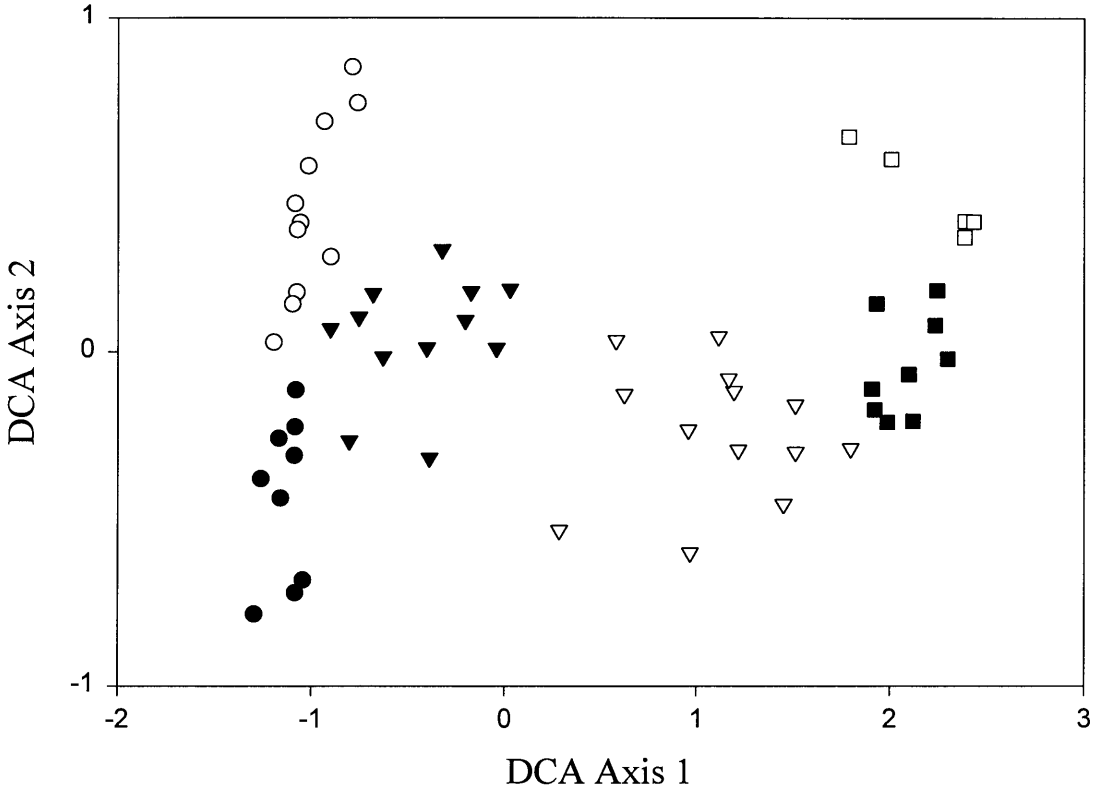
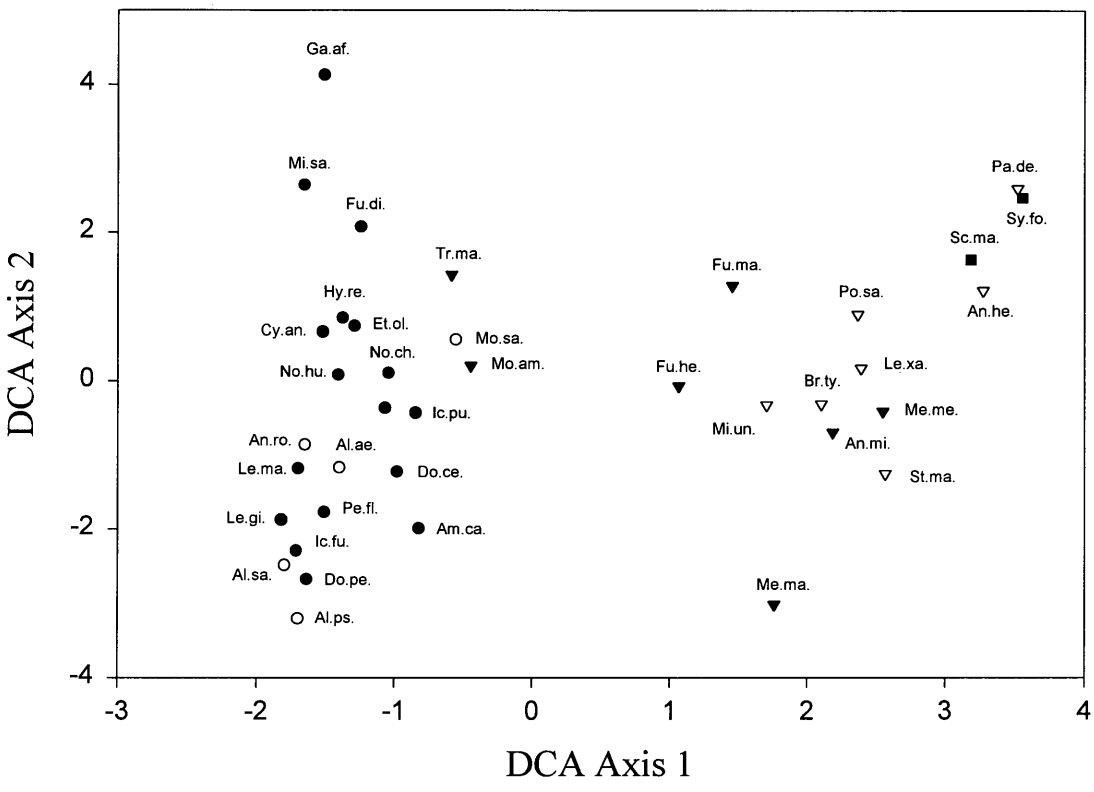


Figure 4: Axes 1 and 2 of DCA ordination of the 38 Rappahannock River species included in the gradient analysis. Symbols correspond to the modified ecological groups of McHugh (1967). Species labels are the first f our letters of genus and species names respectively (see Appendix 2 for a complete alphabetical list). Units are standard deviations in species turnover rate.

Rappahannock River Species Scores
(Ecological Affinity Groups)



- Freshwater Species
- Diadromous Species
- Estuarine Species
- Estuarine-Marine Species
- Marine Species

Table 3: Direct comparison of DCA and DCCA axes via Spearman rank correlation for the Rappahannock River stations. DCA scores are weighted average scores and DCCA scores are linear combination scores predicted from the multiple regression.

	Eigenvalue		Gradient Length		
Ordination Axis	**DCA**	**DCCA**	**DCA**	**DCCA**	r^2
1	0.61	0.56	3.73	2.67	0.95 ***
2	0.13	0.10	1.64	1.27	0.66 ***

*** $p < 0.001$

Table 4: Results of the detrended canonical correspondence analysis of fish assemblages from the Rappahannock River. Significance values of correlation and canonical coefficients correspond to a two-tailed students *t*-test.

Variable	Axis 1	Axis 2
Canonical Coefficients for Environmental Variables		
Salinity	0.2178 *	0.0652
Temperature	0.0044	0.0035
Dissolved O_2	0.0060	-0.0035
pH	-0.0587	0.0028
Substrate Grain Size	-0.0645	-0.3399 ***
Channel Width	0.1949	-0.2987 ***
6' Contour	-0.0048	-0.0494
Distance to Bay Mouth	-0.3356 ***	-0.0878
Correlations of Environmental Variables with Axes		
Salinity	0.9093 ***	0.0040
Temperature	-0.4770 ***	0.1117
Dissolved O_2	0.0561	-0.2131
pH	-0.0827	-0.1462
Substrate Grain Size	-0.4499 ***	-0.6711 ***
Channel Width	0.9124 ***	-0.1572
6' Contour	0.3944 ***	-0.1503
Distance to Bay Mouth	-0.9332 ***	0.0657
Summary Statistics for Ordination Axes		
Eigenvalue	0.558	0.098
Species-environment correlation	0.963	0.886
Cummulative % of species-environment variance explained	67.0	78.8
Monte Carlo probability for significance of the sum of all eigenvalues (10^3 pemutations): 0.001		

*** $p < 0.005$ ** $p < 0.01$ * $p < 0.05$

Figure 5: Axes 1 and 2 of DCCA ordination of the 38 Rappahannock River species included in the gradient analysis. Environmental variables are indicated with vectors. Only statistically significant variables are included in the ordination diagram. Abbreviations are the first four letters in both the genus and species names (see Appendix 2 for a complete list).

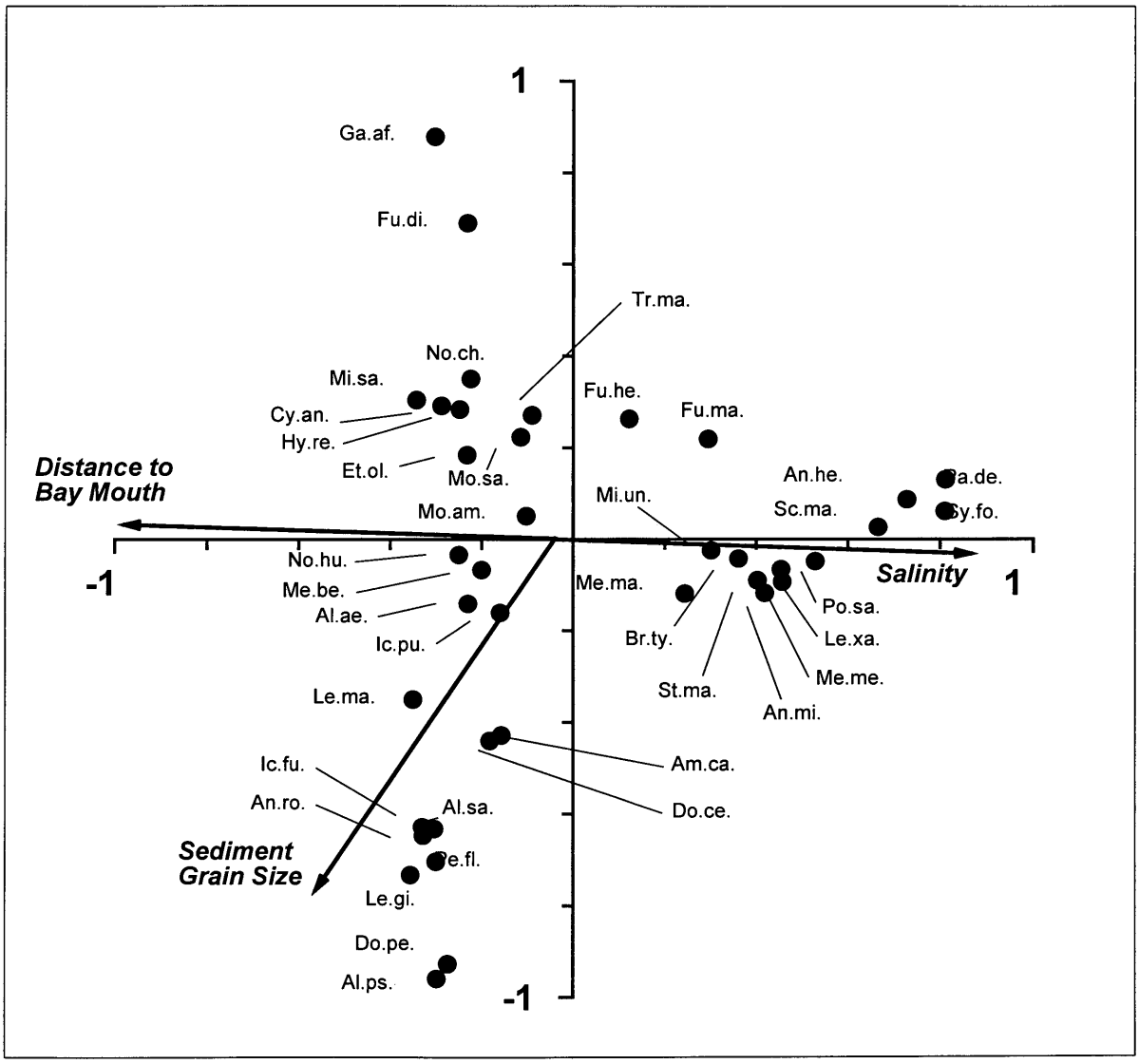

1
-1
1
-1
Distance to Bay Mouth
Salinity
Sediment Grain Size
Ga.af.
Fu.di.
Tr.ma.
No.ch.
Mi.sa.
Cy.an.
Hy.re.
Et.ol.
Mo.sa.
Mo.am.
Fu.he.
Fu.ma.
An.he.
Sc.ma.
Mi.un.
No.hu.
Me.be.
Al.ae.
Ic.pu.
Le.ma.
Me.ma.
Br.ty.
St.ma.
Po.sa.
Le.xa.
Me.me.
An.mi.
Ic.fu.
An.ro.
Al.sa.
Le.fl.
Le.gi.
Do.pe.
Al.ps.
Am.ca.
Do.ce.

Table 5: Dominant and indicator taxa for TWINSPAN groups of Rappahannock River stations. Density is mean (+/- 1 standard error) abundance per 1000 m^2 swept area calculated for all stations included in the TWINSPAN group. FOC = frequency of occurence in the stations from the TWINSPAN group. Indicator species are denoted with an asterisk.

TWINSPAN Group	Dominant & Indicator Taxa					
	Species	Density (#/10^3 m^2)		FOC	Fork Length (mm)	
1	*Notropis hudsonius*	71.66	(13.09)	0.97	70.17	(0.47)
	Dorosoma cepedianum *	29.50	(10.51)	0.74	78.16	(1.76)
	Morone americana	27.84	(3.72)	0.90	91.73	(1.30)
	Menidia beryllina	22.47	(8.55)	0.54	66.43	(0.25)
	Ictalurus furcatus	19.02	(5.99)	0.59	119.18	(2.59)
	Perca flavescens *	17.70	(2.89)	0.90	106.50	(1.96)
	Cyprinella analostana	12.32	(2.79)	0.74	61.09	(0.75)
	Hybognathus regius	8.60	(2.97)	0.67	68.36	(1.12)
	Alosa aestivalis	5.30	(1.97)	0.38	49.56	(0.54)
	Etheostoma olmstedii	4.81	(0.94)	0.64	67.75	(1.03)
	Morone saxatilis	4.66	(0.80)	0.72	64.88	(3.44)
	Trinectes maculatus	3.50	(0.80)	0.64	53.61	(1.73)
	Lepomis gibbosus *	3.20	(1.23)	0.51	111.59	(2.47)
	Ictalurus punctatus	2.52	(0.50)	0.54	150.59	(10.48)
	Alosa pseudoharengus	2.30	(0.97)	0.26	61.24	(1.64)
	Lepomis macrochirus	1.77	(0.47)	0.41	75.00	(7.29)
	Anguilla rostrata *	1.45	(0.37)	0.41	208.74	(5.65)
	Fundulus diaphanus	1.07	(0.30)	0.31	62.47	(2.63)
2	*Morone americana*	160.85	(28.81)	0.93	64.60	(0.62)
	Notropis hudsonius	63.01	(12.61)	0.89	69.43	(0.63)
	Morone saxatilis	46.35	(8.55)	0.91	54.61	(0.56)
	Cyprinella analostana	38.68	(8.82)	0.82	58.67	(0.48)
	Hybognathus regius	36.71	(12.09)	0.60	63.68	(0.72)
	Fundulus diaphanus *	32.60	(5.92)	0.73	65.88	(0.57)
	Trinectes maculatus *	22.91	(5.45)	0.84	44.25	(0.88)
	Menidia beryllina	11.69	(4.61)	0.53	63.43	(0.77)
	Etheostoma olmstedii	5.23	(1.00)	0.53	67.10	(1.02)
3	*Morone saxatilis*	44.62	(8.14)	0.94	57.51	(0.58)
	Notropis hudsonius	36.50	(4.87)	0.94	68.1	(0.97)
	Morone americana	31.40	(5.95)	0.95	70.99	(0.78)
	Alosa aestivalis	27.35	(13.42)	0.37	50.48	(0.12)
	Hybognathus regius	16.00	(7.42)	0.47	67.08	(0.56)
	Cyprinella analostana	9.40	(1.82)	0.61	56.45	(0.55)
	Menidia beryllina	7.04	(1.13)	0.74	62.76	(0.62)
	Etheostoma olmstedii	6.35	(0.90)	0.81	66.47	(0.49)
	Trinectes maculatus	5.53	(2.09)	0.60	57.16	(1.50)
	Micropogonias undulatus *	4.52	(1.10)	0.40	105.22	(1.01)
	Leiostomus xanthurus *	2.58	(0.76)	0.32	101.70	(1.80)
	Ictalurus punctatus	2.46	(0.47)	0.55	140.87	(9.99)

TWINSPAN Group	Dominant & Indicator Taxa					
	Species	Density (#/10^3 m^2)		FOC	Fork Length (mm)	
3	*Fundulus diaphanus*	2.00	(0.61)	0.40	65.67	(1.25)
cont'd	*Dorosoma cepedianum*	1.67	(0.60)	0.26	116.57	(7.84)
	Fundulus heteroclitus	1.30	(0.30)	0.34	61.00	(1.49)
4	*Brevoortia tyrannus*	131.37	(59.14)	0.41	92.68	(0.11)
	Menidia menidia	48.75	(11.93)	0.83	65.18	(0.13)
	Morone americana *	28.82	(4.08)	0.89	80.99	(1.14)
	Leiostomus xanthurus	16.64	(2.88)	0.86	88.46	(1.30)
	Micropogonias undulatus	15.06	(3.41)	0.59	103.25	(0.74)
	Morone saxatilis	14.96	(4.08)	0.74	59.35	(0.79)
	Fundulus heteroclitus	10.70	(3.35)	0.50	60.09	(0.48)
	Anchoa mitchelli	4.78	(1.48)	0.44	55.28	(0.47)
	Membras martinica	2.47	(1.23)	0.24	83.33	(0.81)
	Trinectes maculatus	1.52	(0.45)	0.26	54.01	(1.42)
	Dorosoma cepedianum	1.03	(0.28)	0.32	173.49	(10.87)
	Ictalurus punctatus *	0.69	(0.17)	0.27	242.16	(22.88)
5	*Brevoortia tyrannus*	264.80	(151.20)	0.42	81.74	(0.14)
	Menidia menidia *	109.30	(28.74)	0.98	68.22	(0.17)
	Anchoa mitchelli *	28.55	(7.03)	0.72	55.43	(0.43)
	Leiostomus xanthurus	21.86	(4.01)	0.84	102.47	(2.16)
	Micropogonias undulatus	5.50	(1.48)	0.44	123.49	(2.66)
	Anchoa hepsetus	2.72	(1.30)	0.33	71.36	(1.79)
	Fundulus majalis	1.30	(0.41)	0.33	101.38	(3.76)
	Morone americana	1.08	(0.55)	0.26	180.47	(6.70)
	Synodus foetens	0.59	(0.19)	0.23	123.54	(7.54)
6	*Leiostomus xanthurus*	60.23	(17.40)	0.96	106.47	(0.68)
	Brevoortia tyrannus	55.53	(52.12)	0.25	100.81	(0.29)
	Menidia menidia	20.41	(9.15)	0.75	70.15	(0.42)
	Anchoa hepsetus	5.62	(2.93)	0.33	62.16	(1.15)
	Synodus foetens *	3.57	(0.87)	0.67	120.28	(14.52)
	Trinectes maculatus	2.80	(1.26)	0.33	96.86	(1.44)
	Anchoa mitchelli	2.64	(1.33)	0.33	56.07	(0.92)
	Micropogonias undulatus	2.40	(0.94)	0.33	149.65	(3.97)
	Fundulus majalis	1.37	(0.68)	0.25	111.63	(2.55)
	Paralicthys dentatus *	0.78	(0.25)	0.33	162.46	(15.09)

Table 6: Average environmental values by TWINSPAN group for stations from the Rappahannock River. Quantitative variables are mean ± one standard error. Channel measurements are given as a range.

TWINSPAN Group	Salinity (ppt)	Temperature (°C)	Dissolved O_2 (mg ℓ^{-1})	pH
1	0.00 ∓ 0.00	27.95 ∓ 0.37	7.14 ∓ 0.19	7.58 ∓ 0.10
2	0.00 ∓ 0.00	28.09 ∓ 0.31	6.27 ∓ 0.14	7.40 ∓ 0.07
3	0.45 ∓ 0.11	27.89 ∓ 0.27	7.00 ∓ 0.16	7.31 ∓ 0.14
4	3.75 ∓ 0.34	27.43 ∓ 0.28	6.75 ∓ 0.15	7.22 ∓ 0.09
5	12.42 ∓ 0.43	26.31 ∓ 0.37	6.51 ∓ 0.19	7.38 ∓ 0.08
6	14.42 ∓ 0.55	26.84 ∓ 0.59	6.67 ∓ 0.28	7.60 ∓ 0.09

	Nearshore Sediment	6' Contour (m)	Distance to Bay Mouth (Nm)	SAV Beds
1	Pebble	72 - 178	82.78 - 87.43	No
2	Sand-Granule	16 - 27	72.88 - 93.98	No
3	Sand-Granule	16 - 1231	62.18 - 72.88	No
4	Sand-Granule	161 - 1231	46.18 - 2.18	No
5	Sand	343 - 485	39.08 - 6.18	No
6	Sand	288	29.98	No

Figure 6: Total (a) and rarefied (b) longitudinal species richness in the Rappahannock River, 1990-94. Rarefied values are fit with a LOWESS curve.

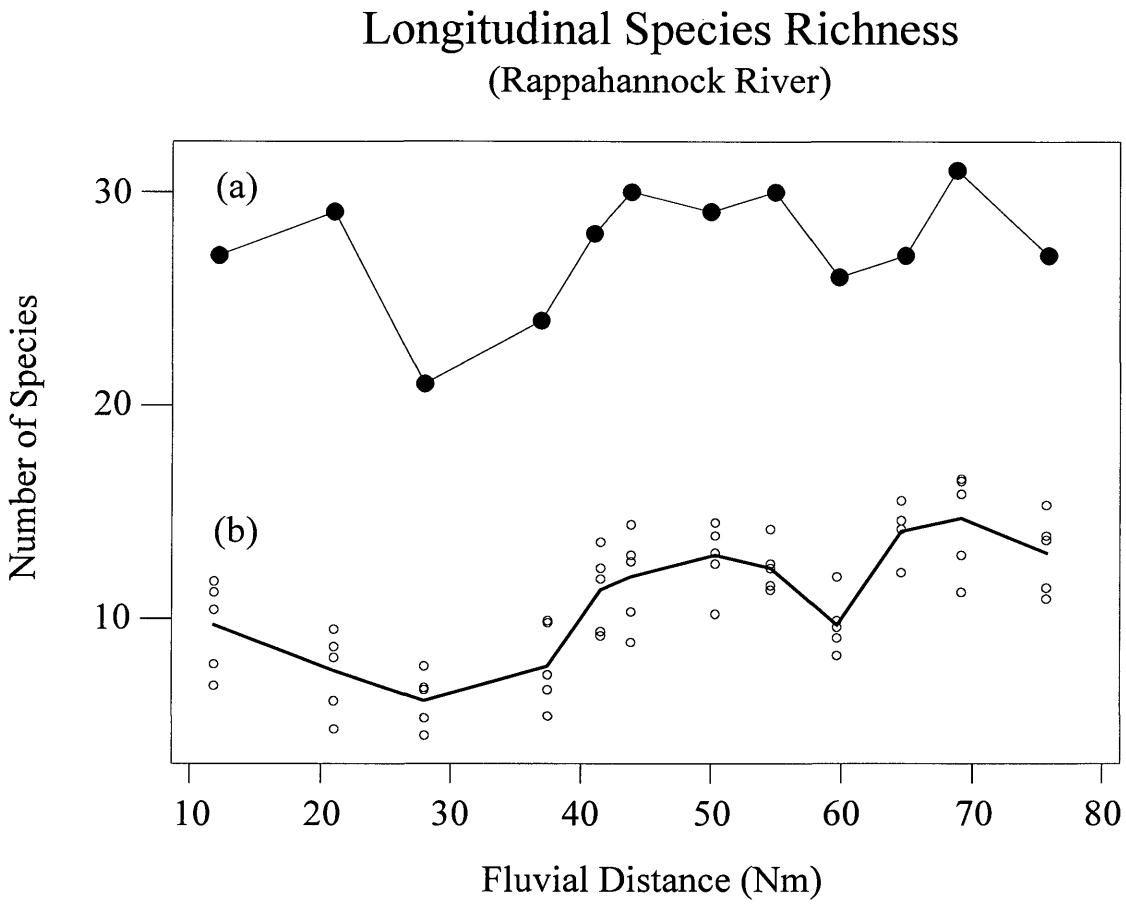

Longitudinal Species Richness
(Rappahannock River)
Number of Species
30
20
10
(a)
(b)
10
20
30
40
50
60
70
80
Fluvial Distance (Nm)

Figure 7: Total species captured and total area swept for Rappahannock River stations, 1990-1994.

Species-Area Relationship
(Rappahannock River)

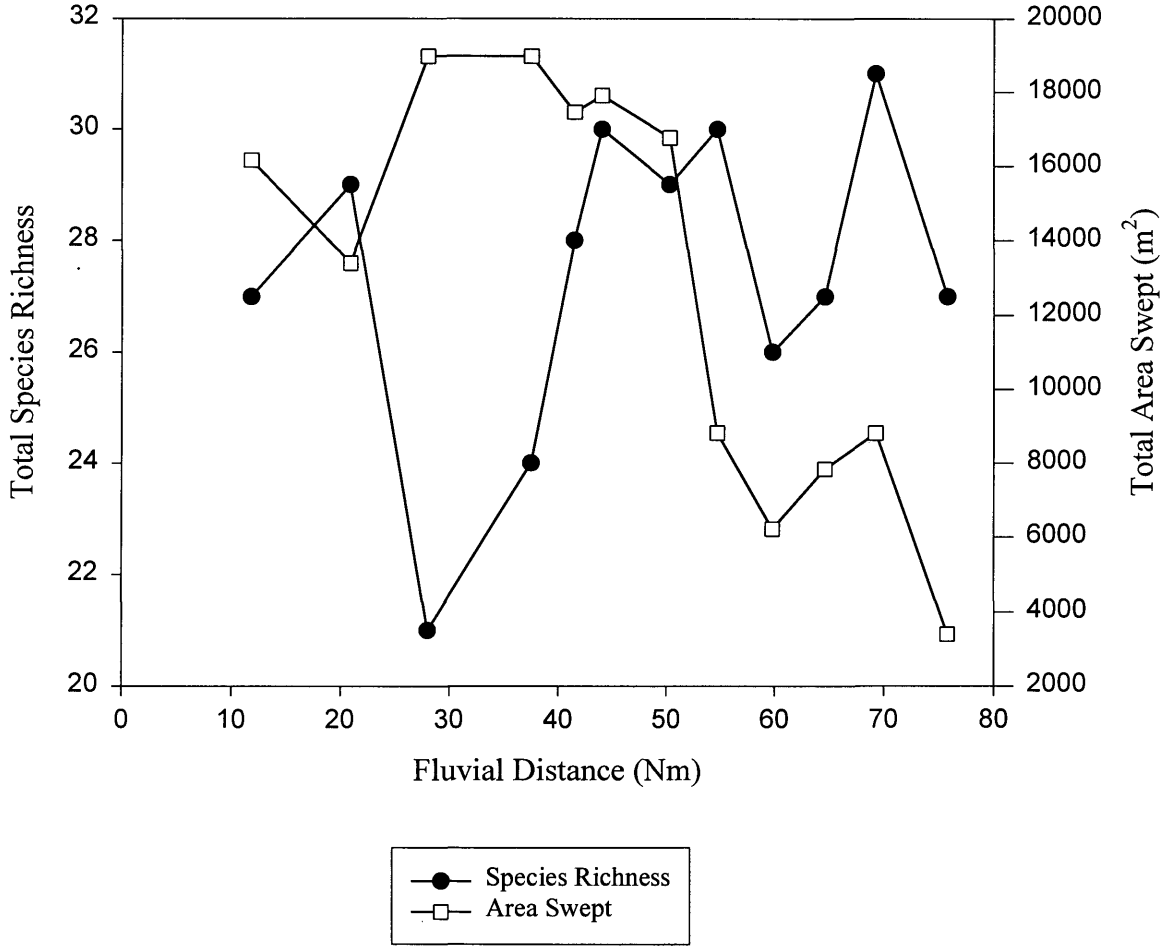


Figure 8: Longitudinal species evenness (Pielou's) in the Rappahannock River, 1990-1994, fit with a LOWESS curve.

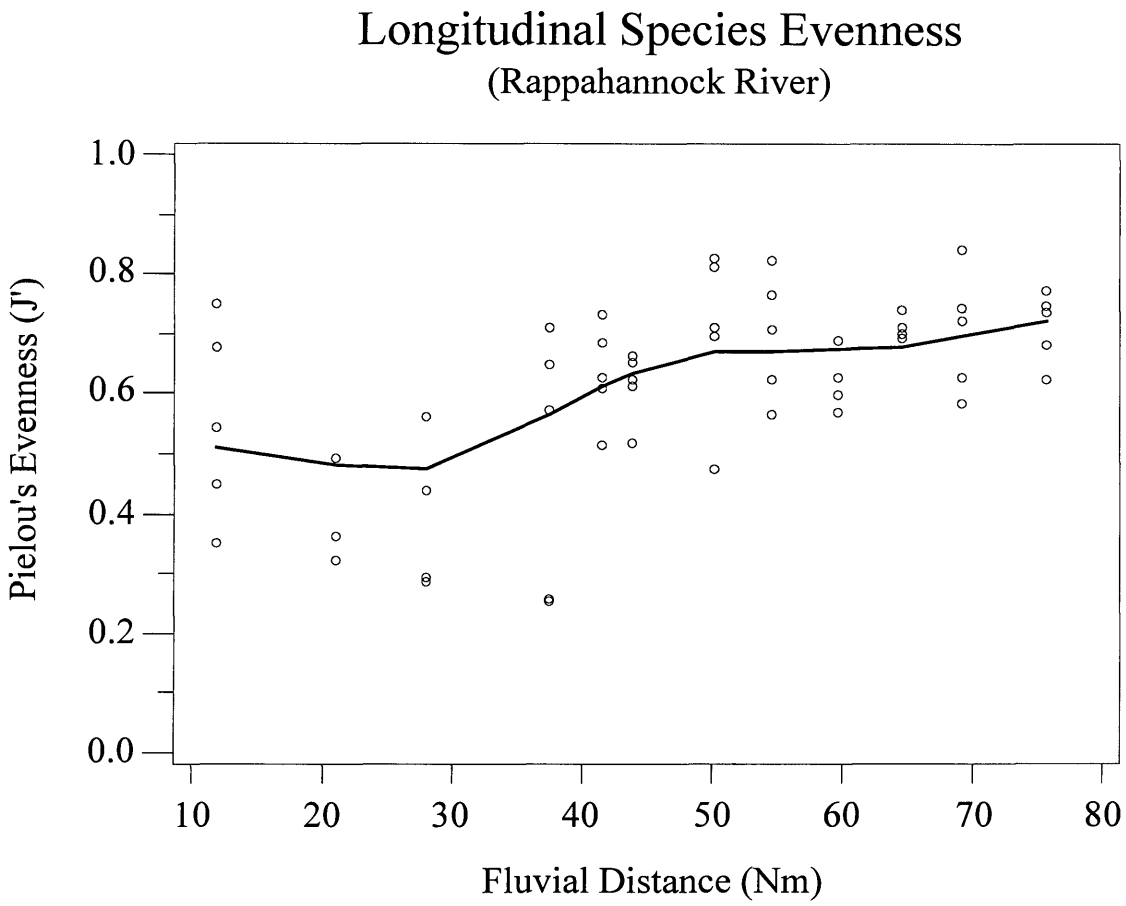

Longitudinal Species Evenness
(Rappahannock River)
Pielou's Evenness (J')
1.0
0.8
0.6
0.4
0.2
0.0
10
20
30
40
50
60
70
80
Fluvial Distance (Nm)

Figure 9: Longitudinal species diversity (Shannon-Wiener) in the Rappahannock River, 1990-1994, fit with a LOWESS curve.

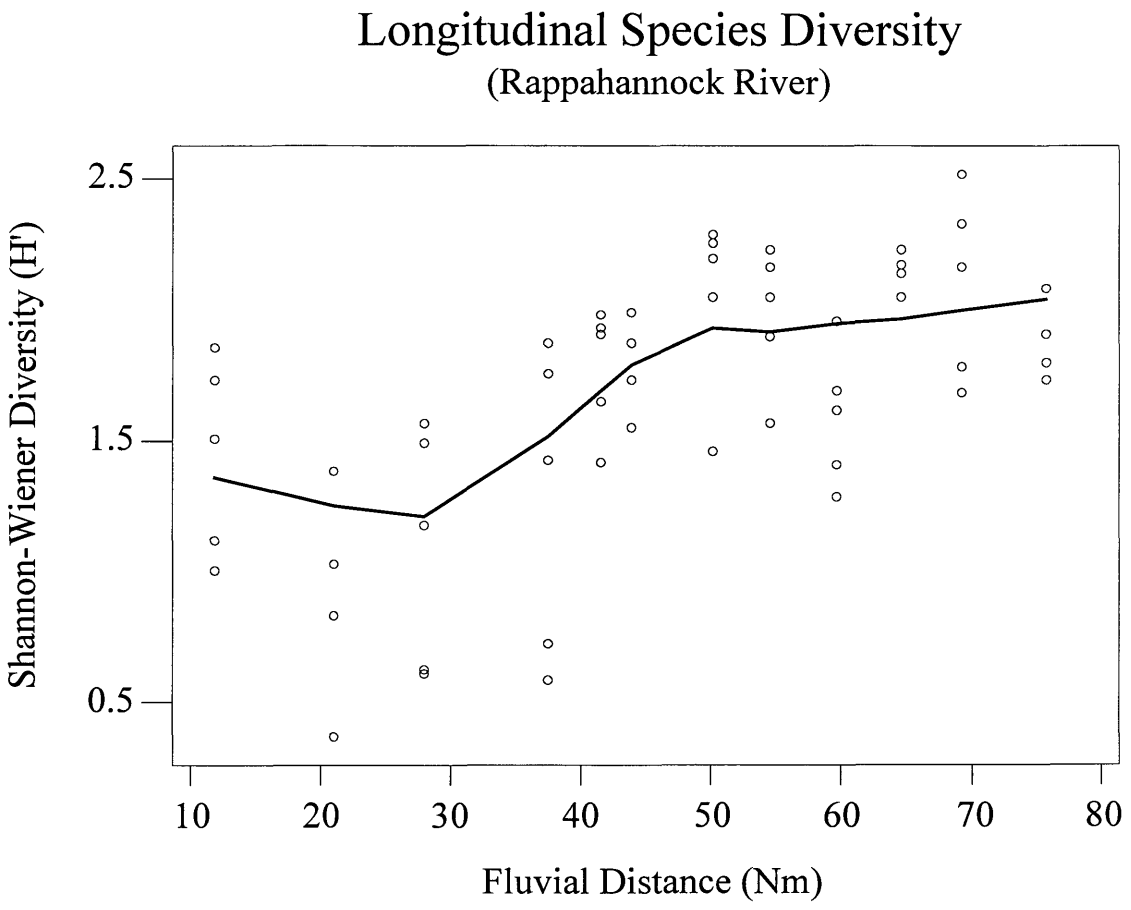
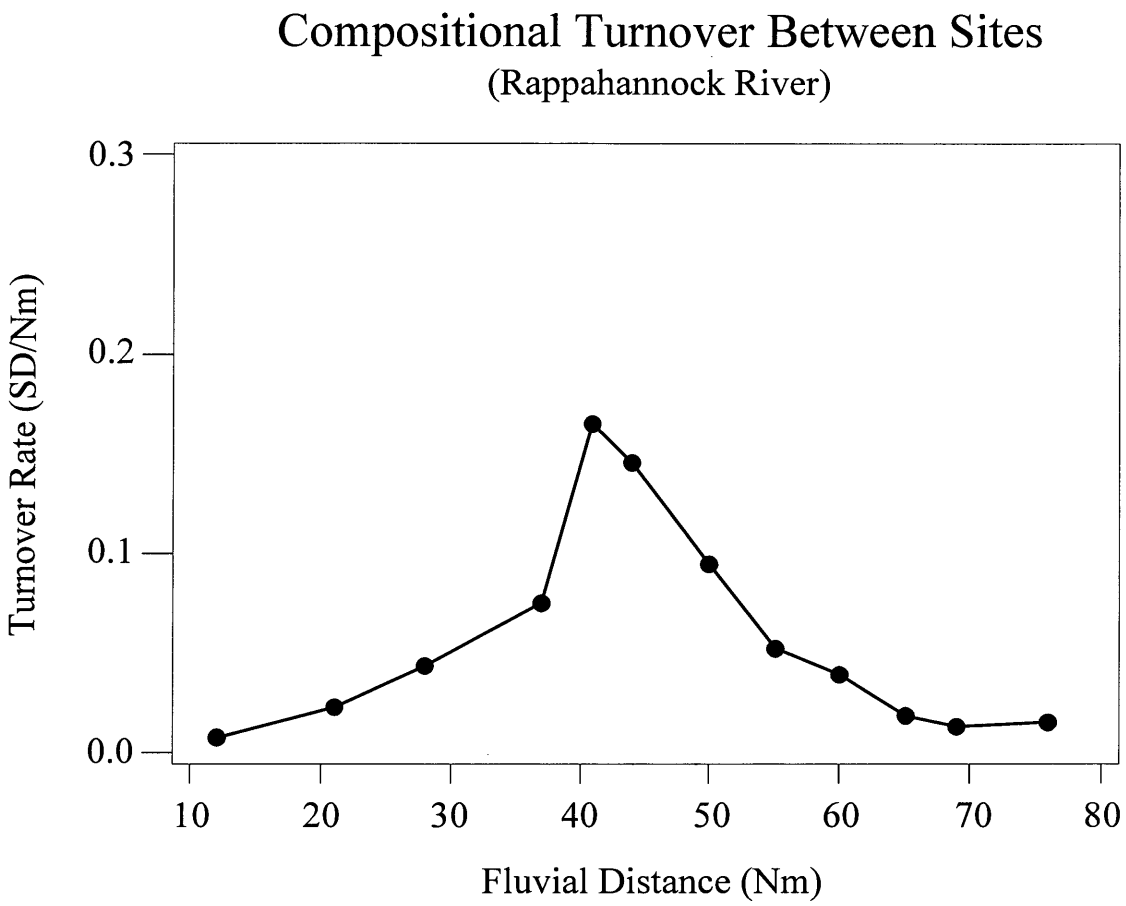

Longitudinal Species Diversity
(Rappahannock River)
Shannon-Wiener Diversity (H')
2.5
1.5
0.5
10
20
30
40
50
60
70
80
Fluvial Distance (Nm)

Figure 10: Longitudinal species turnover (beta diversity) in the Rappahannock River, 1990-94. Units are standard deviations in species turnover per nautical mile from the DCA ordination of all stations.


Compositional Turnover Between Sites
(Rappahannock River)
Turnover Rate (SD/Nm)
0.3
0.2
0.1
0.0
10
20
30
40
50
60
70
80
Fluvial Distance (Nm)

York-Mattaponi River Community Patterns

A total of 65 species of fishes comprising 20,827 individuals were collected (first tow only), of which 22 were represented by 5 or fewer individuals, and 38 met the 3% capture frequency criterion for inclusion in the gradient analysis.

Spatial Assemblage Patterns -- The TWINSPAN classification of all stations generally reflects a longitudinal riverine gradient (Fig. 11), and suggests the presence of five intergrading assemblages of sandy beach fishes. The first dichotomy was very strong (eigenvalue 0.65) and separates tidal freshwater stations (subset 0) from saline stations (subset 1). Subset 0 separated at the second division level into coarser vegetated bottoms (Group 1) vs. sandy bottoms (Group 2) in the permanent tidal freshwater reach of the Mattaponi River. At the second division level for saline stations, subset 11 (mesohaline stations) separated from oligohaline stations (Group 3). Subset 11 further separated at the third division level due primarily to the limited upstream penetration of a few polyhaline species (Groups 4a and 4b). Further divisions of Groups 1-4 were not considered as they seem mainly due to the presence of uncommon species and did not yield distinct groups within the DCA ordination space.

The DCA ordination of all stations is presented in Figure 12. The major TWINSPAN groups are well defined and form a continuum, with some clustering, and stronger separation between groups across the freshwater interface. Station scores along the first axis are generally separated into three regions along the salinity gradient associated with tidal freshwater (Groups 1-2) and oligohaline (Group 3) stations in the

Mattaponi River, and mesohaline stations (Groups 4a-b) in the York River below the confluence at West Point, VA. The eigenvalue of the first axis (0.63) suggests the gradient represented by it was highly significant. The ecological distance of 3.88 SD between the most upstream and downstream groups indicates that the faunas at the extremities of the estuarine gradient were about 97% dissimilar. The second axis had a lower eigenvalue (0.16), is relatively short (1.71 SD; 43% dissimilar), and appears to primarily to separate the tidal freshwater stations longitudinally according to the presence of SAVs and/or coarser bottoms.

Figure 13 shows the DCA ordination of the 38 species from the York and Mattaponi Rivers which met the first tow 3% frequency criterion for retention. Species symbols correspond to the modified ecological affinity groups of McHugh (1967) as defined in the Methods and Materials section. Species scores were aligned in a longitudinal pattern similar to the station scores. Dispersion along the first ordination axis is truncated in permanent tidal freshwater, indicating the presence of a longitudinal salinity gradient, with species scores generally well ordered from freshwater → estuarine → marine taxa. Freshwater species scores are largely dispersed along the second ordination axis in a longitudinal series from sandy to coarse/vegetated bottoms.

Environmental Correlates (DCCA) -- A direct comparison of the distribution of constrained (DCCA) and unconstrained (DCA) station scores is given in Table 7. Spearman rank correlations indicate that the two ordination methods accounted for similar variation. Further support for this interpretation is indicated by the similar gradient lengths and eigenvalues generated by the two methods. The high rank

correlation between the second axis of DCA and DCCA (0.84) is driven by the categorical vegetation variable (presence/absence of SAV). SAV's are only present at MP-52, and this tends to polarize the second DCCA axis. When SAV is not included as a variable, the rank correlation falls to 0.48.

The overall ordination was significant ($p<0.001$) and the first two DCCA axes explained 65.9% of the total variance in the species-environment relations (Tab. 8). Significant correlations and canonical coefficients of species scores on DCCA axis 1 with environmental factors indicated that this axis was positively correlated with salinity (0.87), distance to the bay mouth (-0.94), channel width (0.70) and shoal width (0.50). These variables tend to be highly intercorrelated as salinity, channel width and shoal width all tend to decrease with increasing distance from the bay mouth. However, the truncation of the range of axis 1 scores for freshwater species (Fig. 14) suggests salinity is the primary actor. The presence of SAV's (0.52) and nearshore substrate grain size (0.45) were significant on the second DCCA axis, and served to primarily separate collections from MP-52 (SAV's, sand & pebble substrates) from downstream freshwater stations (no SAV's, sandy substrate). Correlations on third and higher DCCA axes were not considered due to their low eigenvalues.

The arrangement of species scores on DCCA axes 1 and 2 strongly support the results derived from TWINSPAN and DCA (Fig. 14). The order of species scores along the first axis corresponds well with the general salinity preferences and tolerances of McHugh's ecological affinity groups; with species well ordered from freshwater → estuarine → marine taxa. Freshwater taxa are spread primarily on the second axis, with a

few noticeable features. Though widely dispersed in tidal freshwater, three cyprinids (spottail shiner, satinfin shiner and eastern silvery minnow), the banded killifish, juvenile American shad (*Alosa sapidissima*) and juvenile channel catfish form a fairly tight group of fishes commonly found over sandy bottoms in tidal freshwater. Other freshwater species, particularly the blue-spotted sunfish (*Enneacanthus gloriosus*) and juvenile yellow perch, are centered well upstream due to their high abundances in the SAV beds at MP-52.

Species-Environment Associations -- Specific species associations with TWINSPAN station groups are catalogued below and are summarized in Table 9. Environmental values for TWINSPAN groups are summarized in Table 10.

Tidal Freshwater (Coarse & Vegetated Bottom): This group included 6 stations (TWINSPAN Group 1; five are MP-52), and supports primarily freshwater species (26). A total of 35 species and 2,349 individuals were collected. The hogchoker (*T. maculatus*; 22.6%), the spottail shiner (*N. hudsonius*; 19.2%), the banded killifish (*F. diaphanus*; 10.8%), the yellow perch (*P. flavescens*; 7.0%), the eastern silvery minnow (*H. regius*; 6.0%) and the redbreast sunfish (*Lepomis auritus*; 5.4%) accounted for 71.0% of all individuals captured at these sites. Relatively large catches of the tessellated darter (FOC 58%) characterized this group in the TWINSPAN analysis. The most frequently occurring species were the banded killifish (FOC 96%), hogchoker (FOC 85%), spottail shiner (FOC 85%), redbreast sunfish (FOC 77%) and satinfin shiner (FOC 77%). Frequent catches of yellow perch (FOC 73%), largemouth bass (*Micropterus salmoides*; FOC 54%) and the blue-spotted sunfish (FOC 50%) also served to distinguish these sites

from other downstream freshwater stations.

Tidal Freshwater (Sandy Bottoms): This group included 15 stations (TWINSPAN Group 2), and supports primarily freshwater (17), estuarine (8) and diadromous (4) fishes with a total of 36 species and 3,601 individuals captured. The spottail shiner (*N. hudsonius*; 28.5%), juvenile striped bass (*M. saxatilis*; 20.8%), the hogchoker (*T. maculatus*; 12.6%), the eastern silvery minnow (*H. regius*; 8.6%), juvenile white perch (*M. americana*; 8.0%) and the satinfin shiner (*C. analostana*; 7.0%) accounted for 85.5% of all individuals captured at these sites. TWINSPAN identified juvenile striped bass (FOC 90%) as an indicator species. Other frequently occurring species were the spottail shiner (FOC 86%), hogchoker (FOC 61%) and satinfin shiner (FOC 58%). Most of the tidal freshwater reach of the Mattaponi River study area was included in this group.

Oligohaline: This group included 9 stations (TWINSPAN Group 3), and supports primarily estuarine fishes (8 species, 79.5% individuals), although several freshwater (12) and estuarine-marine (5) species occur less frequently. A total of 33 species and 3,405 individuals were collected. The hogchoker (*T. maculatus*; 39.0%), mummichog (*F. heteroclitus*; 14.9%), the bay anchovy (*A. mitchelli*; 8.1%), the Atlantic silverside (*M. menidia*; 7.0%), juvenile white perch (*M. americana*; 6.2%), juvenile Atlantic menhaden (*B. tyrannus*; 5.5%) and juvenile striped bass (*M. saxatilis*; 5.2%) accounted for 85.9% of all individuals captured at these sites. TWINSPAN failed to identify a strong indicator species for this group. The most frequently occurring species were the hogchoker (FOC 95%), mummichog (FOC 84%), juvenile striped bass (FOC 84%) and juvenile white perch (FOC 73%). All of the stations in this group occurred above the confluence with

the York River. The average salinity for this group was 3.66 ± 0.43 ppt.

Mesohaline I: This group included 10 stations (TWINSPAN Group 4a), and supports primarily estuarine (13), estuarine-marine (12) and marine (7) species with a total of 9,089 individuals and 37 species collected. The hogchoker (*T. maculatus*; 42.4%), mummichog (*F. heteroclitus*; 15.8%), the Atlantic croaker (*M. undulatus*; 13.0%), the spot (*L. xanthurus*; 10.9%) and the Atlantic silverside (*M. menidia*; 6.5%) accounted for 88.6% of all individuals captured at these sites. TWINSPAN identified the striped killifish (*Fundulus majalis*; FOC 83%) as an indicator species for both mesohaline assemblages. The other most frequently occurring species included the spot (FOC 94%), hogchoker (FOC 88%), Atlantic croaker (FOC 83%), Atlantic silverside (FOC 79%) and the mummichog (FOC 77%). The average salinity for this group was 13.14 ± 0.47 ppt.

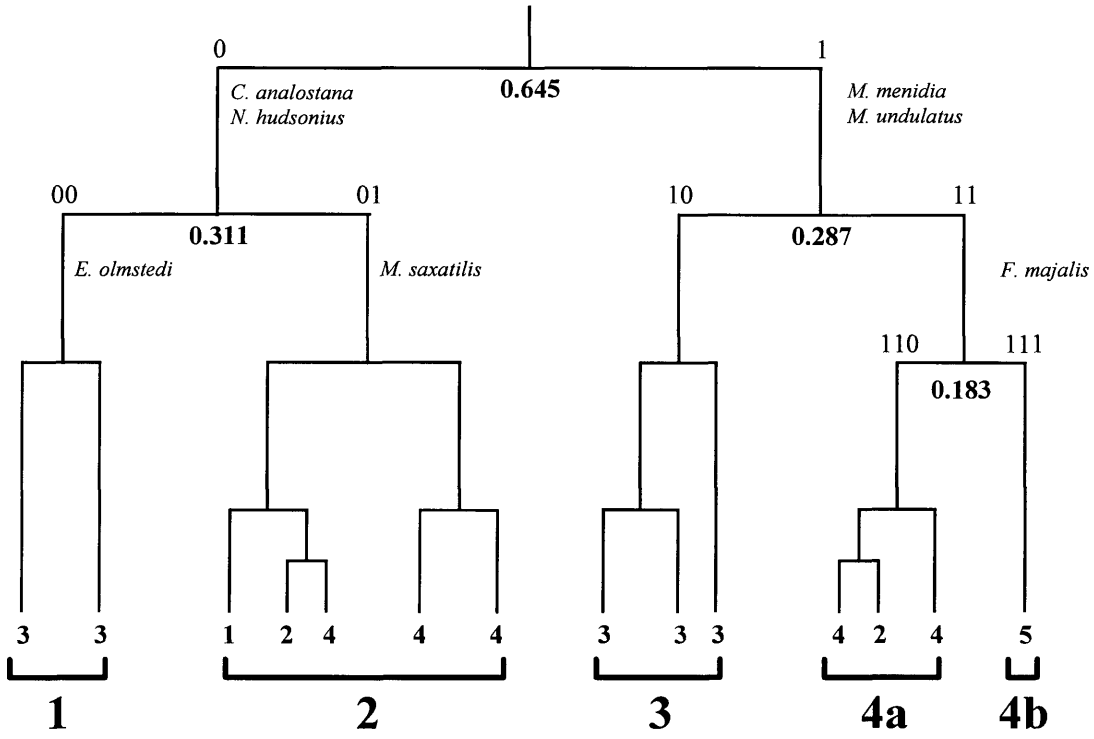
Mesohaline II: This group included 5 stations (TWINSPAN Group 4b; four are from YK-15), and supports primarily estuarine (10), estuarine-marine (9) and marine (5) species with a total of 2,383 individuals and 27 species collected. The Atlantic silverside (*M. menidia*; 51.9%), mummichog (*F. heteroclitus*; 25.0%) and the spot (*L. xanthurus*; 8.4%) accounted for 85.2% of all individuals captured at these sites. Relatively moderate to high standardized densities and FOC of several ubiquitous estuarine species characterized this group in the gradient analysis. Particularly, the Atlantic silverside (FOC 88%), spot (FOC 68%), striped killifish (FOC 64%), and the inshore lizardfish (FOC 64%). The average salinity at these sites was 15.41 ± 0.48 ppt.

Species Diversity -- Rarefied species richness showed a slight increase moving from the saline to tidal freshwater portions of the river system, with a falloff where the

York River divides, and a distinct peak at station MP-52 (Fig. 15b). Total species richness differed somewhat from the rarefaction curve and showed a marked increase at stations YK-21 and YK-28 (Fig. 15a). This increase appears due to the increased capture of relatively rare higher salinity species (e.g., Atlantic thread herring, Atlantic spadefish, northern kingfish) associated with a greater total sample area (i.e., the species-area effect; Fig. 16). The most notable features of the curves are a decrease in total species richness at YK-15, and a peak at MP-52. This peak was a result of the recruitment of many freshwater species to the SAV bed's found at this station. Species evenness and diversity displayed a similar trend of increasing values moving upstream, with a local falloff near the river fork above river mile 28 (Figs. 17 & 18) Interannual variability in both evenness and diversity was high all along the study area. The highest compositional turnover (beta diversity) along the York-Mattaponi River was observed across the freshwater interface between sites MP-33 and MP-41; above and below these sites the rate of change was generally less (Fig. 19). A large increase also occurs at MP-52, primarily due to the high species richness associated with SAV beds.

Figure 11: TWINSPAN classification of York-Mattaponi River stations. Indicator species for each division are shown in decreasing order of importance. Eigenvalues of major divisions are shown in bold under each division. Binary numbers above divisions denote major subsets. Smaller font numbers below final groups are the number of stations within that group. Larger font numbers below brackets are final TWINSPAN group labels. Station labels are rivermile-year.

York-Mattaponi River
(n=43)



1	2	3	4a	4b
MP47-92	MP37-90	MP33-90	YK15-93	YK15-90
		MP33-91		YK15-91
MP52-90	MP41-90	MP33-92	YK21-91	YK15-92
MP52-91	MP41-91	MP33-93	YK21-92	YK15-94
MP52-92	MP41-92	MP33-94	YK21-93	
MP52-93	MP41-93		YK21-94	YK21-90
MP52-94	MP41-94	MP37-91		
		MP37-92	YK28-90	
	MP44-90	MP37-93	YK28-91	
	MP44-91	MP37-94	YK28-92	
	MP44-92		YK28-93	
	MP44-93		YK28-94	
	MP44-94			
	MP47-91			
	MP47-92			
	MP47-93			
	MP47-94			

Figure 12: Axes 1 and 2 of DCA ordination of York-Mattaponi River stations. Symbols correspond to TWINSPAN groups. Units are standard deviations in species turnover rate.

York-Mattaponi River Station Scores
(TWINSPAN Groups)

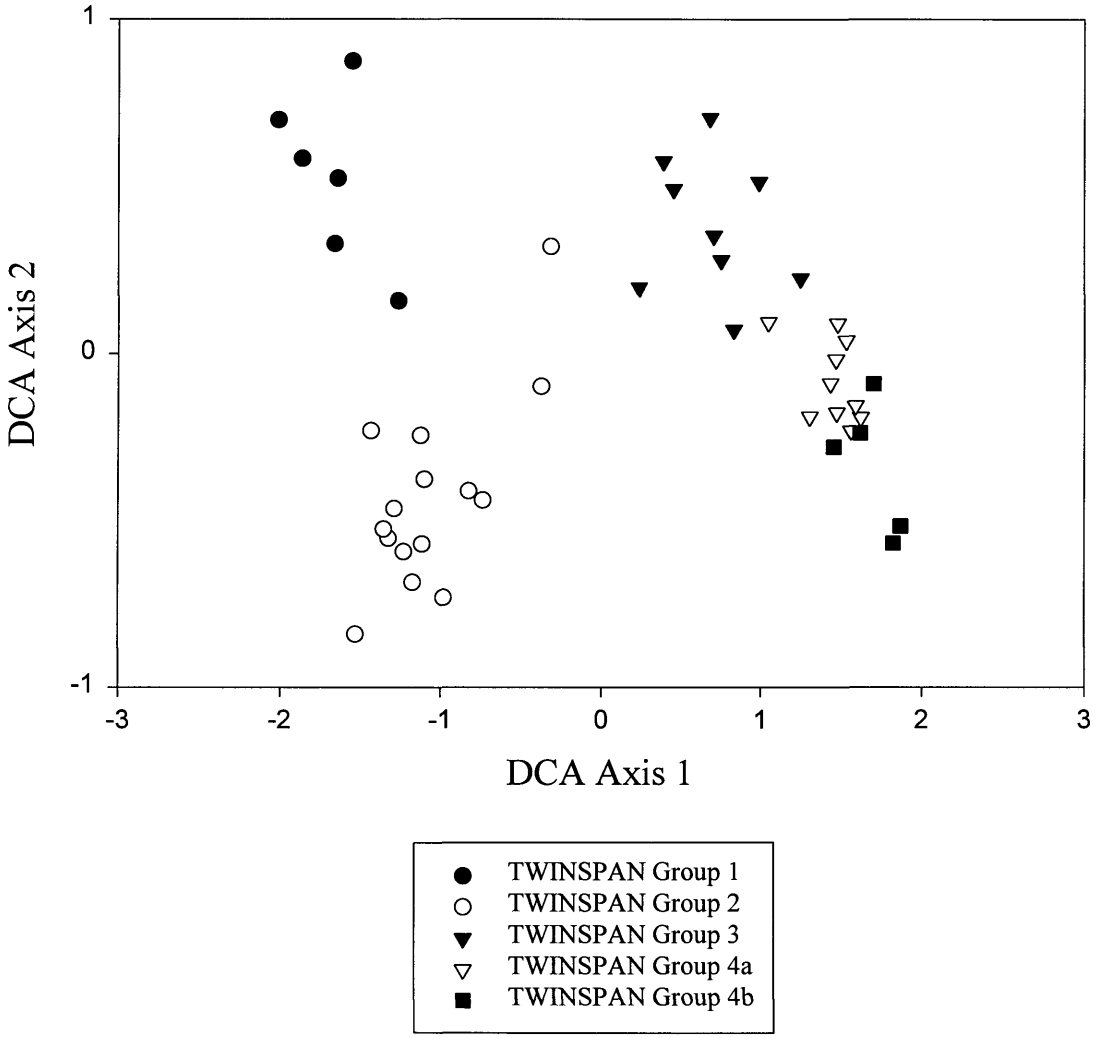


Figure 13: Axes 1 and 2 of DCA ordination of the 38 York-Mattaponi River species included in the gradient analysis. Symbols correspond to the modified ecological groups of McHugh (1967). Species labels are the first f our letters of genus and species names respectively (see Appendix 2 for a complete alphabetical list). Units are standard deviations in species turnover rate.

York-Mattaponi Species Scores
(Ecological Affinity Groups)

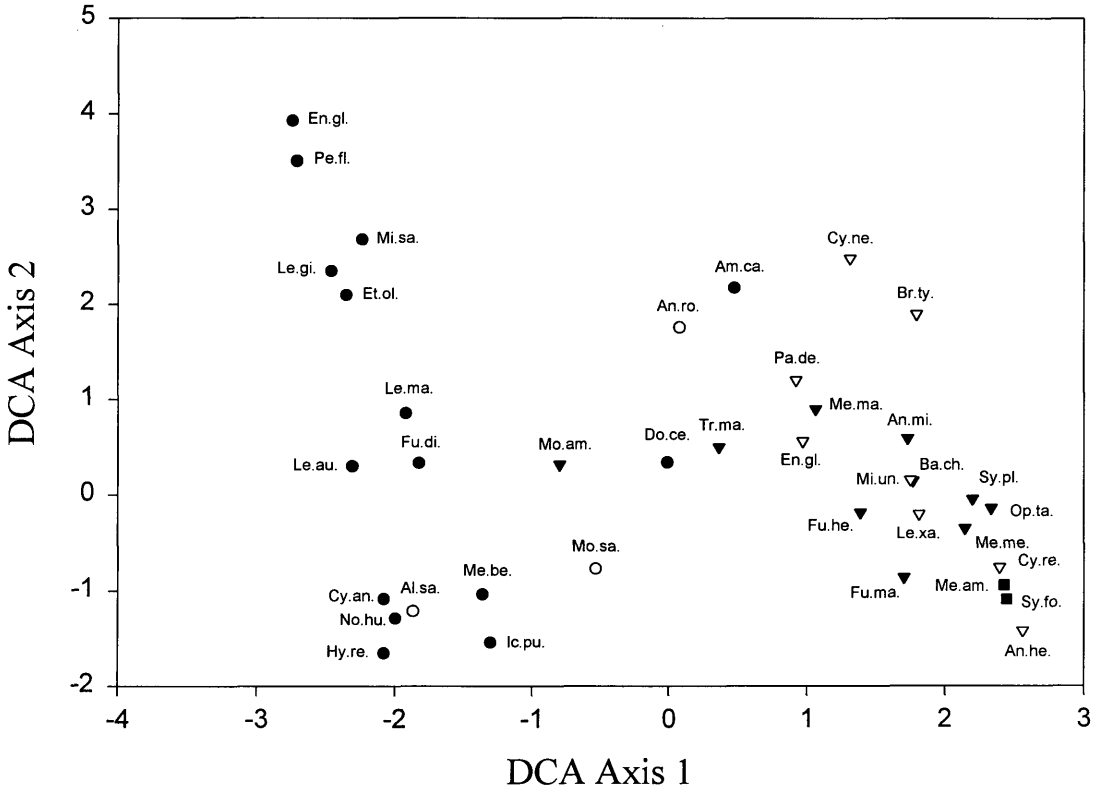


Table 7: Direct comparison of DCA and DCCA axes via Spearman rank correlation for the York-Mattaponi River stations. DCA scores are weighted average scores and DCCA scores are linear combination scores predicted from the multiple regression.

	Eigenvalue		Gradient Length		
Ordination Axis	**DCA**	**DCCA**	**DCA**	**DCCA**	r^2
1	0.63	0.61	3.88	3.71	0.96 ***
2	0.16	0.12	1.71	1.20	0.84 ***

*** $p < 0.001$

Table 8: Results of the detrended canonical correspondence analysis of fish assemblages from the York-Mattaponi River. Significance values of correlation and canonical coefficients correspond to a two-tailed students *t*-test.

Variable	Axis 1	Axis 2
Canonical Coefficients for Environmental Variables		
Salinity	0.4102 ***	-0.0030
Temperature	0.0597	0.0690
Dissolved O_2	-0.0186	0.0926
pH	-0.0054	-0.0674
Substrate Grain Size	-0.0766	-0.2548
Channel Width	-1.3757 ***	-3.1694 ***
6' Contour	0.7192 ***	1.4767 ***
Distance to Bay Mouth	-1.3851 ***	-2.5620 ***
Presence of SAV	0.1266	1.6420 ***
Correlations of Environmental Variables with Axes		
Salinity	0.8673 ***	-0.1162
Temperature	-0.2735	0.1292
Dissolved O_2	-0.0728	-0.0334
pH	0.4647 ***	-0.1659
Substrate Grain Size	-0.1909	0.4474 **
Channel Width	0.6993 ***	-0.1919
6' Contour	0.5030 ***	-0.0735
Distance to Bay Mouth	-0.9378 ***	0.1476
Presence of SAV	-0.5591 ***	0.5237 ***
Summary Statistics for Ordination Axes		
Eigenvalue	0.607	0.117
Species-environment correlation	0.982	0.885
Cummulative % of species-environment variance explained	55.3	65.9
Monte Carlo probability for significance of the sum of all eigenvalues (10^3 pemutations): 0.001		

*** $p < 0.005$ ** $p < 0.01$ * $p < 0.05$

Figure 14: Axes 1 and 2 of DCCA ordination of the 38 York-Mattaponi River species included in the gradient analysis. Environmental variables are indicated with vectors. Only statistically significant variables are included in the ordination diagram. Abbreviations are the first four letters in both the genus and species names (see Appendix 2 for a complete list).

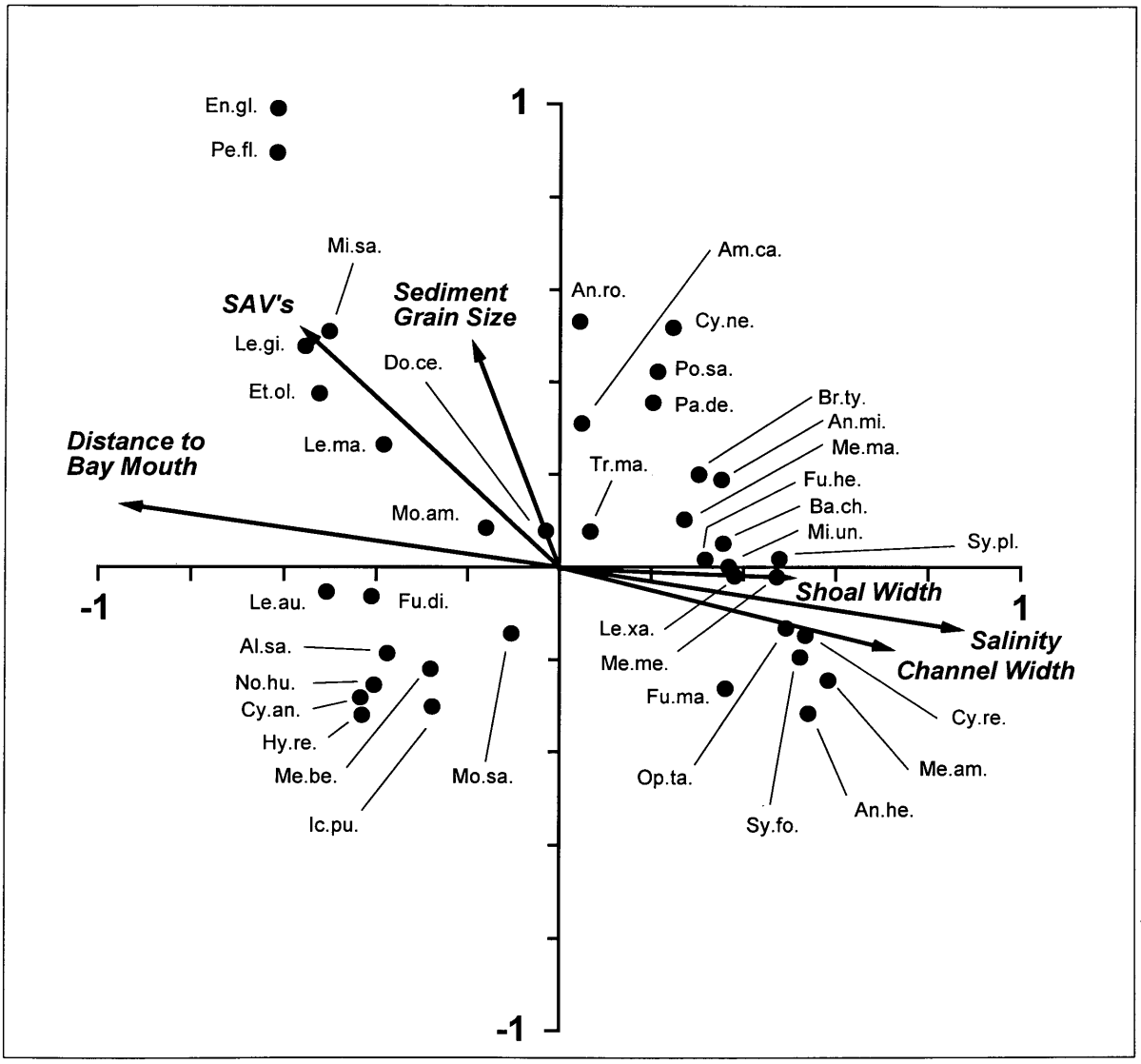

1
-1
1
-1
En.gl.
Pe.fl.
Mi.sa.
SAV's
Sediment
Grain Size
Le.gi.
Et.ol.
Do.ce.
Le.ma.
Distance to
Bay Mouth
Mo.am.
Le.au.
Fu.di.
Al.sa.
No.hu.
Cy.an.
Hy.re.
Me.be.
Ic.pu.
Mo.sa.
An.ro.
Am.ca.
Cy.ne.
Po.sa.
Pa.de.
Tr.ma.
Br.ty.
An.mi.
Me.ma.
Fu.he.
Ba.ch.
Mi.un.
Sy.pl.
Shoal Width
Salinity
Channel Width
Le.xa.
Me.me.
Fu.ma.
Op.ta.
Sy.fo.
An.he.
Me.am.
Cy.re.

Table 9: Dominant and indicator taxa for TWINSPAN groups of York and Mattaponi River stations. Density is mean (+/- 1 standard error) abundance per 1000 m^2 swept area calculated for all stations included in the TWINSPAN group. FOC = frequency of occurence in the stations from the TWINSPAN group. Indicator species are denoted with an asteriks.

TWINSPAN Group	Dominant & Indicator Taxa					
	Species	Density (#/10^3 m^2)		FOC	Fork Length (mm)	
1	*Trinectes maculatus*	79.18	(28.51)	0.85	40.99	(0.58)
	Notropis hudsonius	43.93	(17.12)	0.85	62.30	(0.57)
	Fundulus diaphanus	25.33	(4.28)	0.96	58.39	(0.66)
	Perca flavescens	15.18	(2.98)	0.73	95.32	(3.25)
	Hybognathus regius	13.63	(6.62)	0.54	75.85	(1.28)
	Lepomis auritus	12.08	(2.57)	0.77	89.67	(3.25)
	Alosa sapidissima	11.62	(4.41)	0.46	57.88	(1.08)
	Etheostoma olmstedi *	10.71	(3.53)	0.58	47.93	(1.42)
	Cyprinella analostana	9.57	(1.97)	0.77	59.81	(0.80)
	Morone americana	9.53	(2.13)	0.69	83.40	(3.77)
	Lepomis gibbosus	6.48	(1.50)	0.58	99.34	(3.61)
	Micropterus salmoides	4.70	(1.10)	0.54	112.75	(4.96)
	Enneacanthus gloriosus	3.51	(1.15)	0.50	46.43	(1.65)
	Lepomis macrochirus	2.02	(1.25)	0.31	55.25	(7.88)
	Morone saxatilis	1.91	(0.60)	0.38	84.75	(4.58)
	Fundulus heteroclitus	0.86	(0.37)	0.23	51.33	(5.74)
2	*Notropis hudsonius*	55.79	(10.13)	0.86	72.64	(0.40)
	Morone saxatilis *	40.60	(7.09)	0.90	61.91	(0.74)
	Trinectes maculatus	23.40	(5.31)	0.61	51.22	(0.64)
	Hybognathus regius	16.86	(6.15)	0.42	60.64	(0.89)
	Morone americana	15.37	(4.40)	0.53	67.06	(2.24)
	Cyprinella analostana	13.10	(2.07)	0.58	59.41	(0.54)
	Alosa sapidissima	9.23	(2.42)	0.35	66.48	(0.82)
	Fundulus diaphanus	4.90	(1.32)	0.32	59.60	(0.81)
	Lepomis auritus	3.13	(0.66)	0.32	105.64	(3.97)
	Fundulus heteroclitus	2.15	(0.68)	0.21	52.54	(1.81)
	Menidia beryllina	1.42	(0.32)	0.15	59.52	(1.54)
3	*Trinectes maculatus*	158.38	(39.78)	0.95	49.76	(0.31)
	Fundulus heteroclitus	58.75	(21.86)	0.84	53.79	(0.40)
	Anchoa mitchelli	26.60	(13.86)	0.41	54.46	(0.47)
	Menidia menidia	23.13	(6.44)	0.36	65.14	(0.38)
	Morone americana	22.92	(6.24)	0.73	69.29	(2.76)
	Morone saxatilis	18.92	(3.51)	0.84	65.24	(1.79)
	Leiostomus xanthurus	13.36	(4.28)	0.50	72.73	(1.57)
	Brevoortia tyrannus	10.98	(8.02)	0.09	118.33	(1.00)
	Ameiurus catus	9.08	(3.67)	0.36	96.15	(2.57)
	Micropogonias undulatus	6.77	(2.14)	0.36	106.87	(2.61)
	Dorosoma cepedianum	4.07	(3.01)	0.16	132.93	(11.01)
	Paralichthys dentatus	1.84	(0.65)	0.23	121.87	(15.43)

TWINSPAN Group	Dominant & Indicator Taxa					
	Species	Density (#/10^3 m^3)		FOC	Fork Length (mm)	
4a	*Trinectes maculatus*	109.93	(21.94)	0.88	54.82	(0.15)
	Fundulus heteroclitus	40.95	(10.08)	0.77	62.25	(0.32)
	Micropogonias undulatus	33.62	(7.78)	0.83	108.84	(0.54)
	Leiostomus xanthurus	28.39	(4.80)	0.94	91.12	(0.55)
	Menidia menidia	16.78	(3.38)	0.79	66.87	(0.45)
	Anchoa mitchelli	8.05	(2.51)	0.69	58.16	(0.36)
	Fundulus majalis *	7.16	(1.15)	0.83	83.95	(1.54)
	Morone saxatilis	2.28	(0.45)	0.56	72.35	(3.12)
	Symphurus plagiusa	2.05	(0.33)	0.60	90.74	(2.48)
	Mentichirrus americanus	1.74	(0.87)	0.21	81.95	(2.18)
	Synodus foetens	1.23	(0.33)	0.40	107.93	(5.13)
	Cynoscion regalis	1.11	(0.40)	0.23	63.74	(2.33)
	Brevoortia tyrannus	1.00	(0.50)	0.17	80.31	(5.45)
	Bairdiella chrysoura	0.88	(0.33)	0.23	59.10	(3.67)
	Anchoa hepsetus	0.83	(0.23)	0.33	68.62	(1.58)
4b	*Menidia menidia*	67.80	(35.10)	0.88	7.91	(0.17)
	Fundulus heteroclitus	32.60	(11.98)	0.60	72.39	(0.36)
	Leiostomus xanthurus	10.90	(2.64)	0.68	108.95	(0.76)
	Fundulus majalis *	5.25	(1.73)	0.64	94.56	(2.19)
	Trinectes maculatus	3.19	(0.97)	0.56	71.47	(1.42)
	Anchoa hepsetus	2.96	(0.87)	0.56	66.19	(1.23)
	Synodus foetens	1.69	(0.32)	0.64	106.57	(5.23)
	Anchoa mitchelli	1.26	(0.52)	0.24	58.83	(2.12)

Table 10: Average environmental values by TWINSPAN group for stations from the York and Mattaponi Rivers. Quantitative variables are mean ± one standard error. Channel measurements are given as a range.

TWINSPAN Group	Salinity (ppt)	Temperature (°C)	Dissolved O_2 (mg ℓ^{-1})	pH
1	0.18 ∓ 0.13	27.77 ∓ 0.42	5.21 ∓ 0.15	6.44 ∓ 0.12
2	0.40 ∓ 0.08	27.24 ∓ 0.20	5.08 ∓ 0.07	6.44 ∓ 0.06
3	3.66 ∓ 0.43	27.21 ∓ 0.21	4.52 ∓ 0.11	6.56 ∓ 0.06
4a	13.14 ∓ 0.47	26.45 ∓ 0.31	5.84 ∓ 0.15	7.09 ∓ 0.08
4b	15.41 ∓ 0.48	26.66 ∓ 0.52	6.61 ∓ 0.28	7.44 ∓ 0.15

	Nearshore Sediment	6' Contour (m)	Channel Width (m)	SAV Beds
1	Sand-Pebble	18 - 96	180 - 384	Yes[†]
2	Sand-Silt	10 - 20	162 - 202	No
3	Sand-Granule	10 - 18	162 - 228	No
4a	Sand	72 - 365	1800 - 3516	No
4b	Sand	72 - 360	1800 - 3516	No

[†] Five of six stations have SAV's in Group 1. Only tows from MP-52.

Figure 15: Total (a) and rarefied (b) longitudinal species richness in the York and Mattaponi Rivers, 1990-94. Rarefied species richness is fit with a LOWESS curve.

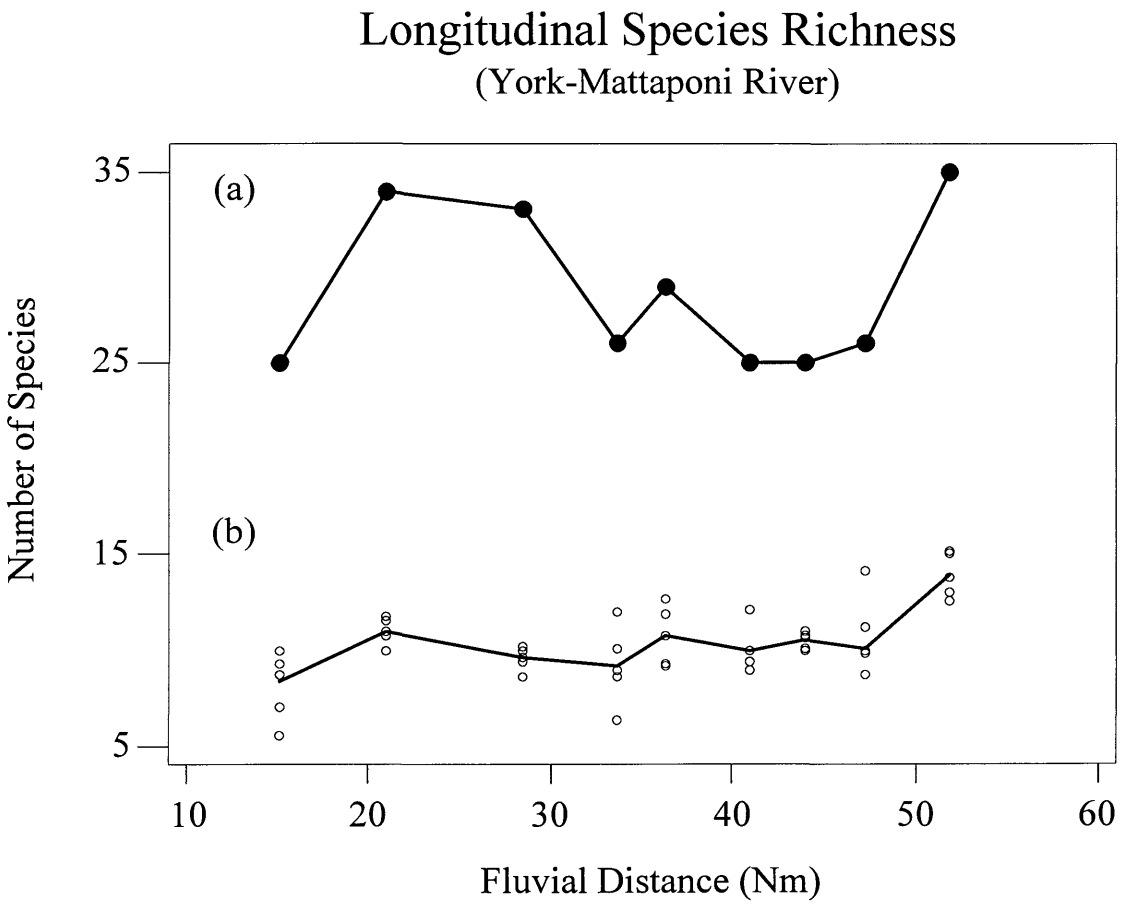

Longitudinal Species Richness
(York-Mattaponi River)
Number of Species
35
25
15
5
(a)
(b)
10
20
30
40
50
60
Fluvial Distance (Nm)

Figure 16: Total species captured and total area swept for York-Mattaponi River stations, 1990-1994.

Species-Area Relationship
(York-Mattaponi River)

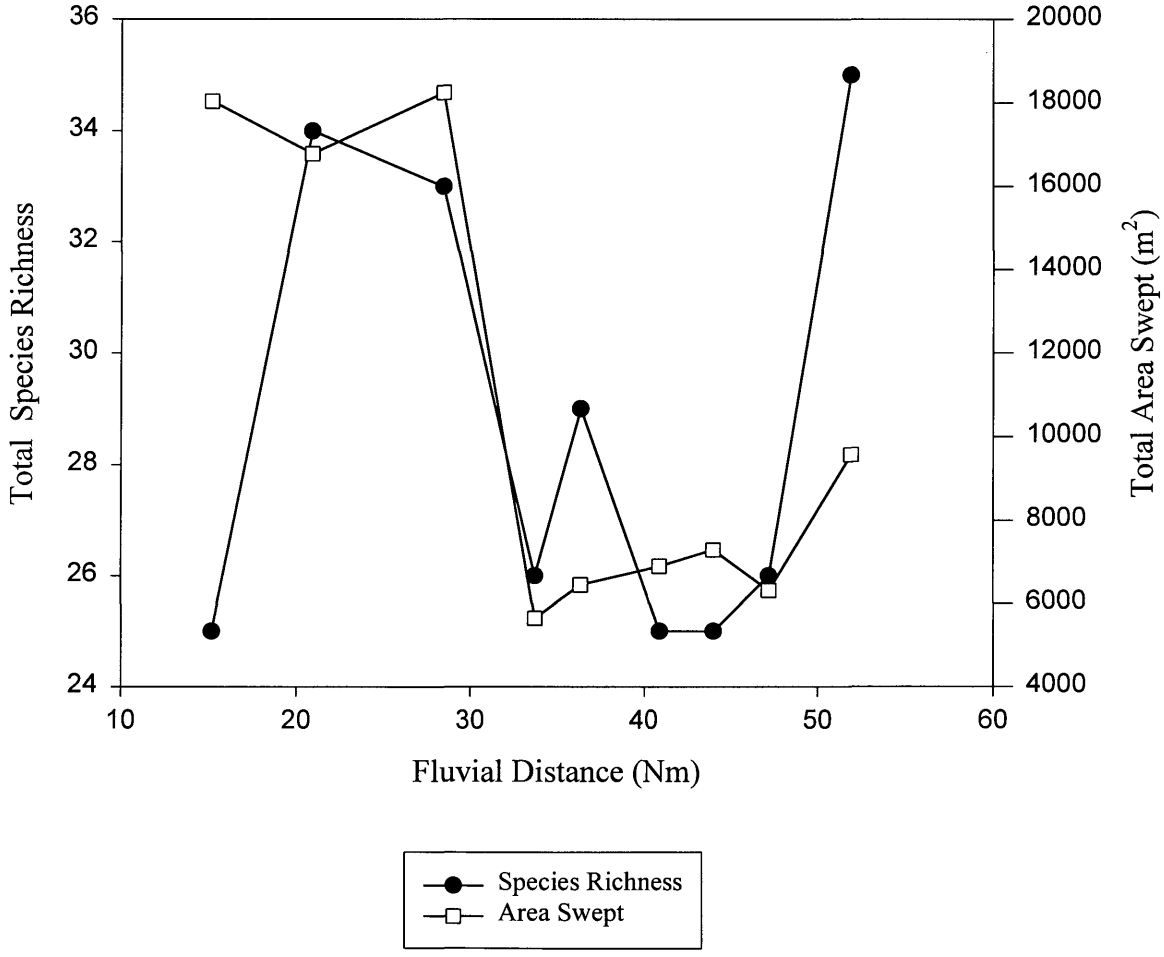


Figure 17: Longitudinal species evenness (Pielou's) in the York and Mattaponi Rivers, 1990-1994, fit with a LOWESS curve.

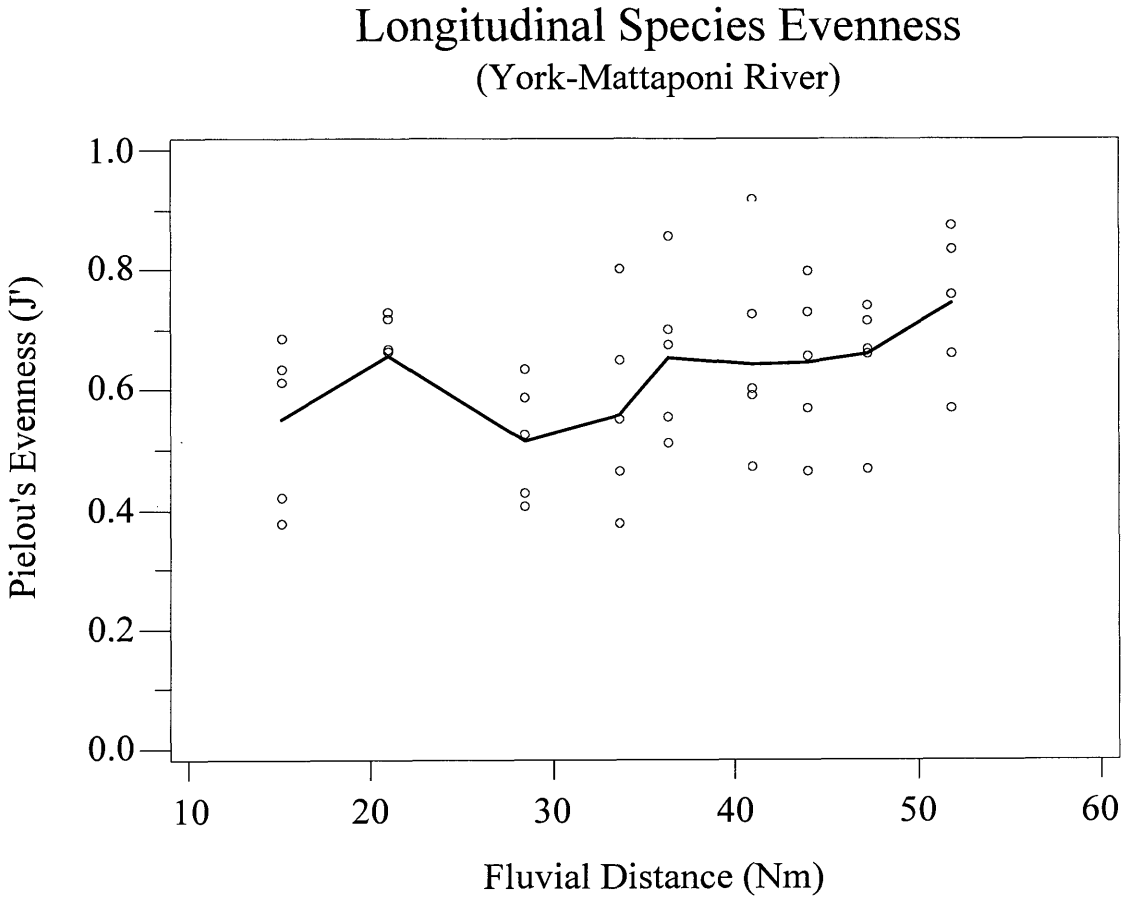

Longitudinal Species Evenness
(York-Mattaponi River)
Pielou's Evenness (J')
1.0
0.8
0.6
0.4
0.2
0.0
10
20
30
40
50
60
Fluvial Distance (Nm)

Figure 18: Longitudinal species diversity (Shannon-Wiener) in the York and Mattaponi Rivers, 1990-1994, fit with a LOWESS curve.

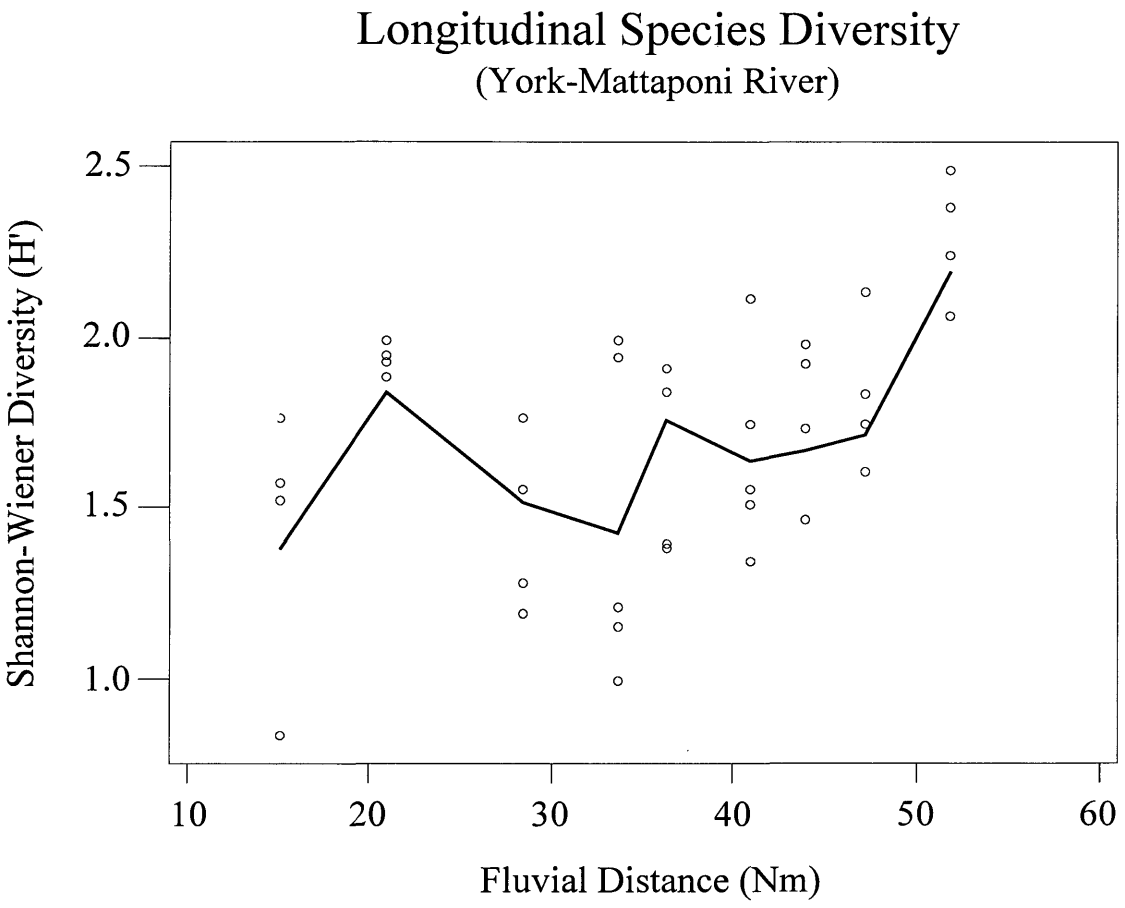
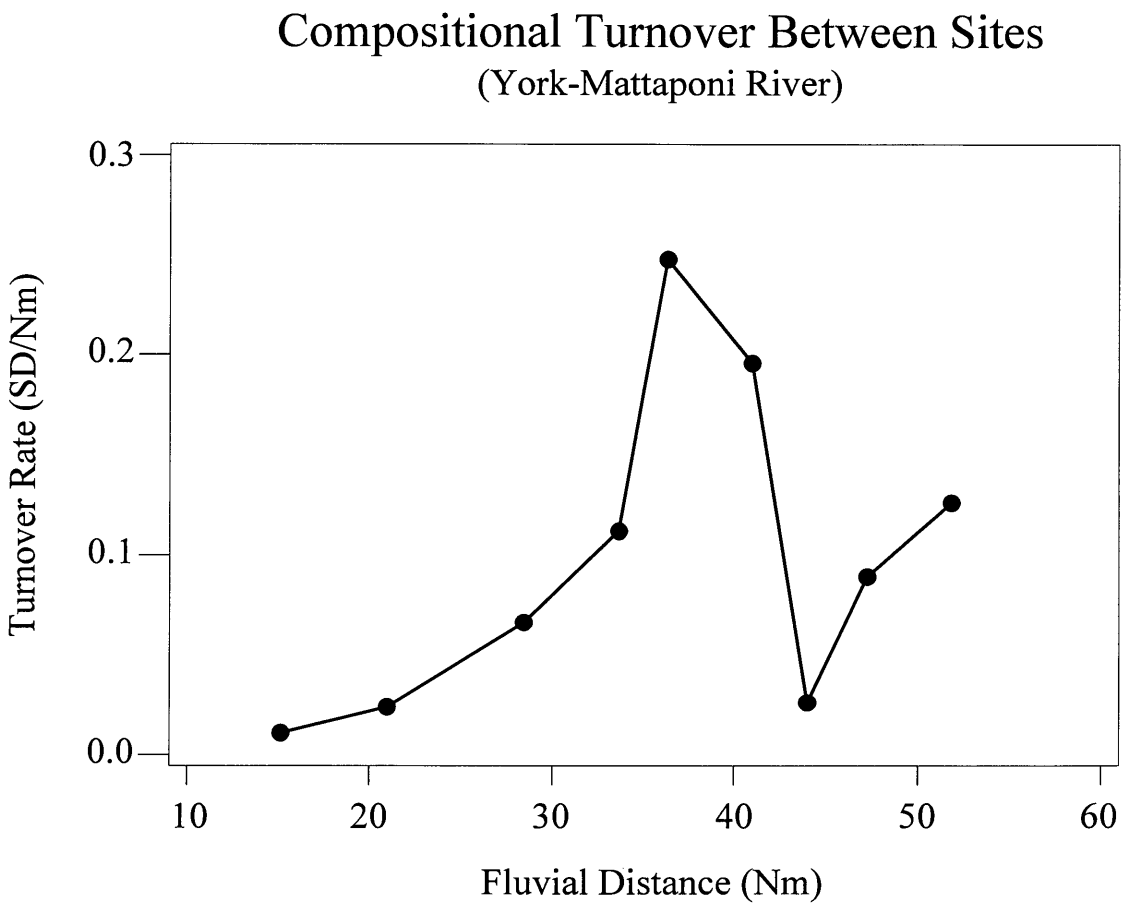

Longitudinal Species Diversity
(York-Mattaponi River)
Shannon-Wiener Diversity (H')
2.5
2.0
1.5
1.0
10
20
30
40
50
60
Fluvial Distance (Nm)

Figure 19: Longitudinal species turnover (beta diversity) in the York-Mattaponi River, 1990-94. Units are standard deviations in species turnover per nautical mile from the DCA ordination of all stations.


Compositional Turnover Between Sites
(York-Mattaponi River)
Turnover Rate (SD/Nm)
0.3
0.2
0.1
0.0
10
20
30
40
50
60
Fluvial Distance (Nm)

York-Pamunkey River Community Patterns

A total of 64 species of fishes comprising 21,834 individuals were collected (first tow only), of which 20 were represented by 5 or fewer individuals, and 35 met the 3% capture frequency criterion for inclusion in the gradient analysis.

Spatial Assemblage Patterns (TWINSPAN and DCA) -- The TWINSPAN classification of all stations generally reflects a longitudinal riverine gradient (Fig. 20), and suggests the presence of six intergrading assemblages of sandy beach fishes. The first dichotomy is strong (eigenvalue 0.55) and separates tidal freshwater stations (subset 0) from saline stations (subset 1). At the second division level, subset 0 was subdivided into a longitudinal series of tidal freshwater stations with separation between upstream (Group 1; PM-55 & PM-61) and downstream (subset 01) stations. Subset 01 separated at the third division level into two groups of tidal freshwater stations (Groups 2 and 3) based on the upstream penetration of several higher salinity taxa. Saline stations (subset 1) separated at the second division level into oligohaline (Group 4) and mesohaline (subset 11) groups. Subset 11 further divided at the third division level into two mesohaline station groups: Group 5a (primarily YK-21 and YK-28) and Group 5b (primarily YK-15). Further divisions of Groups 1-5 were not considered as they seemed mainly due to the presence of less common species and did not yield distinct groups within the DCA ordination space.

The DCA ordination of all stations is presented in Figure 21. The TWINSPAN groups are reasonably distinct; however, many stations in neighboring groups are

adjacent. Overall, the ordination represents a continuum of intergrading assemblages. The faunal break associated with the freshwater interface (origin of the first axis) was relatively indistinct in this river system vs. the James or Rappahannock. Station scores along the first axis were generally separated along the salinity gradient into tidal freshwater (Groups 1-3) and oligohaline (Group 4) stations in the Pamumkey River, and mesohaline stations (Groups 5a & 5b) in the York River below the confluence at West Point, VA. The eigenvalue of the first axis (0.56) suggests the gradient represented by it was highly significant. The ecological distance of 3.59 SD along the first axis indicates that the faunas at the extremities of the estuarine gradient were approximately 90% dissimilar. The second axis had a lower eigenvalue (0.13), is relatively short (1.85 SD; 46% dissimilar), and appears to primarily separate the permanent tidal freshwater stations along the riverine gradient.

Figure 22 shows the DCA ordination of the 35 species from the York and Pamunkey Rivers which met the first tow 3% frequency criterion for retention. Species symbols correspond to the modified ecological affinity groups of McHugh (1967) as defined in the Methods and Materials section. Species scores were generally aligned in a longitudinal pattern similar to the station scores. The dispersion of species centered in permanent tidal freshwater was truncated, indicating the presence of a longitudinal salinity gradient. Species scores were generally well ordered from freshwater → estuarine → marine species. The faunal break at the freshwater interface (origin of axis 1) is more evident in the species plot then the station plot. Freshwater species were largely dispersed along the second ordination axis in a longitudinal series moving upstream.

Environmental Correlates (DCCA) -- A direct comparison of the distribution of constrained (DCCA) and unconstrained (DCA) station scores is given in Table 11. Spearman rank correlations indicate the ordination methods accounted for similar variation. Further support for this interpretation is indicated by the similar gradient lengths and eigenvalues generated by the two methods. The lower correlation between the second axis of DCA and DCCA (0.72) may indicate the importance of unmeasured variables (or spatial scales).

The overall ordination was significant ($p<0.001$) and the first two DCCA axes explained 64.8% of the total variance in the species-environment relations (Tab. 12). Significant correlations and canonical coefficients of species scores on DCCA axis 1 with environmental factors indicated that this axis was positively correlated with salinity (0.86), channel width (0.77) and shoal width (0.66), all of which tend to decrease moving upstream. The first axis was also negatively correlated with distance to the bay mouth (-0.96). Nearshore sediment grain size (0.67) was positively correlated with the second DCCA axis and served primarily to separate upstream (sand with some pebbles) from downstream (sandy) freshwater collections. Correlations on third and higher DCCA axes were not considered due to their low eigenvalues.

The arrangement of species scores on DCCA axes 1 and 2 support the results derived from TWINSPAN and DCA (Fig. 23). The order of species scores along the first axis corresponds well with the general salinity preferences and tolerances of McHugh's ecological affinity groups; species were well order from freshwater → estuarine → marine taxa. Freshwater taxa were centered primarily along the second axis with one notable

exception. The white catfish (*Ameiurus catus*) was commonly observed at oligohaline stations below the freshwater interface.

Species-Environment Associations -- Specific species associations with TWINSPAN groups are catalogued below and are summarized in Table 13. Environmental values for TWINSPAN groups are summarized in Table 14.

Tidal Freshwater I: This group included 9 stations (TWINSPAN Group 1) and supports primarily freshwater (22) and diadromous (5) species. A total of 33 species and 2,677 individuals were collected. The spottail shiner (*N. hudsonius*; 40.0%), hogchoker (*T. maculatus*; 14.3%), the eastern silvery minnow (*H. regius*; 8.4%), the satinfin shiner (*C. analostana*; 5.4%), the redbreast sunfish (*L. auritus*; 5.2%) and juvenile striped bass (*M. saxatilis*; 4.8%) accounted for 78.1% of all individuals captured at these sites. Relatively frequent catches of the redbreast sunfish (FOC 82%) characterized this group in the TWINSPAN analysis. Other frequently occurring species included the spottail shiner (FOC 91%), satinfin shiner (FOC 82%), hogchoker (FOC 76%), bluegill (*Lepomis macrochirus*; FOC 70%) and the banded killifish (FOC 67%). These stations are far upstream in the Pamunkey River and are frequented by several centrarchid species indicative of more stable freshwater environments (e.g., redbreast sunfish, bluegill and pumpkinseed).

Tidal Freshwater II: This group included 6 stations (TWINSPAN Group 2), and supports primarily freshwater (17) and estuarine (7) species with a total of 29 species and 1,645 individuals captured. The spottail shiner (*N. hudsonius*; 48.6%), juvenile striped bass (*M. saxatilis*; 14.8%) and the hogchoker (*T. maculatus*; 14.0%) comprised 77.4% of

all individuals captured at these sites. TWINSPAN identified the tessellated darter (FOC 50%) as an indicator species. The most frequently occurring species were the spottail shiner (FOC 93%), juvenile striped bass (FOC 79%), hogchoker (FOC 71%) and the banded killifish (FOC 64%). This species assemblage was typical of tidal freshwater, sandy bottom environments common in the lower Pamunkey River.

Tidal Freshwater III: This group included 7 stations (TWINSPAN Group 3), and supports primarily freshwater (15), estuarine (6) and anadromous (4) species with a total of 30 species and 1,891 individuals captured. The spottail shiner (*N. hudsonius*; 27.4%), juvenile striped bass (*M. saxatilis*; 23.1%), hogchoker (*T. maculatus*; 14.8%), juvenile white perch (*M. americana*; 11.1%) and the mummichog (*F. heteroclitus*; 5.6%) accounted for 82% of all individuals collected at these sites. TWINSPAN identified the Atlantic croaker (FOC 32%), mummichog (FOC 51%) and juvenile striped bass (FOC 95%) as indicator species. Other frequently occurring species included the spottail shiner (FOC 86%), hogchoker (FOC 73%) and juvenile white perch (FOC 73%). This group is very similar to the Tidal Freshwater II stations, however, higher salinity species more commonly occurred at these sites (e.g., Atlantic croaker, spot).

Oligohaline: This group included 8 stations (TWINSPAN Group 4), and supports primarily estuarine fishes (7 species; 77.5% individuals), although several freshwater (11), estuarine-marine (7) and diadromous (4) species routinely occur in fewer numbers. A total of 31 species and 4,149 individuals were captured. The hogchoker (*T. maculatus*; 38.0%), bay anchovy (*A. mitchelli*; 19.6%), juvenile white perch (*M. americana*; 9.8%), the white catfish *A. catus*; 8.3%), juvenile striped bass (*M. saxatilis*; 6.1%) and the

mummichog (*F. heteroclitus*; 4.9%) accounted for 86.7% of all individuals collected at these sites. TWINSPAN failed to identify a strong indicator species for this group. The most frequently occurring species were the hogchoker (FOC 100%), mummichog (FOC 89%), juvenile striped bass (FOC 81%), bay anchovy (FOC 78%), juvenile white perch (FOC 73%), spot (FOC 70%) and white catfish (FOC 68%). All of the stations in this group occurred above the confluence with the York River. The average salinity for this group was 2.67 ∓ 0.42 ppt.

(NOTE: The next two groups are identical to Groups 4a and 4b from of the York-Mattaponi analysis.)

Mesohaline I: This group included 10 stations (TWINSPAN Group 5a), and supports primarily estuarine (13), estuarine-marine (12) and marine (7) species with a total of 9,089 individuals and 37 species collected. The hogchoker (*T. maculatus*; 42.4%), mummichog (*F. heteroclitus*; 15.8%), the Atlantic croaker (*M. undulatus*; 13.0%), the spot (*L. xanthurus*; 10.9%) and the Atlantic silverside (*M. menidia*; 6.5%) accounted for 88.6% of all individuals captured at these sites. TWINSPAN identified the striped killifish (FOC 83%) as an indicator species for both mesohaline assemblages. The other most frequently occurring species included the spot (FOC 94%), hogchoker (FOC 88%), Atlantic croaker (FOC 83%), Atlantic silverside (FOC 79%) and the mummichog (FOC 77%). The average salinity for this group was 13.14 ± 0.47 ppt.

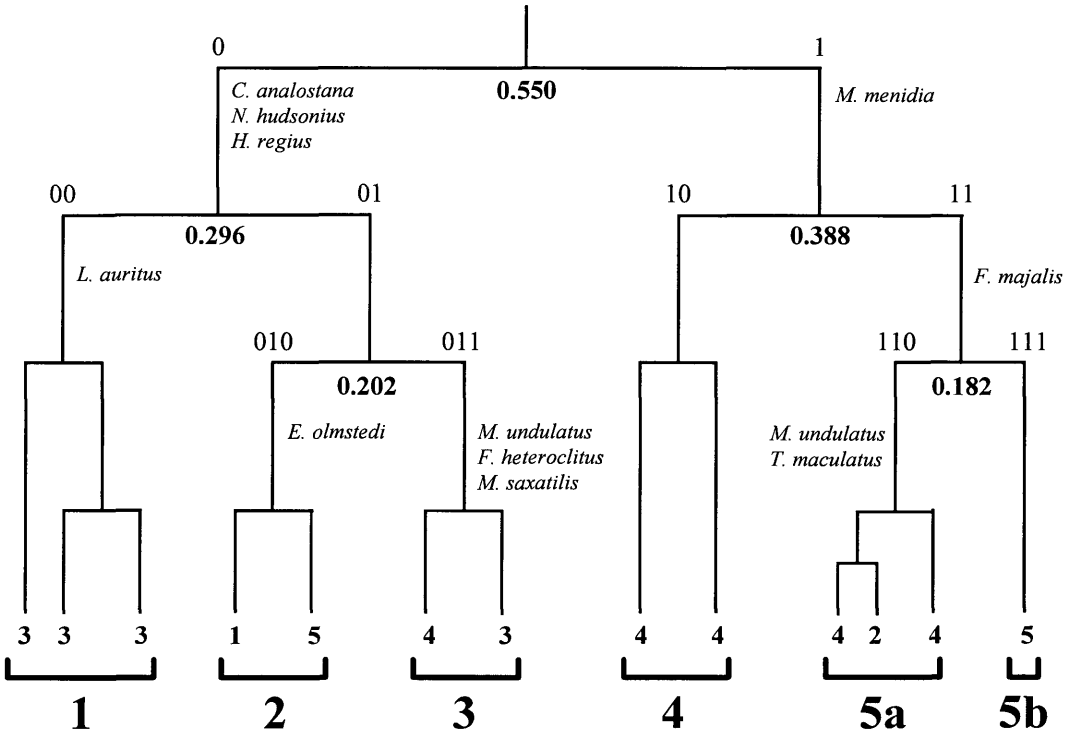
Mesohaline II: This group included 5 stations (TWINSPAN Group 5b; four are

from YK-15), and supports primarily estuarine (10), estuarine-marine (9) and marine (5) species with a total of 2,383 individuals and 27 species collected. The Atlantic silverside (*M. menidia*; 51.9%), mummichog (*F. heteroclitus*; 25.0%) and the spot (*L. xanthurus*; 8.4%) accounted for 85.2% of all individuals captured at these sites. Relatively moderate to high standardized densities and FOC of several ubiquitous estuarine species characterized this group in the gradient analysis. Particularly, the Atlantic silverside (FOC 88%), spot (FOC 68%), striped killifish (FOC 64%), and the inshore lizardfish (FOC 64%). The average salinity at these sites was 15.41 ± 0.48 ppt.

Species Diversity -- Rarefied species richness showed a slight increase moving from the saline to tidal freshwater portions of the river system (Fig. 24b). Total species richness differed from the rarefaction curve, showing a general decline moving upstream, with marked local increases at stations YK-21, YK-28 and PM-55 (Fig.24a). Each of these increases appear due to the increased capture of rare species associated with a greater total sample area (i.e., the species-area effect; Fig. 25). The most notable feature of these curves is the low total species richness at station YK-15. Species evenness and diversity displayed similar trends with values generally increasing moving upstream (Figs. 26 & 27). Interannual variability in both evenness and diversity were high throughout the study area. The highest compositional turnover (beta diversity) along the York-Pamunkey River was observed across the freshwater interface near station PM-42; above and below this site the rate of change was generally less (Fig. 28).

Figure 20: TWINSPAN classification of York-Pamunkey River stations. Indicator species for each division are shown in decreasing order of importance. Eigenvalues of major divisions are shown in bold under each division. Binary numbers above divisions denote major subsets. Smaller font numbers below final groups are the number of stations within that group. Larger font numbers below brackets are final TWINSPAN group labels. Station labels are rivermile-year.

York-Pamunkey River
(n=45)



1	2	3	4	5a	5b
PM55-91	PM42-90	PM42-94	PM36-90	YK15-93	YK15-90
PM55-92			PM36-91		YK15-91
PM55-93	PM45-90	PM45-91	PM36-92	YK21-91	YK15-92
PM55-94		PM45-92	PM36-93	YK21-92	YK15-94
	PM50-90	PM45-93	PM36-94	YK21-93	
PM61-90	PM50-91	PM45-94		YK21-94	YK21-90
PM61-91	PM50-92		PM42-91		
PM61-92		PM50-93	PM42-92	YK28-90	
PM61-93	PM55-90	PM50-94	PM42-93	YK28-91	
PM61-94				YK28-92	
				YK28-93	
				YK28-94	

Figure 21: Axes 1 and 2 of DCA ordination of York-Pamunkey River stations. Symbols correspond to TWINSPAN groups. Units are standard deviations in species turnover rate.

York-Pamunkey River Station Scores
(TWINSPAN Groups)

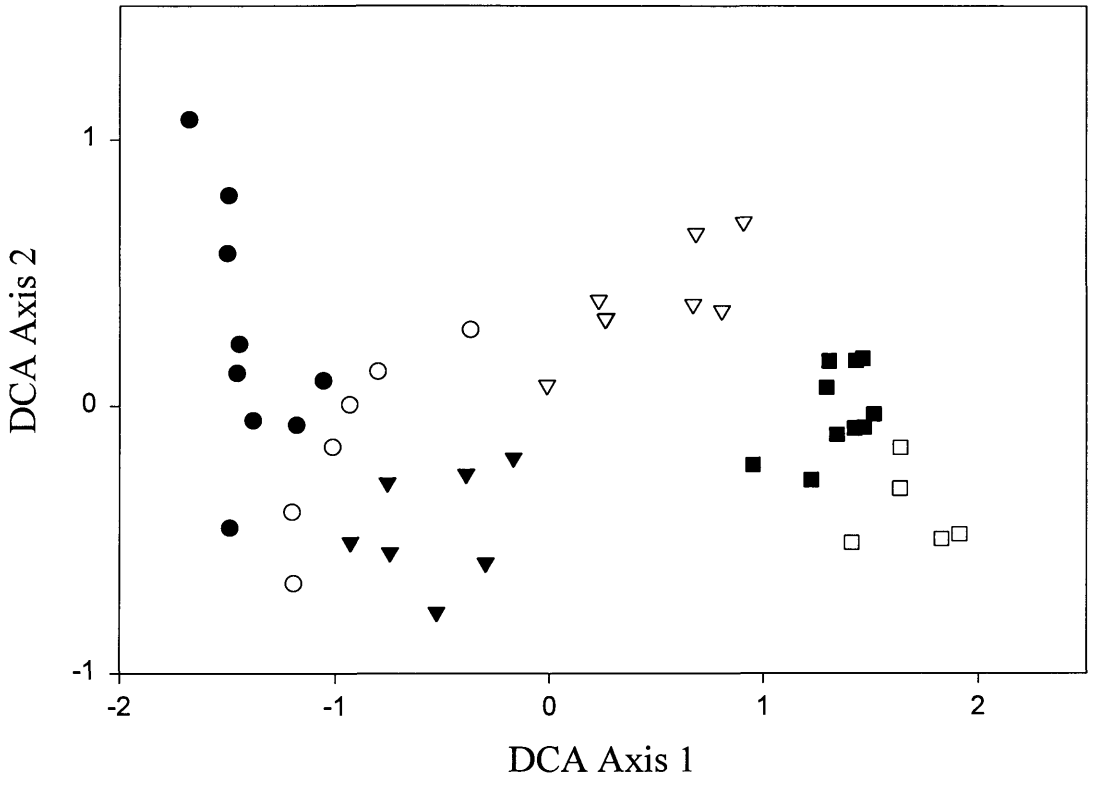
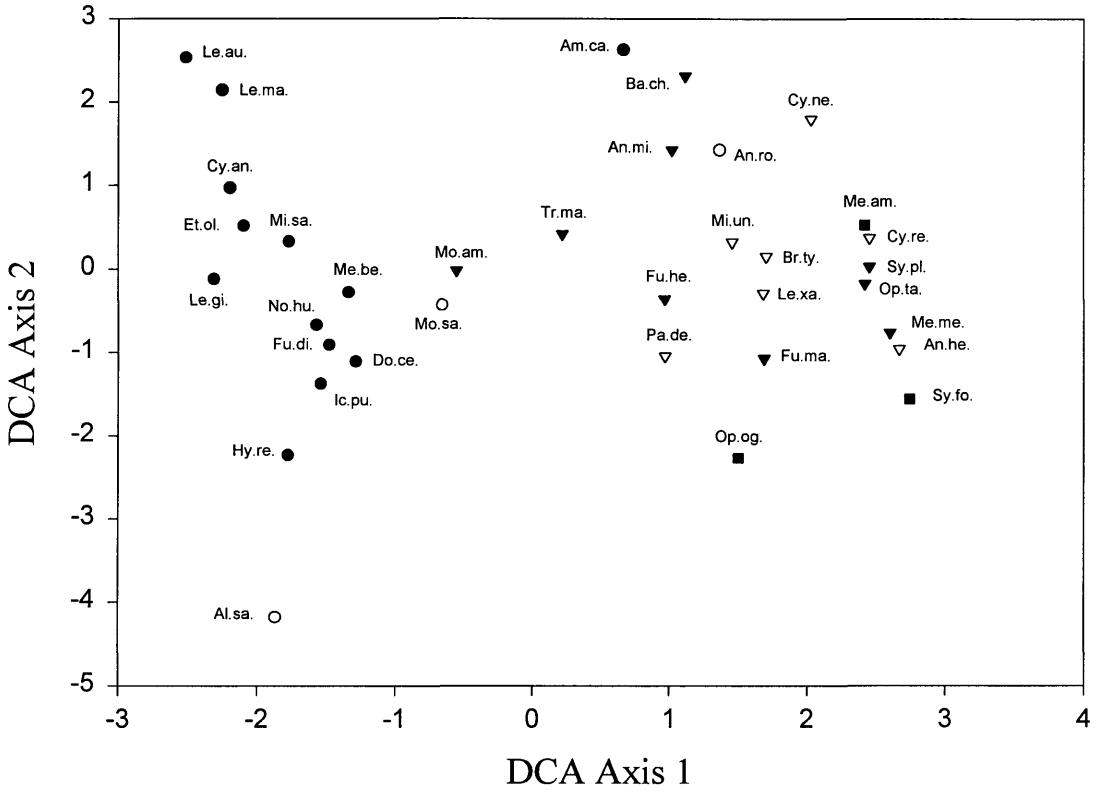


Figure 22: Axes 1 and 2 of DCA ordination of the 35 York-Pamunkey River species included in the gradient analysis. Symbols correspond to the modified ecological groups of McHugh (1967). Species labels are the first f our letters of genus and species names respectively (see Appendix 2 for a complete alphabetical list). Units are standard deviations in species turnover rate.

York-Pamunkey River Species Scores
(Ecological Affinity Groups)



●	Freshwater Species
○	Diadromous Species
▼	Estuarine Species
▽	Estuarine-Marine Species
■	Marine Species

Table 11: Direct comparison of DCA and DCCA axes via Spearman rank correlation for the York-Pamunkey River stations. DCA scores are weighted average scores and DCCA scores are linear combination scores predicted from the multiple regression.

	Eigenvalue		Gradient Length		
Ordination Axis	**DCA**	**DCCA**	**DCA**	**DCCA**	r^2
1	0.56	0.52	3.59	2.15	0.97 ***
2	0.13	0.10	1.85	1.32	0.72 ***

*** $p < 0.001$

Table 12: Results of the detrended canonical correspondence analysis of fish assemblages from the York-Pamunkey River. Significance values of correlation and canonical coefficients correspond to a two-tailed students *t*-test.

Variable	Axis 1	Axis 2
Canonical Coefficients for Environmental Variables		
Salinity	0.2826 ***	0.2118 *
Temperature	0.0015	-0.1294 ***
Dissolved O_2	0.0075	-0.0497
pH	-0.0101	-0.0358
Substrate Grain Size	0.0521	0.2181 ***
Channel Width	-0.5949 ***	-0.6647 ***
6' Contour	0.2947 ***	0.1501
Distance to Bay Mouth	-0.7840 ***	-0.3065 ***
Correlations of Environmental Variables with Axes		
Salinity	0.8642 ***	-0.0908
Temperature	-0.3129 *	-0.1894
Dissolved O_2	0.4028 **	-0.3696 *
pH	0.1107	-0.2161
Substrate Grain Size	-0.3623 *	0.6865 ***
Channel Width	0.7681 ***	-0.2659
6' Contour	0.6317 ***	-0.2220
Distance to Bay Mouth	-0.9634 ***	0.1301
Summary Statistics for Ordination Axes		
Eigenvalue	0.523	0.097
Species-environment correlation	0.984	0.912
Cummulative % of species-environment variance explained	54.6	64.8
Monte Carlo probability for significance of the sum of all eigenvalues (10^3 pemutations): 0.001		

*** $p < 0.005$ ** $p < 0.01$ * $p < 0.05$

Figure 23: Axes 1 and 2 of DCCA ordination of the 35 York-Pamunkey River species included in the gradient analysis. Environmental variables are indicated with vectors. Only statistically significant variables are included in the ordination diagram. Abbreviations are the first four letters in both the genus and species names (see Appendix 2 for a complete alphabetical list).

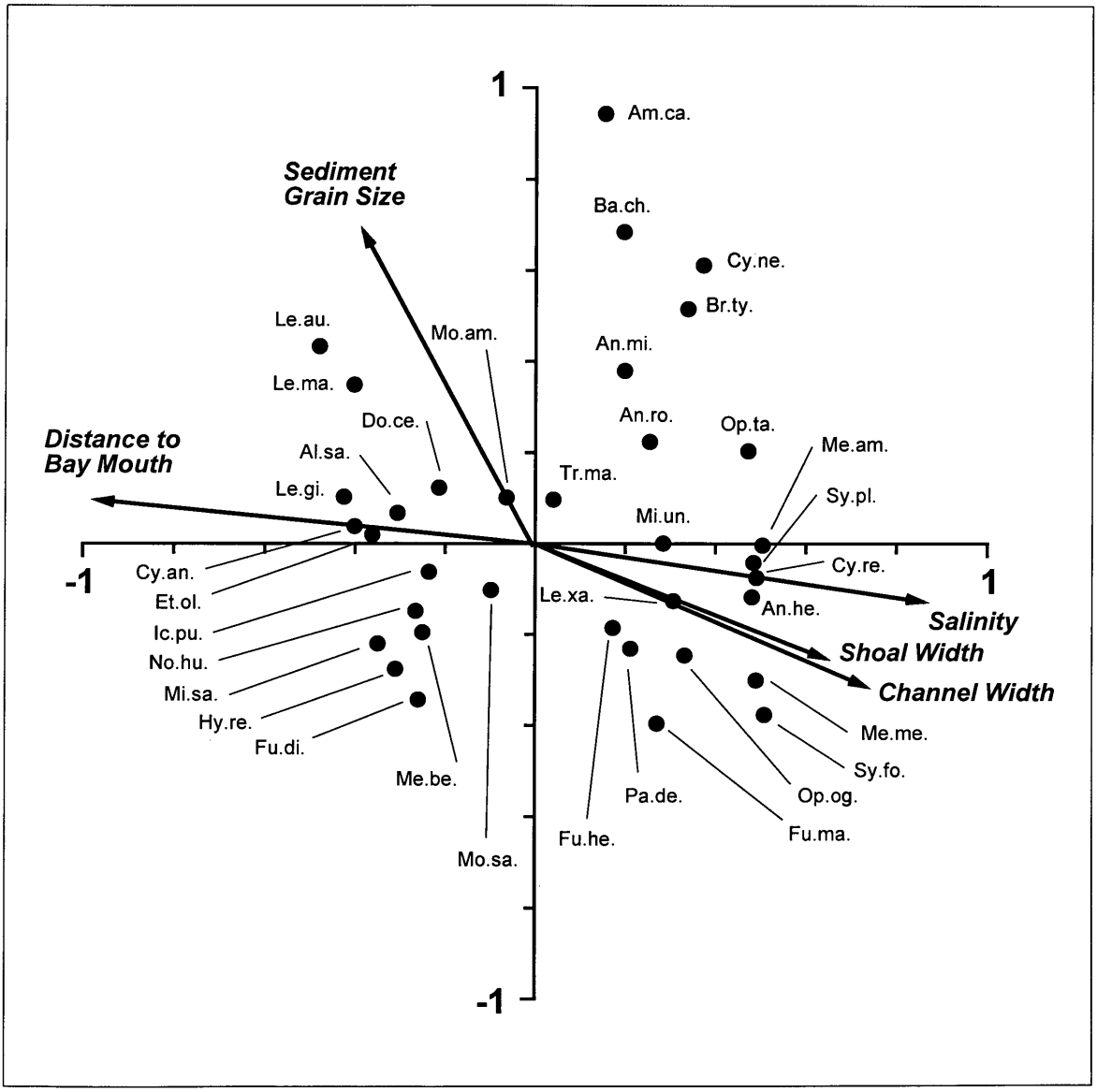

1
-1
1
-1
Sediment
Grain Size
Distance to
Bay Mouth
Salinity
Shoal Width
Channel Width
Am.ca.
Ba.ch.
Cy.ne.
Br.ty.
An.mi.
An.ro.
Op.ta.
Me.am.
Sy.pl.
Cy.re.
An.he.
Tr.ma.
Mi.un.
Le.xa.
Le.au.
Le.ma.
Le.gi.
Al.sa.
Do.ce.
Mo.am.
Cy.an.
Et.ol.
Ic.pu.
No.hu.
Mi.sa.
Hy.re.
Fu.di.
Me.be.
Mo.sa.
Fu.he.
Pa.de.
Op.og.
Fu.ma.
Me.me.
Sy.fo.

Table 13: Dominant and indicator taxa for TWINSPAN groups of York and Pamunkey River stations. Density is mean (+/- 1 standard error) abundance per 1000 m^2 swept area calculated for all stations included in the TWINSPAN group. FOC = frequency of occurence in the stations from the TWINSPAN group. Indicator species are denoted with an asteriks.

TWINSPAN Group	Dominant & Indicator Taxa					
	Species	Density (#/10^3 m^2)		FOC	Fork Length (mm)	
1	*Notropis hudsonius*	62.33	(22.75)	0.91	60.93	(0.51)
	Trinectes maculatus	42.05	(13.14)	0.76	46.09	(2.41)
	Cyprinella analostana	29.79	(9.33)	0.82	55.79	(0.49)
	Lepomis auritus *	18.13	(3.55)	0.82	85.06	(6.29)
	Lepomis macrochirus	12.89	(3.68)	0.70	76.92	(3.03)
	Hybognathus regius	12.67	(6.04)	0.42	63.11	(0.78)
	Fundulus diaphanus	11.44	(4.24)	0.67	57.63	(1.10)
	Morone saxatilis	10.67	(2.72)	0.61	71.79	(2.10)
	Etheostoma olmstedi	6.84	(2.23)	0.48	49.88	(1.66)
	Fundulus heteroclitus	4.20	(2.26)	0.33	61.55	(1.21)
	Ictalurus punctatus	3.17	(1.15)	0.30	177.24	(5.93)
	Morone americana	2.92	(1.02)	0.36	154.49	(17.89)
	Menidia beryllina	2.80	(1.36)	0.39	56.38	(2.20)
	Lepomis gibbosus	2.69	(0.90)	0.33	97.05	(4.16)
2	*Notropis hudsonius*	102.58	(21.08)	0.93	61.95	(0.41)
	Morone saxatilis	40.55	(12.72)	0.79	66.80	(1.31)
	Trinectes maculatus	28.05	(7.61)	0.71	47.85	(1.02)
	Anchoa mitchelli	8.03	(4.36)	0.32	47.22	(1.87)
	Fundulus diaphanus	7.15	(1.72)	0.64	51.98	(1.73)
	Morone americana	5.38	(1.52)	0.46	88.88	(7.16)
	Cyprinella analostana	4.50	(1.42)	0.50	56.88	(1.02)
	Etheostoma olmstedi *	3.01	(0.72)	0.50	52.68	(1.68)
	Menidia beryllina	3.01	(1.17)	0.32	53.05	(2.82)
	Ictalurus punctatus	2.45	(0.91)	0.29	162.67	(20.86)
	Hybognathus regius	2.12	(0.63)	0.36	83.82	(2.88)
	Dorosoma cepedianum	1.35	(0.53)	0.25	169.69	(25.93)
3	*Notropis hudsonius*	73.79	(17.62)	0.86	68.15	(0.49)
	Morone saxatilis *	63.04	(12.46)	0.95	61.89	(0.99)
	Trinectes maculatus	42.58	(11.07)	0.73	51.43	(0.69)
	Morone americana	30.59	(8.42)	0.73	59.31	(2.14)
	Fundulus heteroclitus *	20.41	(6.76)	0.51	59.08	(0.91)
	Hybognathus regius	10.34	(3.36)	0.38	65.70	(1.52)
	Fundulus diaphanus	8.48	(3.10)	0.38	68.37	(11.32)
	Leiostomus xanthurus	6.64	(3.09)	0.30	78.81	(2.77)
	Micropogonias undulatus *	3.33	(1.13)	0.32	98.77	(4.38)
	Menidia beryllina	3.30	(1.05)	0.30	60.86	(1.36)
	Ictalurus punctatus	1.78	(0.57)	0.27	167.75	(40.22)
	Cyprinella analostana	1.61	(0.58)	0.22	56.36	(2.05)

TWINSPAN Group	Dominant & Indicator Taxa					
	Species	Density (#/10^3 m^2)		FOC	Fork Length (mm)	
4	*Trinectes maculatus*	146.17	(27.45)	1.00	47.80	(0.31)
	Anchoa mitchelli	62.46	(17.49)	0.78	57.59	(0.22)
	Morone americana	35.89	(10.97)	0.73	63.03	(1.24)
	Ameiurus catus	31.26	(11.06)	0.68	77.66	(1.64)
	Morone saxatilis	22.35	(5.35)	0.81	63.45	(1.45)
	Fundulus heteroclitus	16.94	(3.24)	0.89	55.00	(0.65)
	Micropogonias undulatus	13.07	(4.40)	0.54	102.86	(1.98)
	Leiostomus xanthurus	9.56	(2.13)	0.70	82.42	(1.72)
	Notropis hudsonius	8.01	(2.87)	0.35	68.59	(1.18)
	Bairdiella chrysoura	7.91	(3.22)	0.35	88.09	(1.75)
	Brevoortia tyrannus	1.67	(1.22)	0.05	115.44	(2.20)
	Menidia menidia	1.54	(0.66)	0.19	67.00	(1.50)
	Menidia beryllina	1.22	(0.42)	0.24	61.08	(2.16)
	Dorosoma cepedianum	0.96	(0.51)	0.19	133.55	(32.33)
	Ictalurus punctatus	0.55	(0.26)	0.14	88.13	(9.84)
5a	*Trinectes maculatus* *	109.93	(21.94)	0.88	54.82	(0.15)
	Fundulus heteroclitus	40.95	(10.08)	0.77	62.25	(0.32)
	Micropogonias undulatus *	33.62	(7.78)	0.83	108.84	(0.54)
	Leiostomus xanthurus	28.39	(4.80)	0.94	91.12	(0.55)
	Menidia menidia	16.78	(3.38)	0.79	66.87	(0.45)
	Anchoa mitchelli	8.05	(2.51)	0.69	58.16	(0.36)
	Fundulus majalis *	7.16	(1.15)	0.83	83.95	(1.54)
	Morone saxatilis	2.28	(0.45)	0.56	72.35	(3.12)
	Symphurus plagiusa	2.05	(0.33)	0.60	90.74	(2.48)
	Mentichirrus americanus	1.74	(0.87)	0.21	81.95	(2.18)
	Synodus foetens	1.23	(0.33)	0.40	107.93	(5.13)
	Cynoscion regalis	1.11	(0.40)	0.23	63.74	(2.33)
	Brevoortia tyrannus	1.00	(0.50)	0.17	80.31	(5.45)
	Bairdiella chrysoura	0.88	(0.33)	0.23	59.10	(3.67)
	Anchoa hepsetus	0.83	(0.23)	0.33	68.62	(1.58)
5b	*Menidia menidia*	67.80	(35.10)	0.88	7.91	(0.17)
	Fundulus heteroclitus	32.60	(11.98)	0.60	72.39	(0.36)
	Leiostomus xanthurus	10.90	(2.64)	0.68	108.95	(0.76)
	Fundulus majalis *	5.25	(1.73)	0.64	94.56	(2.19)
	Trinectes maculatus	3.19	(0.97)	0.56	71.47	(1.42)
	Anchoa hepsetus	2.96	(0.87)	0.56	66.19	(1.23)
	Synodus foetens	1.69	(0.32)	0.64	106.57	(5.23)
	Anchoa mitchelli	1.26	(0.52)	0.24	58.83	(2.12)

Table 14: Average environmental values by TWINSPAN group for stations from the York and Pamunkey Rivers. Quantitative variables are mean ± one standard error. Channel measurements are given as a range.

TWINSPAN Group	Salinity (ppt)	Temperature (°C)	Dissolved O_2 (mg ℓ^{-1})	pH
1	0.00 ∓ 0.00	27.60 ∓ 0.44	5.16 ∓ 0.15	6.91 ∓ 0.11
2	0.13 ∓ 0.08	26.35 ∓ 0.47	5.58 ∓ 0.21	6.84 ∓ 0.13
3	0.17 ∓ 0.06	27.96 ∓ 0.32	5.83 ∓ 0.12	7.04 ∓ 0.11
4	2.67 ∓ 0.42	27.15 ∓ 0.33	5.46 ∓ 0.11	6.73 ∓ 0.09
5a	12.99 ∓ 0.44	26.32 ∓ 0.30	5.92 ∓ 0.16	7.09 ∓ 0.08
5b	15.61 ∓ 0.54	26.90 ∓ 0.54	6.29 ∓ 0.30	7.41 ∓ 0.18

	Nearshore Sediment	6' Contour (m)	Channel Width (m)	SAV Beds
1	Sand/Pebble	32 - 48	108 - 456	No
2	Sand/Pebble	12 - 48	192 - 456	No
3	Sand/Mud	12 - 18	192 - 286	No
4	Mud/Sand	16 - 43	192 - 458	No
5a	Sand	72 - 365	1800 - 3516	No
5b	Sand	72 - 360	1800 - 3516	No

Figure 24: Total (a) and rarefied (b) longitudinal species richness in the York and Pamunkey Rivers, 1990-94. Rarefied species richness is fit with a LOWESS curve.

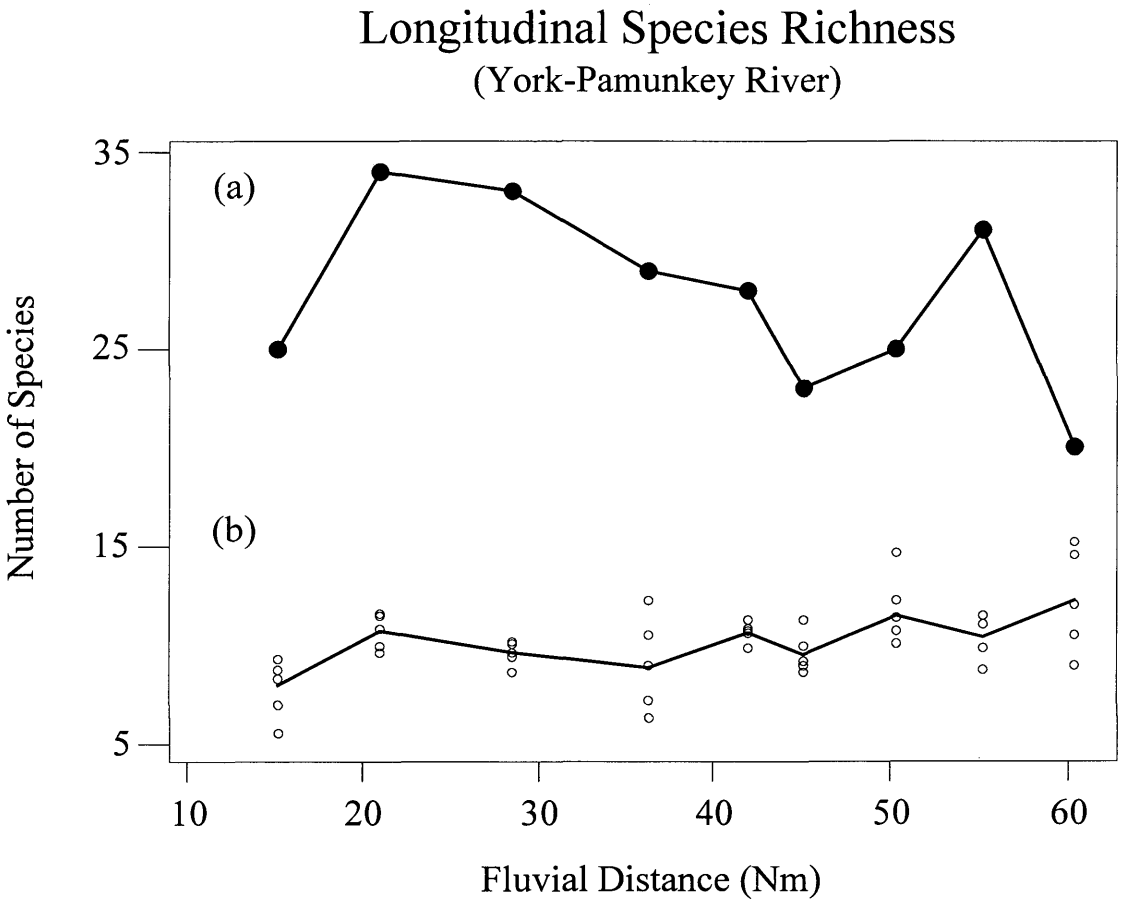

Longitudinal Species Richness
(York-Pamunkey River)
Number of Species
35
25
15
5
(a)
(b)
10
20
30
40
50
60
Fluvial Distance (Nm)

Figure 25: Total species captured and total area swept for York-Pamunkey River stations, 1990-1994.

Species-Area Relationship
(York-Pamunkey River)

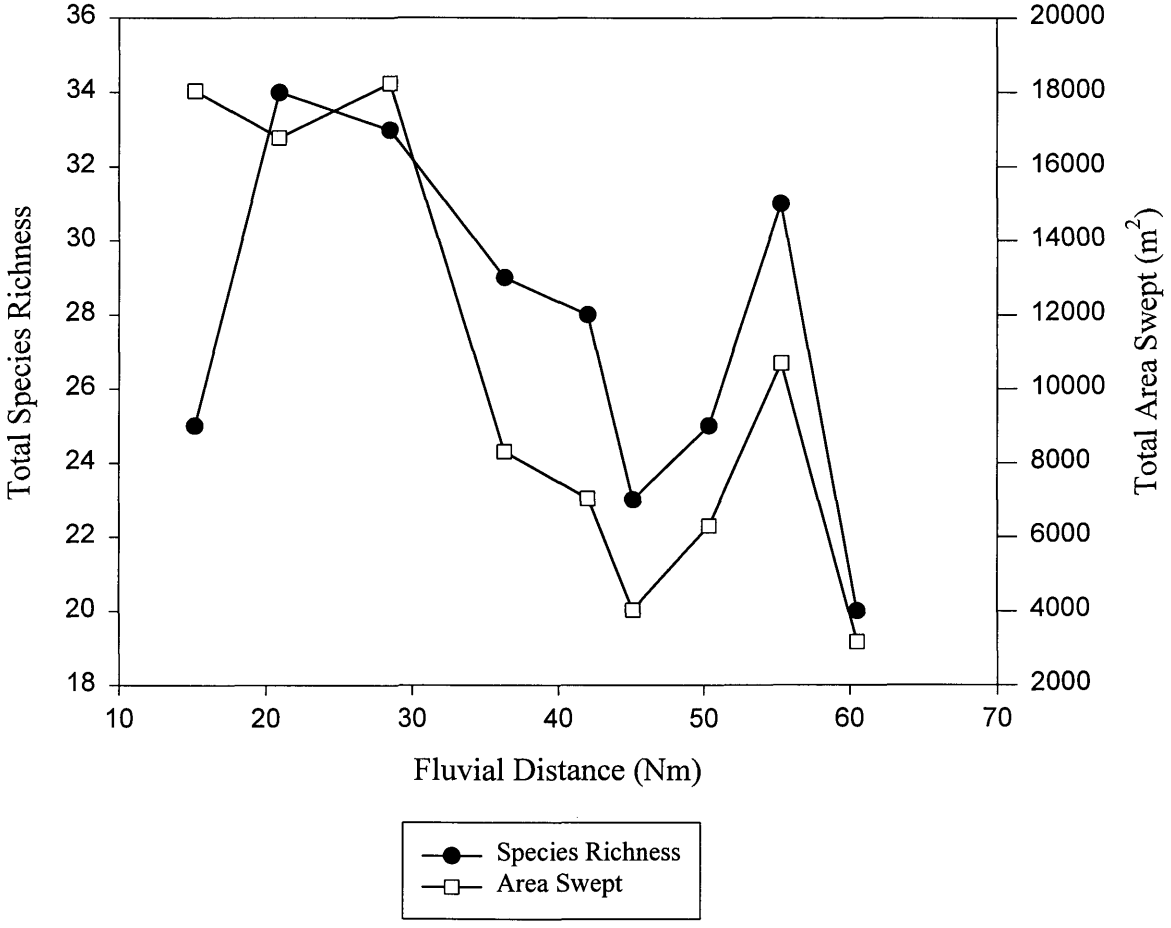


Figure 26: Longitudinal species evenness (Pielou's) in the York and Pamunkey Rivers, 1990-1994, fit with a LOWESS curve.

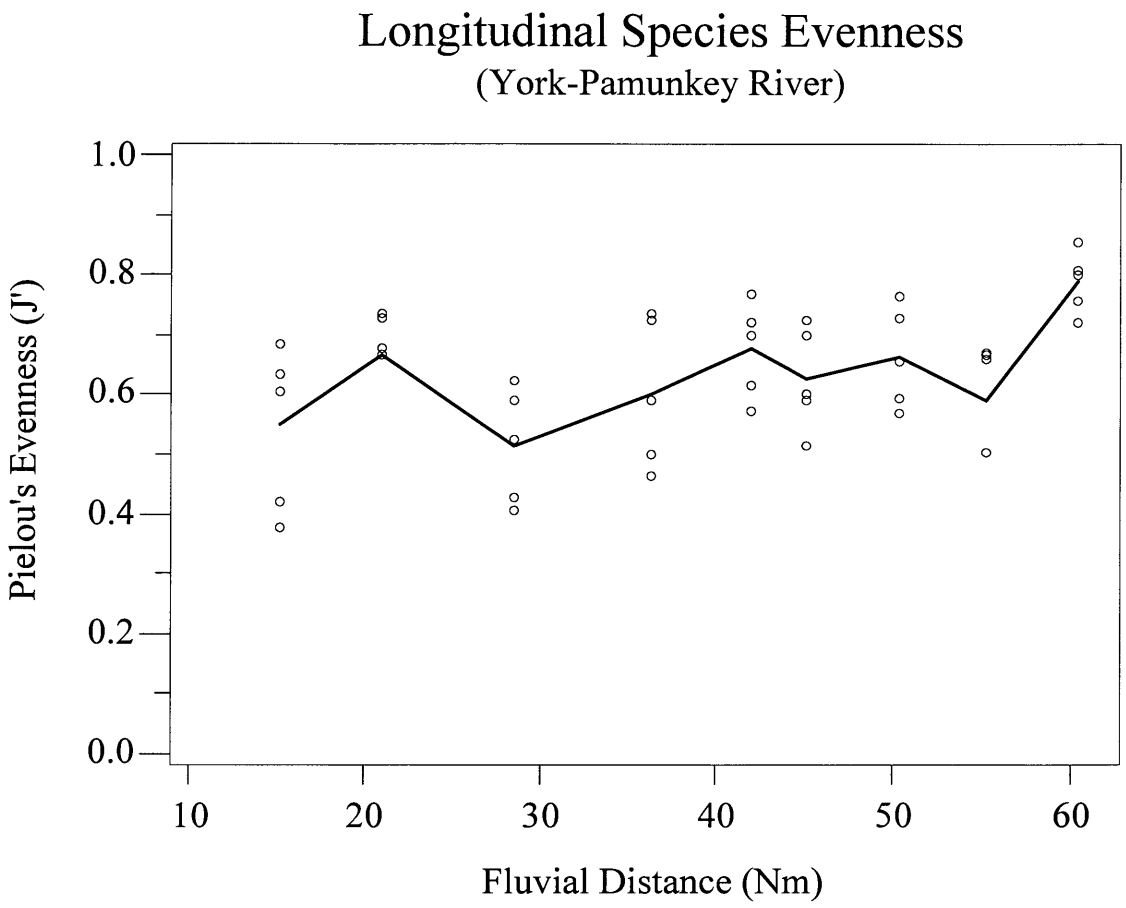

Longitudinal Species Evenness
(York-Pamunkey River)
Pielou's Evenness (J')
1.0
0.8
0.6
0.4
0.2
0.0
10
20
30
40
50
60
Fluvial Distance (Nm)

Figure 27: Longitudinal species diversity (Shannon-Wiener) in the York and Pamunkey Rivers, 1990-1994, fit with a LOWESS curve.

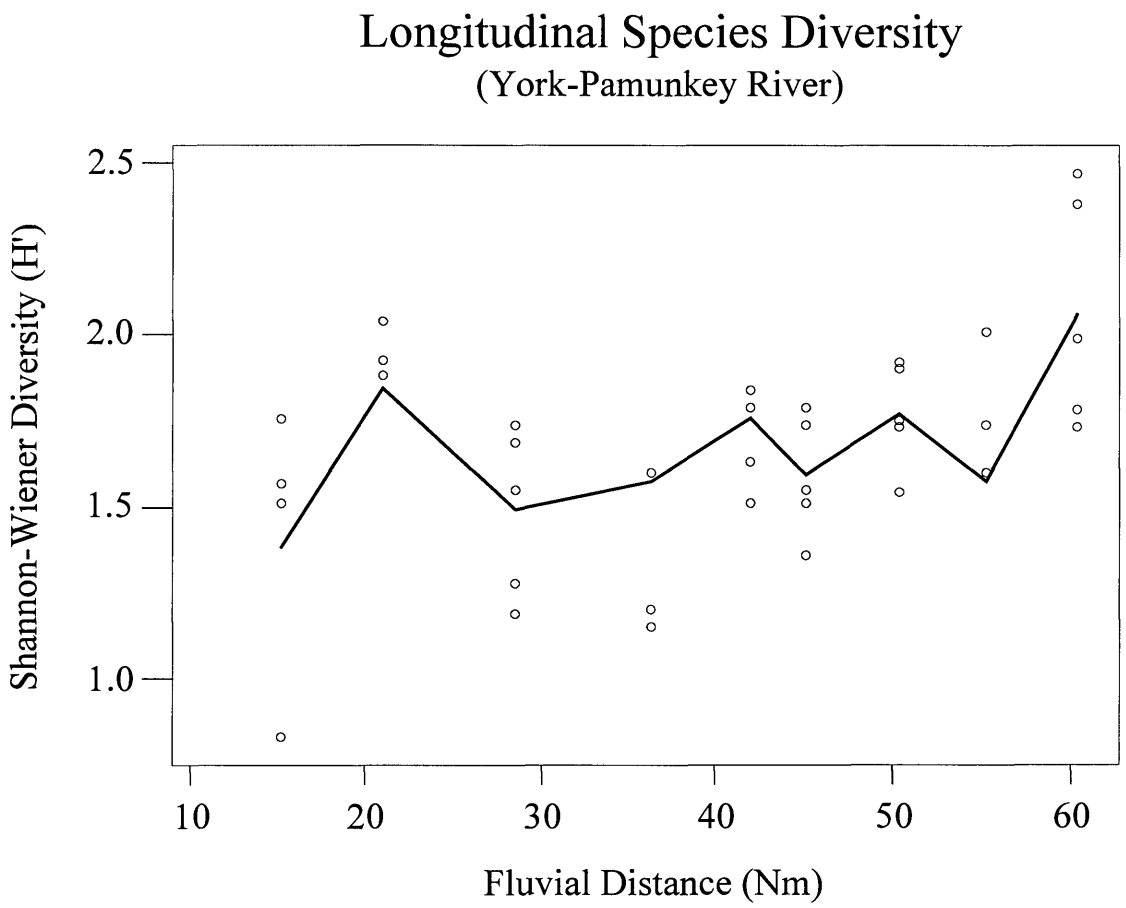
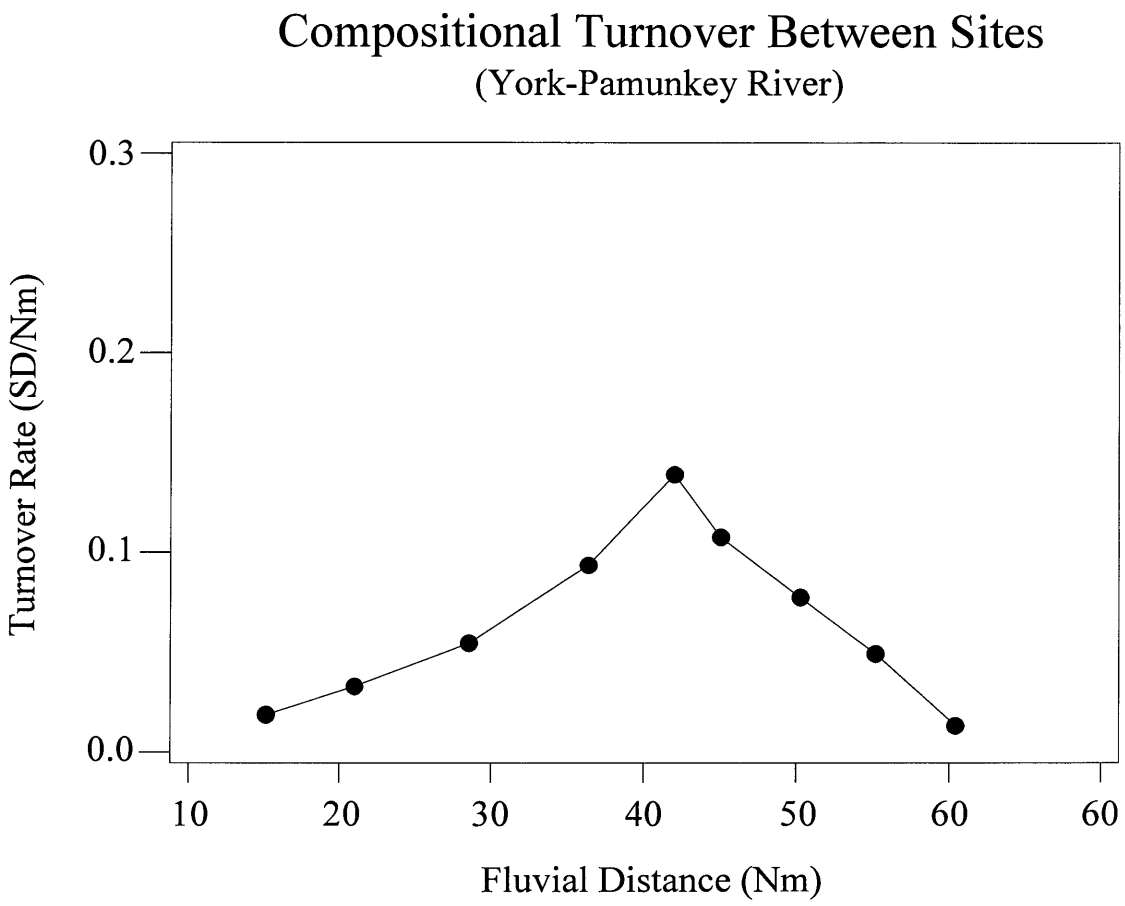

Longitudinal Species Diversity
(York-Pamunkey River)
Shannon-Wiener Diversity (H')
2.5
2.0
1.5
1.0
10
20
30
40
50
60
Fluvial Distance (Nm)

Figure 28: Longitudinal species turnover (beta diversity) in the York-Pamunkey River, 1990-94. Units are standard deviations in species turnover per nautical mile from the DCA ordination of all stations.


Compositional Turnover Between Sites
(York-Pamunkey River)
Turnover Rate (SD/Nm)
0.3
0.2
0.1
0.0
10
20
30
40
50
60
60
Fluvial Distance (Nm)

James River Community Patterns

A total of 65 species of fishes comprising 46,362 individuals were collected (first tow only), of which 26 were represented by 5 or fewer individuals, and 38 met the 3% capture frequency criterion for inclusion in the gradient analysis.

Spatial Assemblage Patterns (TWINSPAN and DCA) -- The TWINSPAN classification of all stations generally reflects a longitudinal riverine gradient (Fig. 29), and suggests the presence of six intergrading assemblages of sandy beach fishes. The first dichotomy is very strong (eigenvalue 0.50) and separates high salinity stations (subset 1) from tidal freshwater and oligohaline stations (subset 0). At the second division level, subset 1 was subdivided into low mesohaline (Group 5) vs. high mesohaline (Group 6) mean salinities. Subset 0 separated at the second division level into silty permanent tidal freshwater stations above the confluence with the Appomattox River at Hopewell, VA (Group 1) and the sandy tidal freshwater and oligohaline waters below Hopewell (subset 01). Subset 01 separated at the third division level into tidal freshwater stations (subset 010) and oligohaline stations (Group 4). Subset 010 further divided at the fourth division level into two permanent tidal freshwater groups (Groups 2 and 3). Further divisions of groups 1-6 were not considered as they seemed mainly due to the presence of less common species and did not yield distinct groups within the DCA ordination space.

The DCA ordination of all stations is presented in Figure 30. TWINSPAN groups below the freshwater interface are relatively well defined (Groups 4-6) while many

stations in neighboring groups above the interface are adjacent. Overall, the ordination represents a continuum of riverine beach assemblages. The largest separation occurs across the origin of axis 1 and corresponds to the faunal break associated with the freshwater interface. Interestingly, the oligohaline stations (Group 4) straddle this faunal break, due primarily to the relatively high abundances and frequencies of occurrence of freshwater species. Station scores along the first axis were generally separated into three regions along the salinity gradient associated with permanent tidal freshwater (Groups 1-3), transition to oligohaline salinities at the interface (Group 3), and mesohaline salinities (Groups 5 and 6). The eigenvalue of the first axis (0.54) suggests the gradient represented by it is very significant. The ecological distance of approximately 3.5 SD along the estuarine gradient indicates the faunas at the extremities of the sample reach were about 88% dissimilar. The second axis has a lower eigenvalue (0.18), is relatively short (2.02 SD; 51% dissimilar), and served primarily to separate downstream from upstream permanent tidal freshwater stations.

Figure 31 shows the DCA ordination of the 38 species from the James River collections meeting the first tow 3% frequency criterion for retention. Species symbols correspond to the modified ecological affinity groups of McHugh (1967) as defined in the Methods and Materials section. The first DCA axis is divided into two regions near the origin typified by species with negative scores (primarily freshwater and diadromous forms), and those with positive scores (estuarine and marine forms). Freshwater species with scores in the permanent tidal freshwater reach of the river are spread along the second axis, while estuarine and marine forms are dispersed along both axes.

Environmental Correlates (DCCA) -- A direct comparison of the distribution of constrained (DCCA) and unconstrained (DCA) station scores is given in Table 15. Spearman rank correlations indicate that the two ordination methods accounted for similar variation. Further support for this interpretation is indicated by the similar gradient lengths and eigenvalues generated by the two methods. The lower correlation between the second axis of DCA and DCCA (0.46) indicates the importance of unmeasured variables (or spatial scales).

The overall ordination was significant ($p<0.001$) and the first two DCCA axes explained 65.9% of the total variance in the species-environment relations (Tab. 16). Significant correlations and canonical coefficients of species scores on DCCA axis 1 with environmental factors indicated that this axis was positively correlated with salinity (0.92) and shoal width (0.93), and negatively correlated with fluvial distance to the bay mouth (-0.93). A strong and unsurprising correlation between salinity and shoal width was observed as both shoal width and salinity tend to decrease with movement upstream. Similarly, these variables were both negatively correlated with fluvial distance to the bay mouth. Nearshore substrate grain size was significant on the second DCCA axis (-0.49) and served primarily to separate muddy from sandy stations in the permanent tidal freshwater reach of the river. Dissolved oxygen was also significantly negatively correlated with the second DCCA axis (-0.29), although its low coefficient makes its importance suspect. The average dissolved oxygen content in the James River was 6.83 ± 0.09 mg ℓ^{-1}, and the lowest measurement was 3.60 mg ℓ^{-1}, above the generally accepted acute stress level of 2.0 mg ℓ^{-1}. Correlations on the third and higher DCCA axes were not

considered due to their low eigenvalues.

The arrangement of species scores on DCCA axes 1 and 2 strongly support the results derived from TWINSPAN and DCA (Fig. 32). The order of species scores along the first axis corresponds well with the general salinity preferences and tolerances of McHugh's ecological affinity groups; with species scores well ordered from freshwater → estuarine → marine taxa. The large variation of freshwater resident species along the second axis may represent small-scale (i.e., 10's-100's of meters) habitat preferences, or simple longitudinal succession into more stable, upstream environments.

Species-Environment Associations -- Specific species associations with TWINSPAN station groups are catalogued below and are summarized in Table 17. Environmental values for TWINSPAN station groups are summarized in Table 18.

Tidal Freshwater I: This group included 14 stations (TWINSPAN Group 1) and is derived entirely from the upstream, permanent tidal freshwater reach of the sample area above the confluence with the Appomattox River (stations JA-68 (except 1992), JA-74 and JA-78). These stations support primarily freshwater (23) and diadromous (5) species with a total of 3,721 individuals and 34 species collected. The blueback herring (*Alosa aestivalis*; 20.0%), spottail shiner (*N. hudsonius*; 16.3%), juvenile threadfin shad (*Dorosoma petenense*; 14.0%), juvenile white perch (*M. americana*; 13.7%), satinfin shiner (*C. analostana*; 7.4%), gizzard shad (*D. cepedianum*; 7.1%), juvenile striped bass (*M. saxatilis*; 6.0%) and the eastern silvery minnow (*H. regius*; 5.8%) comprised 90.3% of all individuals captured at these sites. Large total catch of the blueback herring (FOC 25%) characterized this group in the TWINSPAN analysis. However, the more

ubiquitous juvenile striped bass (FOC 71%), juvenile white perch (FOC 70%) and the spottail shiner (FOC 60%) were the most frequently occurring species. Rare catches of freshwater obligate species such as the bluehead chub (*Nocomis leptocephalus*), the smallmouth bass (*Micropterus dolomieu*) and the quillback (*Carpiodes cyprinnus*) also served to distinguish the upstream collections from other permanent tidal freshwater stations.

Tidal Freshwater II: This group included 10 stations (TWINSPAN Group 2), and supports primarily freshwater (18) and estuarine (6) species with a total of 12,480 individuals and 32 species collected. The gizzard shad (*D. cepedianum*; 34.1%), juvenile striped bass (*M. americana*; 24.3%), juvenile threadfin shad (*D. petenense*; 17.2%) and the hogchoker (*T. maculatus*; 12.4%) comprised 88.0% of all individuals captured at these sites. TWINSPAN identified the satinfin (FOC 58%) and golden (*Notemigonus chrysoleucas*; FOC 28%) shiners as indicator species. The most frequently occurring species were juvenile white perch (FOC 96%), the spottail shiner (FOC 94%) and juvenile striped bass (FOC 92%). Eight of the ten stations are collections taken from JA-46 and JA-56, sites with sandy bottoms, close proximity to submerged woody debris piles and relatively steep drop-offs to deeper water.

Tidal Freshwater III: This group included 9 stations (TWINSPAN Group 3), and supports primarily freshwater (18), estuarine (6) and estuarine-marine (6) species with a total of 4,293 individuals and 34 species collected. The spottail shiner (*N. hudsonius*; 33.7%), juvenile white perch (*M. americana*; 23.4%), juvenile striped bass (*M. saxatilis*; 10.3%) and the inland silverside (*M. beryllina*; 8.3%) comprised 75.7% of all individuals

captured at these sites. TWINSPAN identified the second most frequently occurring species, the hogchoker (FOC 91%), as an indicator species. Other frequently occurring species included juvenile white perch (FOC 100%), spottail shiner (FOC 81%), gizzard shad (FOC 79%) and channel catfish (FOC 74%).

Oligohaline: This group included 7 stations (TWINSPAN Group 4), and supports primarily estuarine (5) and estuarine-marine (8) species, though many freshwater species (14) occur in low numbers. A total of 2,580 individuals and 32 species were collected. Juvenile striped bass (*M. americana*; 29.8%), the Atlantic croaker (*M. undulatus*; 23.6%), juvenile striped bass (*M. saxatilis*; 13.4%) and the spottail shiner (*N. hudsonius*; 7.6%) comprised 74.4% of all individuals captured at these sites. TWINSPAN identified the Atlantic croaker (FOC 68%) and the rough silverside (FOC 22%) as indicator species. The most frequently occurring species were juvenile striped bass (FOC 100%) and white perch (FOC 100%), the spottail shiner (FOC 92%) and the inland silverside (FOC 70%). The low salinity (1.13 ± 0.20 ppt), and the close proximity to freshwater source areas (upstream James and Chickahominy Rivers) allowed for a good mix of estuarine and riverine faunas indicative of the spatially compressed salinity gradient in the James River.

Mesohaline I: This group included 9 stations (TWINSPAN Group 5) taken from JA-22 and JA-29, and supports primarily estuarine (6) and estuarine-marine (8) species, though several freshwater (6) and marine (8) species also occur in low numbers. A total of 5,209 individuals and 30 species were collected. The Atlantic silverside (*M. menidia*; 41.7%), juvenile white perch (*M. americana*; 11.4%), juvenile Atlantic menhaden (*B. tyrannus*; 9.7%), juvenile threadfin shad (*D. petenense*; 9.0%) and juvenile striped bass

(*M. saxatilis*; 6.9%) comprised 78.7% of all individuals captured at these sites. TWINSPAN failed to clearly identify any indicator species for this group. The most frequently occurring species were the Atlantic silverside (FOC 98%) and juvenile striped bass (FOC 91%). Average salinity for the stations in this group was 5.79 ± 0.38 ppt.

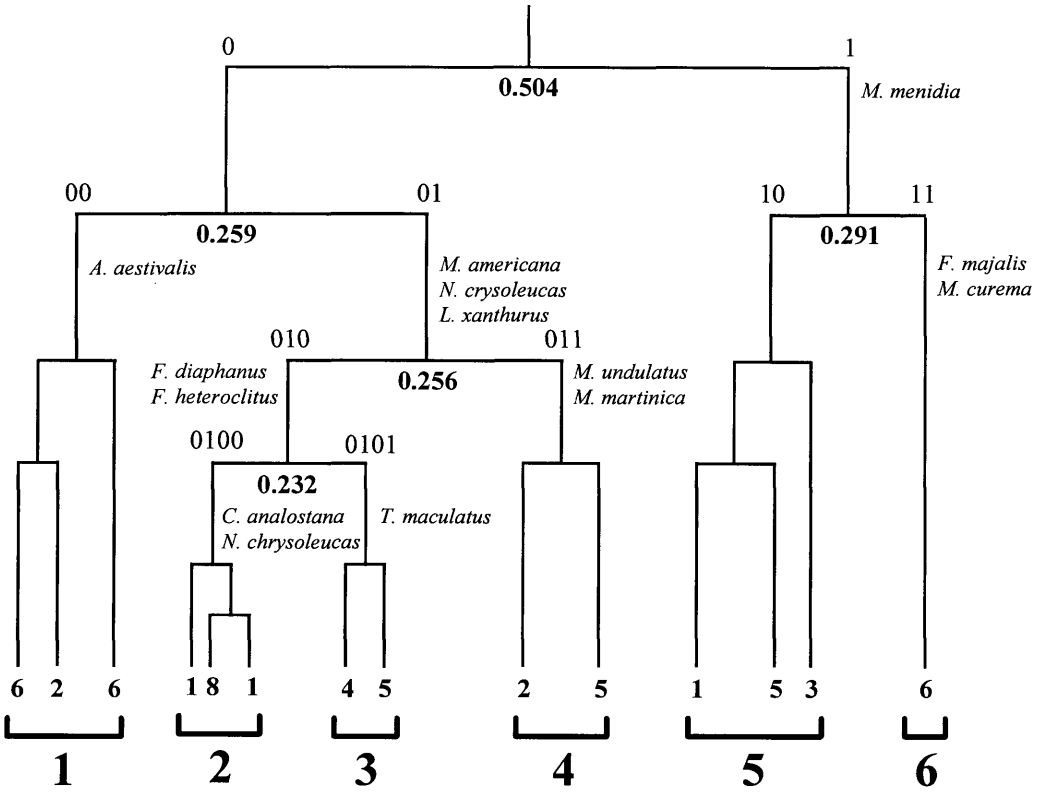
Mesohaline II: This group included 6 stations (TWINSPAN Group 6), taken from JA-12 (5) and JA-22 (1), and supports primarily estuarine (8) and estuarine-marine (11) species. A total of 11,915 individuals and 31 species were collected. The Atlantic silverside (*M. menidia*; 59.2%), the bay anchovy (*A. mitchelli*; 14.3%) and the white mullet (*Mugil curema*; 6.0%) comprised 79.5% of all individuals collected at these sites. TWINSPAN identified the white mullet (FOC 63%) and the striped killifish (FOC 77%) as indicator species. The other most frequently occurring species were the Atlantic silverside (FOC 100%) and the spot (FOC 80%). Average salinity for the stations in this group was 11.78 ± 0.90 ppt.

Species Diversity -- Rarified species richness was markedly hump-shaped with a peak near the tidal freshwater interface (approximately river mile 40) and coincident with the confluence with the Chickahominy River (Fig. 33b). Values were generally lower above and below this region. Total species richness displayed similar patterns (Fig. 33a); although, the lower oligomesohaline portion of the sample area showed a sharp decrease in the total number of species captured that was unrelated to the species-area effect (Fig. 34). Species evenness (Fig. 35) and diversity (Fig. 36) showed a similar hump-shaped pattern near the freshwater interface, although both had local increases above the confluence with the Appomattox River. The highest compositional turnover rate (Beta

diversity) was observed across the freshwater interface near JA-36 (Fig. 37). A small, local increase was also evident above the confluence with the Appomattox River.

Figure 29: TWINSPAN classification of James River stations. Indicator species for each division are shown in decreasing order of importance. Eigenvalues of major divisions are shown in bold under each division. Binary numbers above divisions denote major subsets. Smaller font numbers below final groups are the number of stations within that group. Larger font numbers below brackets are final TWINSPAN group labels. Station labels are rivermile-year.

James River
(n=55)



1	2	3	4	5	6
JA68-90	JA46-90	JA51-90	JA36-90	JA22-90	JA12-90
JA68-91	JA46-92	JA51-91	JA36-91	JA22-91	JA12-91
JA68-93	JA46-93	JA51-92	JA36-92	JA22-92	JA12-92
JA68-94		JA51-93	JA36-93	JA22-93	JA12-93
	JA51-94		JA36-94		JA12-94
JA74-90		JA62-90		JA29-90	
JA74-91	JA56-90	JA62-91	JA46-91	JA29-91	JA22-94
JA74-92	JA56-91	JA62-92	JA46-94	JA29-92	
JA74-93	JA56-92	JA62-93		JA29-93	
JA74-94	JA56-93	JA62-94		JA29-94	
	JA56-94				
JA78-90					
JA78-91	JA68-92				
JA78-92					
JA78-93					
JA78-94					

Figure 30: Axes 1 and 2 of DCA ordination of James River stations. Symbols correspond to TWINSPAN groups. Units are standard deviations in species turnover rate.

James River Station Scores
(TWINSPAN Groups)

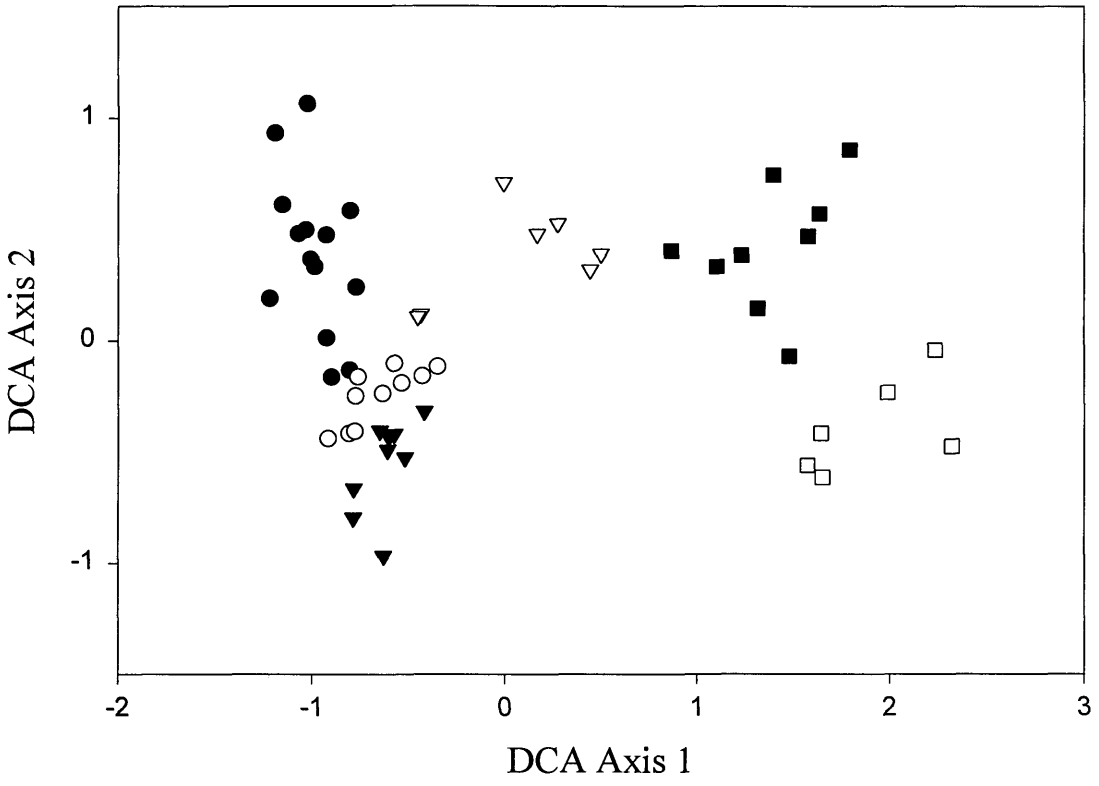
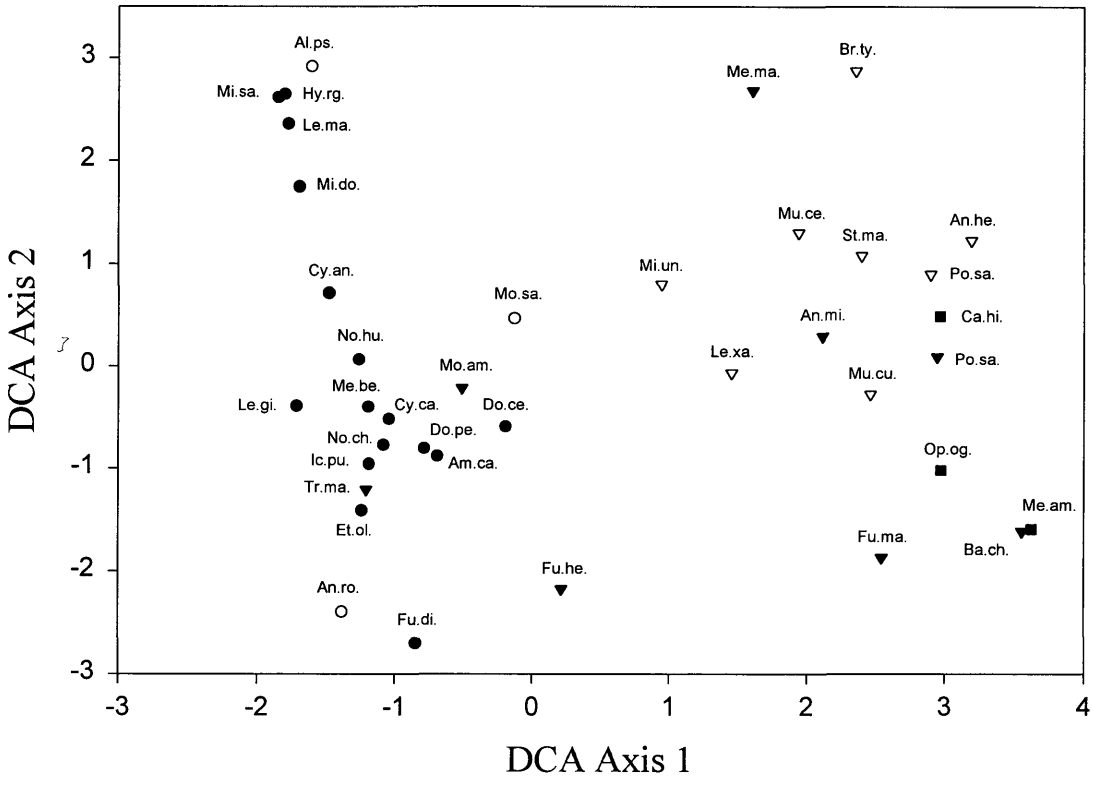


Figure 31: Axes 1 and 2 of DCA ordination of the 38 James River species included in the gradient analysis. Symbols correspond to the modified ecological groups of McHugh (1967). Species labels are the first f our letters of genus and species names respectively (see Appendix 2 for a complete alphabetical list). Units are standard deviations in species turnover rate.

James River Species Scores
(Ecological Affinity Groups)



- Freshwater Species
- Diadromous Species
- Estuarine Species
- Estuarine-Marine Species
- Marine Species

Table 15: Direct comparison of DCA and DCCA axes via Spearman rank correlation for the James River stations. DCA scores are weighted average scores and DCCA scores are linear combination scores predicted from the multiple regression.

	Eigenvalue		Gradient Length		
Ordination Axis	**DCA**	**DCCA**	**DCA**	**DCCA**	r^2
1	0.54	0.50	3.54	2.28	0.93 ***
2	0.18	0.09	2.03	1.04	0.46 ***

*** $p < 0.001$

Table 16: Results of the detrended canonical correspondence analysis of fish assemblages from the James River. Significance values of correlation and canonical coefficients correspond to a two-tailed students *t*-test.

Variable	Axis 1	Axis 2
Canonical Coefficients for Environmental Variables		
Salinity	0.2230 ***	-0.1862
Temperature	0.0215	0.0999 *
Dissolved O_2	-0.0156	-0.1590 ***
pH	-0.0076	0.0241
Substrate Grain Size	0.0220	-0.1135 *
Channel Width	-0.0207	-0.0724
6' Contour	0.2728 ***	0.4047 ***
Distance to Bay Mouth	-0.2789 ***	0.1310
Correlations of Environmental Variables with Axes		
Salinity	0.9213 ***	-0.0602
Temperature	-0.2483	0.2142
Dissolved O_2	-0.1358	-0.2918 *
pH	-0.0605	-0.1983
Substrate Grain Size	0.0697	-0.4926 ***
Channel Width	0.9437 ***	-0.0411
6' Contour	0.9258 ***	0.1953
Distance to Bay Mouth	-0.9325 ***	0.1453
Summary Statistics for Ordination Axes		
Eigenvalue	0.501	0.085
Species-environment correlation	0.986	0.795
Cummulative % of species-environment variance explained	56.4	65.9
Monte Carlo probability for significance of the sum of all eigenvalues (10^3 pemutations): 0.001		

*** $p < 0.005$ ** $p < 0.01$ * $p < 0.05$

Figure 32: Axes 1 and 2 of DCCA ordination of the 38 James River species included in the gradient analysis. Environmental variables are indicated with vectors. Only statistically significant variables are included in the ordination diagram. Abbreviations are the first four letters in both the genus and species names (see Appendix 2 for a complete list).

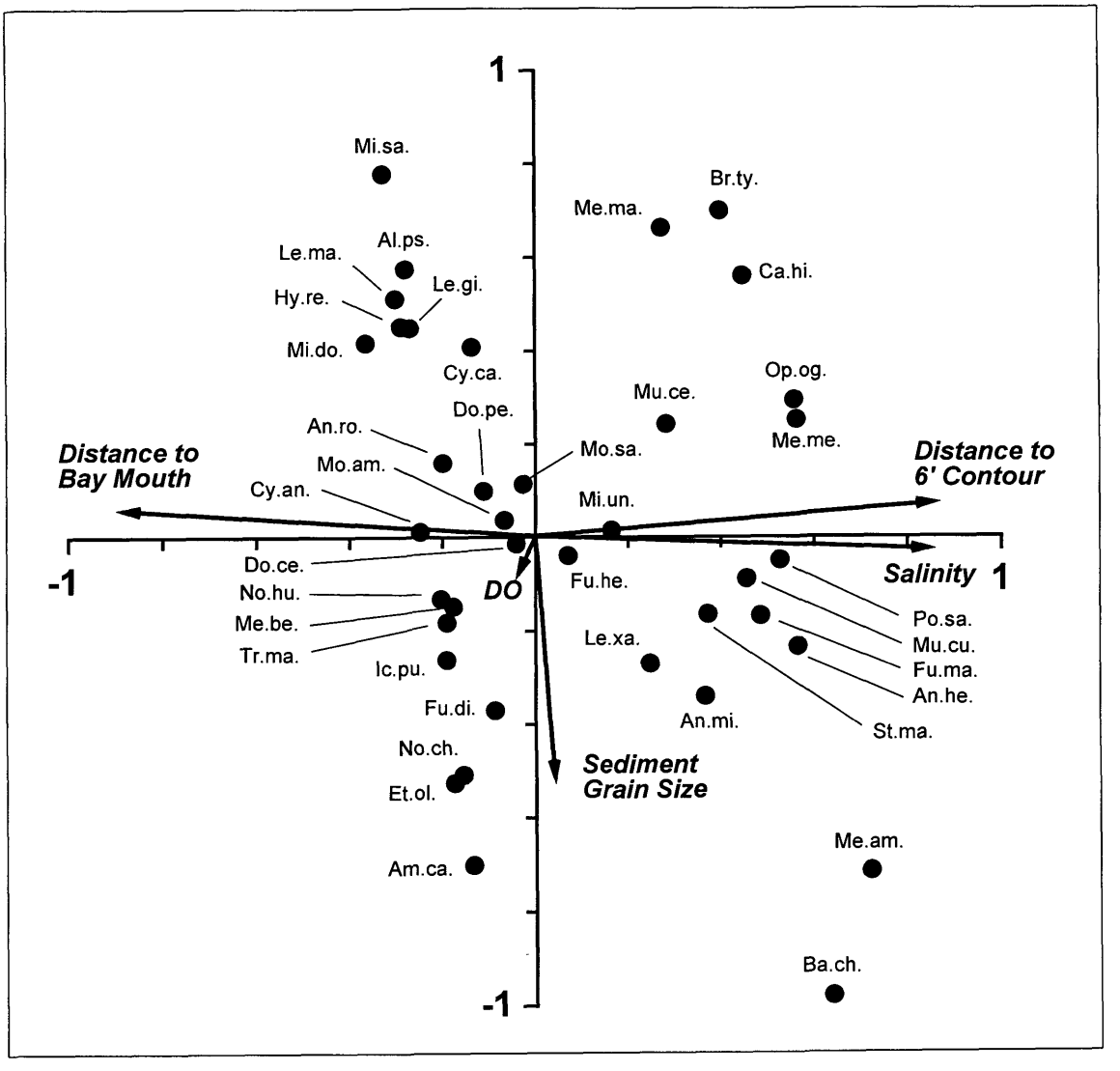

1
-1
-1
1
Distance to
Bay Mouth
Distance to
6' Contour
Salinity
DO
Sediment
Grain Size
Mi.sa.
Br.ty.
Me.ma.
Ca.hi.
Al.ps.
Le.ma.
Le.gi.
Hy.re.
Mi.do.
Cy.ca.
Op.og.
Mu.ce.
Me.me.
Do.pe.
An.ro.
Mo.sa.
Mo.am.
Cy.an.
Mi.un.
Do.ce.
Fu.he.
No.hu.
Po.sa.
Mu.cu.
Me.be.
Fu.ma.
Tr.ma.
An.he.
Le.xa.
Ic.pu.
St.ma.
An.mi.
Fu.di.
No.ch.
Et.ol.
Me.am.
Am.ca.
Ba.ch.

Table 17: Dominant and indicator taxa for TWINSPAN groups of James River stations. Density is mean (+/- 1 standard error) abundance per 1000 m^2 swept area calculated for all stations included in the TWINSPAN group. FOC = frequency of occurence in the stations from the TWINSPAN group. Indicator species are denoted with an asteriks.

TWINSPAN Group	Dominant & Indicator Taxa					
	Species	Density (#/10^3 m^2)		FOC	Fork Length (mm)	
1	*Alosa aestivalis* *	35.02	(14.55)	0.25	51.60	(0.15)
	Dorosoma petenense	30.22	(27.67)	0.08	69.54	(0.30)
	Notropis hudsonius	29.30	(11.43)	0.60	62.71	(0.49)
	Morone americana	24.71	(10.07)	0.70	61.36	(1.19)
	Cyprinella analostana	16.49	(8.34)	0.52	59.02	(0.53)
	Hybognathus regius	13.89	(9.95)	0.17	65.08	(0.67)
	Morone saxatilis	13.67	(4.55)	0.71	56.53	(1.15)
	Dorosoma cepedianum	10.77	(3.95)	0.43	151.08	(3.17)
	Menidia beryllina	5.12	(1.35)	0.35	60.98	(0.87)
	Ictalurus punctatus	3.83	(2.37)	0.16	80.06	(6.86)
	Trinectes maculatus	2.56	(0.82)	0.37	47.03	(1.40)
	Lepomis macrochirus	1.20	(0.36)	0.19	100.52	(8.60)
	Micropterus salmoides	1.04	(0.34)	0.21	97.76	(9.63)
	Micropterus dolomieu	0.39	(0.13)	0.14	67.29	(4.08)
2	*Notropis hudsonius*	54.55	(9.84)	0.94	60.43	(0.55)
	Morone americana	35.70	(5.11)	0.96	61.40	(0.40)
	Menidia beryllina	17.88	(6.16)	0.76	56.98	(0.73)
	Morone saxatilis	16.14	(3.07)	0.92	61.83	(1.36)
	Dorosoma cepedianum	5.89	(1.25)	0.66	108.70	(0.89)
	Ictalurus punctatus	5.49	(1.25)	0.60	85.32	(5.09)
	Cyprinella analostana *	5.26	(1.16)	0.58	59.98	(1.11)
	Dorosoma petenense	3.88	(1.23)	0.38	57.83	(0.36)
	Micropogonias undulatus	3.87	(1.23)	0.26	106.06	(2.31)
	Trinectes maculatus	2.61	(0.71)	0.48	45.79	(0.43)
	Leiostomus xanthurus	2.29	(0.91)	0.28	103.24	(1.07)
	Etheostoma olmstedii	1.80	(0.64)	0.38	64.31	(1.42)
	Notemigonus chrysoleucas *	1.53	(0.43)	0.28	99.00	(6.73)
	Fundulus diaphanus	0.80	(0.32)	0.26	57.29	(2.12)
	Fundulus heteroclitus	0.79	(0.21)	0.28	54.28	(1.20)
3	*Dorosoma cepedianum*	147.57	(54.33)	0.79	134.24	(4.10)
	Morone americana	98.00	(47.40)	1.00	71.49	(0.57)
	Dorosoma petenense	74.03	(29.15)	0.58	58.90	(0.96)
	Trinectes maculatus *	49.57	(10.08)	0.91	54.92	(1.22)
	Notropis hudsonius	10.33	(2.25)	0.81	61.88	(0.25)
	Morone saxatilis	9.13	(2.62)	0.60	64.87	(1.20)
	Ictalurus punctatus	6.75	(1.51)	0.74	101.36	(4.27)
	Menidia beryllina	5.68	(1.35)	0.67	59.24	(0.38)
	Leiostomus xanthurus	4.21	(1.80)	0.30	100.16	(1.52)

TWINSPAN Group	Dominant & Indicator Taxa					
	Species	Density (#/10^3 m^2)		FOC	Fork Length (mm)	
3	*Fundulus heteroclitus*	3.73	(1.68)	0.56	60.87	(1.45)
cont'd	*Cyprinella analostana*	1.46	(0.32)	0.47	60.52	(0.63)
	Fundulus diaphanus	1.45	(0.50)	0.30	69.06	(1.44)
	Etheostoma olmstedii	1.25	(0.34)	0.40	63.71	(0.58)
	Micropogonias undulatus	1.18	(0.50)	0.19	100.93	(1.18)
4	*Morone americana*	33.48	(6.35)	1.00	70.85	(1.00)
	Micropogonias undulatus *	24.80	(5.69)	0.68	105.24	(0.54)
	Morone saxatilis	13.45	(2.03)	1.00	66.92	(1.59)
	Notropis hudsonius	9.77	(1.62)	0.92	68.91	(0.98)
	Menidia beryllina	4.54	(1.07)	0.70	59.67	(0.76)
	Leiostomus xanthurus	4.38	(1.77)	0.46	103.78	(1.46)
	Anchoa mitchelli	3.65	(1.64)	0.35	51.87	(0.86)
	Dorosoma cepedianum	2.73	(1.21)	0.38	144.34	(3.75)
	Ictalurus punctatus	2.16	(0.78)	0.38	157.60	(11.36)
	Mugil cephalus	2.01	(0.98)	0.32	170.20	(8.85)
	Mugil curema	1.66	(0.90)	0.11	128.56	(1.52)
	Trinectes maculatus	1.24	(0.62)	0.27	61.80	(2.09)
	Alosa aestivalis	1.24	(0.85)	0.11	50.16	(1.18)
	Cyprinella analostana	0.78	(0.28)	0.24	66.30	(1.54)
	Dorosoma petenense	0.71	(0.41)	0.11	64.34	(0.73)
	Membras martinica *	0.63	(0.24)	0.22	78.68	(2.23)
	Menidia menidia	0.56	(0.20)	0.24	63.38	(1.30)
	Hybognathus regius	0.45	(0.41)	0.05	98.85	(5.36)
	Notemigonus chrysoleucas	0.43	(0.21)	0.16	92.50	(3.86)
5	*Menidia menidia*	66.69	(13.81)	0.98	67.79	(0.29)
	Morone americana	17.74	(9.43)	0.70	60.24	(0.86)
	Brevoortia tyrannus	15.92	(12.75)	0.20	124.15	(0.45)
	Dorosoma petenense	14.03	(11.43)	0.07	73.64	(0.24)
	Morone saxatilis	10.70	(1.42)	0.91	64.98	(0.73)
	Micropogonias undulatus	8.16	(1.97)	0.57	116.24	(1.11)
	Dorosoma cepedianum	7.90	(2.88)	0.50	162.34	(3.40)
	Leiostomus xanthurus	4.09	(1.03)	0.59	85.63	(1.27)
	Mugil cephalus	3.81	(1.59)	0.33	157.55	(5.54)
	Anchoa mitchelli	2.26	(0.69)	0.37	54.32	(1.02)
	Mugil curema	2.14	(0.78)	0.26	133.58	(2.34)
	Membras martinica	1.19	(0.43)	0.22	75.12	(0.93)
	Fundulus heteroclitus	0.63	(0.23)	0.20	65.66	(1.89)
	Fundulus majalis	0.63	(0.45)	0.13	93.90	(3.63)
	Opisthonema oglinum	0.60	(0.26)	0.13	85.93	(1.12)
	Anchoa hepsetus	0.60	(0.20)	0.24	69.41	(2.14)
	Pomatomus saltatrix	0.33	(0.13)	0.15	112.93	(18.32)
	Strongylura marina	0.18	(0.08)	0.11	297.22	(22.98)

TWINSPAN Group	Dominant & Indicator Taxa					
	Species	Density (#/10^3 m^2)		FOC	Fork Length (mm)	
6	*Menidia menidia*	322.26	(94.42)	1.00	66.15	(0.09)
	Anchoa mitchelli	77.85	(51.59)	0.47	47.37	(0.22)
	Mugil curema *	32.42	(15.23)	0.63	73.90	(0.98)
	Dorosoma cepedianum	22.05	(12.28)	0.43	92.48	(0.80)
	Fundulus majalis *	19.50	(4.53)	0.77	88.62	(1.02)
	Mugil cephalus	18.22	(11.09)	0.23	79.66	(1.37)
	Leiostomus xanthurus	15.48	(3.55)	0.80	105.27	(0.95)
	Opisthonema oglinum	9.82	(6.64)	0.33	90.21	(0.61)
	Morone americana	6.16	(3.48)	0.30	51.45	(0.54)
	Morone saxatilis	6.03	(1.66)	0.67	79.43	(1.47)
	Menticirrus americana	2.69	(1.36)	0.30	78.37	(3.63)
	Micropogonias undulatus	2.37	(0.99)	0.30	157.60	(4.84)
	Anchoa hepsetus	2.05	(1.22)	0.23	58.05	(1.69)
	Fundulus heteroclitus	1.96	(1.14)	0.23	69.51	(1.82)
	Pomatomus saltatrix	1.19	(0.83)	0.17	112.88	(4.75)
	Caranx hippos	0.73	(0.42)	0.13	54.56	(3.48)
	Bairdiella chrysoura	0.73	(0.33)	0.23	65.25	(5.08)
	Strongylura marina	0.64	(0.33)	0.17	214.14	(11.43)
	Brevoortia tyrannus	0.18	(0.11)	0.10	141.75	(20.36)

Table 18: Average environmental values by TWINSPAN group for stations from the James River. Quantitative variables are mean ± one standard error. Channel measurements are given as a range.

TWINSPAN Group	Salinity (ppt)	Temperature (°C)	Dissolved O_2 (mg ℓ^{-1})	pH
1	0.02 ∓ 0.00	29.56 ∓ 0.31	6.58 ∓ 0.11	7.51 ∓ 0.10
2	0.01 ∓ 0.01	28.42 ∓ 0.40	7.85 ∓ 0.33	8.08 ∓ 0.13
3	0.06 ∓ 0.03	27.84 ∓ 0.30	7.14 ∓ 0.19	7.88 ∓ 0.08
4	1.13 ∓ 0.20	26.15 ∓ 0.38	6.71 ∓ 0.22	7.50 ∓ 0.09
5	5.79 ∓ 0.38	28.21 ∓ 0.39	6.38 ∓ 0.25	7.56 ∓ 0.10
6	11.78 ∓ 0.90	27.81 ∓ 0.45	6.58 ∓ 0.27	7.45 ∓ 0.15

	Nearshore Sediment	6' Contour (m)	Distance to Bay Mouth (Nm)	SAV Beds
1	Silt-Sand	22 - 48	75.16 - 85.46	No
2	Sand-Granule	24 - 79	53.61 - 75.16	No
3	Sand-Granule	60 - 384	58.06 - 69.66	No
4	Sand	48 - 384	42.91 - 53.61	No
5	Sand	876 - 1020	29.71 - 36.76	No
6	Sand	876 - 1020	19.26 - 29.71	No

Figure 33: Total (a) and rarefied (b) longitudinal species richness in the James River, 1990-94. Rarefied species richness is fit with a LOWESS curve.

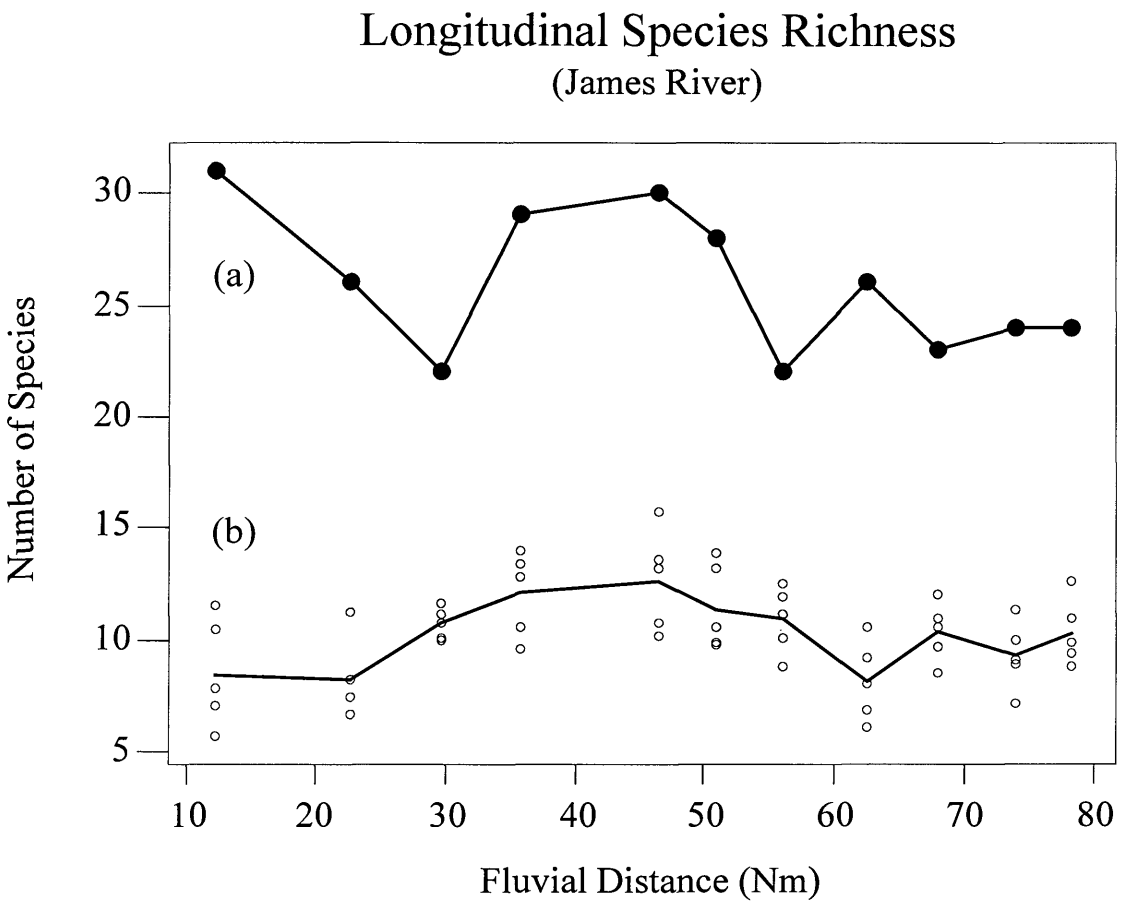

Longitudinal Species Richness
(James River)
Number of Species
30
25
20
15
10
5
(a)
(b)
10
20
30
40
50
60
70
80
Fluvial Distance (Nm)

Figure 34: Total species captured and total area swept for James River stations, 1990-1994.

Species-Area Relationship
(James River)

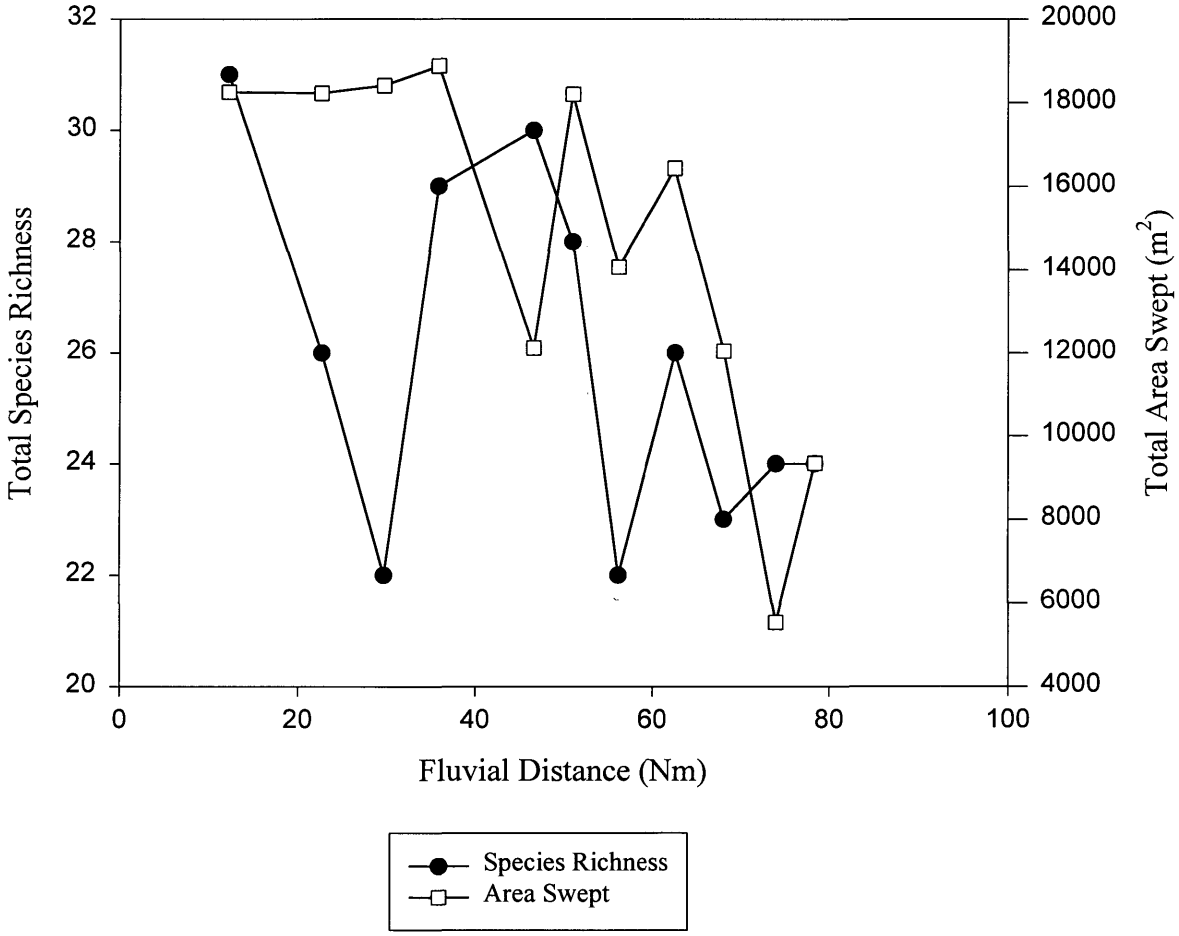


Figure 35: Longitudinal species evenness (Pielou's) in the James River, 1990-1994, fit with a LOWESS curve.

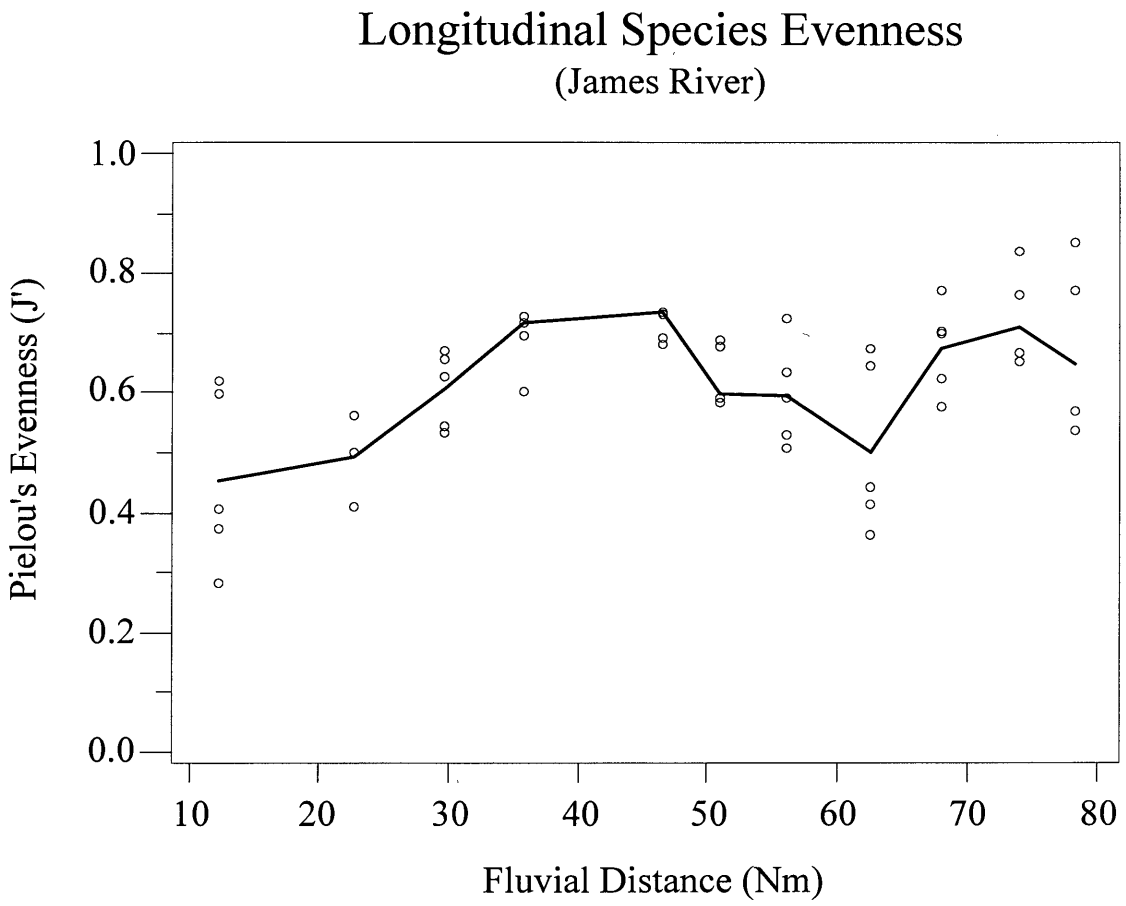

Longitudinal Species Evenness
(James River)
Pielou's Evenness (J')
1.0
0.8
0.6
0.4
0.2
0.0
10
20
30
40
50
60
70
80
Fluvial Distance (Nm)

Figure 36: Longitudinal species diversity (Shannon-Wiener) in the James River, 1990-1994, fit with a LOWESS curve.

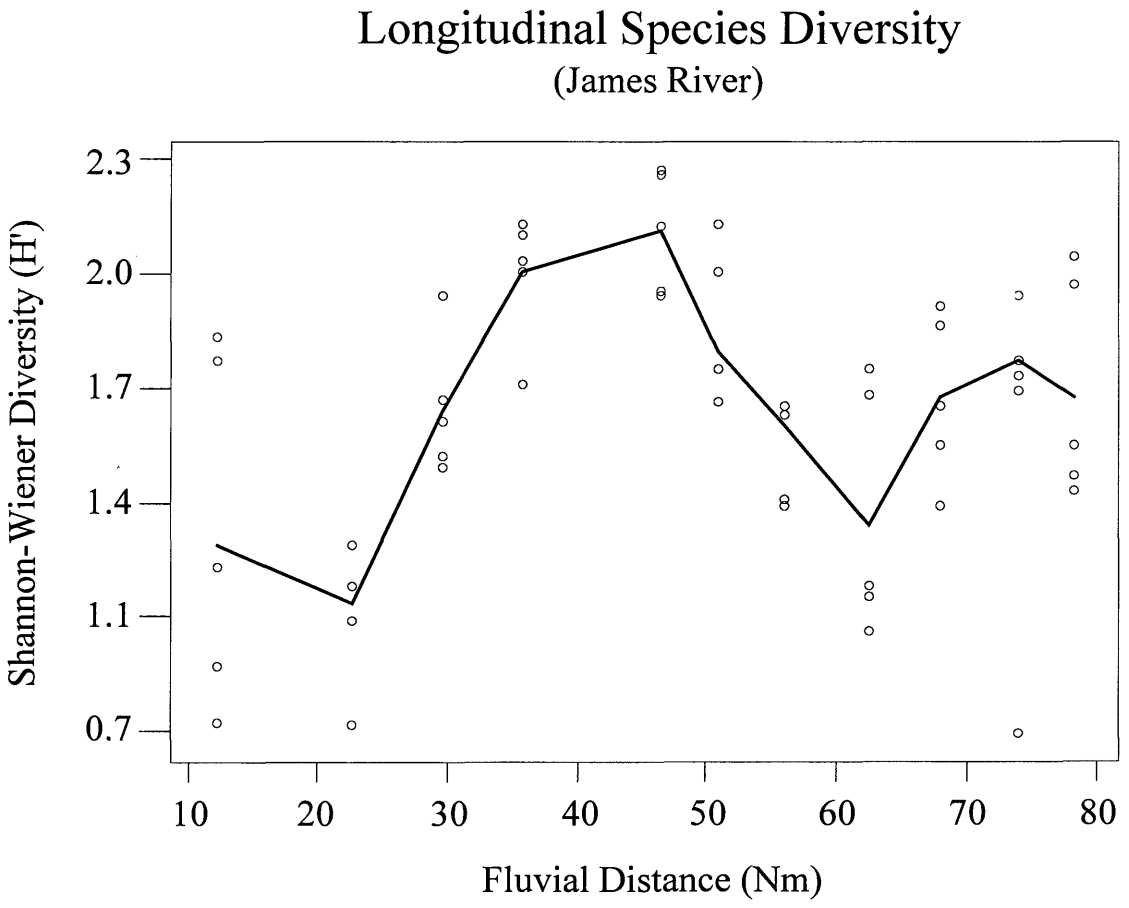
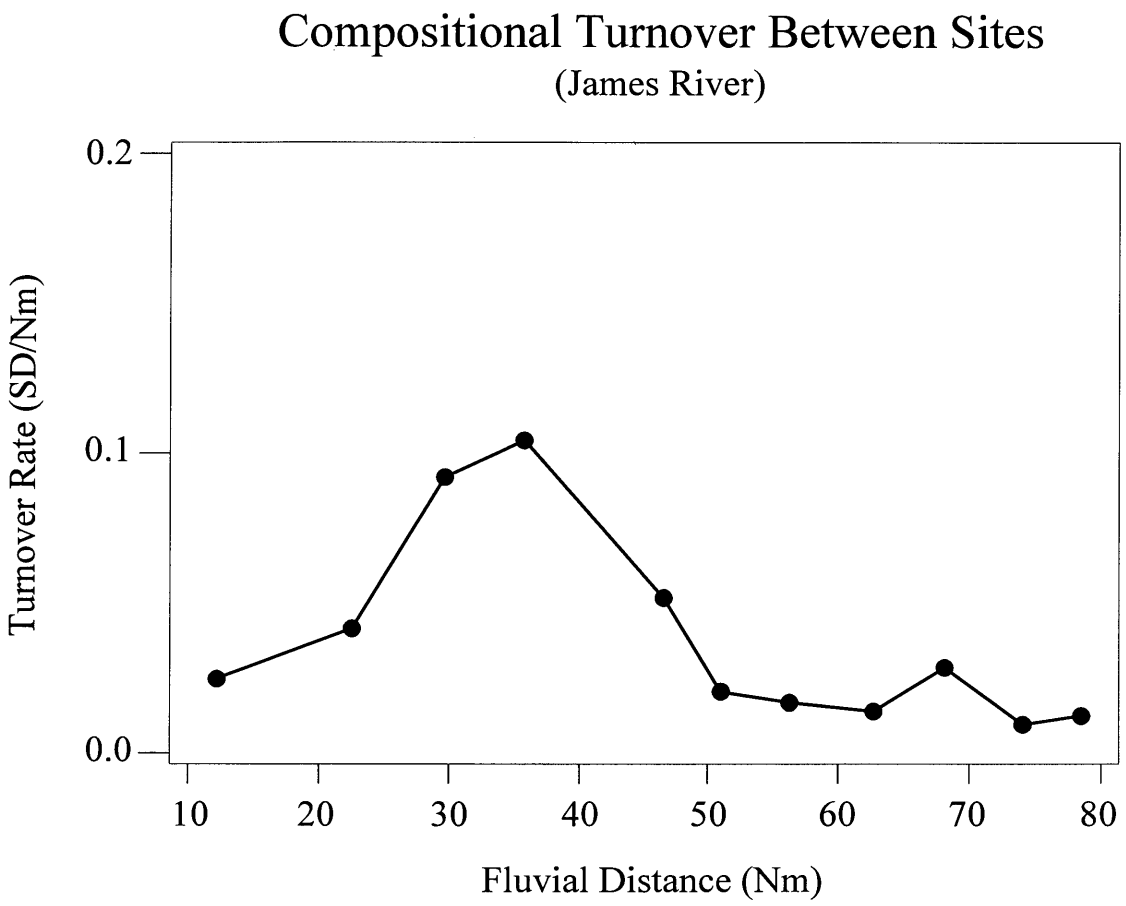

Longitudinal Species Diversity
(James River)
Shannon-Wiener Diversity (H')
2.3
2.0
1.7
1.4
1.1
0.7
10
20
30
40
50
60
70
80
Fluvial Distance (Nm)

Figure 37: Longitudinal species turnover (beta diversity) in the James River, 1990-94. Units are standard deviations in species turnover per nautical mile from the DCA ordination of all stations.


Compositional Turnover Between Sites
(James River)
Turnover Rate (SD/Nm)
0.2
0.1
0.0
10
20
30
40
50
60
70
80
Fluvial Distance (Nm)

DISCUSSION

Longitudinal Patterns in Assemblage Structure

Littoral fish assemblages of the three major tributaries to the lower Chesapeake Bay exhibited a strong pattern of longitudinal transition between permanent tidal freshwater river reaches and the mesohaline portion of the estuary. This coenocline is similar to patterns observed in other temperate and tropical zone coastal faunas (Felley 1987; Rozas & Odum 1987b; Odum 1988; Peterson & Ross 1991; Winemiller & Leslie 1992), and is characterized by a series of species supplements and replacements in successive downstream locations. Fish assemblages generally grade smoothly into each other with one notable exception; the freshwater interface is a boundary with a markedly increased rate of species turnover (=faunal break, Matthews 1986). Fairly distinctive fish assemblages can be mapped over a longitudinal pattern of fluvial zonation that corresponds to the first two axes of DCA/DCCA, and can be clearly seen in the distribution patterns of the more common species (Tab. 19-22). While estuarine fish populations in the Chesapeake Bay are known to undergo large interannual fluctuations in abundance (McHugh 1967; Houde 1993), the spatial structure of these assemblages during summer appears stable from year to year. Large-scale zonation in the river systems corresponded to three basic habitat types: permanent tidal freshwater, the freshwater interface (lower tidal freshwater and oligohaline reaches which straddle the interface) and the mesohaline portion of the estuary (Fig. 38).

Dominant species were widely dispersed within each of the three major ecoregions and few species were characteristic of only one aquatic habitat type. In

general, two types of littoral fishes dominated the collections: juveniles of large migratory species and adults of smaller resident species. Small fishes in riverine and estuarine systems commonly assemble in shallow littoral zone habitats, presumably in response to predation on proximate and maybe even co-evolutionary time scales. Exceptions to this general spatial segregation by small fishes have been noted for schooling mid-water planktivores (clupeidae), schooling surface feeding invertivores (atherinidae) and cryptic or burrowing benthic fishes (e.g., blenniidae, gobiidae) (Ruiz *et al.* 1993). Even so, data from this study indicate that the first two of these groups do occur in significant numbers in shallow littoral waters. Given the selectivity of seine nets for smaller individuals, it would not be appropriate to apply this scheme to the total behavior of the species discussed. However, many of these species exhibit substantial ecological differences between life-history stages, and treatment as ontological entities (vs. species) may bring about more appropriate models (Livingston 1988). I therefore believe this scheme is ecologically meaningful and may be of use for large-scale comparative analyses with the littoral fish assemblages of other river dominated estuarine systems.

Permanent Tidal Freshwater -- Three groups of fishes typified collections from permanent tidal freshwater: (1) a widely distributed resident group of second division freshwater fishes; (2) primary division freshwater fishes largely confined to upstream stations well above the influence of the salt wedge; and, (3) juveniles of non-resident adults who occupy tidal freshwater as a nursery. Group 1 is numerically dominated by a few cyprinid minnows, most particularly the spottail and satinfin shiners and the eastern

silvery minnow. Other important secondary freshwater species include the banded killifish, mummichog, inland silverside, and juvenile white, blue and channel catfishes. Primary division (or obligate) freshwater fishes have essentially no tolerance for high salinity waters and are therefore largely confined to freshwater environments (Darlington 1957). Though never dominant, several primary division freshwater fishes were regular components of permanent tidal freshwater collections. These included several centrarchids (bluespotted sunfish, redbreast sunfish, pumpkinseed, largemouth bass) and two percids (yellow perch and the tessellated darter).

The role as a nursery for annual migrants is a particularly important function of shallow tidal freshwater environments (Odum *et al.* 1984). Many of these anadromous and semi-anadromous fishes are of significant commercial importance in mid-Atlantic estuaries. Anadromous clupeids of the genus *Alosa* are mid-water planktivores with large populations known in the Chesapeake Bay tributaries (Massman 1953; Foerster & Reagan 1977; Loesch 1987). Three species of *Alosa* were captured by the seines, though only the blueback herring was captured in any great number, primarily from the James River. The American shad was a regular subdominant component of the Pamunkey River tidal freshwater assemblage. The semi-anadromous gizzard and thread-fin shads were numerically quite important in all of the rivers. The gizzard shad frequently extended well into the saline estuary, particularly in the James and Rappahannock Rivers.

The Interface Zone -- The waters bracketing the freshwater interface are hydrologically dynamic, range from fresh to oligohaline salinities, and harbor a diverse assemblage of fishes drawn from freshwater and marine source pools. Several secondary

division freshwater fishes routinely penetrated into low salinity waters (e.g., gizzard shad, spottail shiner, satinfin shiner, banded killifish, channel catfish, white catfish). Similarly, several estuarine residents and juveniles of estuarine-dependent marine species were established in the lower tidal freshwater river reaches (e.g., mummichog, spot, Atlantic croaker, hogchoker, bay anchovy, Atlantic silverside). The distribution of three species were noticeably centered in the interface zone: juveniles of the hogchoker, white perch and striped bass.

White perch are semi-anadromous estuarine fishes who spawn in tidal freshwater during the spring and are distributed throughout the mesohaline portions of the estuary (Mansueti 1964; Hardy 1978). The closely related striped bass is fully anadromous with adults spawning in tidal freshwaters during the spring and adults broadly distributed in estuarine and near-coastal marine waters (Hardy 1978; Olney *et al.* 1991). Juvenile white perch and striped bass move towards brackish waters from August through November and are generally found in shallow littoral waters (Setzler-Hamilton 1987). The hogchoker is a common estuarine flatfish which completes its life cycle entirely within one estuary and is the most abundant pleuronectiform fish in the lower Chesapeake Bay (Bonzek *et al.* 1993). Eggs are spawned in saline waters near the mouth of the estuary, and the larvae migrate back to tidal freshwaters (Dovel *et al.* 1969). Life-history trajectories of these three species have fundamental differences in spawning locations and the distribution of adults, but share at least two commonalities: (1) the juveniles of each occupy tidal freshwaters as a nursery zone; and, (2) older juveniles progressively move into more saline waters.

The Mesohaline Mid-Estuary -- The areas above five ppt salinity had assemblages dominated by a variety of euryhaline estuarine residents and juveniles of estuarine-dependent marine species. The Atlantic silverside, bay anchovy and mummichog were the most important estuarine residents and are generally considered to be important forage species for the larger fishes of the Bay system (Murdy *et al.* 1997). Juveniles of the Atlantic menhaden, spot and Atlantic croaker were also numerically dominant and are commercially and recreationally quite valuable species. Most of the secondary freshwater species avoided higher salinity stations. An exception to this pattern was observed for the gizzard shad, which penetrated well into the lower estuary, particularly in the James River.

Upper mesohaline waters (i.e., salinities generally greater than 10 ppt) also housed several species who exhibit preferences for higher salinity portions of the Bay (Musick 1972). These included estuarine residents (e.g., striped killifish, oyster toadfish, blackcheek tonguefish), coastal marine species who regularly utilize the Bay during warm months as nursery and adult feeding habitat (e.g., summer flounder, bluefish, Atlantic needlefish), and marine species who penetrate the high salinity lower reaches during summer (e.g., crevalle jack, inshore lizardfish, Atlantic thread herring). Several of these species are known to exhibit fairly broad tolerances for low salinity, and probably penetrate farther into the rivers in the deeper, more saline waters.

Assemblage Structure Correlation with Environmental Gradients

Four out of nine physical environmental variables included in the DCCA analyses

had high loadings on the first ordination axis. Among these, the physiological constraints imposed by salinity are assumed to be of major importance in the structuring of fish assemblages across the lower reaches of the freshwater/estuarine ecotone. Salinity was probably not a major factor influencing fish assemblages in permanent tidal freshwater well above the interface. The other three statistically important variables on the first DCCA axis were fluvial distance to the bay mouth, and two components of habitat size: shoal width and channel width. Of course, many variables, both measured and unmeasured, may be expected to covary with salinity along an estuarine gradient. The truncation of freshwater species and station scores on the first DCA and DCCA axes generally suggest that those variables which continue to decrease in value moving upstream (i.e., distance to the bay mouth, channel width and shoal width) are not controlling the large scale assemblage patterns between regions. However, each of these may certainly have local effects within a major habitat type. For example, distance to the bay mouth may also be viewed as distance to the source pool for transient marine species. High salinity marine species were present in each of the river systems, yet more typically occurred in the James River vs. the Rappahannock River at similar salinities. This may be a simple distance-related effect on the relationship of local species diversity to the regional species pool, a topic of recent and growing interest (Ricklefs 1987; Ricklefs & Schluter 1993).

The results of this study indicate four general features of littoral fish assemblage structure with respect to salinity: (1) first division freshwater fishes are distributed in upstream, relatively stable freshwater reaches above the influence of the salt-wedge; (2)

second division freshwater fishes dominate in tidal freshwater and make regular but limited penetration of the low-saline areas of the estuary; (3) estuarine residents and some estuarine-marine juveniles are dominant in the estuary and can make significant penetrations into tidal freshwaters; and, (4) high salinity marine species rarely occupy littoral waters below oligohaline salinities (Fig. 39). The degree of overlap between adjacent assemblages appears, in part, to be dictated by the physical strength of the salinity gradient.

Estuarine penetration and establishment of freshwater fish species is a consequence of limitations in physiological mechanisms for dealing with a hypertonic environment (Peterson & Meador 1994). Fifty-five percent of the freshwater fish species were never found in salinities greater than 0.5 ppt, and 82% were never encountered seaward of 5.0 ppt. Most of the second division (or facultative) freshwater species which did penetrate the lower estuary have well-known, if limited, salinity tolerances, and all were most abundant in tidal freshwater. Juveniles of the gizzard and thread-fin shads were commonly encountered in saline waters, particularly in the James River. Both are schooling planktivores which enjoy wide geographic distributions in the Atlantic and Gulf of Mexico coastal drainages of the U.S. (Page & Burr 1991), and whose juveniles regularly penetrate the oligohaline reaches of coastal rivers (Jones *et al.* 1987). The spottail shiner was also commonly captured in oligohaline waters. Other second division freshwater species encountered in low numbers in saline waters included the banded killifish and juvenile bluegill.

The limited upstream penetration and establishment of many marine fishes is

similarly a consequence of their lack of physiological mechanisms for adjusting to a hypotonic environment (Bone *et al.* 1995). Even so, most estuarine residents, and the juveniles of marine species which occupy the estuary as a nursery, are very euryhaline and appear less affected by salinity then their freshwater counterparts (Gunter 1961; Vernberg & Vernberg 1976). It is therefore not surprising that juveniles of two of the most abundant estuarine-marine species (spot, Atlantic croaker) regularly penetrated deep into the tidal freshwater reaches of the rivers, well above the influence of the salt wedge. Migratory juveniles of spot and Atlantic croaker are physiologically well equipped for extreme salinity fluctuations (Moser & Gerry 1989), and are generalist feeders on infauna and epibenthic invertebrates (Chao & Musick 1977). These characteristics make them well-suited for invading tidal freshwater littoral habitats. Juveniles of several essentially marine species with known capabilities for adjusting to low salinity environments were extremely rare above the freshwater interface and dropped out altogether in the permanent tidal freshwater reaches (e.g., *Mugil* spp., *Caranx* spp.). It is possible that these species do sometimes invade the upper river reaches through the higher salinity waters of the deep river channels.

Three of the nine environmental covariables had significant loadings on the second DCCA axis. Dissolved oxygen was significant only in the James River, but does not appear to reach chronic or acute stress levels. The remaining two, nearshore substrate grain size and the presence of SAV's (Mattaponi only), are measures of habitat structure and were important in the upstream tidal freshwater reaches of the rivers. Structural habitat heterogeneity in the form of aquatic vegetation, submerged trees and limbs, coarse

detritus and coarse substrate is often positively correlated with the local diversity and density of fishes in freshwater environments (Gorman & Karr 1978; Capone & Kushlan 1991; Benson & Magnuson 1992; Everett & Ruiz 1993). The effect of substrate was most pronounced in the Rappahannock River ordinations. The DCA ordination of stations extracted stations with pebble substrate (RA-65 and RA-69) from the center of the permanent tidal freshwater reach, while the grouping stations with sandy substrate from either end (RA-60 and RA-76). Numerically, the pebble stations were dominated by the ubiquitous spottail shiner. The distinction arose from the presence of several sub-dominant species which seemed to prefer structure; particularly, juvenile blue catfish, yellow perch and the pumpkinseed.

Substrate grain size was also important to the explanation of species distributions in the upstream tidal freshwater reaches of the James, Pamunkey and Mattaponi Rivers. The presence of pebbles on the littoral shoals tended to increase upstream, though were never the dominant substrate in these rivers. Nevertheless, the presence of several first division freshwater fishes (mostly centrarchids) were correlated with the increase in mean substrate size (or perhaps diversity), and may mark the transition to more stable, riverine environments.

Only one station had significant SAV beds (MP-52). The macrofauna associated with SAV's have been the subject of extensive study in the estuarine and freshwater environments of the Chesapeake Bay (e.g., Orth *et al.* 1984; Rozas & Odum 1988; Sogard & Abele 1991). Though not sampled in previous years, SAV at MP-52 in 1997 was dominated by wild celery (*Vallisneria americana*) and the complex alga *Nitella*

flexilis (Charophyceae). Conversations with survey personnel suggest this plant assemblage has been stable in composition, though interannual fluctuations in coverage are probable. The submerged plant beds at MP-52 were heavily used by several species of fishes. Since this study is limited to only one station with SAV's over a five-year period, I can say little about the large-scale spatial patterns in the use of SAV's. Nevertheless, certain attributes of the fauna at MP-52 are notable and congruent with other studies of SAV use in the tributaries to the Chespeake Bay. For example, juvenile redbreast sunfish and pumpkinseed were much more abundant and frequently captured in the SAV bed vs. downstream unvegetated stations. Juvenile centrarchids are known to concentrate in the vegetated littoral zones of lakes (Werner *et al.* 1977) and tidal freshwater marshes (Rozas & Odum 1987a). The bluespotted sunfish, a small centrarchid, was also consistently captured. Small sunfishes of the genus *Enneacanthus* are almost invariably associated with vegetation in tidal and non-tidal freshwater swamps where they glean small invertebrates (Lee *et al.* 1980; Rozas & Odum 1987a). The banded killifish was also very abundant, and is known to frequent both submerged vegetation beds and flooded marsh surfaces in tidal freshwater (Rozas & Odum 1987b).

Longitudinal Patterns in Species Diversity

The ichthyofaunal diversity of the Chesapeake Bay estuary has been documented by numerous investigators over the past century (e.g., Uhler & Lugger 1876; Everman & Hildebrand 1910; Hildebrand & Schroeder 1927; McHugh 1967; Musick 1972; Weinstein 1985; Vieira & Musick 1993; Murdy *et al.* 1996). These accounts are largely

focussed on the mainstem of the Bay, and often offer little more than annotated species lists for the low salinity and tidal freshwater reaches of the major southern tributaries. Systematic investigations of fish species diversity along estuarine gradients from permanent tidal freshwater to marine salinities have been generally rare, and those from Chesapeake Bay are no exception. Species diversity, evenness and rarefied richness from this study are compiled in Table 23.

The dramatic biological, chemical and physical changes in the low salinity habitats of estuaries (i.e., < 5 ppt) are thought to limit the number of resident faunal taxa (Remane & Schlieper 1971; Dunson & Travis 1994). Remane (1934) first described this phenomena, a species minimum occurring near oligohaline salinities (Fig. 40), and it has been hypothesized as a general feature of strong gradient estuaries (Deaton & Greenberg 1986). In a review of the ecology of salt vs. freshwater marshes, Odum (1988) hypothesized that such a relationship may exist for fishes of western Atlantic estuaries, but was careful to point out the paucity of data from low salinity environments (Fig. 41). Studies along the Gulf of Mexico and Atlantic coasts have generally confirmed the rise in the number of fish species along transects from mesohaline estuaries to nearshore marine environments (e.g., Gunter 1961; Dahlberg 1972), though other gradient studies focussed on the lower estuary have failed to find a minimum (Peterson & Ross 1991). Two possible complications to the location of this pattern in estuarine fishes are: (1) the large number of seasonal migratory species (e.g., Atlantic menhaden, spot, Atlantic croaker) whose various life history stages probably exhibit different salinity preferences; and, (2) the failure to standardize species richness to a measure of sample size (i.e., rarefaction).

Fortunately, beach seines predominantly capture juvenile stages of most of the migratory species. Figure 42 shows the relationship between the mean expected number of species and mean annual summer salinity from the lower Chesapeake Bay tributaries (stations above the first permanent tidal freshwater station were excluded). There is a general trend towards a minimum near 8-10 ppt salinity, but more stations in that salinity range are needed before confirmation may be asserted. In the individual river analyses, this relationship was most apparent in the Rappahannock River. Species richness tends to increase moving from oligohaline salinities into tidal freshwater due to the interfacing of freshwater and estuarine assemblages. Peterson and Ross (1991) noted a similar phenomena in a Mississippi coastal river with seven species comprising 90.1% of the individuals in mesohaline waters, 12 species comprising 91.5% near the interface and nine species comprising 91.0% in tidal freshwater just above the interface. Similarly, Smith *et al.* (1984) documented greater richness and evenness within an oligomesohaline section of the York River estuary when compared to a downstream polyhaline area.

Fish assemblages from upstream localities were more evenly distributed among the species with upper tidal freshwater evenness scores (Pielou's Index, J′) averaging near 0.7 and mesohaline scores averaging closer to 0.5. Overall species diversity values (Shannon-Wiener Index, H') within the tidal freshwater and interface zones were also consistently higher then the mesohaline stations. This may reflect the transition from the estuary, where fewer species have evolved the physiological capacity to deal with variable salinities and are often contagiously distributed in large schools.

Relationships to Existing Models of Fish Assemblage Structure

One of the more striking features of the permanent tidal freshwater assemblages is the low number of species relative to upland lotic freshwater rivers of the piedmont and montane provinces (Fig. 43). Although seine nets do not, as a rule, capture the larger or more pelagic species, over a five-year period many of the larger species will be captured a few times. Hence, the number of freshwater species captured by the survey probably underestimates the total species complement, but not grossly. Several factors contribute to the lower numbers in tidal areas including a reduction in the diversity of structural habitat (particularly substrate), infrequent or absent riffles and runs, and turbid or stained waters (Jenkins & Burkhead 1994). The upper tidal freshwater resident fauna is derivative of piedmont and upland faunas, and no species appear to be specialized for exclusive existence in freshwater below the fall line. Two species do appear to be primarily distributed in tidal freshwater, the freshwater derived banded killifish and the marine derived inland silverside. Members of the resident fauna were widely distributed and exhibited a high degree of substrate eurytopy. Only the bluespotted sunfish appeared largely constrained to the one station with SAV beds. Several essentially marine anadromous species have their life-histories cued to the availability of a free connection to tidal freshwater (e.g., *Alosa* spp., *Morone* spp.), and utilize these waters as the upper end of the estuary. Overall, the patterns observed in the permanent tidal freshwater river reaches generally do not agree with the large-scale non-tidal stream models of discrete longitudinal zonation or the downstream addition of species.

The importance of vegetative cover to freshwater fishes is well documented,

providing refuge from predators, substrate for foraging and suitable spawning sites (Savino & Stein 1982, 1989; Werner *et al.* 1983; Angermeir & Karr 1983; Mittlebach 1986; Rozas & Odum 1987a, 1988). The changes in assemblage structure associated with submerged macrophyte beds at station MP-52 were mainly due to enhanced recruitment of young and adult fishes which were found elsewhere in the river. This suggests that macrophyte beds in the main river channel may serve a similar role as seagrasses in estuarine systems: a structural attractant which tends to concentrate fishes from the local area (Ruiz *et al.* 1993). The enhanced species richness associated with abiotic habitat structure is also a well documented (e.g., Gorman & Karr 1978; Schlosser 1982, 1987; Capone & Kushlan 1991), if not universal (Bart 1989), feature of freshwater fish assemblages. Freshwater fishes are known to make active substrate selections based on mean particle size, and tidal freshwater fishes may exhibit limited local preferences when a preferred substrate is available in large enough patches.

The freshwater interface zone (which may be subdivided into lower tidal freshwater and oligohaline ends) appears to meet the definition of an ecotone. It is a region of sharp transition in the physical and biotic environment where saline and freshwater meet and deposition of the major portion of the alluvial sediment load takes place (turbidity maximum zone of Nichols 1972, 1974). An incipient stress point associated with salinities between 0 and 2 ppt has been described which may serve as a barrier to the egress of species ill-adapted to hypertonic environments (Deaton 1981; Deaton & Greenberg 1994). The rate of species turnover in all of the rivers peaked in this salinity range (Fig. 44), and in general, marine species made larger forays across the

interface then did freshwater species. It then follows that the role of salinity in determining the composition of fish assemblages is dependent upon whether the assemblage is primarily comprised of freshwater- or marine-derived species (Peterson & Meador 1994). Studies in coastal areas of Louisiana (Rousenfell 1964), North Carolina (Rozas & Hackney 1984), Georgia (Rogers *et al.* 1984) and north-western Florida (Subrahmanyan & Coultras 1980) have indicated that salinity may only play a minor role in affecting the primary distribution of marine derived fishes. However, other studies have demonstrated the presence of macrofaunal assemblages which conform to well-defined salinity gradients (Boesch *et al.* 1977; Weinstein *et al.* 1980).

When physiological systems are stressed, fishes often employ behavioral adjustments to overcome the increased metabolic costs associated with unfavorable environments (Slobodkin & Rappaport 1974; Pitcher 1993; Werner & Anholt 1993). However, when the exposure to such stress may be controlled via residence time, the tendency for highly mobile organisms to penetrate physiologically unfavorable environments in order to gain access to some other resource (e.g., food) may increase.

The low salinity zone has historically been viewed as the region of maximum primary and secondary production within an estuary (Day *et al.* 1989), and hence an area of exceptional value to fishes, receiving fish eggs, larvae and juveniles from freshwater, anadromous and estuarine spawners (Horn & Allen 1976; Yáñez-Arancibia *et al.* 1980). This productivity peak has been associated with the "maximum turbidity" or "entrapment" zone; an area of the lower estuary where the hydrodynamics entrain suspended material resulting in higher particle concentrations than in waters both

landward and seaward (Dovel *et al.* 1969; Cronin & Mansueti 1971; Chester 1990). Two contrasting perspectives on the biological role of the maximum turbidity zone (MTZ) have arisen: the first being that it is a zone of stress and mortality for the plankton community (Bousfield *et al.* 1975; Dodson *et al.* 1989), the second that it is a biologically productive area with a complex, structured food web (Barclay & Knight 1981). Though debate continues, recent observations reject the former and suggest the MTZ is a valuable larval fish nursery (Frenette *et al.* 1995).

The diversity in fish eggs and larvae in low salinity reaches of Virginia's major tributaries to the Chesapeake Bay peaks in July (Massman 1954). Rozas and Hackney (1984) further observed that the residence time in low salinity intertidal marsh habitats for the small juveniles of two recruiting species (summer flounder and Atlantic menhaden) is relatively short. Peterson-Curtis (1997) found that juvenile hogchokers are physiologically stressed by very low salinity environments, yet they actively choose these environments during early ontogeny. Hence, individuals of some species may take advantage of productive low-salinity littoral habitats during post-larval and early juvenile development and then move into other areas of the system as larger juveniles when predation threats are reduced.

The lower river reaches (salinity > 5 ppt) support a western Atlantic temperate estuarine fauna which is well described (e.g., Robbins & Ray 1986; Murdy *et al.* 1997). The primary factors influencing the distributional patterns of plants and animals in the Chesapeake Bay estuary are salinity and its correlates (spatial coenoclines) and temperature (seasonal turnover) (Jenkins & Munroe 1994). During summer, the salinity

gradient is relatively stable along the estuarine axis (Schubel & Pritchard 1987), and may serve as part of a continuum of physiological stress, ordering habitats from benign to harsh relative to- species tolerances. Abiotic factors thus serve as a 'physiological sieve' (Remmert 1983), creating a longitudinal mosaic of intergrading, but distinct, faunal assemblages. Descriptions of the distributions of estuarine organisms have yielded at least a dozen salinity classification schemes. Perhaps the most well-known estuarine zonation scheme is the Venice System (Fig. 45a), which has superseded most other schemes (Anonymous 1959). The empirical basis for this system was not reported in the original document, and so its utility is largely descriptive. A recent test of this scheme using 316 reported salinity ranges for fauna from the Chesapeake and Delaware Bays (broken down by species and life-history stage) showed general agreement with the Venice System except in the middle of the salinity range (Fig. 45b: Bulger *et al.* 1993). Components II and III of the 'biologically-based' system reflect a large mesohaline zone overlapping with a lower polyhaline zone. The results of this study generally reflect this type of overlapping zonation with several euryhaline resident and migratory species spread over the range of at least 0 to 20 ppt, and higher salinity preferring marine forms which do not generally penetrate the very low salinity river reaches. However it should be noted that the Bulger *et al.* analysis used reported total salinity ranges which, particularly for secondary freshwater fishes, generally overestimates the behavior of the species. All of the species which dominated the littoral zone at the mesohaline stations are generally known to be widespread in the estuary (e.g., Atlantic menhaden, Atlantic silverside, bay anchovy), and it would not be reasonable to assume their distributions are

truncated at the upper mesohaline range.

Table 19: Common species characteristic of each of the three major faunal zones and ubiquitous species common in two or more adjacent zones of the longitudinal aquatic gradient in the Rappahannock River. The centers of the TWINSPAN station groups are given by the bold numbers. Species names are placed near their abundance peak. Locally dominant species are shown in bold.

Permanent Tidal Freshwater		**Interface**		**Mesohaline**	
Pebble Bottom	Sandy Bottom	Freshwater	Oligohaline	Lower	Upper
1	**2**	**3**	**4**	**5**	**6**
Ictalurus furcatus *					
Lepomis gibbosus					
Lepomis macrochirus					
Perca flavescens					
Etheostoma olmstedi ----------					
Dorosoma cepedianum ----------					
---------- *Cyprinella analostana* ----------					
---------- *Fundulus diaphanus* ----------					
---------- *Hybognathus regius* ----------					
Menida beryllina ----------					
---------- ***Morone saxatilis*** ----------					
Notropis hudsonius ----------					
---------- ***Morone americana*** ----------					
---------- *Trinectes maculatus* ----------					
		---------- *Micropogonias undulatus* ----------			
		---------- *Fundulus heteroclitus* ----------			
		---------- ***Leiostomus xanthurus*** ----------			
				---------- ***Brevoortia tyrannus***	
				---------- ***Menidia menidia***	
				----------*Anchoa hepsetus*	
				---------- *Fundulus majalis*	
				Paralichthys dentatus	
				Pomatomus saltatrix	
				Scomberomorous maculatus	
				Strongylura marina	
				Synodus foetens	

Table 20: Common species characteristic of each of the three major faunal zones and ubiquitous species common in two or more adjacent zones of the longitudinal aquatic gradient in the York and Mattaponi Rivers. The centers of the TWINSPAN station groups are given by the bold numbers. Species names are placed near their abundance peak. Locally dominant species are shown in bold.

Permanent Tidal Freshwater		**Interface**		**Mesohaline**	
Upper and Vegetated	Lower	Freshwater	Oligohaline	Lower	Upper
1	**2**		**3**	**4a**	**4b**

← Mattaponi River → ← York River →

Enneacanthus gloriosus
Lepomis auritus
Lepomis gibbosus
Lepomis macrochirus
Micropterus salmoides
Perca flavescens

Alosa sapidissima ----------
Etheostoma olmstedi ----------
Fundulus diaphanus ----------
------- *Cyprinella analostana* --------
------- *Hybognathus regius* ----------

---------- *Menida beryllina* ----------
---------- *Morone americana* ----------
---------- ***Morone saxatilis*** ----------
---------- ***Notropis hudsonius*** ----------

---------- ***Fundulus heteroclitus*** ----------
---------- ***Trinectes maculatus*** ----------
---------- *Anchoa mitchelli* ----------

---------- *Leiostomus xanthurus* ----------
---------- *Micropogonias undulatus* ------

---------- ***Menidia menidia***
---------- *Fundulus majalis*

Anchoa hepsetus
Synodus foetens
Opsanus tau
Symphurus plagiusa

Table 21: Common species characteristic of each of the three major faunal zones and ubiquitous species common in two or more adjacent zones of the longitudinal aquatic gradient in the York and Pamunkey Rivers. The centers of the TWINSPAN station groups are given by the bold numbers. Species names are placed near their abundance peak. Locally dominant species are shown in bold.

Permanent Tidal Freshwater		**Interface**		**Mesohaline**	
Upper	Lower	Freshwater	Oligohaline	Lower	Upper
1	**2**	**3**	**4**	**5a**	**5b**

← Pamunkey River → ← York River →

Lepomis auritus
Lepomis gibbosus
Lepomis macrochirus

Cyprinella analostana
Etheostoma olmstedi
Hybognathus regius

Fundulus diaphanus
Menida beryllina
Morone americana
Morone saxatilis
Notropis hudsonius

Trinectes maculatus
Anchoa mitchelli
Fundulus heteroclitus

Leiostomus xanthurus
Micropogonias undulatus

Menidia menidia
Fundulus majalis

Anchoa hepsetus
Synodus foetens
Opsanus tau
Symphurus plagiusa

Table 22: Common species characteristic of each of the three major faunal zones and ubiquitous species common in two or more adjacent zones of the longitudinal aquatic gradient in the James River. The centers of the TWINSPAN station groups are given by the bold numbers. Species names are placed near their abundance peak. Locally dominant species are shown in bold.

Permanent Tidal Freshwater		Interface		Mesohaline	
Upper	Lower	Freshwater	Oligohaline	Lower	Upper
1	**3** **2** **3** **2**	**4**		**5**	**6**

Alosa aestivalis
Lepomis macrochirus
Micropterus dolomieu
Micropterus salmoides

Dorosoma petenense ---------- ***D. petenense***
Notemigonus chrysoleucas --- *N. chrysoleucas*

Cyprinella analostana ----------
Menida beryllina ----------
---------- *Ictalurus punctatus* ----------
---------- *Fundulus diaphanus* ----------
---------- *Hybognathus regius* ----------

----------***Notropis hudsonius*** ----------
---------- *Trinectes maculatus* ----------
---------- ***Dorosoma cepedianum*** ----------
---------- ***Morone americana*** ----------
---------- *Morone saxatilis* ----------

---------- ***Micropogonias undulatus*** ----------
---------- *Leiostomus xanthurus*

---------- ***Menidia menidia***
---------- ***Anchoa mitchelli***
---------- *Mugil cephalus*
---------- *Mugil curema*

---------- *Brevoortia tyrannus*
----------*Anchoa hepsetus*

Fundulus majalis
Mentichirrus americanus
Opisthonema oglinum
Pomatomus saltatrix

Figure 38: Major ecoregions along the axial coenocline identified by the multivariate analysis.

General Station Pattern

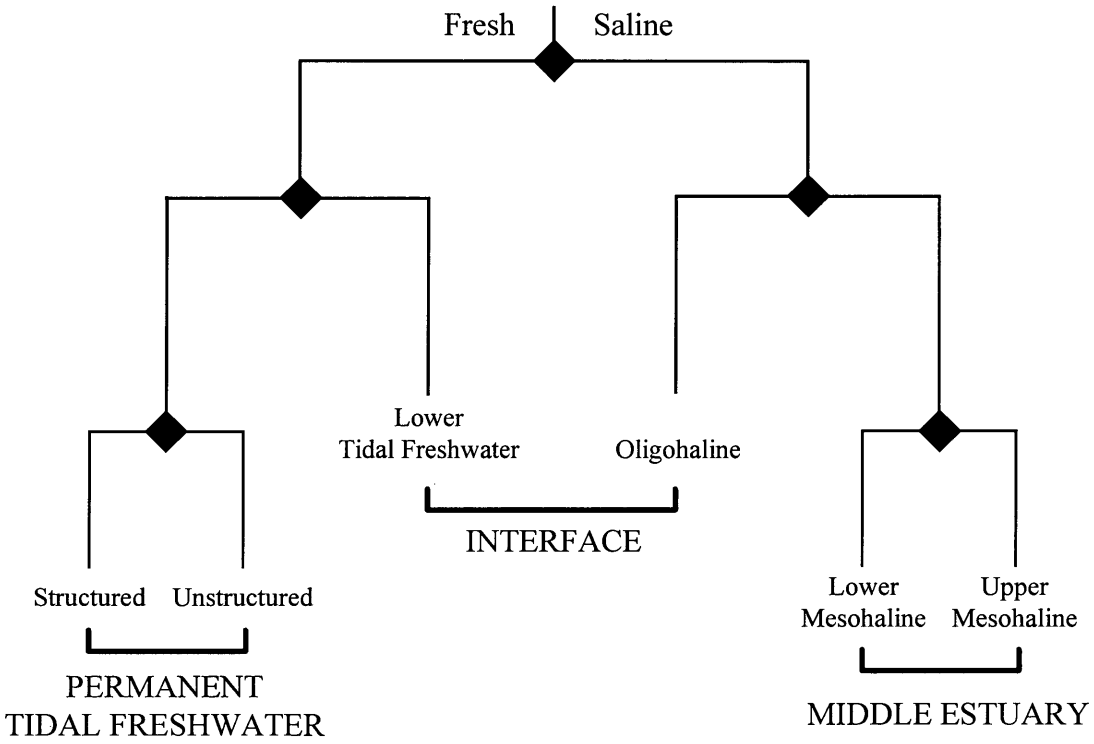


Figure 39: Large-scale distributions of fishes with respect to the strength of the salinity gradient in the tidal portions of the rivers.

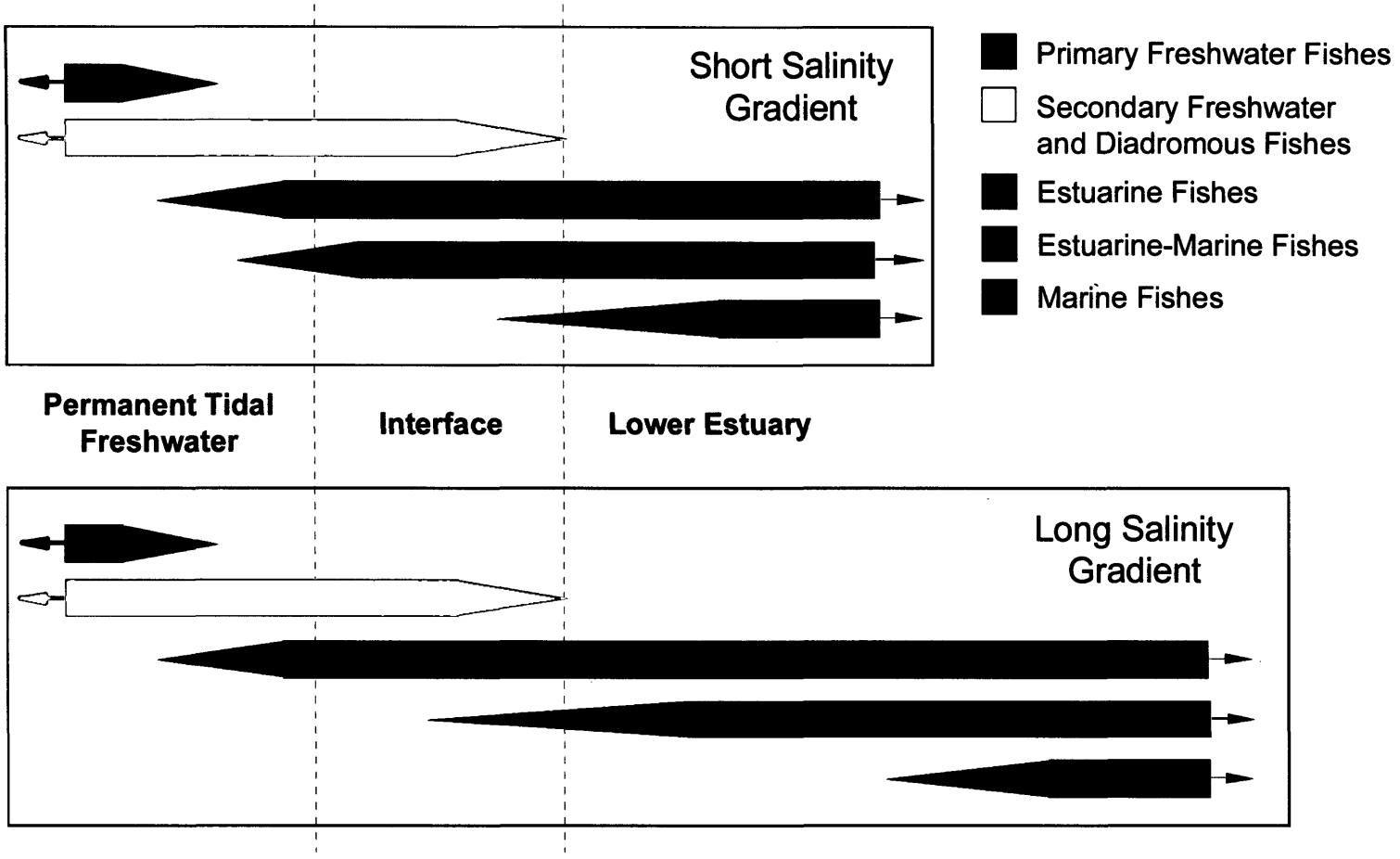

Short Salinity Gradient
Primary Freshwater Fishes
Secondary Freshwater and Diadromous Fishes
Estuarine Fishes
Estuarine-Marine Fishes
Marine Fishes
Permanent Tidal Freshwater
Interface
Lower Estuary
Long Salinity Gradient

Table 23: Diversity of fishes from all rivers expressed as expected number of species per 100 individuals via rarefaction (E(S)), Shannon-Wiener Diversity (H') and Pielou's Species Evenness (J'). All values are the mean annual value ± 1 standard error.

River	Station	Salinity	E(S)	H'	J'
Rappahannock	12	15.01 ± 1.48	9.67 ± 0.97	1.45 ± 0.17	0.55 ± 0.07
	21	13.69 ± 1.14	7.52 ± 0.86	1.07 ± 0.23	0.39 ± 0.09
	28	10.69 ± 1.23	6.22 ± 0.56	1.10 ± 0.21	0.45 ± 0.08
	37	5.68 ± 1.03	7.86 ± 0.89	1.28 ± 0.26	0.49 ± 0.10
	41	3.04 ± 0.85	11.32 ± 0.85	1.78 ± 0.11	0.63 ± 0.04
	44	1.54 ± 0.54	11.89 ± 0.98	1.83 ± 0.08	0.61 ± 0.03
	50	0.30 ± 0.20	12.88 ± 0.72	2.05 ± 0.15	0.70 ± 0.06
	55	0.09 ± 0.08	12.44 ± 0.50	1.98 ± 0.12	0.70 ± 0.05
	60	0.00 ± 0.00	9.82 ± 0.61	1.59 ± 0.12	0.58 ± 0.04
	65	0.00 ± 0.00	14.13 ± 0.70	2.15 ± 0.04	0.71 ± 0.01
	69	0.00 ± 0.00	14.60 ± 1.04	2.10 ± 0.16	0.70 ± 0.05
	76	0.00 ± 0.00	13.10 ± 0.80	1.97 ± 0.10	0.71 ± 0.03
York	15	16.30 ± 0.39	8.10 ± 0.81	1.36 ± 0.17	0.55 ± 0.06
	21	13.52 ± 0.57	11.00 ± 0.33	1.82 ± 0.12	0.65 ± 0.05
	28	11.92 ± 1.35	9.56 ± 0.27	1.51 ± 0.12	0.52 ± 0.04
Mattaponi	33	4.16 ± 1.40	9.18 ± 0.93	1.46 ± 0.21	0.57 ± 0.07
	37	1.88 ± 0.85	10.78 ± 0.70	1.77 ± 0.18	0.66 ± 0.06
	41	0.63 ± 0.38	10.06 ± 0.55	1.65 ± 0.13	0.66 ± 0.08
	44	0.24 ± 0.13	10.48 ± 0.19	1.65 ± 0.15	0.64 ± 0.06
	47	0.14 ± 0.12	10.77 ± 0.94	1.70 ± 0.15	0.65 ± 0.05
	52	0.00 ± 0.00	13.94 ± 0.53	2.18 ± 0.14	0.74 ± 0.06
Pamunkey	36	3.75 ± 0.85	9.03 ± 1.07	1.58 ± 0.18	0.60 ± 0.06
	42	0.87 ± 0.20	10.65 ± 0.24	1.76 ± 0.09	0.68 ± 0.04
	45	0.20 ± 0.09	9.59 ± 0.48	1.59 ± 0.08	0.63 ± 0.04
	50	0.05 ± 0.03	11.84 ± 0.80	1.77 ± 0.07	0.66 ± 0.04
	55	0.02 ± 0.02	11.55 ± 1.38	1.56 ± 0.16	0.57 ± 0.06
	61	0.00 ± 0.00	12.25 ± 1.19	2.07 ± 0.15	0.79 ± 0.02
James	12	13.02 ± 0.58	8.51 ± 1.08	1.31 ± 0.21	0.46 ± 0.07
	22	7.17 ± 0.51	8.39 ± 0.78	1.27 ± 0.20	0.50 ± 0.07
	29	4.51 ± 0.43	10.74 ± 0.31	1.64 ± 0.08	0.61 ± 0.03
	36	1.56 ± 0.18	12.08 ± 0.85	1.98 ± 0.07	0.72 ± 0.04
	46	0.10 ± 0.07	12.70 ± 1.00	2.10 ± 0.07	0.74 ± 0.03
	51	0.02 ± 0.02	11.47 ± 0.87	1.74 ± 0.16	0.59 ± 0.05
	56	0.02 ± 0.02	10.91 ± 0.65	1.61 ± 0.11	0.60 ± 0.04
	62	0.03 ± 0.03	8.19 ± 0.80	1.35 ± 0.15	0.51 ± 0.06
	68	0.02 ± 0.02	10.35 ± 0.60	1.66 ± 0.10	0.68 ± 0.03
	74	0.02 ± 0.02	9.34 ± 0.69	1.58 ± 0.20	0.65 ± 0.09
	78	0.02 ± 0.02	10.36 ± 0.66	1.68 ± 0.13	0.66 ± 0.06

Figure 40: The relative number of species in relation to salinity. The number of species corresponds to the vertical extent of the respective areas (after Remane 1934).

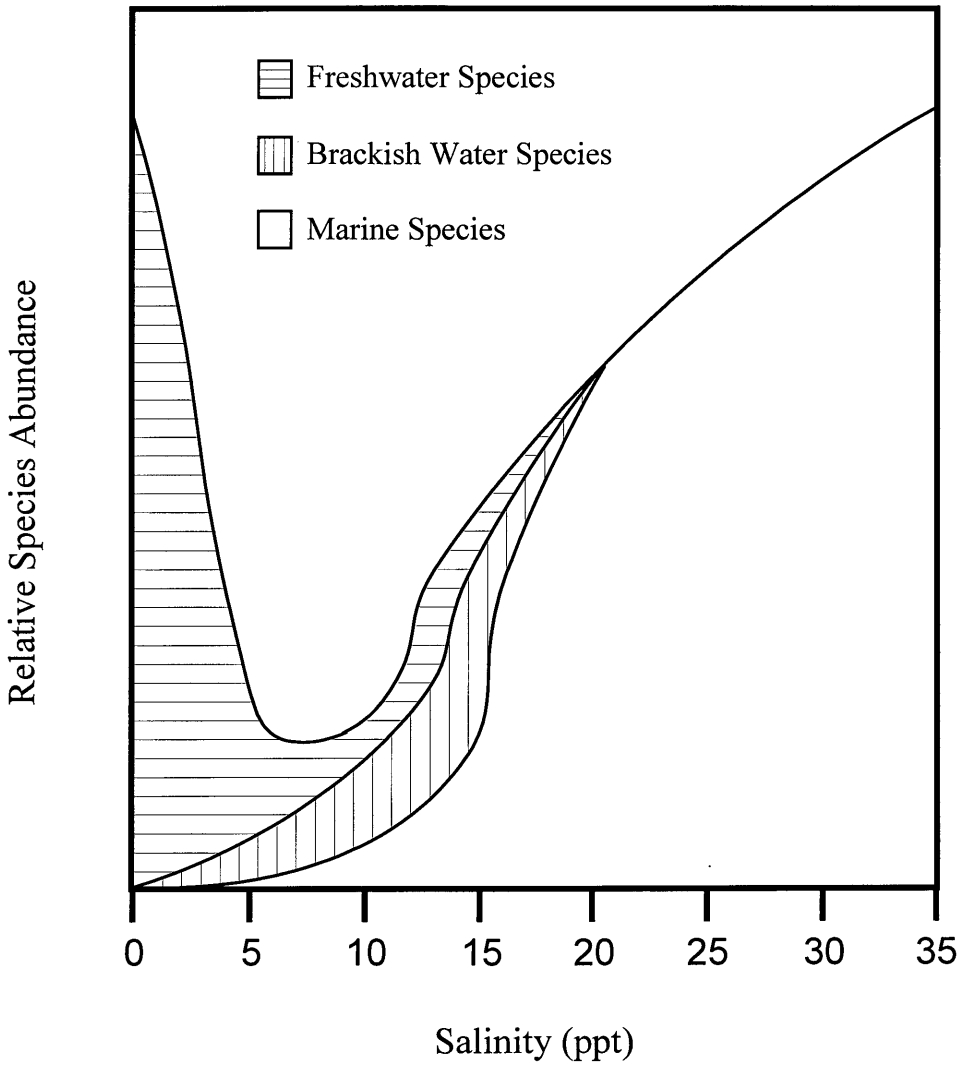

Freshwater Species
Brackish Water Species
Marine Species
Relative Species Abundance
0
5
10
15
20
25
30
35
Salinity (ppt)

Figure 41: The relative number of fish species in relation to salinity along the estuarine gradient (after Odum 1988).

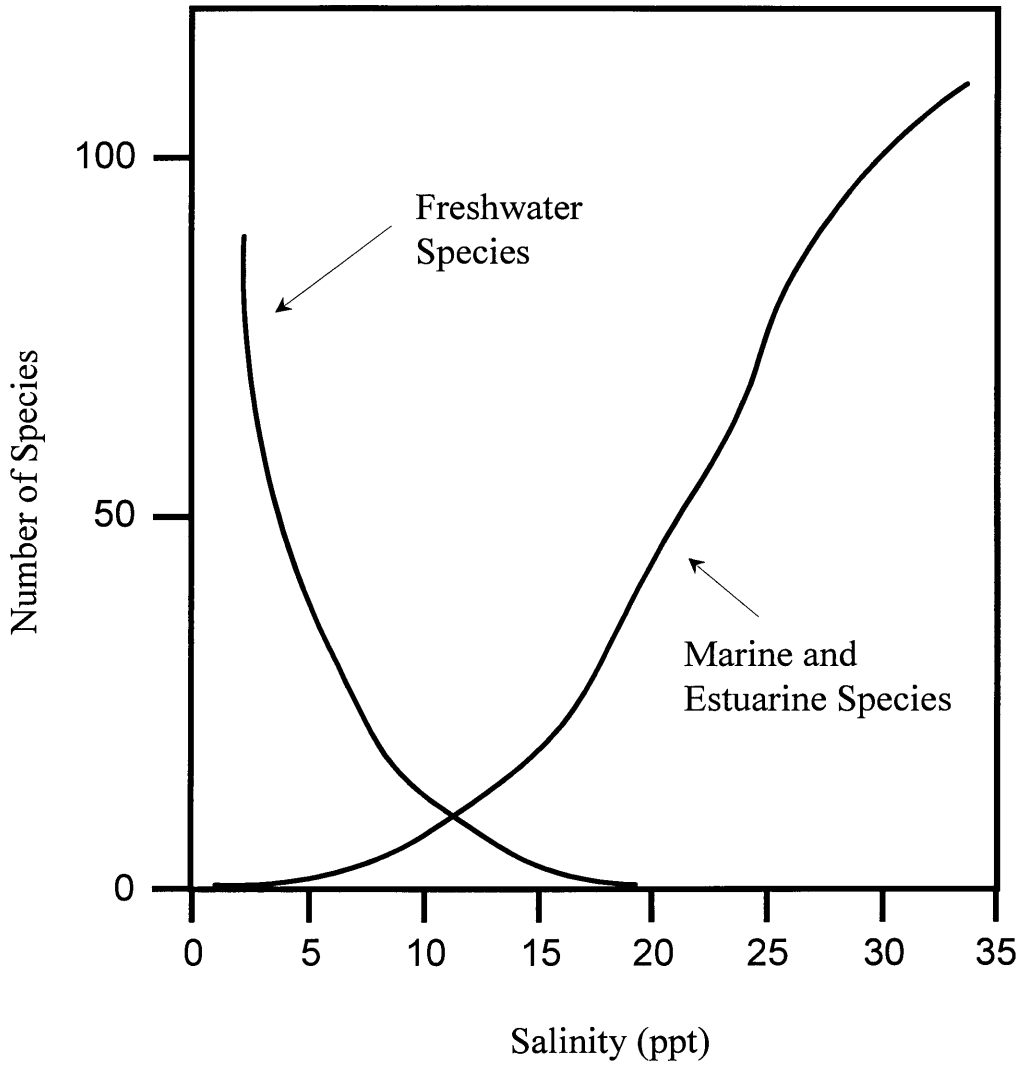

100
50
0
Number of Species
Freshwater
Species
Marine and
Estuarine Species
0
5
10
15
20
25
30
35
Salinity (ppt)

Figure 42: The relationship between the mean expected number of fish species (ES100) via rarefaction and the mean annual summer salinity for all stations.

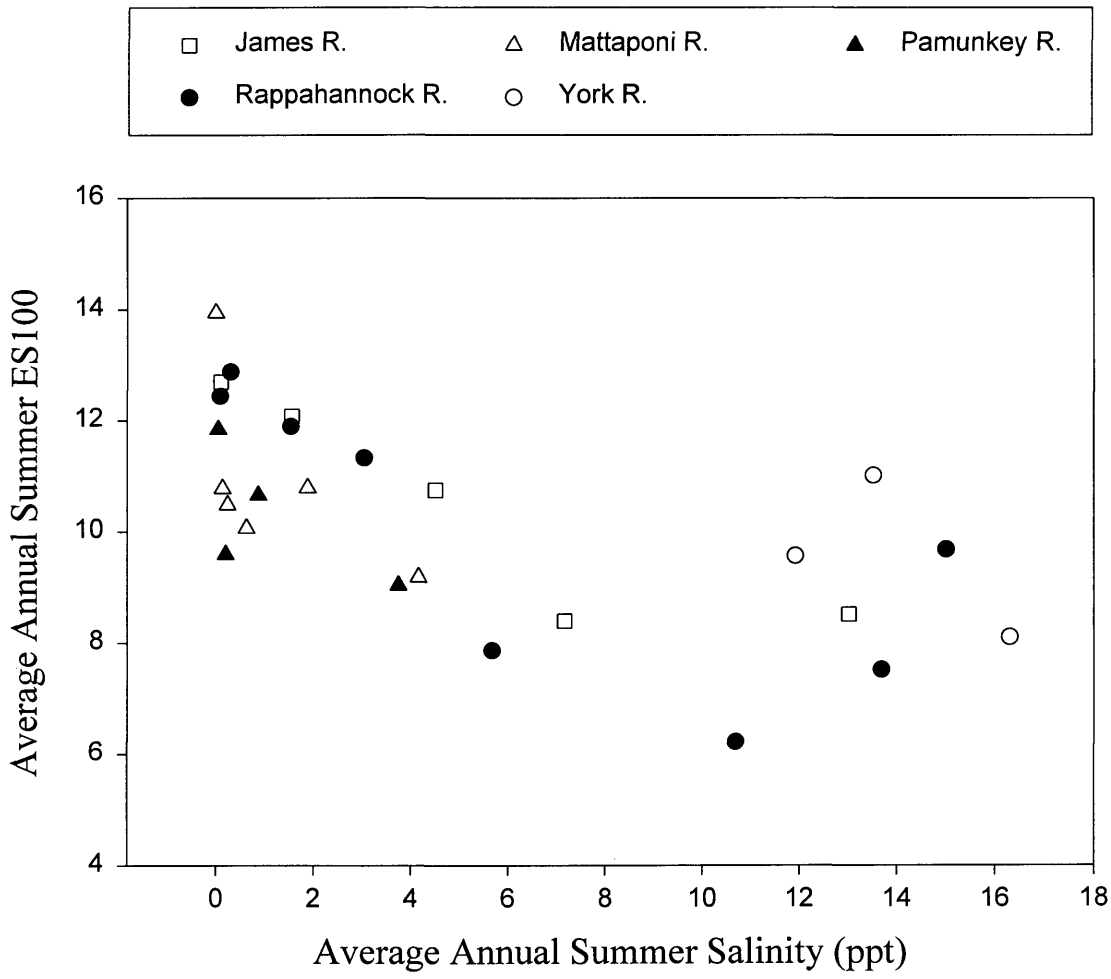
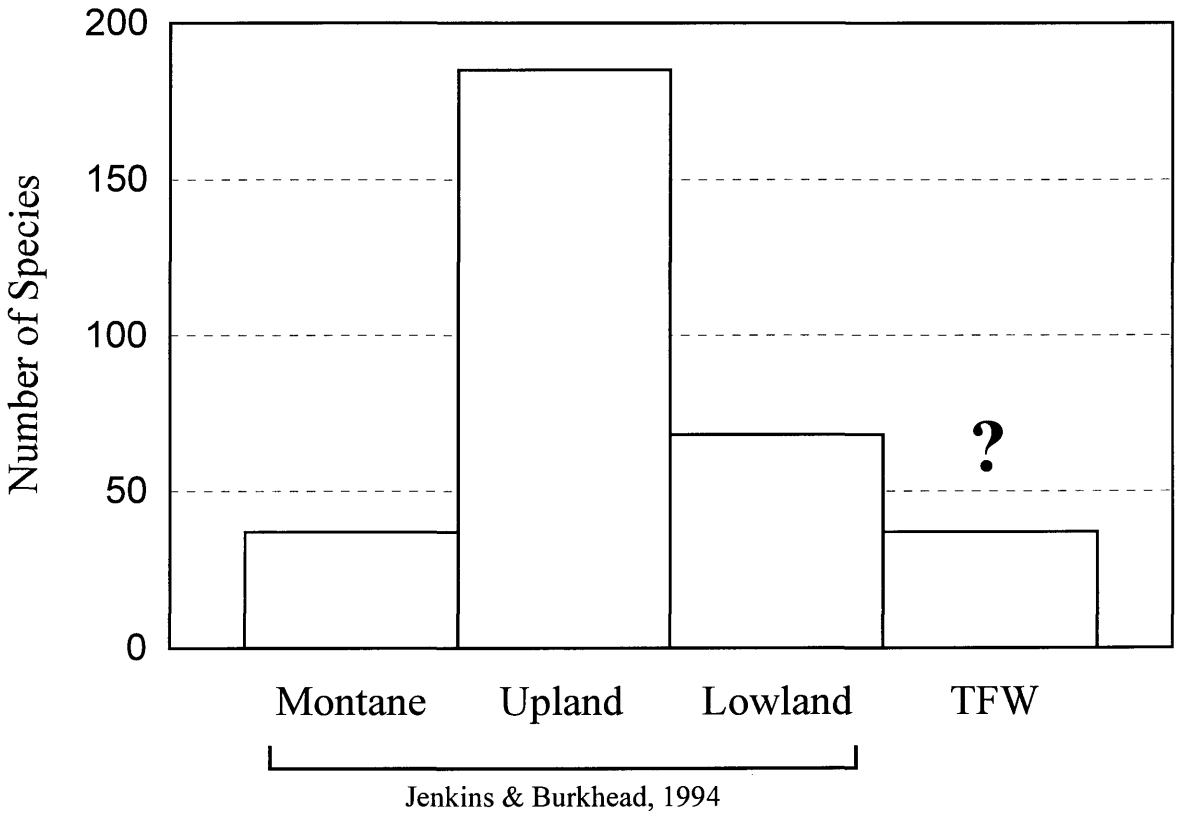

James R.
Mattaponi R.
Pamunkey R.
Rappahannock R.
York R.
Average Annual Summer ES100
16
14
12
10
8
6
4
0
2
4
6
8
10
12
14
16
18
Average Annual Summer Salinity (ppt)

Figure 43: Large-scale distribution of freshwater fish species in Virginia streams and rivers.

Freshwater Fish Species in Virginia Drainages



Jenkins & Burkhead, 1994

Figure 44: The relationship of species turnover rate to the incipient stress point which arises at 0-2 ppt salinity.

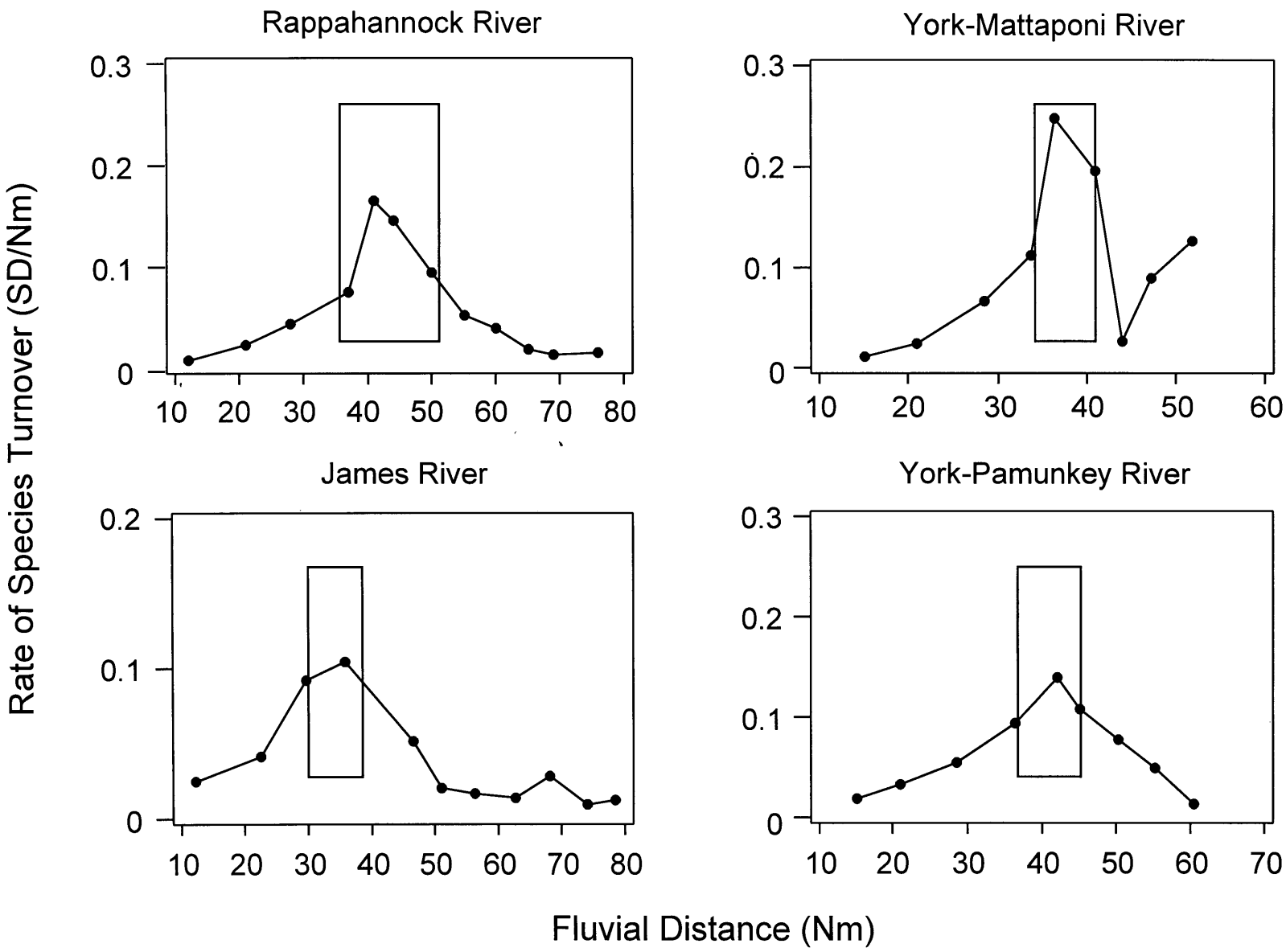
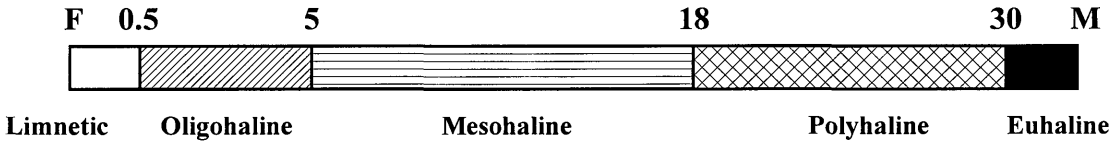
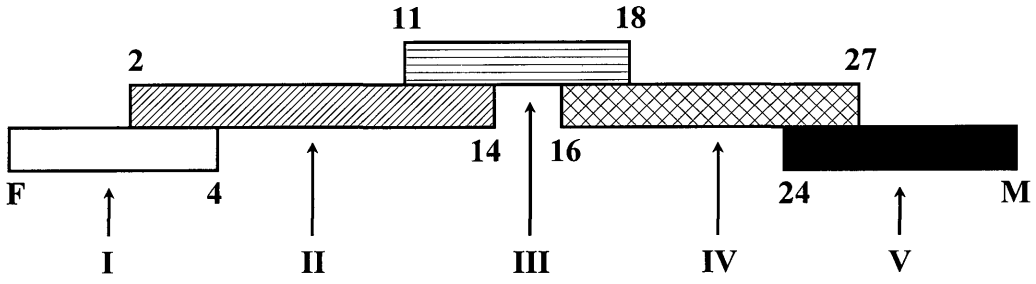

Rappahannock River
York-Mattaponi River
James River
York-Pamunkey River
Rate of Species Turnover (SD/Nm)
Fluvial Distance (Nm)
0.3
0.2
0.1
0
10 20 30 40 50 60 70 80
10 20 30 40 50 60
0.2
0.1
0
10 20 30 40 50 60 70 80
0.3
0.2
0.1
0
10 20 30 40 50 60 70

Figure 45: Comparison of Venice System and the estuarine salinity zones derived from multivariate analysis by Bulger *et al.* 1993.

Venice System



Biologically-Based Estuarine Salinity Zones



CONCLUSIONS

An important caveat of the approach I applied here is that pattern detection methods, such as canonical correspondence analysis (multiple regression) and correlation, do not necessarily imply causal relationships. Such analyses may be essential, however, to the formation of causal hypotheses and the progression to more experimental, process-oriented study in estuarine systems (Ludwig & Reynolds 1988; Coull 1985).

Results of the above analyses strongly suggest that large-scale littoral fish assemblage structure is related to site level and river level habitat variation (at least with respect to those species and variables included in the gradient analysis). Three ecological regions with recognizable fauna arose along the longitudinal river coenocline: permanent tidal freshwater, the freshwater interface, and the lower estuary. The influence of the physical environment in the tidal portions of the rivers probably overwhelms strong biotic interactions, and resident species are generally eurytopic within the ecological regions. Shallow water fishes were predominantly small residents and juveniles of larger migratory and resident species which presumably occupy the littoral zone as a refuge from predation.

The resident fauna of the tidal freshwater reaches are derivative of the non-tidal lowland rivers above the fall line (except *Menidia beryllina*) with no endemic species. Most species were not distinctly associated with a particular habitat, and there was no evidence for distinct longitudinal faunal zones or the downstream addition of species. Two factors which may explain these patterns are: (1) most of the individuals are secondary freshwater species who exhibit generalist patterns in feeding and spawning

requirements; and, (2) it would be disadvantageous for a tidal freshwater river species to specialize to a particular habitat since habitat availability and quality frequently change with the dynamic flow regimes and shifting substrates characteristic of these systems.

The freshwater interface serves as an ecotone which separates the resident faunas derived from freshwater and marine source areas. Several species of each group have the capacity to penetrate less favorable environments, though this capacity is asymmetric. Estuarine species appear more capable of withstanding a hypotonic environment while most salt-tolerant freshwater species made only shallow penetrations into oligohaline waters. The life-histories of the hogchoker, striped bass and white perch appear to be specifically cued to occupy this region as juveniles.

The lower estuary above five ppt salinity conforms well to existing models which suggest salinity (or its correlates) as the controlling factor, particularly during summer when a relatively stable salinity gradient is in place. There is evidence for a species minimum in the range of 8-10 ppt which generally agrees with the assertion of Remane (1934).

APPENDIX 1

Guidelines for Interpreting Community Structure Plots

The spatial community patterns are represented in a three-step graphical process designed to associate stations according to the distribution and abundance of common species, and then position species along gradients in environmental condition. Specifically,

1) Stations are classified in a TWINSPAN dendrogram.
2) Stations and species are ordinated via detrended correspondence analysis to associate specific species with the TWINSPAN station groups.
3) Species are associated with attributes of the environment via detrended canonical correspondence analysis.

Each of these methods generate graphical plots which require some explanation for proper interpretation. For the following simple example, imagine a hypothetical river-dominated estuary which floods in the spring. The data are a transect trawl samples of fishes taken in the central portion of the estuary across a single year.

TWINSPAN Classification -- The primary result of TWINSPAN is a two-way classification table of sites and species. The station or species classifications may also be represented as dendrograms where each level represents sequential dichotomies of the previous levels. Divisions are made successively according to the scheme shown in Figure 46.

The data are first ordinated by reciprocal averaging (i.e., correspondence analysis). Species which characterize the extremes of the ordination are used to split the

data set near the middle. The division process is then repeated on the two sample subsets (0 and 1) to give four clusters, and so on, until each cluster has no more then a preset number of samples (e.g., 10). the results are plotted in a dendrogram of sequential dichotomies, coded in binary. The species used to polarize the groups are called *Indicator Species*, and are plotted in decreasing order of importance at each division. Indicator species are those species which best serve to separate the groups and are not necessarily the most abundant taxa. The relative strength of the division is given by an eigenvalue which ranges from zero to one. Generally, an eigenvalue is considered strong above 0.3, and very strong above 0.5. In the example, the stations have split into two primary groups with species A and B suggested as indicators for station group 1, and species C and D are suggested for station group 2.

DCA Ordination -- The primary result of DCA is an ordination diagram, i.e. a graph with a coordinate system formed by the ordination axes (synthetic gradients extracted by the analysis). A DCA diagram only consists of points for stations and/or species. The coordinates of the station points are the values (termed scores) of the stations on the two best synthetic gradients (axes 1 and 2). Station scores reside at their distributional center for each axis, i.e., by the weighted average of the axis-scores of species which occur at the station (weight is determined by the actual abundance value). Consequently, each station point in the diagram is at the centroid (weighted average) of the species scores (i.e., the relative center of the two-dimensional distribution of the species in the ordination space). A consequence of this algorithm is that all station scores will reside within the range of species scores. Scaling of the axes is based on Hill &

Gauch's (1980) original formulation where one unit represents a standard deviation (SD) in the rate of species turnover. Thus, stations separated by two SD units share approximately 50% of their species composition whereas stations separated by four SD units may have no species in common. Gradients of greater than 3 SD are considered long (Gauch 1982).

In the example, the stations are spread along two synthetic gradients (DCA axes 1 and 2), with the greater turnover (5 SD's or >100% turnover) along axis 1 (Fig. 47). The two groups of stations are distinct within the ordination space, and the scores of species A-D tend to polarize the samples. Species E-G are distributed near the origin, suggesting they are common to both station groups.

DCCA Ordination -- The allocation of station scores and species scores in DCCA is similar to DCA with one major exception. As the station scores are constrained by a multivariate regression on the environmental variables, species scores now represent a niche center within the environmental space (to the extent that the species niche may be defined by the set of environmental covariables included in the analysis). DCCA allows the simultaneous plotting of species and/or site scores with environmental variables in a joint plot. Environmental gradients are represented by vectors, and sites or species by symbols. The axes are based on the species composition (as in DCA), but are rescaled to a range of zero to one. The environmental vectors may now be projected onto the axes, and the X-Y coordinates of the vectors' terminus equal the correlation coefficients for the variable with the species composition axes. The angle between vectors indicates the strength of intercorrelations between variables (90° = no correlation). The location of

site scores relative to the vectors indicates the environmental characteristics of the sites, and the proximity of species scores relative to the vectors indicates the environmental "preferences" of each species. Species scores may be projected onto a vector such that the ordering of species along the axis of the vector are maximum likelihood estimates of species modes under the assumption that species abundance is a Gaussian function of environmental gradients.

In the example, species scores and environmental vectors are plotted for the trawl data (Fig. 48). The first species compositional gradient (axis 1) is most highly correlated with salinity (~ 0.90), and the second with water temperature (~ 0.70). The relative distribution of species scores is preserved. Species E-G reside near the origin suggesting limited preferences along gradients of salinity or temperature. These species are likely estuarine residents with broad tolerances. Species A and B occur primarily in higher salinity, lower temperature stations, and are probably boreal species which penetrate the estuary during winter months. Species C and D occur at lower salinity, higher temperature stations. These are probably facultative riverine species which penetrate the estuary during the spring flood, retreating during the later part of the year.

Figure 46: Example of a TWINSPAN classification dendrogram.

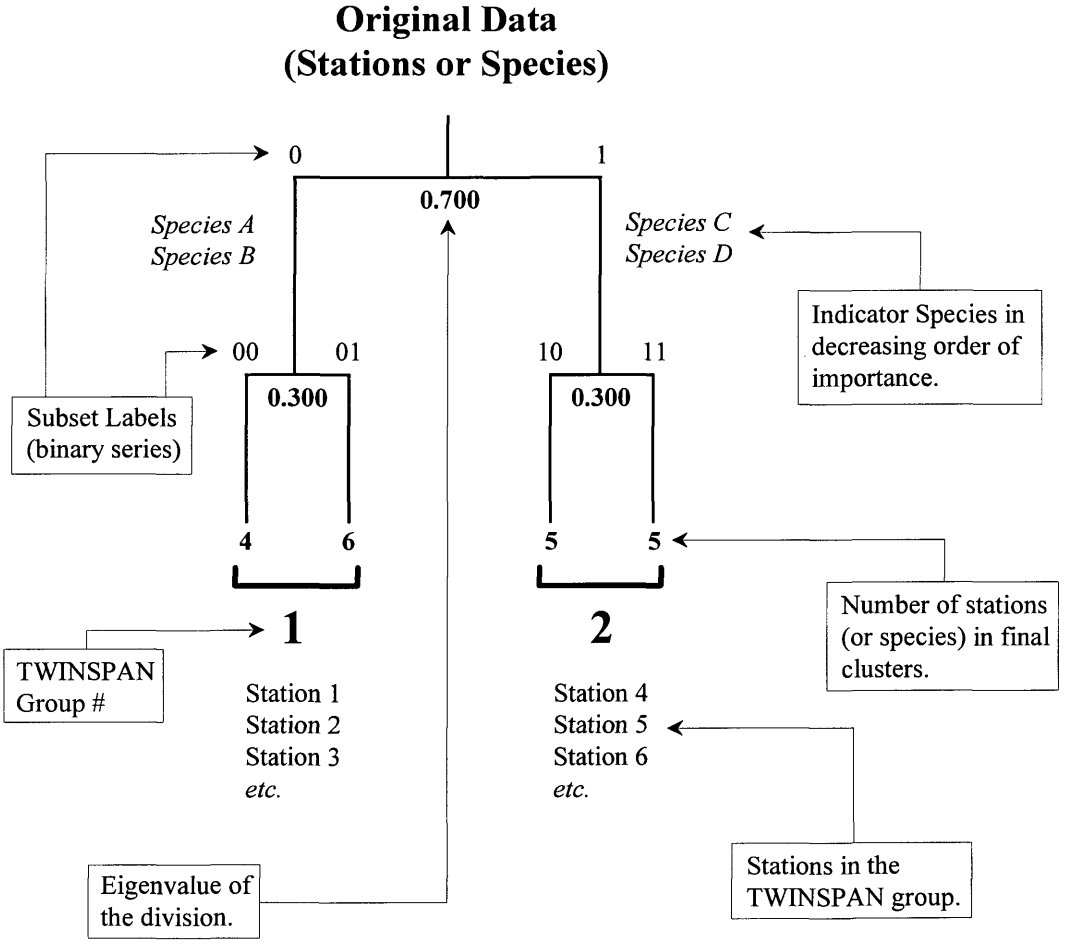

Original Data
(Stations or Species)
0
1
0.700
Species A
Species B
Species C
Species D
Indicator Species in decreasing order of importance.
00
01
10
11
0.300
0.300
Subset Labels (binary series)
4
6
5
5
Number of stations (or species) in final clusters.
1
2
TWINSPAN Group #
Station 1
Station 2
Station 3
etc.
Station 4
Station 5
Station 6
etc.
Eigenvalue of the division.
Stations in the TWINSPAN group.

Figure 47: Example of a detrended correspondence analysis biplot of station scores and species scores.

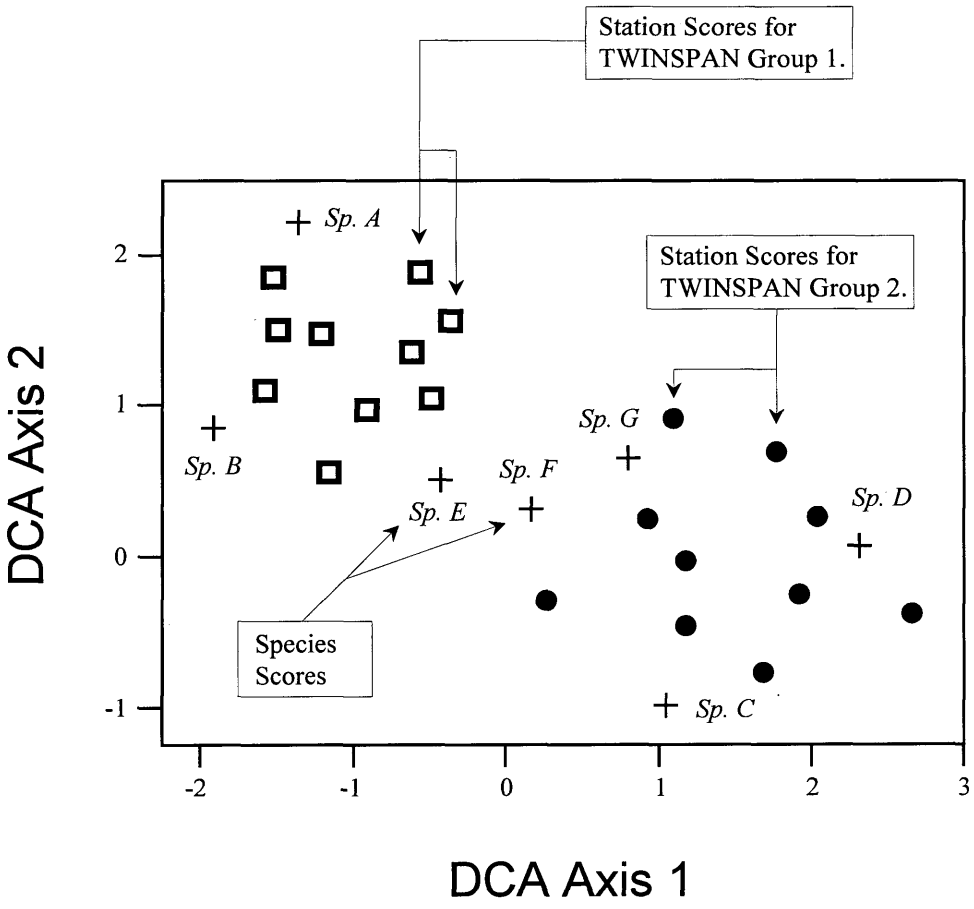
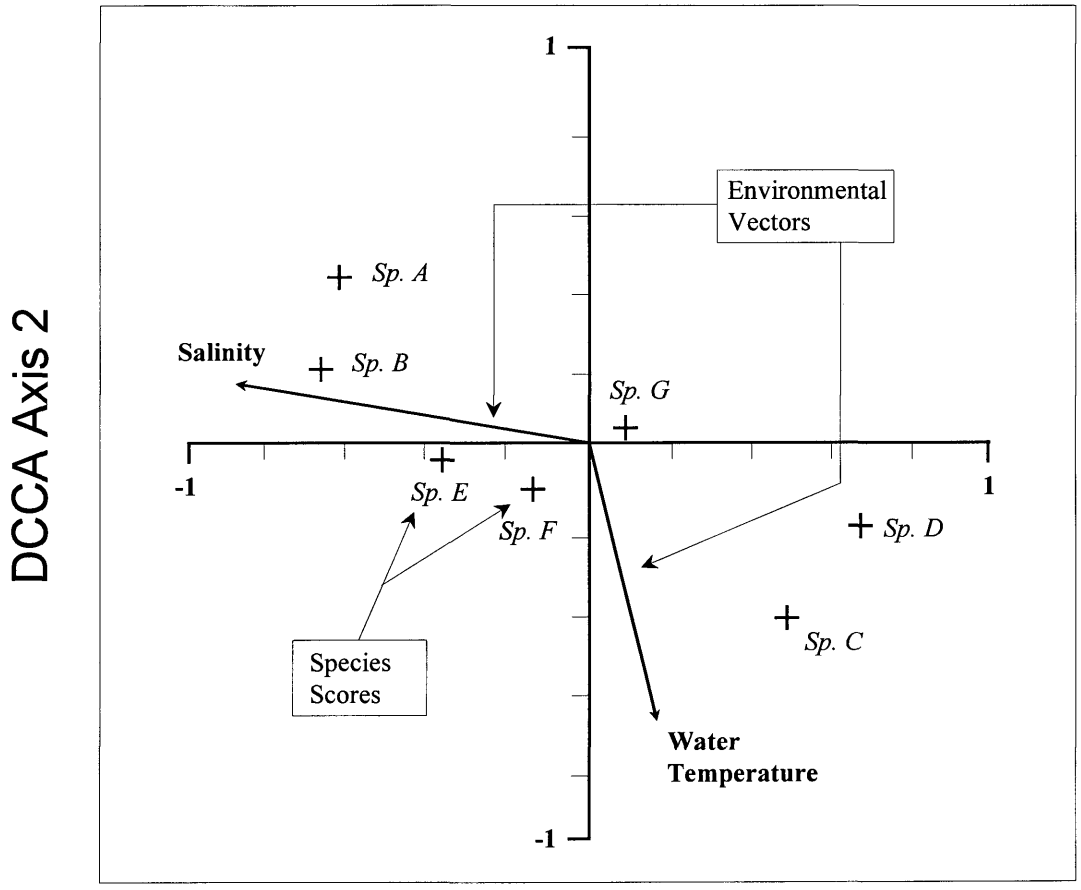

Station Scores for TWINSPAN Group 1.
Station Scores for TWINSPAN Group 2.
Species Scores
Sp. A
Sp. B
Sp. C
Sp. D
Sp. E
Sp. F
Sp. G
DCA Axis 2
DCA Axis 1
2
1
0
-1
-2
-1
0
1
2
3

Figure 48: Example of a detrended canonical correspondence analysis biplot of species scores and environmental vectors.


1
-1
1
-1
Environmental Vectors
Sp. A
Salinity
Sp. B
Sp. G
Sp. E
Sp. F
Sp. D
Sp. C
Species Scores
Water Temperature
DCCA Axis 2
DCCA Axis 1

APPENDIX 2: Species codes used in DCA and DCCA plots.

Code	Scientific Name	Common Name
Al.ae.	*Alosa aestivalis*	blueback herring
Al.ps.	*Alosa pseudoharengus*	alewife
Am.ca.	*Ameiurus catus*	white catfish
An.he.	*Anchoa hepsetus*	striped anchovy
An.mi.	*Anchoa mitchelli*	bay anchovy
An.ro.	*Anguilla rostrata*	American eel
Ba.ch.	*Bairdiella chrysoura*	silver perch
Br.ty.	*Brevoortia tyrannus*	Atlantic menhaden
Ca.hi.	*Caranx hippos*	crevalle jack
Cy.an.	*Cyprinella analostana*	satinfin shiner
Cy.ca.	*Cyprinnus carpio*	common carp
Cy.ne.	*Cynoscion nebulosus*	spotted seatrout
Cy.re.	*Cynoscion regalis*	weakfish
Do.ce.	*Dorosoma cepedianum*	gizzard shad
Do.pe.	*Dorosoma petenense*	threadfin shad
En.gl.	*Enneacanthus gloriosus*	bluespotted sunfish
Et.ol.	*Etheostoma olmstedi*	tessellated darter
Fu.di.	*Fundulus diaphanus*	banded killifish
Fu.he.	*Fundulus heteroclitus*	mummichog
Fu.ma.	*Fundulus majalis*	striped killifish
Ga.af.	*Gambusia affinis*	mosquitofish
Hy.re.	*Hybognathus regius*	eastern silvery minnow
Ic.fu.	*Ictalurus furcatus*	blue catfish
Ic.pu.	*Ictalurus punctatus*	channel catfish
Le.au.	*Lepomis auritus*	redbreast sunfish
Le.gi.	*Lepomis gibbosus*	pumpkinseed
Le.ma.	*Lepomis macrochirus*	bluegill
Le.xa.	*Leiostomus xanthurus*	spot
Me.am.	*Mentichirrus americanus*	southern kingfish
Me.be.	*Menidia beryllina*	inland silverside
Me.ma.	*Membras martinica*	rough silverside
Me.me.	*Menidia menidia*	Atlantic silverside
Mi.do.	*Micropterus dolomieu*	smallmouth bass
Mi.sa.	*Micropterus salmoides*	largemouth bass
Mi.un.	*Micropogonias undulatus*	Atlantic croaker
Mo.am.	*Morone americana*	white perch
Mo.sa.	*Morone saxatilis*	striped bass
Mu.ce.	*Mugil cephalus*	striped mullet
Mu.cu.	*Mugil curema*	white mullet
No.ch.	*Notemigonus chrysoleucas*	golden shiner
No.hu.	*Notropis hudsonius*	spottail shiner
Op.og.	*Opisthonema oglinum*	Atlantic thread herring
Op.ta.	*Opsanus tau*	oyster toadfish
Pa.de.	*Paralichthys dentatus*	summer flounder
Pe.fl.	*Perca flavescens*	yellow perch
Po.sa.	*Pomatomus saltatrix*	bluefish
Sc.ma.	*Scomberomorous maculatus*	Spanish mackerel
St.ma.	*Strongylura marina*	Atlantic needlefish
Sy.fo.	*Synodus foetens*	inshore lizardfish
Sy.pl.	*Symphurus plagiusa*	blackcheek tonguefish
Tr.ma.	*Trinectes maculatus*	hogchoker

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