ABSTRACT

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                            COMPOSITION AND COMMUNITY
                            STRUCTURE OF FISHES IN ESTUARINE
                            ECOSYSTEMS

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Fishing, other human activities, and natural perturbations can alter the

species composition and size structure of fish communities in coastal

ecosystems. Normalized biomass size spectra (NBSS) and other metrics based

on size and abundance of fish communities are sensitive to effects of fishing and

have been proposed as useful tools for ecosystem-based management.

However, these approaches based on size and abundance are unevaluated at

temporal and spatial scales relevant for management within estuaries. Because

individual species have important ecological and economic value, tracking

temporal and spatial changes in the species composition of the fish communities

using multivariate analyses, such as principal component analysis (PCA), can

facilitate interpretation of patterns observed in the NBSS. A goal of my

dissertation was to determine if indicators suitable for ecosystem-based

management can be derived from NBSS parameters and other metrics based on size and abundance for estuarine fish and plankton communities at relatively small temporal and spatial scales. Additionally, I sought to elucidate effects of temporal and spatial variability in species composition on community size structure of estuarine fish communities by combining multivariate and NBSS analyses. Analyzing data from multiple fisheries-independent surveys and water quality monitoring programs, the objectives of my dissertation were 1) to describe and quantify the size distribution and community composition of fish and plankton in Chesapeake Bay at temporal scales ranging from months to over a decade and at spatial scales ranging from 18 km to 100 km, 2) to evaluate long-term trends in abundance, size distribution, and species composition of fish communities in Chesapeake Bay and Pamlico Sound, and 3) to analyze environmental variables and their effects on community structure and size distribution of biological communities in the Chesapeake and Pamlico Sound estuaries. Results supported the conclusion that NBSS combined with traditional community analyses permits detection of changes in ecosystem status, facilitates identification the species associated with the observed variability, and provides a framework to establish management reference points.

SCALES OF VARIABILITY IN THE SIZE COMPOSITION AND COMMUNITY STRUCTURE OF FISHES IN ESTUARINE ECOSYSTEMS

By

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DEDICATION

To my wife, Amy Ford.

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> yours is the light by which my spirit's born:
> yours is the darkness of my soul's return
> -you are my sun,my moon,and all my stars

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Figure 16. Regression tree for annual species richness. The number on the end of each leaf of the tree is the mean annual species richness for that leaf. The bar plots below each leaf show the annual richness for each year in each system associated with that leaf. Gray bars = lower Chesapeake Bay, red bars = James River, blue bars = Rappahannock River, and green bars = York River.

Figure 17. Regression tree for annual species diversity. The number on the end of each leaf of the tree is the mean diversity for that leaf. The bar plots below each leaf show the annual diversity for each year in each system associated with that leaf. Gray bars = lower Chesapeake Bay, red bars = James River, blue bars = Rappahannock River, and green bars = York River.

Chapter 5

Figure 1. Map of the area sampled by the North Carolina Department of Marine Fisheries Pamlico Sound Survey (from Moore 2000). The gray grid squares are selected randomly for sampling before each cruise. See text for more information.

Figure 2. Salinity and temperature trends for Pamlico Sound and its tributaries. A) June salinity, B) September salinity, C) June temperature, and D) September temperature. Error bars are +/- 1 standard error.

Figure 3. June survey data: (A) species richness and (B) diversity by year for the Pamlico Sound and its tributaries. Solid lines indicate significant trend, and dashed lines indicate no trend. The data points for 2002 and 2003 were excluded from the Pungo River richness analysis.

Figure 4. (A) June and (B) September PCA biplots for the Pamlico Sound. The data from 1992-1998 are shown in blue, the 1999 data are in green, and the 2000-2003 data are in red. The percentage following each axis label is the percent of the variance represented by each PC. The variable label format is sp.age where "sp" is the species abbreviation and "age" is the numeric age estimate based on visual inspection of annual length histograms. The possible ages are blank (all ages combined), 0, 1, or 2. Species abbreviations are am = Atlantic menhaden, ba = bay anchovy, bc = blue crab, bf = bluefish, bs = brown shrimp, bu = butterfish, bw = bay whiff, cr = Atlantic croaker, hc = hogchoker, hf = harvestfish, lf = lizardfish, pf = pinfish, pg = pigfish, ps = pink shrimp, sf =

spadefish, sk = southern kingfish, si = silver perch, so = southern flounder, sp = spot, su = summer flounder, wf = weakfish, ws = white shrimp.

Figure 5. (A) June and (B) September PCA biplots for the Pamlico River. The data from 1992-1995 and 1997 are shown in blue, and the 1996 and 1998-2003 data are in red. The percentage following each axis label is the percent of the variance represented by each PC. The variable label format is sp.age where "sp" is the species abbreviation and "age" is the numeric age estimate based on visual inspection of annual length histograms. The possible ages are blank (all ages combined), 0, 1, or 2. Species abbreviations are am = Atlantic menhaden, ba = bay anchovy, bc = blue crab, bs = brown shrimp, bu = butterfish, bw = bay whiff, cr = Atlantic croaker, hc = hogchoker, hf = harvestfish, lf = lizardfish, pf = pinfish, pg = pigfish, ps = pink shrimp, si = silver perch, so = southern flounder, sp = spot, su = summer flounder, wf = weakfish, ws = white shrimp.

Figure 6. (A) June and (B) September PCA biplots for the Pungo River. The data from 1992-1995 and 1997 are shown in green, the data from 1996, 1998, and 2001-2003 are shown in orange, the 1999 data are shown in red, and the 2000 data are shown in blue. The percentage following each axis label is the percent of the variance represented by each PC. The variable label format is sp.age where "sp" is the species abbreviation and "age" is the numeric age estimate based on visual inspection of annual length histograms. The possible ages are blank (all ages combined), 0, 1, or 2. Species abbreviations are am = Atlantic menhaden, ba = bay anchovy, bc = blue crab, bf = bluefish, bs = brown shrimp, bu = butterfish, bw = bay whiff, cr = Atlantic croaker, hc = hogchoker, hf = harvestfish, lf = lizardfish, pf = pinfish, ps = pink shrimp, si = silver perch, so = southern flounder, sp = spot, su = summer flounder, wf = weakfish, ws = white shrimp.

Figure 7. (A) June and (B) September PCA biplots for the Neuse River. Assemblages discussed in the text are labeled here. The percentage following each axis label is the percent of the variance represented by each PC. The variable label format is sp.age where "sp" is the species abbreviation and "age" is the numeric age estimate based on visual inspection of annual length histograms. The possible ages are blank (all ages combined), 0, 1, or 2. Species abbreviations are am = Atlantic menhaden, ba = bay anchovy, bc = blue crab, bf = bluefish, bs = brown shrimp, bu = butterfish, bw = bay whiff, cr = Atlantic croaker, hc = hogchoker, hf = harvestfish, lf = lizardfish, pf = pinfish, pg = pigfish, ps = pink shrimp, si = silver perch, so = southern flounder, sp = spot, su = summer flounder, wf = weakfish, ws = white shrimp.

Figure 8. (A) Mean size June and (B) mean biomass September per tow. Solid lines indicate significant trend, and dashed lines indicate no trend.

Figure 9. Examples of June NBSS biomass domes from (A) Pamlico Sound, (B) the Pamlico River, (C) the Pungo River, and (D) the Neuse River. The years

shown for each system were selected from each of the temporal assemblages defined by the June PCAs and shown in Figures 7-10 and are color-coded accordingly. The numbers shown witin the axes of A and B are the nontransformed values for the size classes and number per tow, respectively.

Figure 10. June survey data: NBSS biomass dome estimated size at peak abundance by year. Solid lines indicate significant trend, and dashed lines indicate no trend. The Pamlico River trend represents the regression with the 1997 data point estimate excluded as an outlier.

Figure 11. June survey data: trends in mean number per tow for (A) age 1+ spot, (B) age 2+ Atlantic croaker, (C) pinfish, and (D) brown shrimp. Note that the y-axis scales of each plot differ and that the y-axis for Atlantic croaker (B) is in $\log_{10}$ units. Error bars are +/- 1 standard error.

Supplementary Figures

Figure S1. Scree plots for the principal components analyses based on (A) data from all cruises, (B) data from May cruises, (C) data from July cruises, and (D) data from October cruises. The slope of the curve represents the decline in the amount of variance explained by each additional PC. The point at which the slope begins to level off represents the boundary between the dominant signals and noise.

Figure S2. Scree plots for the principal components analyses based on (A) data from the summer cruises and (B) data from all cruises in 2003 and 2004. The slope of the curve represents the decline in the amount of variance explained by each additional PC. The point at which the slope begins to level off represents the boundary between the dominant signals and noise. In these plots, the dominant signals are represented by the first 3-4 PCs.

Figure S3. Scree plots for the annual principal components analyses for (A) the lower Chesapeake Bay mainstem, (B) the James River, (C) the Rappahannock River, and (D) the York River. The slope of the curve represents the decline in the amount of variance explained by each additional PC. The point at which the slope begins to level off represents the boundary between the dominant signals and noise. In these plots, the dominant signals are represented by the first two PCs.

Figure S4. Scree plots for the June principal components analyses for (A) Pamlico Sound, (B) the Pamlico River, (C) the Pungo River, and (D) the Neuse River. The slope of the curve represents the decline in the amount of variance explained by each additional PC. The point at which the slope begins to level off represents the boundary between the dominant signals and noise. In these plots, the dominant signals are represented by the first two PCs.

Figure S5. Scree plots for the September principal components analyses for (A) Pamlico Sound, (B) the Pamlico River, (C) the Pungo River, and (D) the Neuse River. The slope of the curve represents the decline in the amount of variance explained by each additional PC. The point at which the slope begins to level off represents the boundary between the dominant signals and noise. In these plots, the dominant signals are represented by the first 2-4 PCs.

CHAPTER 1

Introduction

The structure of fish communities, including richness, diversity, size structure, and trophic levels represented, can vary across temporal and spatial scales. In addition, effects of fishing and other human activities can alter structure and productivity of fishes in coastal ecosystems. The goal of this dissertation is to describe and evaluate structure of fish and associated plankton communities in Chesapeake Bay (CB) and its tributaries, and in the Pamlico Sound (PS) estuarine system (Figure 1). Biomass size spectra (BSS) and multivariate statistical analyses were conducted to determine if these approaches were effective and complementary in describing structure and shifts in it at the spatial scales represented in estuarine ecosystems and to determine if the approaches could be used to develop indicators of status and trends in fish and plankton communities.

Introduction to biomass size spectra

Predator-prey interactions in aquatic systems follow predictable patterns of changes in metabolism with body size, relationships between the sizes of predators and their prey, and physiological processes common in aquatic organisms (Sheldon et al. 1973; Silvert and Platt 1978; Dickie et al. 1987; Thiebaux and Dickie 1993; Kerr and Dickie 2001). In early research on particle size distributions for particles ranging from 1 - 4,000 μm in the Atlantic, Pacific, and Southern Oceans, Sheldon et al. (1972) discovered that the biomass

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distribution for the logarithmic sizes representing the size range encompassing

phytoplankton was approximately equal to the biomass distribution for logarithmic

sizes representing zooplankton. Sheldon et al. (1972) also examined standing

stock estimates for larger organisms, including fish and whales, and found that

their biomass distributions were similar to those of smaller organisms. Biomass

size spectra (BSS) evaluated to date for both freshwater and marine ecosystems

of widely varying productivity, over size ranges encompassing phytoplankton,

zooplankton, and fish, have strikingly similar patterns despite differences in

species composition (Sheldon et al. 1972; Sheldon et al. 1973; Sprules and

Munawar 1986; Sprules et al. 1991; Boudreau and Dickie 1992; Sprules and

Goyke 1994; Sprules and Stockwell 1995). It is this similarity in BSS from

different ecosystems and the strong correspondence between empirical

observation and theory that suggest BSS is a widely applicable and powerful tool

to interpret the state of ecosystems. Deviations from theoretical expectations

may indicate a change in predator-prey relationships, either through alterations of

biomass production or via mortality, that mediate energy flow through an

ecosystem (Kerr and Dickie 2001).

In a BSS, weight classes are scaled along the x-axis, usually in equal $\log_2$

units, and biomass is portrayed along the y-axis (Figure 2A). Presented in this

manner, the overall slope of the BSS generally lies between 0 and –0.22. The

near-zero slope results because biomass estimates for the trophic levels

corresponding to phytoplankton, zooplankton, and fish are often approximately

equal (Kerr and Dickie 2001). These empirical observations were confirmed in

mathematically-derived predictions by Platt and Denman (1977, 1978) based on

the dependence of metabolism and turnover time on body size presented by

Fenchel (1974).

It is difficult to compare peaks and gaps within a BSS with the peaks and

gaps in spectra from another ecosystem. Accordingly, a method to normalize a

biomass spectrum was proposed to transform the y-axis by dividing biomass in a

size class by mass of an individual in the class (Platt and Denman 1977, 1978).

This transformation results in a normalized biomass size spectrum (NBSS)

(Figure 2B), which is equivalent to an abundance-based, size-frequency

distribution for sizes represented in the community. Normalizing the spectrum is

a mathematical convenience that provides a generalized form permitting

statistical comparison of spectra from different points in time or from different

ecosystems (Kerr and Dickie 2001). The overall slope of a NBSS, which is

referred to as the integral spectrum, is represented by a linear regression through

the data. The slope of the integral spectrum predicted by the theoretical

developments of Platt and Denman (1977, 1978) and further refined by

Borgmann (1983, 1987) was found to be −1. The slopes of the NBSS integral

spectra quantified from many different marine and freshwater ecosystems have

ranged between −0.8 and −1.2 (Sprules and Munawar 1986; Gaedke 1992; Kerr

and Dickie 2001) (Figure 1B). However, vertical locations, as indicated by the y-

intercept, may differ widely from ecosystem to ecosystem (Sprules and Munawar

1986; Gaedke 1992; Kerr and Dickie 2001). The level of the y-intercept is thought to be representative of overall productivity of the ecosystem (Sprules and Munawar 1986; Gaedke 1992; Kerr and Dickie 2001). The slope and y-intercept are two of several parameters that are descriptive of community structure in a NBSS analysis.

The major advantage of normalizing biomass size spectra is that the peaks in unnormalized spectra are transformed into parabolic domes, referred to as biomass domes. These biomass domes indicate density adjustments resulting from variations of production and mortality rates within trophic levels and represent "ecological scaling" (Kerr and Dickie 2001). In an unperturbed ecosystem, the horizontal and vertical spacing of the biomass domes, as well as the shape of the domes, should be similar from one trophic level to the next (Figures 2 and 3; Kerr and Dickie 2001). There are three readily estimated parameters that describe location and shape of these domes, that can be obtained by regression techniques (Sprules and Goyke 1994; Sprules and Stockwell 1995; Kerr and Dickie 2001; Duplisea and Castonguay 2006). The y-coordinate of the vertex of the dome is referred to as the peak abundance and is the abundance of the most common size class in the dome. The x-coordinate of the biomass dome vertex is the size at peak abundance and represents the most common size class in the dome. The curvature of the biomass dome describes the breadth of the dome. The slope and intercept of the integral spectrum as well as the curvature, size at peak abundance, and peak abundance of the biomass

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domes provide a suite of parameters that describe community structure, exhibit predictable relationships with one another, and may provide important information about the energy flow through an ecosystem. These attributes may vary both intra- and inter-annually for a given ecosystem (Rodriguez et al. 1987; Boudreau and Dickie 1992; Gaedke 1992; Duplisea and Kerr 1995) (Figure 2) depending on ecosystem responses to environmental variability. Observation and quantification of changes or variability in NBSS parameters through time can provide insight into the nature and magnitude of the variability within and between trophic levels of an ecosystem under fluctuating environmental conditions (Boudreau and Dickie 1992). In effect, variability in the biomass domes may indicate shifts in species, sizes, and community structure that can be quantified and further investigated.

Size spectrum theory is based upon several of the same fundamental concepts as metabolic theory (Brown et al. 2004). However, the two theories differ in some key functional concepts as well as in the ecological characteristics the theories attempt to describe. Both theories begin by acknowledging the observed relationships between body size and metabolism, but size spectrum theory focuses on explaining the size distribution of organisms in aquatic ecosystems while the goal of metabolic theory is to explain a variety of individual, population, community, and ecosystem processes in aquatic and terrestrial ecosystems based on processes related to body size and temperature. Given the strongly size-structured nature of trophic interactions in aquatic ecosystems,

predator-prey size ratios, predation rates, and predator production efficiency are explicitly included in size spectrum theory (Kerr and Dickie 2001). Predator-prey interactions are not explicitly included in metabolic theory, which emphasizes the relationships between body size and metabolism as influenced by kinetic energy and temperature (Brown et al. 2004). The two theories similarly predict that the slope of the relationship between body size and abundance across trophic levels in aquatic ecosystems is −1 (Kerr and Dickie 2001; Cohen et al. 2003; Brown et al. 2004). However, ecological scaling in NBSS that reveals the biomass domes observed in many aquatic ecosystems is not explained by any aspect of the metabolic theory framework.

Other approaches, for example ecosystem network analyses, have been taken to evaluate and compare ecosystems (Baird et al. 2009). However, NBSS analyses have advantages in terms of data requirements. Ecosystem network analyses trace energy flow through ecosystems via trophic interaction between different compartments within the ecosystem (Fath et al. 2007). The compartments may be highly aggregated into trophic levels (primary producers, consumers, decomposers) or disaggregated into individual species (Fath et al. 2007). Results of network ecosystem models are limited by the accuracy and precision of the data used in its development (Ulanowicz and Baird 1999; Fath et al. 2007). In contrast, the underlying basis of NBSS models is that large organisms eat smaller organisms in aquatic ecosystems, and, with the exception of reproduction, the flow of energy is from smaller to larger organisms (Kerr and

Dickie 2001). As a result, only estimates of body size and abundance are required for NBSS analyses. These kinds of data are routinely collected by monitoring surveys, and can be used to evaluate seasonal and annual variability of ecosystem structure.

NBSS parameters and other metrics based on size and abundance have been used to quantify perturbations, especially the effects of fishing, on fish communities in large marine ecosystems (Bianchi et al. 2000; Duplisea and Castonguay 2006; Yemane et al. 2008; Blanchard et al. 2010; Bundy et al. 2010). Based on the theoretical predictions noted earlier, the slope of the integral spectrum of an unperturbed ecosystem is −1 (Kerr and Dickie 2001). Using data from long-term, fisheries-independent monitoring surveys, the slope of the integral spectrum has been demonstrated to steepen (more negative) with increasing fishing pressure and selective removal of the largest size classes (Figure 3; Rice and Gislason 1996; Bianchi et al. 2000; Jennings et al. 2002; Daan et al. 2005; Yemane et al. 2008). Duplisea and Castonguay (2006) reported that the biomass dome parameters also were sensitive to effects of fishing. The biomass domes in six heavily fished North Atlantic ecosystems exhibited trends indicating a shift toward smaller sizes and reduced abundance accompanied by reduced peak abundance, reduced size at peak abundance, and narrower biomass domes (Figure 3; Duplisea and Castonguay 2006).

In addition to using NBSS parameters, other metrics based on size and abundance, such as mean size of fish in survey catches and mean abundance or biomass per tow, have been proposed and successfully evaluated as indicators of community status (Rochet and Trenkel 2003; Trenkel and Rochet 2003; Blanchard et al. 2010; Bundy et al. 2010; Shin et al. 2010). However, the monitoring data used in reported findings in NBSS and other size-abundance approaches to describe structure of fish communities have been representative of fish communities analyzed over large spatial scales and multiple decades. Piet and Jennings (2005) assessed the status of North Sea fish communities using several size and abundance metrics, including mean length, mean biomass, and the slope of the integral spectrum from data collected in two fisheries-independent monitoring surveys that spanned 17 and 22 years. They found that the power of the surveys to detect changes in the North Sea fish communities was low at temporal scales < 5 - 10 years and spatial scales < 30 - 70 ICES rectangles (30 rectangles are approximately equal to 102,600 km^2) due, in part, to the migratory nature of fish populations in the North Sea and the time required to sample the survey area each year (Piet and Jennings 2005). Therefore, Piet and Jennings (2005) recommended caution when using size-based indicators at short temporal scales and small spatial scales until more is known about the behavior of the indicators at these scales.

In the first reported BSS analysis of fishes in Chesapeake Bay, Jung and Houde (2005) analyzed spectra from the mainstem Bay based on midwater trawl

collections of primarily juvenile fishes from 1995-2000. They identified two peaks

in biomass for fishes in the pelagic and bentho-pelagic communities in each

region (upper, middle, lower) of the Chesapeake Bay. One corresponded to

small, planktivorous fishes and one corresponded to larger, piscivorous and

benthivorous fishes. The mean slope of the baywide, annual NBSS for the

pelagic species was –1.05 (Jung and Houde 2005), an average value close to

theoretical expectation, but the slope and intercept of the integral spectra varied

seasonally and annually in relation to environmental conditions and the

abundance of dominant species.

Combining NBSS and multivariate techniques

Because no species-level information is included in NBSS analyses,

additional analyses may be necessary to quantify or recognize changes in the

species composition of the aquatic community. From the point of view of size-

spectrum theory, all 2 g fish, for example, are equivalent and occupy the exact

same ecological niche. Theoretically, the species composition of an entire

aquatic community could change completely without affecting the NBSS and

without compromising the transfer of energy through the ecosystem. However,

we know that species richness and species composition clearly have important

effects on the productivity and stability of communities (Tilman 1996, 1999;

Naeem and Li 1997; Tilman et al. 1997; Lehman and Tilman 2000; Worm and

Duffy 2003). Furthermore, the sociological and economic values of harvested

fish and invertebrate species vary widely. Therefore, adopting a method to track

changes in species composition is desirable. One solution is to apply

multivariate ordination of the abundance of age or size classes of represented

species through time, which provides information on changes and trends in

species composition and size/age structure of the community. Multivariate

ordination approaches, i.e., principal components analysis (PCA), can 1)

quantitatively describe relative changes in time or space of the abundance or

size distribution of species included in the analysis, 2) quantify the primary axes

of variability of those species in the PCA, and 3) simplify the display of

community-structure information. In this manner, multivariate analyses served to

link changes in NBSS parameters, or the lack thereof, to changes in species

composition.

Dissertation overview

Two hypotheses were evaluated in my research: 1) Indicators of changes

and trends in estuarine fish and plankton communities at short temporal scales

and small spatial scales can be derived from NBSS parameters and other

metrics based on size and abundance; and 2) Combining multivariate and NBSS

analyses provides a complementary link that explains and quantifies the temporal

and spatial variability in biodiversity with respect to the size distribution of

estuarine fish communities.

The Chesapeake and Pamlico systems represent timely test cases for

evaluating NBSS as potential indicators of fish community structure for two

reasons. First, management agencies are currently working on fisheries

ecosystem-based management plans, particularly in the CB (Chesapeake Bay

Fisheries Ecosystem Advisory Panel 2006), and require ecosystem-level

indicators to help judge effectiveness of such plans (Lipcius and Latour 2006).

Secondly, there are several independent, long-term datasets available in the CB

and PS ecosystems that provide seasonal information on abundance and sizes

of organisms expected to be represented in each of the biomass domes. The

Virginia Institute of Marine Science and the North Carolina Department of Marine

Fisheries have conducted fish abundance monitoring surveys for several

decades in the Virginia portions of the CB and in the PS, respectively (Moore

2000; VIMS 2011). Monitoring by the Chesapeake Bay Program has collected

data on nutrients, phytoplankton, and zooplankton several times per year from

fixed locations throughout the CB since 1984 (CBP 2000), and these data were

used to identify potential causes of the variability observed in the CB fish

community.

This dissertation consists of six chapters that address three objectives:

1) To describe and quantify the size distribution and community composition of

fish and plankton in CB at temporal scales ranging from months to over a decade

and at spatial scales ranging from 18 km to > 100 km.

2) To evaluate and explain causes of long-term trends in abundance, size

distribution, and species composition of fish communities in CB and PS.

3) To analyze environmental variables and their effects on community structure and size distribution of biological communities in CB and PS.

Chapter 2. *How does fish community structure vary at small spatial scales in an estuarine transition zone?*

Fish communities in the upper Chesapeake Bay, in the vicinity of the salt front and Estuarine Turbidity Maximum, are analyzed. The chapter focuses on the seasonal and annual variability in composition and size structure of the fish community on a small spatial scale (18 - 50 km) at seasonal and annual time scales by analyzing three years of data that are highly spatially resolved. The inherent spatial and seasonal variability in the environment of the Chesapeake estuarine transition zone and apparent variable production of fish presented an opportunity to evaluate the efficacy of NBSS when combined with PCA to describe and discriminate fish communities at finer temporal and spatial scales.

Chapter 3. *Structure and Variability of Fish and Plankton Communities in Two Chesapeake Bay Tributaries*

A comparison of biological communities in an Eastern Shore and a Western Shore tributary of Chesapeake Bay was undertaken. My objective was to evaluate size-spectrum parameters with respect to temporal variability in the fish, zooplankton, and phytoplankton communities of two subestuaries of

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Chesapeake Bay at a spatial scale of approximately 50 km using data from the Choptank and Patuxent Rivers. PCA of the species composition of the fish community was used in conjunction with NBSS analyses to determine if changes in species composition accompanied observed seasonal and annual variability of size-spectrum parameters in 2002-2004.

Chapter 4. Decadal-scale variability in size structure and species composition of fish and zooplankton communities in the lower Chesapeake Bay and its tributaries

NBSS parameters, mean abundance, mean biomass, and mean size were estimated for the fish and zooplankton communities of the lower Chesapeake Bay and its tributaries using fisheries-independent monitoring data collected from 1991 to 2003 by the Virginia Institute of Marine Sciences and zooplankton data collected by the Chesapeake Bay Program from 1991 to 2001 (CBP 2007). PCA of abundance data on ecologically and economically important fish species was used to track temporal and spatial changes in species composition of the fish communities in relation to observed patterns in the size and abundance metrics. My objective was to compare community composition and size structure of fish and zooplankton communities at spatial scales of 50 – 100 km in the lower CB and its tributaries at seasonal, annual, and decadal time scales to evaluate the utility of NBSS parameters as indicators of ecosystem status for the mainstem Bay and three tributaries using long-term monitoring data.

Chapter 5. *Decadal-scale variability in the species composition and size structure of fish and crustacean communities in Pamlico Sound and its tributaries*

In Pamlico Sound, North Carolina and its tributaries, NBSS parameters, mean abundance, mean biomass, and mean size of the fish and crustacean communities were estimated using fisheries-independent monitoring data collected from 1992 to 2003 by the North Carolina Department of Marine Fisheries (Moore 2000). PCA of abundance data for ecologically and economically important species was applied to track the temporal changes in species composition in relation to observed patterns in the size and abundance metrics. Long-term fish community monitoring data from PS and its tributaries were analyzed to determine if observed patterns resembled those observed in Chesapeake Bay (Chapter 4), and to evaluate the utility of size-based indicators and ordination methods in the PS, which is subject to a different suite of natural and anthropogenic stresses, including frequent hurricanes and associated environmental perturbations,

Chapter 6. *Synthesis and Conclusions*

The primary results from the previous four chapters are summarized and integrated to address the two hypotheses presented in Chapter 1. Advantages and disadvantages of NBSS parameters and size and abundance metrics are discussed, and their potential utility in an ecosystem-based management

framework are considered. Suggestions are made to improve the plankton

NBSS performance and topics for future research are noted.

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Chesapeake Bay Estuarine Transition Zone

2001-2003, < 50km

Seasonal & annual variability of fish community

Choptank & Patuxent Rivers

2002-2004, ~ 50 km

Seasonal and annual variability of

phyto, zoop, ichthyo, and fish communities

Lower Chesapeake Bay & tributaries

1991-2003, 50-100 km

Seasonal, annual, decadal-scale variability

of zooplankton and fish communities

Pamlico Sound & tributaries

1992-2003, 50-100 km

Seasonal, annual, decadal-scale variability

of fish communities

Figure 1. Study locations, temporal scales, and spatial scales of dissertation analyses.

Figure 2. (A) Hypothetical biomass size spectrum. (B) Hypothetical normalized biomass size spectrum (NBSS) resulting from the normalization of (A). The integral spectrum in (B) is based on a linear regression through the data. The biomass domes of the normalized spectrum (B) are fit by quadratic regressions through the data of each trophic level.

Figure 3. Hypothetical NBSS from phytoplankton to fish. The integral spectrum (red line) shows the linear decrease in abundance with size. The biomass domes (black parabolas) correspond to peaks in abundance associated with each trophic level, i.e. phytoplankton, zooplankton, and fish. The theoretical slope of the integral spectrum is −1 in an unperturbed ecosystem (left), and the biomass domes are equally spaced and similarly shaped. The slope of the integral spectrum in a perturbed ecosystem (right) is steeper, and the parameters of the biomass domes are no longer similar. Peak abundance has decreased, size at peak abundance has decreased, and biomass dome curvature has become narrower for the fish community under heavy exploitation. Phytoplankton have become more abundant (higher peak abundance) due to eutrophication.

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CHAPTER 2

How does fish community structure vary at small spatial scales in an

estuarine transition zone?

Abstract

The Chesapeake Bay estuarine transition zone (ETZ) is an important

spawning, nursery, and feeding area for numerous ecologically and economically

important migratory and resident fishes. A strong and interannually variable

gradient in salinity in this ~50-km zone was hypothesized to exercise control over

community structure of fishes in the ETZ. The inherent spatial and seasonal

variability in the environment of the Chesapeake ETZ and variable production of

fish provided an opportunity to evaluate the efficacy of Normalized Biomass Size

Spectra (NBSS), when combined with traditional principal components analysis

(PCA), to describe and discriminate fish communities at fine temporal and spatial

scales. NBSS models were developed to depict the pattern of abundance of

fishes with increasing body size and to quantify the complex size structure of fish

communities. NBSS rarely has been applied or evaluated at short temporal

scales and small spatial scales. The fish community in the ETZ was sampled

with a midwater trawl in May, July, and October of 2001-2003. The PCA was

conducted to highlight effects of variability in species composition on size

structure of the fish community. The PCA results indicated that recruitment

strength of young-of-the-year (YOY) anadromous fishes drove variability in

species composition, based on the consistently high loading of these species on the first principal component. Fluctuations in abundance of the estuarine bay anchovy and young-of-the-year (YOY) anadromous fishes strongly influenced parameters of the NBSS integral spectra, biomass domes, and biomass subdomes. Effects of recruitment variability in YOY anadromous species remained detectable in the NBSS of following years. NBSS and PCA captured and explained ecologically relevant variability in size structure and species composition of the fish community at the spatial scale of the ETZ, but not for smaller segments within the ETZ.

Introduction

The Chesapeake Bay, like many estuaries, serves as a nursery, feeding, and spawning ground for migratory and resident species. Accordingly, its fish community exhibits substantial temporal and spatial variability in terms of species composition and size structure. Describing the variability and interpreting its relationships to fluctuations in recruitment of key species or to environmental variability associated with shifts in fish distribution and productivity are important needs to support evolving ecosystem-based fisheries management.

Biomass size spectra (BSS) depict the relationship between distribution of biomass and body sizes of constituent taxa. BSS can be analyzed to quantify and describe variability in size distribution, sources of variability, and relationships to environmental factors in fish communities. Developments in size

spectrum theory have been validated by empirical observations from both freshwater and marine ecosystems of varying productivity and taxonomic composition (Sheldon et al. 1972, 1973; Sprules and Munawar 1986; Sprules et al. 1991; Boudreau and Dickie 1992; Sprules and Goyke 1994; Sprules and Stockwell 1995). Evaluation of spectra for fish (Jung and Houde 2005) and zooplankton communities (Kimmel et al. 2006) in Chesapeake Bay on a baywide scale has been conducted. Notable similarities and consistencies of biomass size spectra from different aquatic ecosystems and the strong correspondence between theory and empirical observations suggest that biomass size spectra may be effective tools for quantifying and comparing the state of ecosystems (Pope and Knights 1982; Pope et al. 1988; Rice and Gislason 1996; Gislason and Rice 1998; Bianchi et al. 2000; Kerr and Dickie 2001).

A normalized or integral biomass size spectrum (NBSS) relates abundance of organisms to size. The slope and intercept of the integral NBSS describe the linear relationship between $\log_2$ transformed size and abundance and provide information on productivity and effects of perturbations on the size structure of organisms within an ecosystem (Figure 1). Comparisons of marine and freshwater ecosystems have demonstrated that ecosystems with higher productivity tend to have higher NBSS intercepts (Sprules and Munawar 1986; Boudreau and Dickie 1992; Bianchi et al. 2002). In addition, effects of perturbations, for example fishing, on fish communities often result in a steepening of the slope (more negative) with increasing fishing pressure that

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selectively depletes larger individuals from stocks (Rice and Gislason 1996; Bianchi et al. 2000; Jennings et al. 2002; Daan et al. 2005; Duplisea and Castonguay 2006). The intercept of the integral spectrum in observed (Rice and Gislason 1996; Bianchi et al 2000; Jennings et al. 2002; Nicholson and Jennings 2004) and modeled ecosystems (Gislason and Rice 1998; Pope et al. 2006) has been found to increase with fishing intensity, which can reflect increased abundance of smaller size classes as well as the correlation between the slope and intercept estimates. In an attempt to reduce the correlation between slope and intercept, Daan et al. (2005) centered the x-axis of the normalized size spectrum by rescaling the x-axis so that the mean of the size range was set at 0 for the North Sea Fish community and found that the height (intercept of the centered size spectrum) declined through time as the slope became steeper, indicating reduced productivity of the fish community.

Quantifying variability of NBSS attributes, which may vary both seasonally and annually (Rodriguez et al. 1987; Boudreau and Dickie 1992; Gaedke 1992; Duplisea and Kerr 1995; Jung and Houde 2005; Kimmel et al. 2006), may provide insight into the response of an ecosystem under fluctuating environmental conditions (Boudreau and Dickie 1992; Bianchi et al. 2000; Duplisea and Castonguay 2006). NBSS may exhibit parabolic deviations from the linear regression of abundance on size, which correspond to peaks in abundance of represented trophic levels (phytoplankton, zooplankton, fish) and are referred to as "biomass domes" (Figure 1; Boudreau and Dickie 1992;

Sprules and Goyke 1994; Kerr and Dickie 2001; Duplisea and Castonguay 2006)). Variability in production and mortality rates within each trophic level may result in biomass domes that are indicative of "ecological scaling" (Kerr and Dickie 2001). Parabolic deviations within the biomass domes themselves, referred to as "biomass subdomes" have also been observed and may represent structure induced by predation within each trophic level (Figure 1; Boudreau and Dickie 1992; Sprules and Goyke 1994; Kerr and Dickie 2001). Regression techniques can quantify the location and shape of biomass domes and subdomes (Sprules and Goyke 1994; Sprules and Stockwell 1995; Kerr and Dickie 2001; Duplisea and Castonguay 2006) whose location and shape provide a suite of parameters that are informative about size structure of the aquatic community and probable predator-prey relationships.

The properties and variability of NBSS parameters have not been well evaluated at temporal and spatial scales relevant to estuarine fish communities. Piet and Jennings (2005) found that the statistical power of indicators derived from size spectra for detection of trends in the North Sea fish communities was higher for temporal scales > 5-10 years and spatial scales > 30-70 ICES rectangles (one rectangle = 0.5 degree latitude x 1.0 degree longitude, 30 rectangles = approximately 265800 km^2). They recommended caution when using size-based indicators at short temporal and small spatial scales until more is known about behavior of size spectra at these scales. However, initial analyses of NBSS parameters for estuarine communities suggest that NBSS

theory is applicable and informative at estuarine spatial and temporal scales. For example, in one of the first applications of size spectrum theory in estuaries, Jung and Houde (2005) analyzed the NBSS for the fish community from 1995-2000 in the mainstem Chesapeake Bay (approximately 11,400 km^2) based on midwater-trawl collections. Their NBSS for bay-wide and within-bay regions depicted two biomass subdomes, one corresponding to small, planktivorous fishes and one corresponding to larger, piscivorous and benthivorous fishes. The mean slope of the annual normalized biomass size spectra, based only on pelagic species, was –1.05 (Jung and Houde 2005), which is in accord with size spectrum theory that predicts a slope of -1.

Because all taxa of similar size are categorized as ecologically and metabolically equivalent in NBSS, the species composition of a community in theory could change completely without affecting its NBSS parameters if the size distribution remained constant. Accordingly, an analysis of the temporal and spatial variability of the species composition of a community is required to fully evaluate and understand the ecological consequences of changes in the NBSS parameters. Principal components analysis (PCA), or other multivariate ordination techniques, can effectively quantify changes in abundance of taxa through time and space, depict the primary axes of variability of the data, and display this information. Combining NBSS and multivariate analyses, as conducted herein, provides a more complete portrayal of variability of the size distribution and its relationship to species composition of the community.

Within the upper portion of Chesapeake Bay, the estuarine transition zone (ETZ) (Figure 2) is an important spawning area for many anadromous and semi-anadromous fishes as well as a nursery for larval and juvenile anadromous, resident, and coastal-spawning fishes (Dovel 1971; North and Houde 2001, 2003; Jung and Houde 2005; Martino and Houde 2010). The estuarine turbidity maximum (ETM) and the salt front are prominent physical features of the ETZ in Chesapeake Bay and other coastal plain estuaries that exercise control over the spatial distribution of ichthyoplankton and their zooplankton prey (Boynton et al. 1997; North and Houde 2001, 2003; Roman et al. 2001). Concentrations of zooplankton and ichthyoplankton in the ETM, especially striped bass and white perch, are positively related to freshwater flow and interannual variability in freshwater flow strongly affects recruitment dynamics in the fish community (North and Houde 2001, 2003; Martino and Houde 2010). This effect is attributable to increased temporal and spatial overlap between larval striped bass and white perch and their zooplankton prey in the ETM during high flow years (North and Houde 2003, 2006; Martino and Houde 2010).

The information available on recruitment processes and observed sensitivity of the fish community in the upper Chesapeake Bay ETZ to variable environmental conditions provided an opportunity to evaluate the utility of NBSS analyses to describe and serve as indicators of responses of fish communities in estuarine ecosystems. The objectives of the present study were: 1) to evaluate the variability of size structure and species composition of an estuarine fish

community at small spatial scales (<50 km) and short temporal scales

(seasonally and annually) using NBSS and PCA, and 2) to examine and explain

how variability in species composition relates to size structure of the fish

community in the upper Chesapeake Bay.

Methods

Data collection

Eight research cruises were conducted in the upper Chesapeake Bay.

Individual cruises were conducted on the 50-ft RV *Orion*, *the* 68-ft R/V *Aquarius*,

and the 120-ft RV *Cape Henlopen*, in May, July, and October 2001-2003 as part

of the NSF-sponsored BITMAX project (Figure 2). The monthly freshwater flow

regime, which was variable during the study period, was documented from data

compiled by the United States Geological Survey (USGS 2011; Table 1). The

ETM and its hydrography were defined and mapped in an initial CTD survey

conducted on the first day of each cruise. Trawl sampling of juvenile and adult

fishes began after the location of the ETM and salt front were established. Table

2 provides summarizes of the number of stations sampled with a midwater trawl

and accompanying hydrographic data for each cruise.

A CTD cast was made prior to biological sampling at each station. Due to

the drafts of the research vessels, sampling was limited to sites > 4 m deep. A

midwater trawl was used to sample juvenile and adult fishes. The trawl had a

square mouth opening, 6-m on each side when fully stretched, and 3-mm cod

end mesh. The trawl was fished obliquely in steps from surface to bottom in 20-min tows, with the water column divided into 10 depth increments, each sampled for 2 min. On deck, fish were sorted by species, enumerated, and an aggregate weight of each species was obtained. Total lengths (mm) of up to 30 individuals of each species in a trawl tow were measured and recorded, from which length-frequency distributions were obtained.

Data analyses

Principal components analysis (PCA) was applied to describe and evaluate spatial variability of the fish communities and their size structure. Based on modes in the length-frequency distributions, individuals of each species were placed in 1 to 3 size classes that spanned the size range for that species (Table 3). The size classes used in this analysis successfully separated age classes, typically distinguishing between YOY and age 1+ fishes. However, YOY striped bass (*Morone saxatilis*) and Atlantic menhaden (*Brevoortia tyrannus*) could occupy multiple size classes (small and medium) during a single year. The purpose of assigning species to multiple size classes was to evaluate the extent of size-specific spatial segregation of a cohort. The first PCA was run on the data from all eight cruises. Seasonal PCAs were conducted for data collected during May, July, and October. Species and size classes were included in a PCA if the frequency of occurrence of species/sizes in tows was ≥10%. The observations in these analyses were abundance in size classes of each species at each station. The observations in the PCA biplots were labeled with the river

kilometer of station and the salinity and turbidity measured at the station to identify patterns in the spatial variability of the fish community. All PCAs were conducted using the correlation matrix of the data in S-Plus 2000 (MathSoft 1999).

The NBSS for the ETZ fish community were examined for each cruise. The abundances of each species at each station were binned into $\log_2$ weight classes (g wet wt), and the mean abundance (number m^{-3}) by size class estimated based on all stations sampled. Because size classes at the extremes of the size spectrum have strong statistical leverage that can disproportionately affect model fits and may be poorly sampled by the gear, the size data were censored using the coefficient of variation (CV) of abundance to include only the most consistently collected size classes. The CV was calculated by size class based on the pooled data from all cruises. The CV profile was U-shaped with most of the CV of most of the size classes varying around 200% and size classes at the extremes having much higher CVs. Only size classes with a CV < 500% (fish weighing 0.09 to 724 g) were retained for NBSS analyses because the increase in the CV of size classes outside the selected range indicated they were not consistently retained by the midwater trawl.

Following Kerr and Dickie (2001), the primary, or physiological, scaling of abundance with body size in the NBSS integral spectrum for each season was parameterized using linear regression to estimate the slopes and y-axis

intercepts. The biomass domes and subdomes, which were presumed to be

symmetrical and represent ecological scaling, were modeled and parameterized

using quadratic regression:

$$y = 0.5c(x-h)^2 + k$$

where y = $\log_2$(number/m^3)
x = $\log_2$ size classes (g wet weight)
c = curvature of the biomass dome or subdome
h = size at peak abundance, i.e. the x-coordinate of the parabola
vertex
k = peak abundance, i.e. the y-coordinate of the parabola vertex

The h parameter represents the most common size class in a dome or sub-dome

of a size spectrum while the k parameter is the estimated abundance of the most

common size class in a dome or sub-dome of a NBSS (Duplisea and

Castonguay 2006). The curvature parameter c is a complex metric related to

gross production efficiency of a trophic level, predation mortality of prey

organisms, and the predator-prey size ratio (Thiebaux and Dickie 1993). In

explaining curvature, Thiebaux and Dickie (1993) stated that curvature of a

biomass dome or subdome is an index of food supply available to a trophic level,

and Sprules and Goyke (1994) noted that broader curvature indicated greater

ecosystem productivity.

The particular locations of the biomass subdomes were defined by the

presence of parabolic patterns in the residuals from the fitting of the integral

spectrum and biomass domes for the NBSS data from each cruise. Two or more

consecutive data points were required to define the local minimum where two

biomass subdomes meet (see Figure 1). For a given pair of biomass subdomes,

quadratic regressions were run for all combinations of potential locations for a local minimum. The pair of quadratic regression with the lowest mean Akaike's Information Criterion (AIC) and highest mean coefficient of determination (r^2) were retained as the regressions that defined a parir of subdomes.

Additionally, the NBSS of the fish community in the ETZ region were analyzed at smaller spatial scales to determine if size structure within the ETZ exhibited spatial variability. The ETZ sampling area was divided into three 18-km segments that were sampled with approximately equal trawling effort (Figure 2). The ETM and salt front were located in the middle segment during most cruises. The ETZ was delineated by km, rather than by salinity, because the ETM and salt front exhibited 5-10 km excursions during a tidal cycle, and there was substantial seasonal and annual variability in the salinity gradient and range (Table 2). Mean abundance, mean biomass, and mean size of fishes were estimated for each segment in each year for July and October. The estimates of mean abundance, biomass, and size were log_{10} -transformed, and quantile-quantile plots (Q-Q plots) were used to confirm the normality of the transformed estimates before analyzing with analysis of variance (ANOVA) with year, month, and segment as factors. The data from May 2001 and 2002 were not included in these analyses because the absence of data from May 2003 (Table 2) resulted in multiple interactions that inhibited interpretation of the results. The analysis comparing the size spectrum parameters among the three 18-km segments of the upper Bay ETZ was conducted on data from the October cruises because

quadratic regressions for the biomass dome and subdome from May and July cruises often were not significant or produced nonsensical parameter estimates.

The slopes and intercepts of the NBSS integral spectrum for each cruise were tested for differences among years and seasons by pairwise comparisons of the 90% confidence intervals that were estimated by bootstrapping (Manly 1991). Confidence intervals for each pairwise comparison of slope and intercept of the integral spectrum for each cruise were estimated by randomly selecting with replacement the stations sampled during each cruise and estimating the slope and intercept based on data from the randomly selected set of stations. This process was repeated 2000 times and the 5th percentile and 95th percentile values were used to derive the 90% confidence interval. A separate randomization was performed for each pairwise comparison (Manly 1991; Sprules and Goyke 1994). Based on the quadratic regressions, the curvature, peak abundance, and size at peak abundance of the biomass domes and subdomes were estimated and then compared across seasons and years applying the bootstrapping procedure described above. The same procedure also was used to compare biomass domes and subdomes from NBSS for the three 18-km segments within each year and for each segment across years.

Results

A total of 172 stations were sampled from May 2001 to October 2003, and 301,813 fish weighing a total of 1002.8 kg and representing 36 species were

collected. Total length ranged from 18 mm to 780 mm, and the weights of individual fish ranged from 0.04 to 7,000 g. Bay anchovy (*Anchoa mitchilli*) dominated the catches numerically and represented 77.3% of the catch in numbers. Blueback herring (*Alosa aestivalis*) was the second most abundant species and accounted for 14.3% of the catch in numbers. White perch (*Morone americana*) dominated the catch in terms of biomass, and represented 47.2% of the total biomass caught. Bay anchovy was the second most abundant species in terms of biomass and accounted for 18.2% of the total biomass collected. Other important species in terms of abundance or biomass were Atlantic menhaden, striped bass, and Atlantic croaker (*Micropogonias undulatus*).

The species composition and size distribution of the Chesapeake ETZ fish community varied seasonally and annually. The seasonal variability in the species composition and size distribution reflected the life history patterns of the species that use the Chesapeake ETZ as a spawning for anadromous species and nursery ground for anadromous, coastal spawning, and resident species. The interannual variability in species composition and size distribution resulted primarily from the varying reproductive success of the aforementioned species groups each year. Variability in the abundance of the anadromous species drove the interannual patterns observed in the PCAs while variability in the abundance of bay anchovy and anadromous species were responsible for the seasonal and interannual patterns observed the size distributions.

Fish community analyses

Patterns were detected in the combined and seasonal PCAs. Scree plots of the eigenvalues from each PCA (Figure S1) depicted 4-7 principal components with eigenvalues greater than one, which indicates that the PC captures as much variance as a single standardized variable (Kaiser 1960). However, the slopes of the scree plots for PCs beyond PC1 and PC2 tended to change, which indicated that PC1 and PC2 captured the dominant axes of variability (Johnson 1998). Furthermore, examination of additional PCs did not provide any additional insights into patterns of temporal or spatial variability. Loadings for the PCs with eigenvalues > 1 are listed in Tables S1-S4. Several taxa consistently clustered in all PCAs. Small (young-of-the-year, YOY) size classes of the anadromous moronids and alosines were often strongly correlated and loaded highly on PC1 (Figures 3-6), indicating that variability in their abundances, termed the "YOY anadromous group," was the primary source of variability in the fish community of the Chesapeake Bay ETZ.

The abundance of anadromous fishes tended to be negatively correlated with, or independent of, the abundance of a "forage fish group" consisting of bay anchovy and Atlantic menhaden (Figures 3-6). Lastly, a "benthic group" consisting of American eel (*Anguilla rostrata*), hogchoker (*Trinectes maculatus*), and channel catfish (*Ictalurus punctatus*) was frequently collected at the same stations, which usually had the lowest salinities (Figures 3-6).

The full range of size classes of individual species generally clustered together, with notable exceptions of striped bass and Atlantic menhaden). In those species, the medium and large size classes in the PCA biplots often were separated from the small size class, indicating different habitat preferences. Based on visual inspection of the PCA biplots with the observations labeled with station salinity, turbidity, and river kilometer, the only apparent spatial patterns were related to salinity. There were no consistent patterns related to turbidity or river kilometer.

Considering all eight cruises, seasonal variability in species composition of the fish community was the most obvious pattern in the PCA (Figure 3), providing a clearer signal than interannual differences. Taxa contributing substantially to variability in the species composition and size structure were the YOY anadromous group, which loaded strongly on the negative side of PC1, and large bay anchovy and large Atlantic menhaden (forage fish group), which loaded positively on PC1. The first PC captured 19.5% of the variability. The negative correlation between YOY anadromous and forage fish groups was driven by the relatively low abundance of YOY anadromous fishes in 2002. The PC2 reflected the seasonal variability in species composition and explained 13.8% of the variability. Medium size Atlantic menhaden and striped bass, large Atlantic croaker (*Micropogonias undulatus*), and the YOY anadromous group occurred most commonly in July (Figure 3) while all sizes of the benthic group, as well as gizzard shad (*Dorosoma cepedianum*), weakfish (*Cynoscion regalis*), and blue

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crab (*Callinectes sapidus*) occurred in October (Figure 3). Large Atlantic

menhaden and bay anchovy also were prevalent in October. The fish community

in May was intermediate between July and October (Figure 3). At this level of

analysis, I detected no clear spatial patterns attributable to salinity or location of

the turbidity maximum in the Chesapeake ETZ.

Species composition and abundances in May of 2001 and 2002 differed

strongly and were negatively correlated (Figure 4). PC1 and PC2 of the May

analysis accounted for 55% of the variance. All sizes of the benthic group and

small and large white perch were negatively correlated with all sizes of the forage

group on PC1 (35.4% of the variance, Figure 4). All sizes of American eel, large

Atlantic menhaden, and large and medium hogchoker were more common in

2001 than in 2002. In 2002, small Atlantic menhaden, large bay anchovy, large

striped bass, and small Atlantic croaker were more common than in 2001. No

trawl collections were available for May 2003 to compare with May catches in

2001 and 2002.

In both July and October, the YOY anadromous group loaded highly on

PC1, which represented 28.2% and 23.3% of the variance, respectively (Figures

5 and 6). The low abundance of recruiting YOY anadromous fishes in July and

October 2002 is evident from the relatively tight clustering of observations in that

year on the negative side of PC1 (Figures 5 and 6). The effect of the strong

recruitment of YOY anadromous fishes in 2003 on the PCA was most obvious in

the October biplot (Figure 6). During July, the YOY anadromous group and the benthic group were more common in 2001 and 2003 and were negatively correlated with the forage fish group, large Atlantic croaker, and large striped bass, which were more common in 2002. In July, small bay anchovy, small weakfish, and bluefish (*Pomatomus saltatrix*) loaded negatively on PC2 (14.5% of the variance) and were negatively correlated with medium striped bass. These four species loaded almost completely on PC2 in July indicating that their abundance was less variable and not correlated with species that had high loadings on PC1. In contrast, during October, Atlantic croaker and the forage fish group loaded on PC2 (13.9% of the variance) and were negatively correlated with large striped bass and gizzard shad (Figure 6). Small weakfish (YOY) loaded highly on PC2 in July and October indicating that their variability in abundance was consistently lower than, and uncorrelated with, the variability in abundance of the YOY anadromous group.

The salinity gradient was a factor controlling representation and distribution of fishes in the Chesapeake Bay ETZ. Its effect, though not always consistent, is apparent in the PCA biplots (Figures 4-6). Salinity appeared to be a controlling factor in May 2002, in all years during July, and in October 2003. When a relationship to salinity was observed, the forage fish group occurred at stations with salinity > 3. Low catches of all fishes occurred at locations where salinity was < 2 in July 2002. The benthic group occurred at salinities < 1 in July 2001 and 2003 and at salinities < 7 in October 2003. The YOY anadromous

group occurred in highest abundance at salinities from 1 to 4 in July of all years.

This group became less cohesive in October 2003 when YOY white perch and

alewife were most abundant at the lowest salinities but YOY blueback herring

and striped bass occurred at salinities between 5 and 7. The relationship

between species composition and salinity in October 2001 was weak, but the

benthic group was found at the lowest salinity stations. There was no clear

pattern between species composition and salinity in October 2002.

Normalized size spectra

Overview of results

Parameters of the integral spectra, biomass domes and subdomes for the

fish community in the Chesapeake Bay ETZ varied seasonally and inter-annually.

The peaks in abundance at weights corresponding to YOY and to age-1+ fish

resulted in well-defined biomass subdomes. The parameters describing the

integral spectra (slopes and intercepts) and biomass domes (curvature and

peaks) were a reflection of the combined variability of the YOY and age-1+ size

groups, while parameters of the biomass subdomes (curvature and peaks)

described seasonal and inter-annual variability contributed by each of these size

groups.

Integral spectrum

Inter-annual variability in slopes and intercepts of the integral spectra was

greater than seasonal variability (Table 4, Figure 7). In 2002, the slopes of the

May integral spectra were positive and in 2001 the May slopes were not significantly different from zero (Figure 7a). Therefore, these results were not included in comparison analyses. The slope in July 2002 was less steep and its intercept lower than in either July 2001 or July 2003 (Figure 7b) because relatively few < 4 g fish, such as bay anchovy and YOY anadromous fish, were represented in July 2002. The slope of the NBSS in July 2003 was steeper and its intercept higher than in July 2001 because of higher abundance of fish < 0.5 g in July 2003, which were primarily YOY bay anchovy and white perch.

Inter-annual variability of the slope and intercept estimates for October followed a different pattern than observed in July. The slope for the October 2003 integral spectrum was less steep than for either October 2001 or 2002 because more relatively large fish weighing 32-256 g, such as American eel, gizzard shad, age 1+ white perch, and age 1+ striped bass, occurred in October 2003 (Figure 7c). Slope estimates for October 2001 and 2002 were similar. The intercept estimate for October 2001 was significantly higher than for October 2002 and 2003 because fish from 0.25 to 1 g size classes were more abundant in 2001. Comparing seasonal patterns within years, there were no significant differences between the slopes or intercepts of the integral spectra for July and October in 2001 and 2002. In July 2003, the slope was significantly steeper and the intercept higher than in October because fish < 0.5 g, primarily bay anchovy, were relatively more abundant in July while fish from 64 - 128 g, such as age 1+ white perch, were relatively more abundant in October.

<u>Biomass domes</u>

Quadratic regression describing the biomass domes explained 12-76% of the variance in the NBSS data (Table 5). Although significant in all cases except one, the dome parameters were not very helpful to explain variability in size structure of the ETZ fish community. The dome parameters in the normalized size spectra varied seasonally and inter-annually (Table 5, Figure 8), primarily responding to the differential recruitment strengths of YOY anadromous fishes in 2002 and 2003. However, the quadratic regression for May 2002 was not significant (Table 5) and the curvature estimate for July 2003 was broad and essentially linear (Figure 8b), resulting in bootstrapped intervals so wide (Table 5) that there was no confidence in the curvature estimate. The biomass subdomes, particularly the first subdome, which was dominated by YOY fishes and bay anchovy, provided a better description of the structure and variability than did the biomass domes.

<u>Biomass subdomes</u>

Biomass subdomes were well defined and their structure was similar among years. Three subdomes were identified in May and two subdomes were present in July and October (Table 6, Figure 9). The subdome parameters varied seasonally and inter-annually. Size at peak abundance for the first biomass subdome increased consistently from July to October as YOY anadromous species and bay anchovy increased in size. Size at peak abundance for the second biomass subdome decreased from July to October in

2001 and 2003, which was likely the result of some larger individuals of YOY

anadromous species growing into the second biomass dome by October. There

was no consistent seasonal progression for peak abundance or the curvature of

the biomass subdomes. There also were no correlations between parameters of

the first subdome (which was dominated by YOY fishes) and parameters of the

second subdome (which primarily consisted of age 1+ fishes) in the following

year.

In the May NBSS, three subdomes were identified. The first biomass

subdome (Figure 9a) was composed of YOY Atlantic menhaden, bay anchovy,

and small hogchokers weighing < 4 g. These species were more abundant in

May 2002 than in 2001. Fish weighing 4 – 16 g were in the second subdome

and included age 1+ alosines, hogchokers, and white perch. The third May

subdome was populated by American eel, age 1+ alosines, age 1+ Atlantic

menhaden, channel catfish, hogchoker, age 1+ striped bass, and age 1+ white

perch, all of which were in the 32 – 724 g size classes. The second subdome in

May 2001 had significantly broader curvature and larger size at peak abundance

than the second biomass subdome in May 2002 (Figure 9a) because small age

1+ white perch were more abundant in 2002. Peak abundances in the second

subdomes for the two years were similar because similar numbers of fish were

collected despite the lower catch of white perch in 2001. The third biomass

subdome parameters were similar in May of the two years, suggesting that this

component of the May size spectrum, which is composed of more than one year

class of fishes, is more stable than components contributing to the first two subdomes.

Two biomass subdomes were evident in the July and October for each year (Figure 9b and 9c). The first subdome spanned the size range occupied by YOY anadromous fishes, such as white perch, striped bass, and alosines, and YOY and age 1+ bay anchovy. The second biomass subdome represented size classes occupied by age 1 and older striped bass, white perch, hogchokers, American eel, channel catfish, white catfish, and weakfish although large YOY alosines and weakfish occasionally were included in the second biomass subdome.

Weak recruitment of YOY anadromous fishes in 2002 and strong recruitment in 2003 notably affected parameters of the first biomass subdome in July and October of those years. High abundances in 2003 were associated with parameters indicating high peak abundance and small size at peak abundance, whereas the low abundance of these species in July and October 2002 produced opposite effects (Table 6; Figures 9b and 9c). Abundance of YOY bay anchovy also influenced the subdome parameters in July and October. In July 2003, YOY bay anchovy contributed to the high peak abundance of the first subdome. Its abundance had declined substantially by October 2003. In contrast, in October 2001, abundance of YOY bay anchovy was the highest in the three years, which supported the high peak abundance of the first subdome (Table 6).

There was no clear or consistent progression of parameter estimates from July to October for the second subdome (Table 6, Figures 9b and 9c). Abundance of age 1+ white perch had the greatest impact on parameters of the second subdome. Peak abundance in the second biomass subdome in July did not differ among years. By October, peak abundance differed substantially among years. It was highest in 2003 and lowest in 2002, primarily because of abundant age 1+ white perch in 2003. Age 1+ white perch also dominated the second biomass dome in July 2003, which resulted in a significantly narrower curvature and higher size at peak abundance than in 2001 or 2002. Other species, for example large YOY Atlantic croaker and Atlantic menhaden, were more abundant in July 2002, contributing to a broad curvature of the second subdome (Table 6). However, by October 2002, croaker and menhaden were absent and the respective second subdome curvatures were similar for October 2001 and 2002.

Spatial analyses

Overview of spatial analysis results

The results of finer scale spatial analyses in the 18-km segments did not provide much additional insight into the variability of the size distribution of the Chesapeake ETZ fish community. Similar to the full ETZ analyses, the dynamics of the biomass subdomes drove much of the variability of the biomass domes. No coherent spatial patterns for subdomes parameters were detected across years. The lack of spatial pattern in the subdome parameters at this scale

resulted from inter-annual variability in the spatial distribution of numerically dominant species in each biomass subdome and was consistent with the lack of consistent spatial patterns in the PCAs.

Effects of dominant taxa on NBSS

Given the lack of apparent spatial patterns in the analyses of the biomass subdome parameters, the $\log_{10}$-transformed abundance of the dominant species from each segment were used to predict the parameters of the biomass subdomes. Bay anchovy was the dominant species in the first biomass subdome. Regression relationships were developed to estimate curvature, size at peak abundance, and peak abundance from each of the ETZ segments. With abundance of bay anchovy as the independent variable, 39.3% of the variance in curvature, 47.6% of the variance in size at peak abundance, and 82.9% of the variance in peak abundance of the first biomass subdome were explained (Table 7). Age 1+ white perch and YOY and Age 1+ Atlantic menhaden were the two most common species in the second biomass subdome and had similar abundances. Their combined abundance explained 91.8% of the variance in the estimated peak abundance in the second biomass subdome across years and segments (Table 7), but did not provide significant regression relationships that could explain size at peak abundance or curvature of the second biomass subdome.

There was a consistent temporal pattern in size at peak abundance for both the first and second subdomes in the three designated ETZ segments. For the first biomass subdome in the upper, middle, and lower 18-km segments, the size at peak abundance was significantly larger in 2003 than in 2002 or 2001, attributable to higher abundance of YOY alosines and moronids in 2003. Size at peak abundance was larger and peak abundance was higher for the second biomass subdome in the middle and lower segments of the ETZ in 2003 than in 2002, attributable to the high abundance of age 1+ white perch in 2003. The most up-estuary segment in 2003 was not included in this analysis because not all bootstrapped regressions for the second biomass subdome in the uppermost segment in 2003 were significant, a consequence of too few sites being sampled.

Abundance, biomass, and mean weight

Based on the July and October data, there were significant temporal and spatial patterns for fish biomass and abundance (Table 8) that reflected the patterns described for the biomass domes and subdomes. Mean biomass differed significantly by year, month, and segment (Table 9). Biomass was significantly lower in 2002 than in 2001 or 2003, lower in July than in October, and lower in the uppermost segment than in the lower segments. For mean abundance, there was a significant effect of year, month, segment, and the interactions between year and month and year and segment (Table 9). Mean abundance was significantly lower in 2002 than in the other two years and lower in July than October. A significant interaction between year and month resulted

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because mean abundances were similar in July and October 2003 but were significantly higher in October than in July in both 2001 and 2002. A significant interaction between year and segment resulted from inconsistent spatial patterns in segment-specific abundances among years.

There were no spatial differences in mean weight (Tables 8 and 9), but the effect of month and the interaction between year and month on mean weight were significant (Table 9). In 2001 and 2002, mean weights were heavier in July than in October. Mean weight in October 2003 was similar to mean weights in July 2001 and 2002 while mean weight in July 2003 was similar to the October mean weights for 2001 and 2002.

Discussion

There were notable seasonal differences and inter-annual variability in the species composition and abundance of fishes in the estuarine transition zone (ETZ) of Chesapeake Bay that primarily were driven by variable and contrasting recruitment success of YOY anadromous fishes, bay anchovy, and Atlantic menhaden. Recruitment variability apparently was influenced by the differing freshwater flow regimes attributable to Susquehanna River discharges in 2001 - 2003 (Martino and Houde 2010). Here, I have demonstrated that these conditions affected species composition and size distribution of the fish community in the ETZ of upper Chesapeake Bay. The PCA results and NBSS parameters quantitatively described changes in assemblage structure and size

distributions that accompanied the seasonal and inter-annual variability in species composition.

The distinct seasonal and inter-annual differences in species composition of fishes in the Chesapeake Bay ETZ was revealed by the PCA of data from all cruises. The abundance of YOY moronids and alosines was an important source of variability as demonstrated by the high loadings of these species on PC1. The seasonal variations in species composition and size groups was captured by PC2, which suggested that the seasonal differences were less variable than, and uncorrelated with, abundance of the YOY moronids and alosines. Seasonal variability was driven by spawning periods, life histories, and species-specific behaviors, including in particular spawning migrations of adult moronids and alosines to the upper Bay, and the subsequent utilization of the Chesapeake ETZ as a nursery ground by YOY moronids and alosines. YOY of numerous other species also utilized the ETZ as a nursery, e.g., Atlantic croaker, Atlantic menhaden, and bay anchovy.

The high loadings of YOY anadromous fishes on the first PC for July, October, and annual PCAs indicated the strength of contributions made by these species to variability in the Chesapeake Bay ETZ fish community. Effects of the forage fishes, bay anchovy and Atlantic menhaden, abundance were less consistent because these two species loaded highly on PC1 in July but had low to intermediate loadings on PC2 in October. The relationship between the YOY

anadromous species and the forage fish group observed in the July PCA and their contributions to variability in species composition of the fish community were similar to effects on multi-decadal patterns of recruitment variability observed by Wood and Austin (2009). Wood and Austin (2009) analyzed multi-decadal summer (July through September) YOY abundance data for species collected consistently by four fisheries-independent juvenile finfish monitoring surveys from the Maryland and Virginia portions of Chesapeake Bay and its tributaries. Using PCA, they found that recruitment levels of YOY anadromous species and YOY coastal spawning species, including Atlantic menhaden, were strongly and negatively correlated on PC1 (Wood and Austin 2009). Given the difference in life histories and spawning locations of anadromous and coastal spawning species, Wood and Austin (2009) concluded that variability in winter-spring synoptic-scale climate patterns that affect freshwater flow variability (Austin 2002; Kimmel et al. 2006, 2009; Miller et al. 2006; Miller and Harding 2007) was the likely driving force behind differential recruitment success in these two fish groups.

While variability of YOY anadromous species had a dominating influence on species composition of the Chesapeake ETZ fish community, the abundance of bay anchovy shaped the size distribution. The effect of bay anchovy on the NBSS parameters was most evident in the small spatial scale analyses where the abundance of bay anchovy explained large proportions of the variance in the parameters of the first biomass subdome across the three designated segments

of the Chesapeake ETZ. Jung and Houde (2005) in a baywide analysis found that bay anchovy dominated the first biomass subdome in the fish NBSS regionally and seasonally from 1995 through 2000 and exerted strong influence on the steepness of the slope parameter in the NBSS integral spectra for fish in the mainstem of the entire Chesapeake Bay. In the Jung and Houde (2005) analysis, variability in the annual mortality and annual mean biomass of bay anchovy affected the peak abundance and size at peak abundance of the first biomass subdome, and the predator-prey ratio as measured by the size differential between subdomes. My results confirmed these effects but also illustrated how variability in abundance of bay anchovy had a major influence on the size distribution of the fish community at the relatively small spatial scale of the ETZ in Chesapeake Bay.

The slope and intercept estimates of integral spectra of NBSS are sensitive to changes in abundance at the extremes of the size range. Accordingly, Duplisea and Castonguay (2006) postulated that the biomass dome and subdrome parameters provide additional and more robust metrics of community size structure than the integral spectrum parameters. Peak abundance and size at peak abundance in biomass domes or subdomes are measures of where the "bulk of ecologically active" biomass lies (Duplisea and Castonguay 2006) and are, therefore, potentially less sensitive to variability or errors in estimating biomass and abundance of fishes in extreme size categories. In Chesapeake Bay, the bay anchovy is the most abundant fish (Houde and

Zastrow 1991; Able and Fahay 1998) and certainly represents an important

fraction of the "ecologically active" biomass due to its high abundance and

important role as prey for many predators in the bay ecosystem (Houde and

Zastrow 1991). The first biomass subdome in either a baywide (Jung and Houde

2005) or my spatially-restricted analysis in the Chesapeake Bay ETZ represents

predominantly bay anchovy at sizes near the lower end of the range used in

NBSS analyses. Variability in bay anchovy abundance strongly affects

parameters of the integral spectrum and of the biomass dome and first biomass

subdome.

Freshwater flow is an important driver of productivity in Chesapeake Bay

(Harding 1994; Kemp et al. 2005; Miller and Harding 2007; Kimmel et al. 2009).

The positive relationship between freshwater flow and the abundance of YOY

alosines and moronids in Chesapeake Bay has been convincingly established

(Secor and Houde 1995; North and Houde 2001, 2003; Jung and Houde 2003;

Hoffman et al. 2007; Martino and Houde 2010), and response of these species to

freshwater flow variability that I observed are consistent with previous findings.

However, the relationship between bay anchovy abundance and freshwater flow

is less clear, particularly its regional occurrence in the Chesapeake ETZ. In a

six-year analysis of abundance, biomass, and spatial distribution in the mainstem

Chesapeake Bay, Jung and Houde (2004) found that environmental factors

affecting the bay anchovy population were complex and differed seasonally and

by life stage. The distribution of the bulk of bay anchovy adult biomass shifts in

relation to freshwater flow levels occurring 6-9 months before the summer

spawning period and is influenced by subpycnocline dissolved oxygen and

spring-summer temperature levels (Jung and Houde 2004). These factors can

affect the fraction of the adult population and dispersal by recruiting YOY bay

anchovy (Kimura et al. 2000) to the upper Bay and its ETZ. In a multi-decadal

PCA on YOY fishes for the entire Bay, bay anchovy loaded strongly on PC2

while anadromous species and coastal spawning species were negatively

correlated on PC1 (Wood and Austin 2009), further suggesting that factors

controlling bay anchovy recruitment are not correlated or closely linked to those

controlling recruitment of anadromous and coastal spawning species.

Years with high temporal and spatial overlap between larval striped bass,

white perch, and zooplankton prey in the Chesapeake Bay ETM resulted in

strong recruitment of YOY striped bass and white perch (North and Houde 2003,

2006; Martino and Houde 2010). YOY alosines likely respond in a similar

manner (Wood 2000). The results of these studies suggest that recruitment

success of YOY anadromous species in the Chesapeake Bay ETM responds

primarily to bottom-up effects and are illustrative of the size spectrum context of a

successful survival strategy outlined by Pope et al. (1994). In a simulation of

seasonal trophic dynamics following the spring phytoplankton bloom in a high

latitude marine ecosystem, Pope et al. (1994) tracked the fate of several cohorts

of zooplankton and fish larvae to determine the effects of spawning time on

growth and survival. The most successful strategy in terms of growth and

survival was to "surf" the wave of abundant prey to grow fast enough to keep ahead of the wave of predators (Pope et al. 1994). Years in which the temporal and spatial overlap between larval anadromous species and their zooplankton prey is high likely allow fish larvae to successfully surf through the size spectrum. Additionally, reduced predator abundance, as indicated by the narrower curvature of the second biomass subdome in Chesapeake Bay during July and October 2003, may have further enhanced YOY anadromous recruitment.

NBSS analyses provide information about bottom-up and top-down processes in estuarine ecosystems. Bottom-up effects that change productivity levels will likely affect the intercept estimate the integral spectrum and the peak abundance estimates of the biomass domes and subdomes (Sprules and Goyke 1994; Kerr and Dickie 2001). The positive relationship between freshwater flow, which is tied to increased productivity in Chesapeake Bay (Harding 1994; Harding et al. 2002; Miller and Harding 2007; Kimmel et al. 2009), and recruitment strength of YOY anadromous fishes was reflected in the differences between the intercept and peak abundance estimates from 2002 when spring freshwater flow was low compared to flows in 2001 and 2003. Except for effects of fishing activities on NBSS, top-down effect may not be as readily apparent in NBSS. Predator-prey interactions are described in NBSS theory using a fixed size ratio (Kerr and Dickie 2001), which means that predation is not size selective, e.g. the smallest or largest individuals are not preferentially preyed upon. Based on theory, the phytoplankton, zooplankton, and fish biomass

domes occur at regular intervals on the predator-prey size ratio, and the spacing

of the biomass subdomes occurs at the same interval or at a harmonic of that

interval (Kerr and Dickie 2001). Deviations from this predicted regularity may

indicate size selective predation and the presence of a top-down forcing.

An objective of my research was to determine if a combination of PCA and

NBSS approaches would produce complementary information to explain

variability in the fish community of the Chesapeake Bay ETZ. Results indicate

that the combined analysis did have value. The PCA described the fish

community in terms of the variability of each species' abundance while the NBSS

parameters categorized effects of those changes on the size distribution and

contribution to biomass structure of the fish community. This point is clear when

comparing observations from each year in the July and October PCAs with the

July and October NBSS biomass dome and subdome parameters. In the July

PCA, observations from 2001 and 2003 cluster close together and are separated

from 2002 observations, but in October the 2001 and 2002 observations cluster

and are separated from the 2003 observations. This seasonal shift in PCA

outcome is mirrored and explained in the July and October NBSS biomass dome

parameters, which document effects of the variable recruitments of anadromous

species and bay anchovy, and indicate that variability in the size distribution

arising from changes in species composition can be quantified by the NBSS

parameters.

The instances of imprecise or nonsensical NBSS parameter estimates were likely the result of a combination of the characteristics and constraints of the sampling gear and methodology, the statistical limitations of NBSS analyses, and potential theoretical limitations of the temporal and spatial scales at which NBSS analyses can be conducted. The poor fits of the integral spectra and biomass domes for the May data reflect the low abundance of small fishes in the sampling area in the spring. It is possible that habitats occupied by smaller fishes were inadequately sampled during the May cruises, but this scenario seems unlikely given the life history characteristics of the species frequently encountered in the Chesapeake ETZ. Anadromous species spawn through May, and the YOY do not recruit to the MWT until summer. Additionally, the abundance-weighted mean latitude of occurrence for bay anchovy tends to be down-bay of the Chesapeake ETZ during May (Jung and Houde 2004). The flat slopes and low peak abundances of the biomass subdomes occupied by small fishes may indicate that organisms not included in the NBSS, such as benthic organisms, may be important for maintaining the flow of energy from plankton to the larger fishes during the spring. Unfortunately, data on benthic organisms in the Chesapeake ETZ were not available for the spring sampling periods.

Censoring the smallest and largest size classes likely contributed to the poor fit to data in the July 2003 biomass dome as well as the ETZ segment domes and subdomes. Prior to censusing, the abundance of the smallest and largest size classes tended to emphasize the parabolic nature of the biomass

domes. Including these size classes may have reduced the number of poor model fits. However, the high variability in abundance of these relatively uncommon size classes raised questions about reliability of the abundance estimates.

A primary objective was to evaluate NBSS as a tool to quantify and describe the fish community in the Chesapeake Bay ETZ at spatial scales ≤ 50 km and at seasonal temporal scales. The NBSS, based on data from the entire ETZ, did exhibit coherent behavior at seasonal time scales and spatial scales of 50 km. NBSS worked well for quantifying seasonal changes in the size distribution of the fish community resulting from changes in the species composition and the recruitment and growth of YOY fishes. Additionally, the effects of weak and strong year classes were registered and remained detectable in NBSS parameters in the following years. At the spatial scale of the entire ETZ, NBSS parameters were estimated with sufficient precision to detect ecologically relevant variability in size distributions. An analysis to categorize and evaluate biomass dome and subdome parameters in a spatial analysis on three 18-km segments within the upper Bay's ETZ was less successful and did not provide information about the size distribution of the fish community in addition to analyses based on the entire ETZ. For analyses of fish communities at such small scales, the simpler metrics, mean abundance, mean biomass, and mean size, offered more reliable performance. In my research, the lower spatial limit for statistically robust NBSS analyses appears to be the spatial scale at which

the size classes of interest consistently occur. That spatial scale appears to be the entire ETZ in the mainstem Chesapeake Bay and, based on other analyses I conducted (see Chapter 3), tributaries of similar spatial scale with similar salinity gradients, such as the Patuxent and Choptank Rivers.

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Table 1. Monthly and annual mean Susquehanna River flow ($m^3 s^{-1}$) at Conowingo Dam. (USGS 2011).

Month	2001	2002	2003
January	447.41	449.95	1287.28
February	998.74	1262.08	781.26
March	1337.97	1153.06	2956.28
April	2193.71	1335.42	2162.84
May	532.64	2297.35	1299.74
June	651.85	1331.74	2384.84
July	309.50	315.45	784.09
August	161.24	136.01	1205.73
September	225.88	146.48	1538.17
October	238.17	716.13	1363.46
November	208.21	1027.05	2125.46
December	752.10	1206.30	2682.45
Annual mean	671.45	948.09	1714.30

Table 2. Research cruises: months, numbers of stations sampled, station depths, and ranges of temperature and salinity.

Year	Month	Midwater Trawl Samples	Depth Range (m)	Temperature Range (°C)	Salinity Range
2001	May	12	5.6-13.0	15.5-20.9	0.1-7.2
2001	July	29	5.0-14.0	23.8-26.6	0.10-9.9
2001	October	27	5.2-14.0	16.5-17.9	2.4-12.7
2002	May	11	6.0-13.5	14.2-17.6	0.1-11.8
2002	July	33	5.0-13.5	23.5-27.2	0.1-13.5
2002	October	33	6.0-14.5	19.0-22.8	0.6-15.4
2003	July	12	6.6-13.8	25.6-27.7	0.2-7.6
2003	October	11	5.0-13.5	14.8-16.6	0.1-7.1

Table 3. Size-class length limits (mm total length) for species in the Principal Components Analyses. NA indicates that a size class was not included in the analysis.

Common Name	Scientific Name	Small	Medium	Large
alewife	*Alosa pseudoharengus*	<150	NA	NA
American eel	*Anguilla rostrata*	≤250	NA	>250
Atlantic croaker	*Micropogonias undulatus*	≤100	NA	>100
Atlantic menhaden	*Brevoortia tyrannus*	≤52	53-126	>126
bay anchovy	*Anchoa mitchilli*	≤42	NA	>42
blue crab	*Callinectes sapidus*	≤75	76-130	>130
blueback herring	*Alosa aestivalis*	<100	NA	NA
bluefish	*Pomatomus saltatrix*	≤150	NA	NA
channel catfish	*Ictalurus punctatus*	≤150	151-300	>300
gizzard shad	*Dorosoma cepedianum*	≤112	NA	>112
hogchoker	*Trinectes maculatus*	≤58	59-112	>112
striped bass	*Morone saxatilis*	≤125	126-220	>220
weakfish	*Cynoscion regalis*	≤150	NA	>150
white perch	*Morone americana*	≤100	NA	>100

Table 4. Integral normalized biomass size spectra. Slope and intercept estimates by cruise. Intercept estimates have been back-transformed from $\log_2$ units. Values in parentheses represent the 90% confidence interval. The listed p-values represent the regression p-value.

Year	Month	Slope	Intercept (number m^{-3} x 1000)	r^2	p-value
2001	May	0.37 (0.24, 0.39)	0.023 (0.021, 0.042)	40.40%	0.001
2002	May	-0.04 (-0.13, 0.05)	0.26 (0.18, 0.32)	0.71%	0.68
2001	July	-0.67 (-0.70, -0.57)	3.24 (2.63, 3.64)	67.52%	<0.0001
2002	July	-0.44 (-0.49, -0.36)	1.30 (1.03, 1.48)	39.58%	0.0004
2003	July	-0.86 (-0.87, -0.75)	5.82 (4.49, 6.71)	75.29%	<0.0001
2001	October	-0.63 (-0.65, -0.52)	3.30 (2.63, 3.70)	48.19%	<0.0001
2002	October	-0.58 (-0.60, -0.45)	1.74 (1.23, 2.11)	48.18%	<0.0001
2003	October	-0.31 (-0.33, -0.17)	2.41 (1.93, 2.72)	17.0%	0.04

Table 5. Normalized biomass size spectra. Biomass dome parameters by cruise. Size at peak abundance and peak abundance are back-transformed from $\log_2$ units. Values in parentheses are the 90% confidence intervals, which were obtained by bootstrapping. The listed p-values are for the quadratic regression.

Year	Month	Curvature	Size at Peak Abundance (g wet wt)	Peak Abundance (number m^{-3} x 1000)	r^2	p-value
2001	May	-0.09 (-0.12, -0.07)	63.56 (40.22, 99.73)	0.17 (0.14, 0.24)	62.7%	<0.0001
2002	May	-0.05 (-0.06, -0.03)	5.90 (1.93, 10.56)	0.39 (0.27, 0.48)	11.8%	0.22
2001	July	-0.06 (-0.07, -0.04)	0.21 (0.05, 0.41)	5.30 (4.04, 7.49)	75.00%	<0.0001
2002	July	-0.12 (-0.14, -0.10)	2.23 (1.59, 3.01)	2.40 (1.87, 3.00)	74.9%	<0.0001
2003	July	-0.03 (-0.03, 0.002)	0.000059 (0, 971598.00)	204.78 (0.010, 24661960)	76.1%	<0.0001
2001	October	-0.11 (-0.12, -0.09)	1.08 (0.71, 1.62)	5.26 (4.25, 6.17)	65.7%	<0.0001
2002	October	-0.10 (-0.12, -0.09)	1.02 (0.66, 1.72)	2.74 (2.11, 3.42)	66.6%	<0.0001
2003	October	-0.17 (-0.18, -0.14)	3.53 (3.12, 4.17)	7.49 (5.96, 8.32)	72.0%	<0.0001

Table 6. Normalized biomass size spectra. Biomass subdome parameters. Subdome 1 corresponds to the subdome dominated by YOY fishes. Subdome 2 corresponds to the subdome primarily composed of age 1+ fishes. Values in parentheses are the 90% confidence interval. Size at peak abundance and peak abundance are converted from log_2 units. The listed p-values are for the quadratic regression.

Year	Month	Subdome	Curvature	Size at Peak Abundance (g wet weight)	Peak Abundance (numbers m^{-3} x 1000)	r^2	p-value
2001	May	1	-2.28 (-3.76, 0)	1.36 (1.19, 1.77)	0.033 (0.020, 0.068)	87.0%	0.13
2002	May	1	-0.83 (-0.90, -0.73)	0.72 (0.66, 0.77)	1.78 (1.04, 2.50)	97.7%	<0.0001
2001	May	2	-0.79 (-0.93, -0.39)	14.09 (12.07, 19.92)	0.15 (0.11, 0.21)	81.2%	<0.0001
2002	May	2	-1.65 (-2.28, -1.16)	7.98 (7.40, 8.97)	0.19 (0.14, 0.29)	91.8%	<0.0001
2001	May	3	-0.48 (-0.57, -0.42)	92.94 (80.96, 104.55)	0.38 (0.33, 0.48)	95.3%	0.05
2002	May	3	-0.55 (-0.65, -0.49)	99.49 (91.74, 108.33)	0.62 (0.47, 0.84)	89.0%	<0.0001
2001	July	1	-0.33 (-0.39, -0.29)	0.53 (0.45, 0.64)	10.13 (8.50, 11.91)	77.2%	<0.0001
2002	July	1	-0.78 (-0.94, -0.68)	0.58 (0.55, 0.64)	5.41 (4.16, 6.68)	83.2%	<0.0001
2003	July	1	-0.31 (-0.35, -0.24)	0.42 (0.29, 0.49)	24.46 (16.66, 29.38)	92.3%	<0.0001
2001	July	2	-0.51 (-0.58, -0.43)	44.11 (38.59, 48.93)	0.87 (0.70, 1.02)	94.5%	<0.0001
2002	July	2	-0.24 (-0.29, -0.20)	12.82 (9.24,15.02)	1.31 (0.93, 1.80)	88.3%	<0.0001
2003	July	2	-0.86 (-1.22, -0.64)	90.95 (76.57, 101.77)	0.48 (0.37, 0.87)	79.5%	<0.0001
2001	October	1	-1.01 (-1.17, -0.96)	0.67 (0.62, 0.72)	42.89 (38.00, 52.64)	85.6%	<0.0001
2002	October	1	-0.64 (-0.70, -0.59)	0.83 (0.80, 0.93)	13.13 (10.54, 15.48)	76.4%	0.0002
2003	October	1	-0.37 (-0.41, -0.34)	1.78 (1.60, 1.95)	12.94 (11.01, 15.15)	77.6%	<0.0001
2001	October	2	-0.27 (-0.34, -0.20)	18.47 (12.57 ,25.93)	1.02 (0.78,1.35)	90.4%	<0.0001
2002	October	2	-0.33 (-0.34, -0.23)	29.07 (22.61, 30.88)	0.41 (0.35, 0.48)	95.3%	<0.0001
2003	October	2	-0.85 (-0.95, -0.71)	61.87 (56.92, 66.51)	1.83 (1.48, 2.40)	98.9%	<0.0001

Table 7. Relationships between biomass subdome parameters and abundances of numerically dominant species for the ETZ segments in October, all years combined. x_{ba} = mean abundance (number m^{-3}) of bay anchovy, x_{wp} = mean abundance of white perch, x_{am} = mean abundance of Atlantic menhaden. curv = curvature of the biomass subdome, pa = peak abundance, sap = size at peak abundance.

Subdome	Equation	r^2	p-value
1	curv = $-0.43\log_{10}x_{ba} - 1.19$	39.34%	0.071
1	pa = $1.10\log_{10}x_{ba} - 4.78$	47.56%	0.040
1	sap = $-1.08\log_{10}x_{ba} - 0.85$	82.9%	0.00064
2	pa = $1.91\log_{10}x_{wp} - 0.88\log_{10}x_{am} - 12.26$	91.8%	0.00056

Table 8. Summarized data for midwater-trawled fishes in upper Chesapeake Bay. Standard errors are shown in parentheses. Mean weight, mean abundance, and mean biomass by year, month, and section.

Factor	Level	Mean Weight (g)	Mean Abundance (number m^{-3})	Mean Biomass (g m^{-3})
year	2001	8.97 (1.91)	0.20 (0.03)	0.50 (0.06)
	2002	5.69 (0.91)	0.10 (0.01)	0.33 (0.05)
	2003	5.06 (0.76)	0.19 (0.02)	0.71 (0.09)
month	July	9.25 (1.34)	0.10 (0.01)	0.44 (0.05)
	October	4.34 (1.05)	0.21 (0.02)	0.48 (0.05)
section	upper	4.73 (0.88)	0.14 (0.02)	0.30 (0.03)
	middle	7.49 (1.49)	0.13 (0.01)	0.48 (0.06)
	lower	8.35 (1.99)	0.20 (0.03)	0.59 (0.07)

Table 9. ANOVA results for mean abundance per tow, mean biomass per tow, and mean individual weight for the comparison of ETZ segments. Numbers are p-values for the effects and interactions for each analysis. Bold entries indicate effects retained in the final ANOVA model. *The year effect was retained in the ANOVA model for mean weight because of the significant interaction between the year and month effect.

Effect	Abundance	Biomass	Mean weight
year	**0.020**	**<0.0001**	**0.712***
month	**<0.0001**	**0.058**	**0.007**
segment	**0.090**	**0.023**	0.596
year-month interaction	**0.010**	0.452	**0.0002**
year-segment interaction	**0.007**	0.309	0.140
month-segment interaction	0.174	0.140	0.144

Figure 1. Hypothetical NBSS illustrating the integral spectrum (diagonal solid line), biomass dome (parabolic dotted line), and biomass subdomes (dashed lines). The NBSS parameters "size at peak abundance" and "peak abundance" are labeled for the first and second biomass subdomes (dashed parabolas).

Figure 2. The Chesapeake Bay and its estuarine transition zone. Sampling stations for each year are indicated by the symbols. The solid lines indicate the segment breaks (at 18 and 36 km) used for the spatial analyses. The estuarine turbidity maximum is depicted by the shaded ellipse.

Figure 3. PCA biplot of the species data for the May, July, and October cruises. The numbers marking the observations represent the year sampled: 1 = 2001, 2 = 2002, 3 = 2003. The color of the observation label indicates the month: blue = May, green = July, red = October. Percentages following the axes labels indicate the amount of variance represented by each axis. Species labels: ac = Atlantic croaker, ae = American eel, am = Atlantic menhaden, aw = alewife, ba = bay anchovy, bb = blueback herring, bc = blue crab, cc = channel catfish, gs = gizzard shad, hc = hogchoker, sb = striped bass, wf = weakfish, wp = white perch. Size class abbreviations: s = small, m = medium, l = large, t = all sizes combined. See Table 2 for lengths of each size class.

Figure 4. PCA biplot of the species data for the May 2001 and May 2002 cruises. No trawl collections were obtained in May 2003. The numbers marking the observations represent the salinity at the station. The color of the observation label indicates the year: green = 2001, red = 2002. Percentages following the axes labels indicate the amount of variance represented by each axis. Species labels: ac = Atlantic croaker, ae = American eel, am = Atlantic menhaden, aw = alewife, ba = bay anchovy, bb = blueback herring, bc = blue crab, cc = channel catfish, gs = gizzard shad, hc = hogchoker, sb = striped bass, wp = white perch. Size class abbreviations: s = small, m = medium, l = large. See Table 2 for lengths of each size class.

Figure 5. PCA biplot of the species data for the July cruises. The numbers marking the observations represent the salinity at the station. The color of the observation label indicates the year: green = 2001, red = 2002, blue = 2003. Percentages following the axes labels indicate the amount of variance represented by each axis. Species labels: ac = Atlantic croaker, ae = American eel, am = Atlantic menhaden, aw = alewife, ba = bay anchovy, bb = blueback herring, bc = blue crab, bf = bluefish, cc = channel catfish, gs = gizzard shad, hc = hogchoker, sb = striped bass, wf = weakfish, wp = white perch. Size class abbreviations: s = small, m = medium, l = large. See Table 2 for lengths of each size class.

Figure 6. PCA biplot of the species data for the October cruises. The numbers marking the observations represent the salinity at the station. The color of the observation label indicates the year: green = 2001, red = 2002, blue = 2003. Percentages following the axes labels indicate the amount of variance represented by each axis. Species labels: ac = Atlantic croaker, ae = American eel, am = Atlantic menhaden, aw = alewife, ba = bay anchovy, bb = blueback herring, bc = blue crab, cc = channel catfish, gs = gizzard shad, hc = hogchoker, sb = striped bass, wf = weakfish, wp = white perch. Size class abbreviations: s = small, m = medium, l = large. See Table 2 for lengths of each size class.

Figure 7. Integral spectra for upper Bay fish community in (a) May, (b) July, and (c) October 2001-2003. Dashed line for May 2002 indicates that the regression was not significant at $\alpha = 0.10$. See Table 4 for parameter estimates.

Figure 8. Regression model fits for biomass domes for upper Bay fish community in (a) May, (b) July, and (c) October 2001-2003. Dashed lines indicate that a regression was not significant at $\alpha = 0.10$. See Table 5 for parameter estimates.

Figure 9. Biomass subdomes for upper Bay fish community in (a) May, (b) July, and (c) October 2001-2003. Dashed line (May 2001) indicates that this quadratic regression was not significant at $\alpha = 0.10$. See Table 4 for parameter estimates.

CHAPTER 3

Structure and Variability of Fish and Plankton Communities in Two Chesapeake Bay Tributaries

Abstract

The temporal variability in fish, zooplankton and phytoplankton communities in two tidal tributaries of Chesapeake Bay was investigated and compared. Principal components analysis (PCA) of the species composition of the fish community was used in conjunction with normalized biomass size-spectrum (NBSS) analyses to determine if changes in species composition accompanied observed seasonal and annual variability of size-spectrum parameters in 2002-2004. Biomass size spectra describe the structure and responses of biological communities to perturbations in marine ecosystems. Size-spectra parameters and their variability rarely have been evaluated at the small temporal and spatial scales represented by the Choptank and Patuxent Rivers. PCA detected high recruitments of anadromous fishes in response to high flow conditions in 2003 and served to link changes in species composition to the variability of size-spectrum parameters for the fish community. Size-spectrum parameters for each trophic level responded to interannual variability of freshwater flow and to the phenology of shifts in species composition and size structure. Size-spectrum parameters described ecologically relevant changes in the size structure of plankton and fish communities at seasonal and annual time

scales while PCA identified the species associated with the size structure variability.

Introduction

The variable size structure and species composition of estuarine fish communities are sensitive to natural and anthropogenic stresses and may change over time in relation to fishing pressure, eutrophication, and ongoing climate change. Variability can occur at several temporal and spatial scales. Describing and quantifying such variability is important for fundamental understanding of factors that control fish community structure and for ecosystem-based fisheries management plans where it is necessary to develop community-level indicators that are responsive to management actions. In this regard, size-based metrics have been proposed as alternatives to traditional biological reference points (Trenkel and Rochet 2003; Jennings and Dulvy 2005; Link 2005).

Normalized biomass size spectra (NBSS) represent the change in abundance of organisms with increasing body size and provide an effective way to summarize and quantify size distributions of fish communities and their variability. Normalized biomass size spectra of biological communities have been evaluated for both freshwater and marine ecosystems of widely varying productivity. Spectral patterns are strikingly similar despite differences in taxonomic composition (Sheldon et al. 1972; Sheldon et al. 1973; Sprules and

Munawar 1986; Sprules et al. 1991; Boudreau and Dickie 1992; Sprules and Goyke 1994; Sprules and Stockwell 1995). The similarity in biomass size spectra from different ecosystems, their strong adherence to empirical observation and theory, and their responsiveness to perturbations suggest that properties of biomass size spectra may be widely applicable and powerful tools to interpret the state of ecosystems (Pope and Knights 1982; Pope et al. 1988; Rice and Gislason 1996; Gislason and Rice 1998; Bianchi et al. 2000; Kerr and Dickie 2001).

Fisheries ecosystem plans require indicators that are sensitive to environmental and anthropogenic effects on ecosystems (Trenkel and Rochet 2003; Jennings 2005; Link 2005). Observation and quantification of changes or variability in NBSS parameters through time can provide insight into the nature and magnitude of the variability within and between trophic levels of an ecosystem under fluctuating environmental conditions (Boudreau and Dickie 1992) or effects of fishing (Bianchi et al. 2000; Trenkel and Rochet 2003; Shin et al. 2005). In effect, variability in NBSS parameters may indicate shifts in species, sizes, and community structure that can be quantified and further investigated. Deviations from theoretical expectations (described in Chapter 1) indicate altered predator-prey relationships in response to variability in biomass production or mortality that mediates energy flow through the ecosystem (Kerr and Dickie 2001).

The properties and variability of NBSS parameters have not been thoroughly evaluated across temporal and spatial scales. Size and abundance based indicators used to assess the status of North Sea fish communities detected the effects of fishing effort on the fish community more consistently over temporal scales > 5 - 10 years and spatial scales > 30 - 70 ICES rectangles (one rectangle = 0.5 degree latitude x 1.0 degree longitude, or approximately 3420 km^2) than did indicators based on trophic level or species diversity (Piet and Jennings 2005). Because of uncertainties in sampling effectiveness in the monitoring surveys used to collect the North Sea data and potential effects of migrations, Piet and Jennings (2005) recommended caution when using size-based indicators at short temporal and small spatial scales until more is known about behavior of size spectra at these scales.

Seasonal variability of size spectra has been reported in several ecosystems, including Georges Bank (Boudreau and Dickie 1992), Lake Constance (Gaedke 1992), and Chesapeake Bay (Jung and Houde 2005; Kimmel et al. 2006). Size-spectrum analyses and modeling in estuaries have been uncommon (but see Jung and Houde 2005; Kimmel et al. 2006). Jung and Houde (2005) analyzed spectra for the fish community from the mainstem Chesapeake Bay based on midwater-trawl collections from 1995-2000. They found two peaks in biomass of pelagic and bentho-pelagic fishes included in their analysis, one corresponding to small, planktivorous fishes and one corresponding to larger, piscivorous and benthivorous fishes. While there was

interannual variability, the mean slope of the annual normalized biomass size

spectra, based only on pelagic species, was –1.05 (Jung and Houde 2005),

which is in accord with size-spectrum theory. The difference in the slope of the

integral spectra that include and exclude benthivorous species reported by Jung

and Houde (2005) suggested that the slope parameter of the fish NBSS may also

be sensitive to shifts in abundance of feeding guilds, for example the abundance

of benthivorous fishes. Overall, the interannual variability of both the slope and

intercept of the normalized biomass size spectra in Chesapeake Bay was

correlated with salinity and recruitment level of the abundant bay anchovy,

Anchoa mitchilli (Jung and Houde 2005).

Most analyses of fish community size spectra derive only the slope and

intercept parameters of the normalized spectrum. However, many size spectra

have parabolic deviations from the linear regression of abundance on size

(Figure 1; Boudreau and Dickie 1992; Sprules and Goyke 1994; Kerr and Dickie

2001; Duplisea and Castonguay 2006). The parabolic deviations correspond to

peaks in abundance of represented trophic levels (phytoplankton, zooplankton,

fish) and are referred to as "biomass domes" (Figure 1). These biomass domes

and their characteristics reflect density adjustments resulting from variability in

production and mortality rates within trophic levels and indicate "ecological

scaling" (Kerr and Dickie 2001). According to the underlying metabolic

relationships described by Thiebaux and Dickie (1992; 1993a; 1993b), the shape

and location of any biomass dome is predictable given the parameters of any

other biomass dome. Specifically, curvatures of the normalized biomass domes

should be similar and the spacing between consecutive biomass domes should

be consistent (Thiebaux and Dickie 1992; Boudreau and Dickie 1992; Thiebaux

and Dickie 1993a; Kerr and Dickie 2001). Parabolic deviations within the

biomass domes, called "biomass subdomes" have also been observed and may

represent predator-prey interactions within each trophic group (Figure 1;

Boudreau and Dickie 1992; Sprules and Goyke 1994; Kerr and Dickie 2001).

The location, size, and shape of biomass domes and subdomes are

readily parameterized using regression techniques (Sprules and Goyke 1994;

Sprules and Stockwell 1995; Kerr and Dickie 2001; Duplisea and Castonguay

2006), providing additional metrics that describe community structure. The

vertical location of the integral spectrum and the location, size, and shape of

biomass domes and subdomes provide a suite of parameters that provide

important information about structure and energy flow through an ecosystem.

These attributes may vary both intra- and inter-annually for a given ecosystem

(Rodriguez et al. 1987; Boudreau and Dickie 1992; Gaedke 1992; Duplisea and

Kerr 1995) depending on ecosystem responses to environmental variability.

Observation and quantification of changes or variability in NBSS parameters

through time can provide insight into the nature and magnitude of the variability

or shifts in species, sizes, and community structure within and between trophic

levels of an ecosystem under fluctuating environmental conditions (Boudreau

and Dickie 1992; Bianchi et al. 2000; Duplisea and Castonguay 2006).

Multivariate statistical models are complementary to NBSS analyses as an approach to describe and quantify aquatic communities. NBSS alone describes the distribution and flow of energy through an ecosystem as mediated by size-dependent production and predation relationships (Thiebaux and Dickie 1993a). In NBSS, all similar-sized taxa are categorized as being ecologically and metabolically equivalent. In theory, the species composition of a community could change completely without affecting the NBSS for that ecosystem if there were no changes in size distribution. To evaluate and understand consequences of community changes, an analysis of how taxa vary in time and space relative to one another is required. Principal components analysis (PCA), or other multivariate ordination techniques, can quantify changes in abundance or biomass of taxa through time and space, depicting the primary axes of variability of the data and facilitating display of this information.

The goal of this component of my research was to develop understanding of the temporal and spatial variability of estuarine fish and plankton community size structure and species composition in two tidal tributaries of Chesapeake Bay. Objectives were: 1) to estimate, evaluate and compare biomass size-spectrum parameters of fish communities at small spatial scales (< 50 km) and short temporal scales (seasonally and annually) using NBSS and PCA; 2) to evaluate relationships between the phytoplankton, zooplankton, and fish communities in the two subestuaries; and 3) to compare the two tributaries using NBSS analyses and PCA.

Methods

Study sites

      The two subestuaries sampled in this research are the Choptank and Patuxent Rivers (Figure 2). They are tidal tributaries of the Chesapeake Bay, each with watersheds of approximately 2000 km^2 (MDNR 2007a, MDNR2007b). Land use, population density, and the land:water ratio differ between the two tributaries (Fisher et al. 2006; Table 1). Salinity of these subestuaries during the research program ranged from 0 to 15, with some interannual variability. Bottom depths of sampling stations ranged from 4-15 m. Research activities in each river were conducted in 2002, 2003, and 2004, when freshwater flow conditions were below average, above average, and near average, respectively (Table 2).

Data collection

      From three to six surveys were conducted in the Patuxent and Choptank Rivers in 2002-2004 as part of the Atlantic Coast Estuarine Indicators Consortium[1] (ACE INC) research program. Three to five fixed stations were sampled from the salt front to the mouth of each river (Figure 2) during the ACE INC surveys, and most sampling effort occurred in spring and summer. The ACE INC surveys included sampling for phytoplankton, zooplankton, ichthyoplankton, and juvenile-adult fish. In 2004, only the Choptank River was sampled as part of the ACE INC project. Sampling of the fish community in the Patuxent River in 2004 was conducted by the Patuxent River Fishery Independent Multispecies

Survey (PAXFIMS) using the same gear and sampling protocols. However, the 12 PAXFIMS stations were located from down-estuary of the salt front to the mouth of the river. No ichthyoplankton, gelatinous zooplankton or zooplankton data were available from the PAXFIMS surveys in 2004. Vessel problems prohibited sampling the Choptank River in April 2004.

At each station, a CTD cast was conducted prior to ichthyoplankton, zooplankton, and fish collections to provide hydrographic data on salinity, temperature, and dissolved oxygen. Ichthyoplankton and gelatinous zooplankton were collected in deployments of a 1-m^2, 280-μm mesh Tucker trawl that was fished in oblique, 2-min tow segments. The two nets on the trawl were fished sequentially, with segments below and above the pycnocline, respectively, at each station. Samples were preserved in ethanol. In the laboratory, larval fish were identified, enumerated from counts of whole samples or aliquots, and standard lengths were measured using ImageJ software (Rasband 2008). Standard lengths (mm) of larvae were corrected for shrinkage (Theilacker 1980; Hjörleifsson and Klein-Macphee 1992; Paradis et al. 2007) and abundance estimates adjusted for losses due to extrusion through the net (Rutherford et al. 1997).

The biovolumes and abundances of each taxon of gelatinous zooplankton collected by the Tucker trawl were recorded on the deck of the vessel at time of collection. The lengths of ctenophores, *Mnemiopsis leidyi*, or the bell diameters

of sea nettles *Chrysaora quinquecirrha*, or a subsample of 30 individuals when abundant, were recorded along with the biovolume of the measured individuals.

Zooplankton abundance and biomass in the two rivers were estimated acoustically using a Tracor Acoustical Profiling System (TAPS-6), which records back-scattering strength using six frequencies (Roman et al. 2001). The instrument measures back-scatter from a 0.01-m^3 spherical volume situated 1.5-m from the transducer surface and measures particles ranging in size from approximately 0.225 - 200 mm (Roman et al. 2001). A narrower size range that was more appropriate for the zooplankton community in the two rivers was selected for this study (0.25 - 2.2 mm). The zooplankton community in the size range recorded by TAPS in the Patuxent and Choptank Rivers is dominated by the calanoid copepods *Eurytemora affinis* and *Acartia tonsa* (Herman et al. 1968; Reaugh et al. 2007).

Juvenile and adult fishes and blue crabs collected in a small midwater trawl were counted and measured. The trawl has a 6-m headrope and footrope, and a 3-mm codend liner. It was towed obliquely for 10-min from surface to bottom in 2-min increments in depths ranging from 4 - 15-m. The catches were identified to species at the time of collection. Lengths of up to 30 individuals of each species were measured. Aggregate weights of each species were recorded. In the laboratory, mean lengths and length-frequency distributions

were obtained. The midwater trawl malfunctioned during the April 2002 cruise in the Patuxent River, which prevented collection of fish data.

The Chesapeake Bay Program (CBP) monitored the phytoplankton community in the Choptank and Patuxent Rivers and the upper Chesapeake Bay from 12 - 14 times each year (CBP 2010). Phytoplankton was collected by CBP using a submersible pump that collected 15 L of water from above and below the pycnocline (CBP 2010). CBP phytoplankton sampling generally occurred within 7 days of each ACE INC survey. Phytoplankton species composition and cell count data from two stations in each river were used for the size-spectrum analyses (Figure 2). One of the stations in each river was in the oligohaline (salinity < 5) zone and the other was in the mesohaline (salinity 5-18) zone (CBP 2010).

Data analyses

Mean individual size (length, biovolume, or cell volume), mean individual weight, mean abundance, and mean biomass were calculated for each trophic level or group (fish, ichthyoplankton, gelatinous zooplankton, zooplankton, and phytoplankton) in the Choptank and Patuxent Rivers for each cruise. Within each trophic level or group, differences in mean size, mean weight, mean abundance, and mean biomass among cruises were analyzed using analysis of variance (ANOVA, $\alpha = 0.10$) with river, year, season, and their interactions as factors. Because these metrics and the NBSS are being evaluated for their utility

as ecosystem indicators, the α = 0.10 level was selected for all analyses to lower

the possibility of making a type II error and consequently failing to recognize

important changes in fish or plankton community structure that could be

detrimental to management efforts (Peterman 1990). These variables were

$\log_{10}$-transformed and quantile-quantile plots (Q-Q plots) were visually inspected

to insure that the transformed values met the assumptions of normality. The

Tukey-Kramer multiple comparisons procedure was used to compare means of

significant factors for each of the within-trophic level analyses. Wet weights for

each trophic level group were estimated for the construction of the NBSS.

Principal components analysis (PCA) was used to evaluate the spatial and

temporal variability of the species composition and size distribution of the fish

community based on the midwater trawl collections. In the PCA, species were

the variables for the species composition analysis and abundances of the

species at each sampling station were the observations. Two analyses were

conducted because not all seasons were sampled each year. The first PCA

(summer-only interannual PCA) used the summer fish data from both rivers in

2002-2004 to compare differences among years in the species composition of

juvenile and adult fishes in each river. The second PCA (seasonal PCA) used

the spring, summer, and fall fish community data for both rivers in 2003 and for

the Patuxent River only in 2004 to compare seasonal changes in the species

composition. To determine if there were size-based differences in spatial

distributions, commonly caught species were assigned to size groups (small,

medium, and large, Table 3) based on length-frequency distributions from each survey cruise. The length frequencies indicated that some YOY fishes could be separated into more than one size class, for example alewife, *Alosa pseudoharengus*, Atlantic menhaden, *Brevoortia tyrannus*, and striped bass (Table 3). Only species with a frequency of occurrence > 5% were included in the summer-only, interannual PCA and the seasonal PCA.

Phytoplankton: Phytoplankton cell volume was estimated for each taxon by the CBP following the methods of Hillebrande et al. (1999) and cell carbon content was estimated by the CBP for each taxon according to Smayda (1978) and Strathmann (1967). Taxon-specific algal wet weights for the NBSS were estimated using the taxon-specific cell carbon content estimated by the CBP and an algal wet weight: C ratio of 10:1 (Link et al. 2006 and references therein). Total phytoplankton biomass was estimated by multiplying the taxon-specific wet weight estimates by the cell count for each taxon and summing the taxon biomasses to estimate total biomass. Comparisons of mean phytoplankton size across rivers, years, and seasons were undertaken using cell volume.

Zooplankton: Only total abundance and total biomass were included in the within-trophic level analyses of size, biomass and abundance as these are the primary variables calculated by the TAPS data processing algorithms. The TAPS processing algorithm assigns zooplankton biovolume measured by the transducers to volume-based size classes supplied by the user. The same set of

size classes were used for all NBSS analyses. For the NBSS analyses, the

volume-based size classes were converted to mass-based (wet weight) size

classes using equation 6 in Wiebe (1988):

$$\log(V)\ 0.199 + 1.009 \log(WW)$$

where V = zooplankton volume in cubic centimeters and WW = mg wet weight.

Because estimates of mean size would have varied depending on the size bins

supplied to the TAPS data processing algorithm, mean size was not compared

across rivers, years, and seasons.

Gelatinous zooplankton: To include gelatinous zooplankton in the NBSS, mean

individual wet weight was estimated using the relationship between wet weight

and biovolume reported by Kremer and Nixon (1976). To compare mean size

across rivers, years and seasons, mean individual biovolume was used to

represent mean size for gelatinous zooplankton rather than mean wet weight.

The effect of adding gelatinous zooplankton on NBSS parameters was

determined by comparing the NBSS parameters before and after adding

gelatinous zooplankton to the NBSS using paired t-tests.

Ichthyoplankton and Fish: Species-specific length-weight relationships from

published literature and reports were used to estimate wet weights of individual

fish.

    Normalized biomass size spectra (NBSS) were constructed for each

trophic level during each sampling period based on wet weights. Complete

NBSS that included all size classes and trophic levels could only be constructed

and analyzed for 2002 and 2003 because zooplankton data were unavailable for

2004. Because size classes at the extremes of the size spectrum have strong

statistical leverage that can affect model fits, the size data were censored using

the coefficient of variation (CV) of abundance to include only the most

consistently collected size classes. For each trophic level, the CV of abundance

was plotted against size class. Organisms collected in each of the samplers

exhibited a U-shaped CV profile with the size classes at the extremes having

much higher CVs. Only size classes with similar CVs were retained for analyses.

The actual CV cutoff value varied by sampling gear.

Based on Daan et al. (2005), the x-axis (size class) was centered by

setting the mean of the size range to zero to reduce the correlation between the

intercept and slope estimates for the phytoplankton, zooplankton, fish, and

combined phytoplankton-fish integral spectra. The intercept estimate for the

centered size spectrum was referred to as the "height" of the size spectrum by

Daan et al. (2005).   Slope, height, and the parameters of the biomass domes

and subdomes were estimated with regression techniques and the parameters

compared across rivers, years, and seasons using ANOVA with α = 0.10. The

slope and height parameters of the integral spectrum were estimated with linear

regression. The biomass dome and subdome parameters were estimated using

quadratic regression from the following model:

$$y = c(x - h)^2 + k$$

where y = $\log_2$(number/m^3)

        x = the $\log_2$ size classes (g wet weight)

        c = curvature of the biomass dome or subdome

        h = size at peak abundance, i.e. the x-coordinate of the parabola vertex

        k = peak abundance, i.e. the y-coordinate of the parabola vertex

In early-stage analysis it was apparent that nearly all biomass domes had curvature estimates not significantly different from zero, which led to nonsensical estimates for size at peak abundance. Therefore, the NBSS analyses focused on the integral spectra and on the clearly-defined biomass subdomes.

The biomass subdomes were defined by the presence of parabolic residuals after the integral spectrum was fit to data. Furthermore, two or more consecutive data points in the NBSS were required to define the local minimum abundance between subdomes, i.e. the point at which the two subdomes meet (Figure 1). In other words, a solitary low-lying data point deviating from the integral spectrum fit to the data was insufficient to define a biomass subdome. Biomass subdomes meeting the specified criterion, based on visual inspection, were rarely identified in the phytoplankton and zooplankton data. Therefore, biomass subdome analyses were restricted to the fish data. Parameters for the subdomes were estimated as described in Chapter 2. To determine if the fish biomass subdomes corresponding to each trophic level had similar shapes, as described by Kerr and Dickie (2001), ratios of the curvatures of adjacent biomass subdomes for each survey and system were calculated and tested with ANOVA (at α = 0.10) to determine if the ratios differed significantly from 1.0. A ratio of 1.0

indicates that the subdomes have equal curvature and conform to the theoretical rule of similarity (Kerr and Dickie 2001).

Growth and loss rates of anadromous fish (striped bass, *Morone saxatilis*, white perch, *Morone americana,* river herrings, *Alosa* sp.) were estimated for the Choptank and Patuxent Rivers from the spring larval biomass subdome parameters and summer YOY biomass subdome parameters. Anadromous species were selected for these analyses because their larvae are collected in the spring and juveniles are collected in summer, which permits estimation of growth and mortality rates between sampling periods. Biomass subdome parameters were estimated for larval subdomes based on the spring cruise collections and juvenile fish subdomes based on the summer cruise collections using only the anadromous moronids and alosines collected in both seasons. Because several species potentially are included in each biomass subdome, estimated growth and loss rates are the combined rates for all species. Combined growth rates for the seleced taxa were estimated from the difference in the size at peak abundance between the larval subdome in spring and the young-of-the-year (YOY) juvenile subdome in summer. Loss rates were estimated from the difference in peak abundance in the two subdomes. The difference in abundance between spring and summer is due primarily to mortality because anadromous fishes (moronids and alosines) in these analyses do not migrate from the study areas until fall (Murdy et al. 1997).

Results

Overview of results

There were statistically significant and ecologically relevant, interannual differences for all trophic levels in the analyses of size and abundance metrics as well as the NBSS parameters. Furthermore, in the PCA of the fish community there were substantial differences in the species composition and abundance that were consistent with observed interannual differences in the NBSS parameters. Size structure and abundance of the fish, ichthyoplankton, and gelatinous zooplankton communities were more seasonally variable than were the zooplankton and phytoplankton communities in each river. There were between-river differences in the phytoplankton, zooplankton, and gelatinous zooplankton communities. In contrast to the variability in NBSS parameters observed in the individual trophic levels of each river, the integral spectra for the 2002 and 2003 cruises, based on all size classes, were remarkably invariable across seasons and years.

Multivariate analyses of the fish communities

Principal components analyses of the Choptank and Patuxent fish species data revealed clear seasonal, interannual, and spatial patterns that were similar in each river (Figures 3 and 4). Scree plots of the eigenvalues from each PCA (Figure S2) depicted 5-6 principal components with eigenvalues greater than one, which indicates that the PC captures as much variance as a single standardized variable (Kaiser 1960). The slopes of the scree plots tended to

change after PC3 or PC4, which indicated that PCs 1-4 captured the dominant axes of variability (Johnson 1998). Loadings for the principal components with eigenvalues > 1 are listed in Tables S5 and S6. The characteristics of the first two PCs in each analysis are reported because these PCs most strongly captured the temporal and spatial variability.

The species composition of the fish community in both rivers in 2003 differed from the composition observed in 2002 and 2004 in the summer-only, interannual PCA and also the seasonal PCA (Figures 3 and 4). In 2003, the fish community was dominated by YOY anadromous fishes, which was evident in both summer and fall. The spatial patterns observed in each PCA were driven by the higher abundance of most species at the upriver stations.

There were clear spatial and interannual patterns when the summer fish data from midwater-trawl collections were compared across years (Figure 3). The first principal component represented abundance, with larger catches having more negative scores along PC1 (Figure 3). The differences between 2003 and the other two years are indicated on PC2 (Figure 3). The data from 2003 scored negatively on PC2, while data from 2002 and 2004 had positive scores (Figure 3). By far, the highest catches of fish in each year were made at the most upriver stations, near the salt front, in each river (stations designated sf and umr, Figure 3) while low catches were made at stations closer to the mouth of each river (lr, lmr, mr, Figure 3). The variability in recruitment levels of YOY anadromous

fishes, particularly at the upriver stations, drove the interannual differences observed in the summer analysis. Species in this summer analysis were rare or absent from the lower river stations (observations with black labels). Spot (*Leiostomus xanthurus*), harvestfish (*Peprilus alepidotus*), and Atlantic croaker did occur at the lower river stations but their low frequency of occurrence precluded including them in the summer-only interannual PCA and seasonal PCA.

Anadromous fishes were consistently more abundant in 2003 than in 2004. Catches at the upper river stations were generally higher than at the lower river stations in both the Choptank and Patuxent Rivers. The seasonal PCA for the Choptank River in 2003 and the Patuxent River in 2003 and 2004 (Figure 4) was driven by ontogenetic migrations of the dominant species. The differences among seasons are distributed across both PC1 and PC2 (Figure 4). Data from the spring cruises scored positively on PC1 while summer cruises generally had negative or near-zero scores (Figure 4). Fall data had primarily positive scores along PC2 while spring data had generally negative scores (Figure 4). Summer observations were distributed along the entire PC2 axis, with the upriver data from summer 2003 having negative scores (Figure 4).

Integrated size spectra

The integral spectra for the 2002 and 2003 cruises, based on all size classes, but excluding jellyfishes, were remarkably invariable across seasons

and years given the variability observed in the slope parameter of the respective

trophic levels (Table 4, Figure 5). The slope estimates for the NBSS integral

spectra ranged from -1.23 to -1.10. The slope estimates differed significantly

from 0 in 2002 and 2003 (ANOVA, $p < 0.0001$) but did not differ from each other

(Tukey-Kramer, $p = 0.2132$). The height estimates of the integral spectra were

more variable than the slope estimates and ranged from 4.76 to 8.22. There was

a significant effect of season on the heights of the NBSS (ANOVA, $p < 0.0001$),

but there were no significant differences between rivers in the seasonal analysis

(Tukey-Kramer, $p > 0.10$).

There were no significant correlations among the integral spectrum slope

estimates or the height estimates for the phytoplankton, zooplankton-

ichthyoplankton, and fish communities. Furthermore, the slope and height

estimates of the phytoplankton and zooplankton-ichthyoplankton communities

were not sufficiently consistent to predict the slope or height estimates of the fish

community. Similarly, the parameters for the phytoplankton community could not

be used to predict the parameters of the zooplankton-ichthyoplankton community

integral spectra.

Fish

The life history patterns and occurrences of anadromous fishes and bay

anchovy drove the seasonal signals of mean size, mean weight, mean

abundance, and mean biomass in the fish community in the Choptank and

Patuxent Rivers (Table 5). None of the metrics differed significantly between rivers (p > 0.10). Season was the only significant factor in the ANOVA on mean lengths and mean weights for fish (Table 6). Mean total length and mean weight were significantly larger in spring than in summer or fall. Mature anadromous fishes were collected in the spring and their YOY occurred in July. YOY bay anchovy were collected in abundance during the summer and fall. The interaction between year and season was significant for mean biomass of the fish community (Table 6). Biomass in spring 2003 was significantly higher than in summer 2002 or spring 2004, leading to a significant interaction effect. The effect of season or year alone on mean fish biomass was not significant.

More age 1+ anadromous fishes were collected in spring 2003 than in the spring of the other two years. There were significant season, year, and season x year interaction effects on mean abundances of fishes in both rivers (Table 6). The standing stock of YOY anadromous fishes in summer and fall 2003 was significantly higher than in the spring and summer of 2002 and 2004. Age 1+ white perch, striped bass, and Atlantic croaker *Micropogonias undulatus* were abundant in the April collections whereas YOY fishes, e.g., YOY alosines, YOY moronids, and bay anchovy, dominated in the June, July, and October collections.

There were detectable seasonal and interannual differences in the slopes and heights of the NBSS integral spectra for the fish communities in the

Choptank and Patuxent Rivers (Table 4). The slope estimates for the fish NBSS

ranged from -1.26 to +0.23. Slopes for the fish component of spectra did not

differ between rivers, but did differ between years (ANOVA, p = 0.067) and

seasons (ANOVA, p = 0.003). The slopes and heights of the fish NBSS integral

spectra were sensitive to recruitment patterns of anadromous fishes and bay

anchovy. Spring size spectra were dominated by mature, age 1+ anadromous

fishes preparing to spawn. YOY of anadromous fishes recruited to the midwater

trawl in July and dominated the summer size spectra. YOY bay anchovy

appeared in catches during summer and peaked in fall, making major

contributions to the high abundance of small fishes. Slopes were significantly

steeper (more negative) in 2003 than in 2002 (Tukey-Kramer, p = 0.055) in

response to the strong recruitment of YOY anadromous species in 2003 relative

to the poor recruitment in 2002. No other pairwise comparisons of slopes among

years were significant. Slope values during spring were significantly less

negative (more horizontal) than in summer or fall (Table 4) because few small

fishes were present during spring cruises.

The integral spectrum height estimates for the fish component of the

NBSS followed the same pattern as the slope estimates described above (Table

4). There were no significant differences between rivers, but height estimates

differed significantly between years and between seasons (ANOVA, p = 0.046

and 0.0006, respectively). The height estimates were significantly lower in 2002,

the year of low abundance of YOY anadromous fishes, than in 2003 (Tukey-

Kramer, p = 0.051, Table 4). No other pairwise comparisons of mean height

among years differed significantly. The height estimates for trawl-sampled fish in

spring, before the annual production of most YOY fishes, were significantly lower

than for summer (Tukey-Kramer, p = 0.001) or fall (Tukey-Kramer, p = 0.003).

Two or three fish biomass subdomes were present in all months in the

Choptank and Patuxent Rivers. These subdomes were well described by

quadratic equations in which parameters of the subdomes varied seasonally and

annually in the two rivers. Three biomass subdomes were observed in the fish

NBSS from the Choptank River in April 2002, in both rivers in April 2003, and in

the Choptank River in October 2003. The NBSS from the Patuxent River in April

2004 had only two subdomes. For the April 2002 and 2003 NBSS, the first

subdome contained age-1 bay anchovy and hogchokers, *Trinectes maculatus*,

that weighed 0.25 - 2 g. The second subdome contained almost exclusively

hogchokers that weighed 2 - 32 g and likely represented a different age class.

Age 1+ white perch, striped bass, white catfish *Ameiurus catus*, and striped bass

were the primary species found in the third subdome that included fishes > 32 g.

Because of the inconsistency in numbers of subdomes, the spring NBSS

subdome parameters were excluded from further statistical analyses. The fish

NBSS for surveys in summer and fall had two biomass subdomes. In these

seasons the fish in the first subdome ranged in weight from 0.25 - 8 g. Species

in this size range included YOY of bay anchovy, Atlantic menhaden, alosines,

and moronids. The fish in the second subdome ranged in size from 8 - 1024 g

and included age 1+ moronids, catfishes, and Atlantic menhaden.

Peak abundance of the YOY fish subdomes (Table 7) were responsive to

variation in recruitment strength of anadromous fishes each year. Only "year"

was significant in the analysis of peak abundances (ANOVA, p =< 0.0001). Peak

abundances were higher in 2003 (Figure 6, Table 7) when YOY anadromous fish

had higher recruitments than in 2002 (Tukey-Kramer, p = 0.014). There were no

other significant differences in peak abundance for the YOY subdome in the

among-years analysis. Season was the only significant factor (ANOVA, p =

0.0013) in the analysis of YOY subdome curvature. However, in pairwise

comparisons summer and fall peak abundances did not differ significantly. Sizes

at peak abundance did not differ significantly among years, rivers or seasons.

A residual effect of the high YOY fish abundances in 2003 that was

principally a result of high anadromous fish recruitment was detectable in 2004.

The peak abundance of the age 1+ fish subdome differed significantly by year

(ANOVA, $p < 0.0001$), with peak abundance of age 1+ fishes in 2004

(representing the 2003 year class) significantly higher than in 2002. Size at peak

abundance for the age 1+ subdome also differed significantly by year (ANOVA, p

< 0.0001). Size at peak abundance of age 1+ fish biomass subdome in 2003

was significantly smaller than in 2002 (Tukey-Kramer, p = 0.005, Figure 6) or

2004 (Tukey-Kramer, p = 0.004). The size at peak abundance of the age 1+ fish

biomass subdome in 2003 was significantly smaller because few individuals > 32 g were collected in either river (Figure 6). While curvature differed significantly among years for the age 1+ subdomes (ANOVA, p = 0.0013), no significant pairwise, between-year differences were detected.

The ratios of the NBSS curvatures for subdomes representing each summer and fall survey did not differ significantly from 1.0 and there were no significant differences between rivers for the curvature ratios, indicating the biomass subdome curvatures were similar. Although not significant, the ratios of the biomass subdome curvatures did vary widely, which resulted in broad distributions for the curvature ratio estimates (Figure 7). Furthermore, there were differences between the rivers in the distributions of curvature ratios, shown by the boxplots in Figure 7. The Patuxent River had a broader interquartile range, indicating that the size distributions represented by the two fish biomass subdomes may be more variable than those for the Choptank River; however, the number of cruises represented in each distribution is small (5-7 cruises in each river). Additionally, most of the subdome curvature ratios for Patuxent River fish were > 1.0, indicating that the curvature of the age 1+ subdome was often greater than the YOY subdome and that the size distribution of the age 1+ subdome was more even than that of the YOY subdome. The relative difference (i.e. size ratio) between the YOY and age 1+ subdome sizes at peak abundance for both rivers was approximately 32x (Figure 7). The range of these size ratios

for the Patuxent was much greater than for the Choptank (Figure 7), an indication of the more variable size structure in the Patuxent River.

Phytoplankton

Mean cell volume, mean biomass, and mean abundance of the phytoplankton communities in the Choptank and Patuxent Rivers differed strongly between years (Table 6). Year was the only significant variable (ANOVA, $p < 0.0001$) in the analysis of mean phytoplankton size (cell volume, μm^3). Cell volume was significantly larger in 2003 than in 2002 or 2004 (Tukey-Kramer, $p < 0.10$) because of higher abundances of large diatoms and dinoflagellates such as *Coscinodiscus*, *Rhizosolenia*, and *Protoperidinium* in 2003, and because small chlorophytes and cyanobacteria, such as *Scenedesmus*, *Crucigenia*, *Merismopedia*, and *Microcystis,* were an order-of-magnitude more abundant in 2002 than in the other years. There was a significant river by year interaction that affected mean abundance ($\log_{10}$(cell count/m^3)) (ANOVA, $p = 0.014$). In pairwise comparisons, mean abundance was significantly higher in the Patuxent in 2002 than in the Choptank in 2003 (Tukey-Kramer, $p = 0.032$). In the Patuxent River, phytoplankton abundance was higher in 2002 than in 2003 and 2004 (Tukey-Kramer, $p < 0.10$). Phytoplankton biomass differed among years in both rivers (ANOVA, $p < 0.0001$, Table 6). Despite differences in abundance and size of dominant phytoplankton taxa in 2002 and 2003, mean biomass did not differ between these two years (Tukey-Kramer, $p = 0.31$). Phytoplankton biomass was higher in both rivers in 2002 than

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in 2004 (Tukey-Kramer, $p = 0.0071$), apparently attributable to the high abundance of small chlorophytes and cyanobacteria in 2002.

There was a significant river by year interaction effect on slope estimates for the phytoplankton NBSS integral spectra (ANOVA, $p = 0.034$). In the Patuxent River, the slope estimates of the phytoplankton integral spectra in 2002 were significantly steeper than in 2003 while there were no differences in slopes among years in the Choptank River. The height estimates did not differ significantly between rivers, among years, or among seasons for the phytoplankton integral spectrum (ANOVA, $p > 0.10$, Table 4).

Zooplankton and ichthyoplankton

Zooplankton biovolume and abundance estimates differed between rivers and years (ANOVA, $p < 0.0001$) but did not differ among seasons (Table 6). The Choptank River had significantly higher zooplankton biovolume and abundance than the Patuxent River (Tukey-Kramer, $p < 0.0001$). Biovolume and abundance were higher in 2002 than in 2003 (Tukey-Kramer, $p < 0.0001$). The primary differences between rivers and years occurred in the smallest zooplankton size classes, 0.10 - 0.14 mm ESR (3 - 15 µg wet weight), which were more abundant overall in the Choptank River and more abundant in both rivers in 2002.

Ichthyoplankton taxa in each river differed seasonally. Larval moronids and alosines dominated in spring and bay anchovy and goby larvae dominated

during summer. Few fish larvae were collected in fall. Mean larval abundance differed between rivers (Table 6). Mean abundance of larvae was significantly higher (ANOVA, $p = 0.006$) in the Choptank than in the Patuxent River. In contrast to the larval abundance result, only year had a significant effect (ANOVA, $p < 0.0001$) on larval biomass (Table 6). The substantial numbers of large goby larvae in 2004 resulted in significantly higher biomass estimates for the larval assemblage than in 2002 and 2003 (Tukey-Kramer, $p < 0.10$). Biomass of the larval assemblages did not differ significantly across season or between rivers.

Variability in the mean lengths of fish larvae (Table 6) was related to the seasonal changes in species composition and phenology of the ichthyoplankton community. The occurrence of more and larger late-stage bay anchovy and pipefish (*Syngnathus* sp.) larvae in fall 2003 and smaller moronid and alosine yolk-sac larvae in spring 2002 in the Patuxent River compared to the Choptank River resulted in a significant three-way interaction (ANOVA, $p = 0.067$) among river, year, and season in the analysis of mean larval lengths (Table 6). Larvae from the Patuxent River during fall 2003 were significantly longer (Tukey-Kramer, $p < 0.10$) and larvae from spring 2002 were significantly shorter (Tukey-Kramer, $p < 0.10$) than larvae from all other collections. The large larvae collected in fall 2003 in the Patuxent River also resulted in a significant interaction effect between season and river (ANOVA, $p < 0.0001$) in mean larval weights (Table 6). Larvae collected in the fall from the Patuxent River were significantly heavier

than larvae from any other combination of season and river (Tukey-Kramer, $p <$ 0.0001). Overall, larvae from the Patuxent were significantly heavier than larvae from the Choptank River (Tukey-Kramer, $p < 0.0001$). Additionally, there was a significant increase in mean larval weights as the larval assemblage shifted from alosines and moronids in the spring to bay anchovy and naked goby in the summer and then to larger bay anchovy in the fall (Tukey-Kramer, $p < 0.0001$).

The weight classes of zooplankton and ichthyoplankton overlapped to a degree. The slopes of the NBSS integral spectra for the combined zooplankton-ichthyoplankton were the most negative (steepest) of all the trophic levels (Table 4). The larger zooplankton-ichthyoplankton size classes had consistently negative residuals with respect to the overall integral spectrum (Figure 5), suggesting possible undersampling of these size classes or, alternatively, high loss rates from strong predation pressure. The slope estimates differed between years (ANOVA, $p < 0.0001$) and were more negative in 2003 than in 2002 (Tukey-Kramer, $p = 0.016$, Table 4). The integral spectrum height estimates of the zooplankton-ichthyoplankton component (Table 4) differed significantly among seasons (ANOVA, $p < 0.0001$), but no significant pairwise differences were detected by the multiple comparison tests (Tukey-Kramer, $p > 0.10$).

Gelatinous zooplankton

Abundance and biomass density of gelatinous zooplankton differed seasonally (Table 6). Both metrics were significantly higher in summer than in

spring (Tukey-Kramer, $p = 0.001$) or fall (Tukey-Kramer, $p = 0.09$). Large

Chrysaora in fall of 2003 in the Choptank River generated a significant interaction

between river and season in the analysis of mean individual biovolume of

gelatinous zooplankton (Table 6). Mean biovolumes of individual gelatinous

zooplankters in the Choptank River during fall 2003 were larger than in all other

cruises (Tukey-Kramer, $p < 0.05$).

The gelatinous zooplankton size classes always overlapped fish size

classes. However, including jellyfish in the biomass subdome analyses did not

have consistent effects across seasons or between rivers. Including gelatinous

zooplankton in the fish NBSS did substantially increase the variance of the size

spectra because the high abundances of jellyfish were concentrated in a few size

classes, which resulted in wide confidence intervals that included zero for many

of the parameters. The increased variability prevented rigorous statistical testing

of the effects of jellyfish on the NBSS, but important ecological information was

obtained from the point estimates in the altered NBSS.

Overall, including gelatinous zooplankton in the fish NBSS generally

resulted in higher estimates of production for this trophic level based on the

higher height and peak abundance estimates. The direction and magnitude of

changes in the slope were not consistent (paired t-test, $p = 0.396$). The high

abundances of gelatinous zooplankton did result in significantly higher height

estimates (paired t-test, $p = 0.0005$). Adding the gelatinous zooplankton to the

fish NBSS affected the shape, location and, in three cases, the number of biomass subdomes. Including gelatinous zooplankton in the fish biomass subdomes did not affect the size at peak abundance in a consistent manner (paired t-test, p = 0.831) but did elevate peak abundance estimates for the biomass subdomes (paired t-test, p = 0.0002).

Growth and loss rates of larval and juvenile fish

Recruitment of YOY anadromous fishes was higher in 2003 than in 2002 in each of the rivers (Figures 3, 4, and 8). The mechanisms supporting the high recruitments apparently differed between rivers. In the Choptank River, the estimated loss rate was much higher in 2003 than in 2002 (Table 8) but initial larval concentrations were > 3-fold higher in 2003 (Figure 8a). In contrast, in the Patuxent River, initial larval concentration was nearly twice as high in 2002 than in 2003 (Figure 8b), but the estimated loss rate in 2003 was only half that in 2002 (Table 8). Juveniles of anadromous fishes were relatively uncommon in the Patuxent in 2002, and there was no evidence of a biomass subdome for YOY fish in that year (Figure 8b). The Choptank subdome curvatures for the larval and juvenile fish biomass subdomes in 2002 were narrower than in 2003 (Figure 8a) indicating narrower size distributions. The larval normalized biomass subdome in 2002 and 2003 had similar curvatures and size ranges in each river (Figure 8b), indicating abundance across size classes was similarly even. Estimated growth rates were similar in each year in the Patuxent River while apparent growth was faster in 2002 than in 2003 in the Choptank River (Table 8).

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The higher peak abundance of larval fishes (first subdomes, Figure 8) in the Choptank suggested that overall productivity of fish larvae may be higher there than in the Patuxent.

Discussion

In general, the Choptank and Patuxent River plankton and fish communities were similar, based on size-structure analysis and biomass size spectra modeling. Size distributions of phytoplankton, zooplankton, ichthyoplankton, and juvenile/adult fishes differed relatively little between rivers. The size distribution of the fish community was the most easily quantifiable. Species composition and interannual responses of the fish community in each river were sensitive to interannual variability in freshwater flow regimes and responded similarly. Fish community responses were keyed to interannual differences in larval production of anadromous fishes that varied in response to freshwater flow regime as has been reported in other estuarine research (Kimmerer 2002; North and Houde 2003; Jung and Houde 2003; Kimmel et al. 2009; Martino and Houde 2010). Considering lower trophic levels, mean size, mean abundance, and mean biomass of phytoplankton are responsive to effects of variable flow regimes (Malone et al. 1988; Harding 1994; Kimmerer 2002; Miller and Harding 2006), but the responses I observed of phytoplankton size spectrum parameters were not easily explained. The seasonal and interannual responses of the zooplankton metrics and the combined zooplankton-ichthyoplankton NBSS parameters did not respond positively to higher flow

levels. Despite the variability of NBSS parameters for each trophic level, the slopes and heights of the integral spectra were remarkably stable in both 2002 and 2003.

The parameter estimates of NBSS integral spectra spanning all size classes and trophic levels in 2002 and 2003 were well within the range reported in other NBSS research (Boudreau et al. 1991; Sprules and Goyke 1994). At the temporal and spatial scales of my analysis, there were no significant correlations among the NBSS parameters for any trophic level, which was unexpected because in theory (Kerr and Dickie 2001) the spacing between biomass subdomes and their curvatures should be similar and consistent among trophic levels (Thiebaux and Dickie 1993a; Sprules and Goyke 1994; Sprules and Stockwell 1995). Additionally, there were no correlations among the mean size, mean abundance, and mean biomass metrics for any of the trophic levels in the Choptank and Patuxent Rivers. The lack of correlations may have resulted because parameters were derived and compared on seasonal rather than annual time scales. Given the differences in turnover times of the trophic levels, evaluating relationships at annual time scales may be required to account for lagged effects.

The quadratic regressions used to quantify the biomass dome parameters for the phytoplankton, zooplankton-ichthyoplankton, and fish communities did not fit the data well and produced nonsensical parameter estimates. The

phytoplankton and zooplankton-ichthyoplankton data exhibited minimal

curvature, and the variability among size classes prevented precise estimation of

the curvature. The abundances of consecutive size classes in the phytoplankton

data were particularly variable because fixed sizes were used for each taxon.

Consecutive size classes in the fish data exhibited more coherent behavior, but

the well-defined biomass subdomes may have contributed to the poor precision

of the biomass dome parameters. Additionally, censoring the largest and

smallest size classes, which had high CVs of abundance, reduced the precision

of the biomass dome curvature estimates. This effect was more pronounced in

the fish data than in the phytoplankton or zooplankton data. Removing these

highly variable size classes reduced the parabolic profile of the fish data as well

as reduced the number of size classes, and degrees of freedom, used in the

regressions. However, given the high CVs of the size classes at the extremes,

the parameter estimates obtained from including the censored size classes in

biomass dome regressions would have cast doubt on the reliability of the

parameter estimates.

The strong differences in flow conditions among years influenced

phytoplankton community structure in the two rivers. The phytoplankton

community in both rivers in 2004 appeared to be intermediate to the extremes

observed in 2002 and 2003 when freshwater input to each river was low and

high, respectively. Mean phytoplankton cell volume was highest in both rivers in

2003, most likely due to a diatom bloom resulting from the high freshwater flow

(Harding 1994; Harding et al. 2002; Miller and Harding 2007) in that year

followed by high numbers of large dinoflagellate taxa in the summer. The low-

flow conditions in 2002 may have been unfavorable for a large spring diatom

bloom and may have favored earlier development of the typical summer

phytoplankton community consisting of smaller taxa such chlorophytes and

cyanobacteria (Harding et al. 2002). The slopes of the phytoplankton integral

spectra appeared to be more sensitive to changes in abundance than to changes

in biomass or cell volume. Contrary to results of Sprules and Munawar (1986),

the height of the integral spectra did not respond to variability in abundance. The

behavior of the slopes and heights in the Choptank and Patuxent Rivers

suggests that variability in the phytoplankton size distribution may occur primarily

near the extremes of the size range. The lack of correlation of NBSS parameters

and metrics based on size and abundance between the phytoplankton data and

the zooplankton-ichthyoplankton data suggest that any effects of seasonal or

annual differences in zooplankton grazing rates were not directly detectable at

the temporal and spatial scales of my analyses and may require finer scale

sampling in both time and space. Both the slope of the phytoplankton integral

spectrum and mean abundance were more variable in the Patuxent River than in

the Choptank River, which may be related to more variable flow conditions in the

Patuxent River.

The NBSS of phytoplankton communities in the two rivers may be

reasonable approximations but could be improved with a dedicated analysis.

The phytoplankton monitoring data collected by the CBP was included in this study in an attempt to relate productivity at lower trophic levels to variability in the size structure of the fish community in each river. The integral spectra for the phytoplankton communities were flatter than predicted by theory. This outcome may be due in part to designating fixed size classes for each of the represented taxa in the absence of measured sizes. The estimated slopes of the integral spectra might have been steeper if cell size had been measured directly as in other studies (Rodriguez and Mullin 1986; Sprules and Munawar 1986). The primary focus of the CBP phytoplankton monitoring program is to detect changes in species composition and abundance resulting from variation in water quality conditions (CBP 2010). As such, the sample processing protocols of the CBP phytoplankton program were not specifically designed to detect changes in the size structure of the phytoplankton community. My assumption of a single, fixed value for size in each taxon is likely to be inaccurate because cell sizes can vary in response to light and nutrient limitation (Strathmann 1967) and temperature (Montagnes et al. 1994). Additionally, using fixed size classes likely inhibited detection and quantification of biomass subdomes within the phytoplankton NBSS because the size range was not continuous.

In my research on the two tributaries, anadromous fish abundance and biomass increased as expected with respect to increased freshwater flow in 2003. However, contrary to expectation, zooplankton abundance and biomass were significantly lower in 2003, compared to the low-flow year 2002. The NBSS

heights of the combined zooplankton-ichthyoplankton assemblages reflected

these differences observed in mean abundance and mean biomass, but the high

variability of the height estimates within each year precluded detecting significant

difference between the years. It is possible that the sampling conducted in April

of 2002 and 2003 in the Choptank and Patuxent Rivers was too early in the

season to detect a zooplankton response to the higher flow conditions in 2003.

The slopes of the combined zooplankton-ichthyoplankton NBSS integral

spectra in the two rivers were considerably steeper (more negative) than those

reported for zooplankton by Kimmel et al. (2006) for the mainstem Chesapeake

Bay and those for zooplankton in the Laurentian Great Lakes (Sprules and

Munawar 1986) and oceanic ecosystems (Rodriguez and Mullin 1986; Quinones

et al. 2003). In my analysis, either an overestimation of abundances of small

size classes of zooplankton or underestimation of large size classes by the TAPS

could have steepened spectral slopes. The addition of ichthyoplankton to the

zooplankton data did not consistently result in either increases or decreases in

the zooplankton-only NBSS slopes. Consequently, it seems unlikely that

underestimation of ichthyoplankton abundances was the sole reason for the

steep slopes in this NBSS component.

Zooplanktivorous life stages of several species of fish were present in the

Choptank and Patuxent Rivers throughout the year. Their predation could

reduce the abundance of the largest size classes of zooplankton during the

spring to fall seasons, steepening the slope of the NBSS. Jellyfishes also could

act to control abundance of zooplankton. Kimmel et al. (2006) suggested that

predation occurred across all size classes of zooplankton in Chesapeake Bay

from April to July when the comb jelly *Mnemiopsis leidyi* and the sea nettle

Chrysaora quinquecirrha were the primary predators. For zooplankton, the

NBSS biomass dome curvature increased and the size at peak abundance

generally decreased in upper Chesapeake Bay as the season progressed from

July to October (Kimmel et al. 2006). The reduced abundance of the largest

zooplankton in the Chesapeake mainstem from July to October was proposed to

be from predation by bay anchovy on adult copepods and copepodites (Kimmel

et al. 2006). Predation on zooplankton by bay anchovy and ctenophores, which

were common in summer and fall in the tributaries during my study, may have

contributed to the steepness of the combined zooplankton-ichthyoplankton

integral spectrum slope.

For the fish community, the slopes of many of the seasonal, NBSS integral

spectra in my study were flatter than predicted by theory or reported in other

research (Bianchi et al. 2000; Kerr and Dickie 2001; Jung and Houde 2005). For

the Choptank and Patuxent Rivers, this may be in part a result of including

benthivorous fishes in the size spectra that are not trophically dependent on the

pelagic food web. Jung and Houde (2005) obtained similar results when

benthivorous fishes were included in their size spectra for the fish community in

the mainstem Chesapeake Bay. In the Jung and Houde research (2005), the

slope of the integral spectrum was not significantly different from -1 when it was

estimated using only the data for zooplanktivorous and piscivorous fishes. The

difference between the slopes with and without benthivorous fishes suggested

that zooplanktivorous fishes may support the prey requirements of piscivorous

fishes, but a benthic-pelagic link is required to support a fraction of the fish

community in the second biomass subdome (Jung and Houde 2005).

Underestimated abundance estimates of the largest and smallest fishes

can strongly affect the slope of the integral spectrum (Duplisea and Castonguay

2006). Underestimation of abundance of these sizes, particularly the smallest

fishes, could flatten the slopes of the integral spectra. The effect of small fishes

on the fish component of the NBSS was particularly pronounced in the spring

spectra for the Choptank and Patuxent Rivers when few YOY fishes were

present and during the summers of 2002 and 2004 when recruitments of YOY

anadromous fishes were low. The slope values of the integral spectrum for the

fish community were consistent with expectations of NBSS theory in 2003 when

YOY anadromous fish recruitment was high, suggesting that elevated production

of juvenile fish in that year represents a better example of the theoretical

"unperturbed" condition where the integral spectrum slope is -1 (Kerr and Dickie

2001). The negative residuals of small fish data in the YOY NBSS subdome for

July 2002 (Figure 5) illustrate the anomalously low recruitment of YOY

anadromous fishes in the Patuxent River, and in the Choptank to a lesser

degree, during that year.

The behavior of the NBSS integral spectra slope for juvenile-adult fish estimated in my research on the two tributaries differed from findings of Jung and Houde (2005) on fish in the mainstem of Chesapeake Bay. Slopes of the annual NBSS integral spectra estimated by Jung and Houde (2005) became less negative in years of high freshwater flow whereas the slopes I estimated in the Choptank and Patuxent Rivers steepened significantly during 2003, the high-flow year. The difference in the two studies may have been influenced by the dominant species in the mainstem and tributary habitats, respectively. In the mainstem, abundant bay anchovy consistently dominated the first biomass subdome in the fish NBSS for Chesapeake Bay from 1995 through 2000 (Jung and Houde 2005). However, in the Choptank and Patuxent tributaries, YOY of anadromous fishes dominated the first subdome during summer, especially in 2003, while bay anchovy became increasingly prevalent in the fall. Based on six years of data, Jung and Houde (2003; 2004) reported that bay anchovy abundance was lowest and YOY anadromous fish abundance highest, and the NBSS integral slope lowest during 1996, a year of high freshwater flow (Jung and Houde 2005). Thus, at the scales of analyses being compared, the relationship between freshwater flow and the slope of the integral spectrum for fishes may depend upon the relative contribution of particular species to the smaller end of the fish size spectrum and the particular responses to freshwater flow. The integral spectrum heights for fishes estimated in my research and those estimated by Jung and Houde (2005) became more positive with increased flow. This response is proposed to be a measure of ecosystem productivity (Sprules

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and Munawar 1986; Kerr and Dickie 2001) and is consistent with expected

changes in productivity in estuaries associated with increased freshwater flow

(Harding 1994; Kimmerer 2002; Miller and Harding 2007; Kimmel et al. 2009).

The Choptank and Patuxent Rivers fish communities exhibited multiple,

well-defined biomass subdomes, similar to those described by Dickie et al.

(1987), Thiebaux and Dickie (1993a; 1993b), and Sprules and Goyke (1994).

Jung and Houde (2005) reported two biomass subdomes in the NBSS for the fish

community of the mainstem Chesapeake Bay. The curvature estimates for the

NBSS subdomes in my study were similar to, but more variable than, curvature

values reported for NBSS domes representing the entire fish communities in

Lake Ontario and Lake Michigan (Sprules and Goyke 1994). My curvature

estimates also resembled curvature values reported for size-spectrum biomass

domes in the North Sea, Scotian Shelf, and Georges Bank (Duplisea and

Castonguay 2006). Sprules and Goyke (1994) suggested that more productive

ecosystems have broader biomass domes than less productive ecosystems.

Given similar peak abundances in a dome, an ecosystem with a broader

curvature will have a larger standing stock (area under the curve) than an

ecosystem with a narrow curvature. The similarity of the fish biomass subdome

parameters for the Choptank and Patuxent Rivers suggests that the fish

communities in these two rivers were equally productive on average.

In contrast to results reported for the Great Lakes (Sprules and Goyke 1994), in which spacing of normalized biomass subdomes was a harmonic of the biomass dome spacing, the fish biomass subdomes in the Choptank and Patuxent Rivers were not equally spaced nor always similarly shaped. The size range of the fish included in my research (0.25 g to 1024 g) was broader than that reported by Sprules and Goyke (1994), which ranged from approximately 0.5 g to 90 g, The size ratio between the fish biomass subdomes in my study (Figure 7) were more than twice the ratios reported by Sprules and Goyke (1994) indicating a greater size difference between age classes in the Choptank and Patuxent River fish communities. The greater size difference in the age classes in the Choptank and Patuxent Rivers compared to the two Great Lakes indicates that the combined growth rates of taxa in the fish community of the tidal rivers is faster than rates in Lakes Michigan and Ontario.

The NBSS seasonal integral spectrum slopes and heights of the fish community did not differ between the Choptank and Patuxent Rivers. Moreover, the NBSS biomass subdome parameters and abundance and size metrics for the fish communities in each river also were similar. While there were no significant statistical differences between the two rivers in the curvature of the biomass subdomes and size ratios, the variability in these parameters suggest that the size distribution of the Patuxent River's fish community may be more variable than that of the Choptank River. A potential source of variability of the size distribution of the Patuxent River fish community is recurring low concentrations

of dissolved oxygen in the downriver portion of the Patuxent River (Fisher et al.

2006). Collections at the downriver stations in the Patuxent were consistently

low compared to catches at the upper river stations. There were several hypoxic

events in the Patuxent River during the survey years that were less frequent in

the Choptank River. Summer hypoxic events were documented regularly in the

lower Patuxent from 1985-2003, but there were no hypoxic events in the lower

Choptank during the same period (Fisher et al. 2006). The spatial extent of

hypoxic water is expected to affect distribution of fish. Accordingly, it appears

that abundance estimates in the Patuxent differed, depending on availability of

fish at the downriver stations and the variability in the size distribution of the fish

community in the Patuxent River also may have been, in part, an effect of

hypoxia at the downriver stations.

The substantial seasonal and interannual variability of the YOY subdome

parameters suggests that the fish communities of the Choptank and Patuxent

Rivers were not in steady-state conditions. Duplisea and Castonguay (2006)

noted that large interannual changes in the curvature parameter suggest that

non-equilibrium events, such as large recruitments of fish, may shift an

ecosystem from the steady-state conditions upon which biomass size-spectrum

theory is based. In the Chesapeake tributaries the species composition, overall

abundance, and recruitment of the fish communities in each river exhibited large

seasonal and interannual variability, with some species (e.g., migratory

anadromous fishes) or size classes entirely absent for part of the year, which

could increase variability in biomass subdome parameters that are likely to be inherently less stable than those in ocean ecosystems. The strong seasonal variability, particularly for fish in spring-months NBSS analyses, inhibited parameter estimation of the integral spectra and precluded including the spring data in the seasonal comparision of biomass subdome parameters. These results suggest that estuarine NBSS may be analyzed most effectively at annual time scales. Still, the biomass subdome parameters in the Choptank and Patuxent Rivers distinguished and quantified the effects of high or low recruitment events on the size spectrum of the fish community and allowed tracking those effects into the following year.

Gelatinous zooplankton are important consumers in Chesapeake Bay (Cowan and Houde 1993; Purcell and Decker 2005) but it is not clear how to best include them in a biomass size-spectrum analysis. Adding gelatinous zooplankton to the fish component of NBSS in the Choptank and Patuxent Rivers increased variability in the NBSS integral spectra and variability in biomass subdome parameter estimates. In my analysis, in which gelatinous zooplankton were included in the fish NBSS based on wet weight, peak abundance estimates of biomass subdomes in which gelatinous zooplankton were included increased. These estimates potentially are inflated with respect to the amount of biomass available to pass through the food web because little is known about predation on jellyfish by fish in Chesapeake Bay (Purcell and Arai 2001). Additionally, representing jellyfish biomass as wet weight in a NBSS may not accurately depict

jellyfish as prey in the transport of energy through the food web because gelatinous zooplankton have high water content and low carbon content. Adjusting the wet weight of gelatinous zooplankton to the equivalency for fish, with equivalent carbon content, might better represent the trophic position of jellyfish as predators. In terms of carbon, a 100 g wet weight jellyfish with carbon weight of 5 g would be equivalent to a fish with wet weight of 50 g, assuming carbon weight of fish is 10% of wet weight (Nixon et al. 1986). This adjustment would shift the gelatinous zooplankton toward smaller sizes in a size-spectrum analysis which could steepen slope estimates. Alternatively, applying a similar statistical adjustment for trophic level to the jellyfish abundance data such as that Hechinger et al. (2011) used to include parasite data in food webs from three California estuaries might provide a more accurate representation of jellyfish as predators.

The Choptank River had higher concentrations of larvae of anadromous fishes than the Patuxent in the spring of both 2002 and 2003 but, by summer, had lower abundances of YOY anadromous fish than the Patuxent River. Two possible explanations for these observations are 1) peak larval production in the Patuxent occurred after the spring survey cruises or 2) loss rates that include both mortality and possibly emigration are sufficiently lower in the Patuxent than in the Choptank to overcome lower initial concentrations of anadromous fish larvae. There were no significant differences between rivers for the peak abundances of the YOY fish biomass subdomes including all species, suggesting

that YOY bay anchovy and Atlantic menhaden, which were more prevalent in the YOY biomass subdome in the Choptank River, fulfilled the plankton consumer role carried out more prominently by YOY anadromous fishes in the Patuxent.

Growth rates of late-stage larvae and YOY juveniles derived from NBSS biomass subdome peak weights were higher in both rivers in 2002 than in 2003, with the highest estimated growth rate occurring in the Choptank in 2002. However, the pattern of loss rates, presumed to represent mortality, was not consistent. The estimated larval to YOY stage community mortality rate for fishes was higher in 2002 than in 2003 in the Patuxent while the reverse was true in the Choptank River. The "size spectrum surfing" strategy for larval fish survival posited by Pope et al. (1994) provides a framework for interpreting the contrasting patterns between rivers and years for the growth, loss rates, and recruitment strength of YOY anadromous fishes. Pope et al. (1994) simulated the seasonal trophic dynamics following the spring phytoplankton bloom in a high latitude marine ecosystem and tracked the fate of several cohorts of zooplankton and fish larvae to determine how spawning time affects growth and survival. Simulated survival of larval fish was highest when spawning time and hatch date allowed larvae to "surf" the wave of abundant prey to grow fast enough to keep ahead of the wave of predators (Pope et al. 1994). The estimated growth rate of fish larvae in the Patuxent River was somewhat faster in 2002 than in 2003, but the loss rate in 2003 was nearly half that of 2002, which suggests that the phenology of 2003 allowed for more successful surfing in 2003 in the Patuxent

River. In contrast, recruitment in the Choptank River was higher in 2003 despite

the higher loss rate and lower growth rate in 2003. Larvae were much more

abundant in 2003 than in 2002, suggesting that abundance of larvae

overwhelmed potential predators despite poorer surfing performance.

Alternatively, the larval cohort in the Choptank in 2003 may have already

survived the factors determining recruitment strength by the time sampling

occurred, which could indicate a difference between 2002 and 2003 in abiotic

conditions that affect survival.

Estimating the growth and loss rate from the larval to the juvenile stage for

the anadromous fishes provided insights into the interannual variability in the first

biomass subdome. This approach was adopted to detect potential causes of

different recruitment levels of YOY anadromous fishes in the two rivers, which

were not evident from the analyses of parameters in the first biomass subdomes

or the size and abundance metrics. The time period during which I estimated

loss and growth rates for the anadromous fishes corresponded to the transition

period between larvae and juveniles. The levels of mortality and growth rates

estimated in my research were intermediate between previously reported rates

for larval and juvenile striped bass and American shad (Crecco and Savoy 1983,

1985; Dorazio et al. 1991; Secor and Houde 1995; Rutherford and Houde 1995;

Rutherford et al. 1997). Using an NBSS approach, Edvardsen et al. (2002)

successfully estimated growth and mortality rates for copepods and euphausids

in a Norwegian fjord where advection was minimal. Applying NBSS parameters

to estimate growth and mortality rates may be a promising approach to estimate size-specific accumulation of biomass and losses of numbers and biomass of dominant taxa in an ecosystem, although the losses cannot be partitioned into mortality and emigration.

Principal component analysis complemented the fish NBSS by indicating which species were responsible for the changes in size structure that was quantified by the NBSS parameters. The PCA biplots revealed interannual differences in the species composition of the YOY biomass subdome which indicated that the role of zooplanktivorous fish was filled by either YOY anadromous species or Atlantic menhaden and bay anchovy. Additionally, the PCA biplots demonstrated that the fish abundance, as estimated from the midwater trawl catches, was not homogenously distributed along the lengths of the rivers. An oligohaline assemblage and a mesohaline assemblage were identified in each river. While the species composition of the oligohaline assemblage varied by season and year, the mesohaline assemblage was less distinct and mostly reflected the absence of oligohaline species. Sampling oligohaline and mesohaline regions in these rivers at finer spatial resolution would improve the description of the two assemblages and also comparisons of the fish NBSS in each river.

Piet and Jennings (2005) recommended that size-based indicators be used with caution at short temporal and small spatial scales until behavior of size

spectra at these scales has been evaluated more thoroughly. In my research, ecologically relevant events were detectable on both seasonal and interannual time scales, which may indicate that NBSS, particularly biomass subdome parameters, are useful indicators and possibly interpretive tools for fisheries management, if the parameters can be estimated precisely. Size-spectrum parameters for phytoplankton, zooplankton, and fish communities in the Choptank and Patuxent rivers responded to variable freshwater flow regimes. More research on environmental factors and potential effects on NBSS will be important to understand factors that structure biological communities in these tributaries. Dedicated sampling and measurement of the phytoplankton and zooplankton communities for multiple years will allow imporoved evaluation of the relationships between size structure of the fish community and lower trophic levels. PCA complemented the NBSS analyses of the fish community in each river by explaining how interannual variations in species abundance related to observed changes in the size structure of the fish community provided by the NBSS. Moreover, biomass subdomes describing the fish community exhibited coherent behavior that was projected across years and was dependent on recruitment levels of YOY fish. Biomass size-spectrum theory and derived parameters potentially can provide indicators of fish community structure and productivity at spatial scales less than 50 km on seasonal and annual time scales.

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Table 1. Physical characteristics of the Choptank and Patuxent Rivers. Data compiled from Fisher et al. (2006), MDNR (2007a), and MDNR. (2007b).

River	Length (km)	Mean depth (m)	Watershed area (km^2)	Land:water ratio	Land use (%) ag/forest/urban	population density (#/km^2)
Choptank	114	3.6	1756	5.83	58/29/10	40
Patuxent	177	4.7	2260	16.5	24/43/31	273

Table 2. Annual mean freshwater discharge (m^3/s) for each study year and the long-term average (LTA) for each river. The Choptank River data are from USGS gauging station 01491000, and the LTA is based on data from 1948-2009. Data for the Patuxent River are from USGS gauging station 01594440, and the LTA represents the period 1977-2009.

River	2002	2003	2004	LTA
Choptank	3.11	8.99	6.80	3.85
Patuxent	6.09	22.52	12.20	10.82

Table 3. Length (mm) cut-off values for the different size classes included in the summer-only interannual PCA and seasonal PCA. Approximate age groups are given in parentheses. YOY = young-of-the-year. NA = not applicable.

Species	Small	Medium	Large
alewife	<75 (YOY)	NA	75-150(YOY)
Atlantic croaker	<100 (YOY)	NA	NA
Atlantic menhaden	<90 (YOY)	NA	90-180 (YOY)
bay anchovy	<50	50-70	>70
blueback herring	<150 (YOY)	NA	NA
blue crab	<75	75-130	>130
channel catfish	<120	120-300	>300
hogchoker	<70	70-100	>100
striped bass	<100 (YOY)	100-250 (YOY & age 1+)	250 (Age 1+)
white catfish	<100	100-200	>200
white perch	<100 (YOY)	100-200 (aAge 1+)	>200 (Age 1+)

Table 4. Slope (a) and height (b, $\log_2$ of concentration) for integral spectra linear regressions averaged by river, season, and year. The number of cruises used for calculating each average is listed in the column labeled "n". "NA" indicates that data were not available for analysis.

	Phytoplankton			Zoo- & Ichthyoplankton			Fish			All Trophic Levels		
	a	b	n	a	b	n	a	b	n	a	b	n
Choptank	-0.63	28.40	9	-2.03	9.12	6	-0.41	-10.55	8	-1.15	6.35	6
Patuxent	-0.69	28.62	9	-1.90	7.26	6	-0.51	-10.94	9	-1.18	6.27	5
spring	-0.60	28.70	6	-1.85	9.83	2	0.05	-12.13	4	-1.14	6.03	3
summer	-0.74	28.46	10	-1.95	6.54	3	-0.59	-10.58	10	-1.18	6.06	6
fall	-0.47	28.17	3	-2.24	9.85	2	-0.75	-9.50	3	-1.15	7.50	2
2002	-0.78	28.71	6	-1.77	8.51	6	-0.24	-11.62	5	-1.18	5.90	5
2003	-0.55	28.50	6	-2.16	7.87	6	-0.61	-10.25	6	-1.15	6.66	6
2004	-0.65	28.32	6	NA	NA	0	-0.51	-10.53	6	NA	NA	0

Table 5. Grand means of size, weight, abundance, and biomass estimates for combined across rivers. Values in parentheses are the ranges of means of means from all cruises. Metrics for mean size differed by taxa (trophic level). "NE" indicates that the metric was not estimated.

Trophic Level	Mean Size	Mean Weight	Mean Abundance	Mean Biomass
Fish	98.76 (66.7-177.3) mm TL	21.9 (0.6-71.5) g	0.1 (0.006-0.4) m^{-3}	0.5 (0.1-1.3) g/m^3
Ichthyo.	6.6 (2.8-27.7) mm SL	4.5 (0.07-82. 9) mg	3.2 (0.001-15.5) m^{-3}	1.9 (0.007-7.3) mg/m^3
Jellyfish	21.4 (1.0-103.5) cm^3	NE	3.2 (0-30.8) m^{-3}	19.3 (0-203.2) g/m^3
Zoopl.	NE	NE	2.1 (0.005-13.6) x 10^7 m^{-3}	134.3 (1.5-821.8) cm^3/m^3
Phyto.	528.9 (138.4-3418.0) μm^3	NE	7.1 (0.7-30.5) x 10^7 cells/L	28.5 (4.7-100.8) g/m^3

Table 6. Factors that significantly affected mean size, mean weight, mean abundance, and mean biomass based on ANOVA. Interactions are designated with the "•" symbol. See text for result of Tukey-Kramer comparisons of the levels of each factor. The metric for mean size differed by trophic level. Mean length was used for fish and ichthyoplankton. Mean volume and cell volume were used for gelatinous zooplankton and phytoplankton, respectively. Mean biovolume was the measure of biomass for zooplankton. "NE" indicates that the metric was not estimated.

Trophic Level	Mean Size	Mean Weight	Mean Abundance	Mean Biomass
Fish	season	season	year, season, year • season	year • season
Ichthyoplankton	river • year • season	season • river	river	Year
Zooplankton	NE	NE	river, year	river, year
Gelatinous zooplankton	river • season	NE	season	Season
Phytoplankton	year	NE	river • year	Year

Table 7. Fish NBSS subdome parameters from quadratic regressions averaged by river, season, and year. curv = subdome curvature, pa = peak abundance (number m^{-3}, converted from $\log_2$ units), spa = size at peak abundance (g wet weight, converted from $\log_2$ units), n = the number of surveys used to estimate the mean.

	YOY subdome				Age 1+ subdome			
	curv	pa	spa	n	curv	Pa	spa	n
Choptank	-0.89	0.007	0.66	5	-0.42	0.0007	18.97	5
Patuxent	-0.85	0.010	0.56	7	-0.44	0.0007	22.12	7
summer	-0.85	0.007	0.60	10	-0.45	0.0007	22.63	10
fall	-0.97	0.039	0.58	2	-0.34	0.0007	13.45	2
2002	-0.86	0.025	0.61	4	-0.29	0.0004	32.62	4
2003	-0.94	0.049	0.39	3	-0.51	0.0007	5.41	3
2004	-0.83	0.009	0.76	5	-0.49	0.0012	32.36	5

Table 8. Estimated loss rates and weight-specific growth rates of YOY anadromous fishes in the Choptank and Patuxent Rivers during the period from April to July in 2002 and 2003.

River	Year	Loss, d^{-1}	Growth, d^{-1}
Choptank	2002	0.019	0.096
Choptank	2003	0.062	0.012
Patuxent	2002	0.009	0.019
Patuxent	2003	0.005	0.014

Figure 1. Example normalized biomass size spectrum (NBSS) illustrating the integral spectrum (diagonal solid line), biomass dome (curved dotted line), and biomass subdomes (dashed lines). Data represented here are from the October 2003 Patuxent River survey. NBSS parameters size at peak abundance and peak abundance are labeled for the YOY fish biomass subdome (dashed parabola) and the Age 1+ fish subdome (dashed parabola).

Figure 2. Map of the study area. Atlantic Coast Estuarine Indicators Consortium (ACE INC) sampling stations are shown as black dots. Black triangles indicate CBP phytoplankton stations. ACE INC station abbreviations are as follows: p = Patuxent River, c = Choptank River, sf = salt front, umr = upper middle river, mr = middle river, lmr = lower middle river, lr = lower river.

PC1 species loadings

-0.6   -0.4   -0.2   0.0   0.2   0.4

PC2 tow scores 18.7%

PC1 tow scores 22.8%

PC2 species loadings

Expanded View

Key: river.station.year

Figure 3. PCA biplot of the species data for the summer cruises in the Choptank and Patuxent Rivers from 2002 to 2004. The blue labels indicate data from the up-estuary stations where larger numbers of anadromous fishes and Atlantic menhaden were collected. The red labels indicate the observations when and where non-anadromous species were collected. The data shown in the expanded view is from the area circled in black. Observation labels: p = Patuxent River, c = Choptank River, sf = salt front station, umr = upper middle river station, mr = middle river station, lmr = lower middle river station, lr = lower river station, 02 = 2002, 03 = 2003, and 04 = 2004. Species labels: alewf = alewife, atmen = Atlantic menhaden, banch = bay anchovy, blubak = blueback herring, blucrb = blue crab, chcat = channel catfish, hogch = hogchoker, stbass = striped bass, whcat = white catfish, whper = white perch. Size abbreviations: S = small, M = medium, L = large.

Figure 4. PCA biplot of the species data for the spring, summer, and fall cruises in the Choptank River in 2003 and the Patuxent River 2003 and 2004. The green labels indicate data from the spring cruises. The blue labels indicate data from the summer cruises. The red labels indicate data from the fall cruises. The data shown in the expanded view is from the area circled in black. p = Patuxent River, c = Choptank River, sf = salt front station, umr = upper middle river station, mr = middle river station, lmr = lower middle river station, lr = lower river station, 02 = 2002, 03 = 2003, and 04 = 2004. Species labels: alewf = alewife, atmen = Atlantic menhaden, banch = bay anchovy, blubak = blueback herring, blucrb = blue crab, chcat = channel catfish, hogch = hogchoker, stbass = striped bass, whcat = white catfish, whper = white perch. Size abbreviations: S = small, M = medium, L = large.

Figure 5. NBSS of three trophic levels for the Choptank and Patuxent Rivers in summer 2002 and 2003. Integral spectra are shown for each trophic level (colored lines) as well as for all trophic levels combined (black line).

Figure 6. Fish NBSS integral spectra and biomass subdomes from the Choptank and Patuxent Rivers during summer 2002 and 2003. Log$_2$ weights are on the x axis and log$_2$ numbers are on the y axis. Wet weight in grams is on the top scale of the x axis. Abundance is given on the inside scale of the y axis.

Figure 7. Box plots of the ratios of the NBSS fish biomass subdome curvatures and the size ratio for the NBSS fish biomass subdomes. The box indicates the first and third quartiles, the brackets indicate the range, and the white line designates the median. The solid line indicates a ratio of 1 on the curvature ratio axis for the fish biomass subdomes and trophic level biomass domes. A curvature ratio of 1 indicates that the fish biomass subdomes have equal curvature as predicted by NBSS theory. The dotted line at 4x on the size ratio axis indicates the predator-prey size ratio between the fish biomass subdomes estimated for Lakes Michigan and Ontario by Sprules and Goyke (1994). The dashed line at 32x on the size ratio axis indicates the predator-prey size ratio between trophic level biomass domes observed by Sprules and Goyke (1994).

Figure 8. Biomass subdomes for larvae of anadromous fishes in April and juvenile anadromous fishes in July. Loss and growth rates were estimated from the NBSS subdome parameters as shown in the top panel.

CHAPTER 4

Decadal-scale variability in size structure and species composition of fish and zooplankton communities in the lower Chesapeake Bay and its tributaries

Abstract

Variability and trends in the size structure and abundance of the fish and zooplankton communities in lower Chesapeake Bay and its tributaries were investigated. Normalized biomass size spectrum (NBSS) parameters, mean abundance, mean biomass, and mean size were estimated using fisheries-independent monitoring data collected from 1991 to 2003. Principle component analysis (PCA) of abundance data on ecologically and economically important fish species were used to track temporal and spatial changes in species composition of the fish communities in relation to observed patterns in the size and abundance metrics. Several fish species, including bay anchovy, hogchoker, and spot, declined in abundance during the study period, with concomitant declines in mean biomass, and changes in the NBSS parameters related to abundance. Some fish species that declined in abundance, such as, bay anchovy and hogchoker, were at the small end of the size spectrum. Their decline resulted in significant increases in mean size of fish in tributaries of the lower Bay. Variability in species composition of the fish communities detected in the PCAs explained the trends observed in the NBSS parameters and size-

based metrics. Similar to patterns in the fish communities, metrics related to abundance and biomass of the zooplankton communities declined in the lower Bay and tributaries. Regression tree analyses of the size and abundance metrics of the fish communities and environmental variables detected few strong patterns and did not identify causes of the observed declines. Fish biomass was predicted by summer pH, summer ammonium concentrations, and winter specific conductance. Regression trees developed to predict species richness and diversity primarily separated the data from the lower Bay from its tributaries. Combining size-based and abundance metrics with multivariate ordination approaches commonly used in community analyses facilitated detection of changes in ecosystem structure and identification of the species and trends driving the observed variability.

Introduction

The species composition and size distribution of the fish community in Chesapeake Bay vary across spatial and temporal scales. The community structure is influenced strongly by the transitory nature of juvenile and adult stages of many migratory species that use the estuary as nursery, feeding, or spawning habitat and by short-lived resident species that vary in abundance interannually. Fish communities in estuarine ecosystems are shaped by environmental conditions resulting from hydrographic, habitat and climatic variability, and also anthropogenic influences such as changes in nutrient loading, contaminants, and fishing intensity. However, these forcing factors do

not operate in isolation (Kemp et al. 2005; Paerl et al. 2006). Temporal and

spatial variability in species composition and size distribution and their effects on

standing stock and productivity of estuarine fish communities must be considered

when developing ecosystem-based fisheries management plans (Houde 2011).

Long-term fishery-independent monitoring surveys are an important source of

data required to develop and evaluate such plans.

Metrics based on size and abundance data from fisheries independent

monitoring surveys have been proposed as alternatives and supplements to

reference points traditionally estimated for single-species stock assessment

methods. New metrics are needed that monitor not only individual stocks but the

broader fish community (Overholtz and Tyler 1985; Rice and Gislason 1996;

Haedrich and Barnes 1996; Kerr and Dickie 2001; Rochet and Trenkel 2003).

Long-term analyses of fishery-independent survey data in large marine

ecosystems often reveals reduced abundance of many size classes and biomass

distributions that have shifted toward smaller body sizes with increasing fishing

pressure (Haedrich and Barnes 1997; Bianchi et al. 2000; Jennings and

Blanchard 2004; Blanchard et al. 2005; Daan et al. 2005; Duplisea and

Castonguay 2006; see Duplisea et al. 1997 for an exception). This shift results

primarily from the selective removal of larger fish species and larger individuals

of a species, but also may reflect an increase in abundance of smaller fishes that

have been released from high predation pressure (Jennings and Blanchard 2004;

Blanchard et al. 2005).

Changes in species composition and decreased abundance of both targeted and non-targeted species resulting from fishing can negatively affect the stability of an ecosystem (Blaber et al. 1990). Jennings and Blanchard (2004) suggest that shifting the biomass distribution toward dominance by smaller fishes shortens the turnover time of a fish community, which, in turn, leads to greater interannual variability of biomass and production. Jennings et al. (1999) compared abundance trends and von Bertalanffy growth model parameters for pairs of phylogenetically related species with opposing abundance trajectories in the North Sea from 1925 to 1996. In most cases, the species with a declining abundance trend had larger maximum size and slower growth rate than the species that increased in abundance. Jennings et al. (1999) concluded that the significant decline in mean size of North Sea fishes reported by Rice and Gislason (1996) was due to fishery removals of larger individuals and a shift in species composition toward species with faster growth rates, smaller maximum size, lower age at maturity, and smaller length at maturity.

Biomass size spectra and, especially, normalized biomass size spectra (NBSS), provide a theoretical foundation, based on the predator-prey size ratios and changes in metabolism and turn-over rates with size, that depict and quantify the decline in abundance with increasing size for aquatic organisms (Kerr and Dickie 2001; Figure 1B in Chapter 1). The NBSS parameters and variability in them provide several metrics based on size and abundance that give insights into changes in the productivity and size structure of aquatic ecosystems. The

slope and intercept of the integral NBSS, which describes the linear relationship between abundance and body size, are the most studied NBSS parameters. Freshwater and marine ecosystems with higher productivity have higher intercepts (Sprules and Munawar 1986; Boudreau and Dickie 1992; Bianchi et al. 2002).

The slope of the integral spectrum is sensitive to perturbations on the ecosystem such as fishing that alter size distributions (Figure 2 in Chapter 1; Rice and Gislason 1996; Bianchi et al. 2000; Jennings et al. 2002; Daan et al. 2005; Duplisea and Castonguay 2006), and the slope of the integral spectrum becomes steeper as fishing intensity increases. The intercept of the integral spectrum in observed (Rice and Gislason 1996; Bianchi et al 2000; Jennings et al. 2002; Nicholson and Jennings 2004) and modeled ecosystems (Gislason and Rice 1998; Pope et al. 2006) increases with fishing intensity, which can reflect increased abundance of smaller size classes as well as the correlation between the slope and intercept estimates. To reduce the correlation between slope and intercept, Daan et al. (2005) centered the x-axis of the normalized size spectrum by rescaling the x-axis so that the mean of the size range was set at 0 for the North Sea fish community and found that the height (intercept of the centered size spectrum) declined through time as the slope became steeper, indicating reduced productivity of the fish community. Lastly, Yemane et al. (2008) found that the intercept of the integral spectrum mirrored catch rates from a fisheries-

independent survey, confirming that the intercept is an index of abundance of the fish community.

Parabolic deviations from the integral spectrum often are observed (Figure 1B in Chapter 1; Boudreau and Dickie 1992; Sprules and Goyke 1994; Kerr and Dickie 2001; Duplisea and Castonguay 2006). These deviations, which correspond to peaks in abundance of represented trophic levels (phytoplankton, zooplankton, fish), are referred to as "biomass domes", and they result from variability in production and mortality rates within each trophic level (Kerr and Dickie 2001). Parameters that quantify the biomass domes are sensitive to ecosystem perturbations (see Figure 2 in Chapter 1) as shown by Duplisea and Castonguay (2006), who reported trends in these parameters from multiple large marine ecosystems in response to fishing intensity.

Based on size spectrum theory (see Chapter 1), the biomass domes for the different trophic levels should have similar curvatures, and the vertical and horizontal displacement between consecutive trophic levels along the size spectrum should be consistent (Kerr and Dickie 2001). Therefore, in theory the location of the biomass dome for one trophic level can be predicted based on the parameters of the biomass dome of the next largest or smallest trophic level (Kerr and Dickie 2001). Sprules and Goyke (1994) successfully predicted the biomass dome parameters for the fish communities of Lakes Ontario and Michigan based on the biomass dome parameters of the zooplankton community in each respective lake.

The variability of size spectrum parameters in estuaries seldom has been reported. Kimmel et al. (2006) quantified the seasonal and annual variability of the zooplankton biomass dome parameters for the upper, middle, and lower Chesapeake Bay over a 4-yr period. The zooplankton dome parameters were sensitive to variability in freshwater flow to the Chesapeake Bay and variability in abundance of predators such as bay anchovy (*Anchoa mitchilli*), the comb jelly ctenophore (*Mnemiopsis leidyi*), and the sea nettle medusa (*Chryasaora quinquecirrha*) (Kimmel et al. 2006). For bentho-pelagic fishes, Jung and Houde (2005) found that the slope and intercept of the integral spectrum in Chesapeake Bay fish from 1995 to 2000 responded to variability in freshwater flow and recruitment level of bay anchovy.

There have been several analyses of the temporal or spatial variability of fish communities in Chesapeake Bay (Wagner 1999; Wagner and Austin 1999; Jung and Houde 2003; Wingate and Secor 2008; Wood and Austin 2009). While these studies provided insight into the response of fish communities to environmental gradients and sources of temporal variability in species composition, the analyses were limited by the habitats, seasons, age classes included, or the short duration of the study. Similarly, the temporal and spatial variability of size distribution and abundance of the zooplankton community in the mainstem Chesapeake Bay have been quantified (Kimmel and Roman 2004; Roman et al. 2005; Kimmel et al. 2006), but the long-term variability of the size

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distribution of zooplankton communities in the tributaries of the lower Bay has not received the same attention.

I hypothesized that changes in the metrics and NBSS parameters representing mean size, as well as measures of abundance, of the fish and zooplankton communities of the lower Chesapeake Bay and its tributaries are responsive to natural and anthropogenic perturbations to the ecosystem. The direction of the response of the size distribution of the fish community in terms of size and abundance will depend upon species affected by the perturbation and their contribution to the size structure of the fish community. My objectives were to analyze a 13-year, fishery-independent data set to 1) determine if there were shifts in community structure of the fish and zooplankton communities in Lower Chesapeake Bay, 2) quantify changes in the size distribution of the zooplankton and fish communities based on size and abundance metrics, 3) link observed changes in size structure to changes in the species composition of the fish community, and 4) evaluate relationships between variability in the size and abundance metrics of the fish community to zooplankton metrics and water quality data.

Methods

Data collection

Virginia CBP mesozooplankton survey

The Chesapeake Bay Program (CBP) Virginia Mesozooplankton survey, initiated in July 1985, sampled zooplankton retained by a 202-μm mesh at four fixed stations each month in the Virginia mainstem Chesapeake Bay (Figure 2). Monthly sampling at three fixed stations in the James, Rappahannock, and York Rivers began in January 1986 (Figure 2). Starting in 1995, a second round of sampling was added for stations in the nursery areas of anadromous fish species. This second round of sampling was not used in my analyses because it started midway through the time series and potentially could have resulted in analytical artifacts.

Mesozooplankton were collected in oblique 5-min tows of a $0.5m^2$, 202-μm bongo net. Zooplankton were identified to species and developmental stage, enumerated, and expressed as concentration (number m^{-3}). From 1985 until December 1997, samples were enumerated using the coefficient of variation stabilizing method (Alden et al. 1982) in which zooplankton were sieved using five different sieve sizes (200, 300, 600, 850, and 2000 μm) and the zooplankton retained by the sieves were split using a Folsom plankton splitter and enumerated (CBP 2007). This method was found to underestimate abundance of small zooplankton (CBP 2000, ICPRB 2007). A 64-μm sieve was added in 1998 (CBP 2007), but the method was still biased (ICPRB 2007). The Hensen-

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Stempel pipette method (Harris et al. 2000), in which zooplankton are enumerated from 1-10 ml aliquot subsamples (CBP 2007), was adopted in 2000 and taxon-specific conversion factors were developed to permit numerical comparison among the 1985-1997 data and 2000-2002 data (Carpenter et al. 2006, ICPRB 2007). The CBP Mesozooplankton Survey was discontinued in October 2002. Because no correction factors were developed for the 1998 and 1999 data (ICPRB 2007), my analyses utilized only the data from 1991 to 1997 and 2000-2001.

VIMS trawl survey

The Virginia Institute of Marine Science Juvenile Finfish and Blue Crab Trawl Survey (henceforth "VIMS trawl survey") has conducted a bottom-trawl survey in the tributaries and Virginia mainstem of Chesapeake Bay since 1955. Prior to 1991, the numerous changes in gear and sampling protocols inhibit analyzing these data as a single time series (Hata 1997). Since 1965, the survey sampled 8-9 fixed stations in each of the James, Rappahannock, and York Rivers. By 1997, 13-14 stratified random stations in each tributary were sampled each month in addition to the fixed stations. The Virginia mainstem Bay has been sampled monthly, except during January and March, at 39-45 stations using a random-stratified design since 1988. Only the data from 1991-2003 are included in my analyses because the sampling gear and protocols were consistent during this period. Only the most consistently sampled fixed stations

in the tributaries, and all mainstem Bay stations, were included in the analyses (Figure 1).

Fish were collected using a 9.14-m semi-balloon otter trawl with 38.1-mm stretch mesh for the body, 6.35-mm stretch mesh cod-end liner, tickler chain, 18.29-m bridle, and steel China-Vee doors (71 cm x 48 cm) towed with a 3:1 warp for 5 min at 2.5 knots. Depth, dissolved oxygen (DO), salinity, Secchi depth, temperature, latitude, and longitude were recorded at each station in addition to the abundance and lengths of trawled fishes. Salinity, temperature, and dissolved oxygen (DO) were measured at the surface and within one meter of the bottom using a Hydrolab Surveyor II. Fish lengths were recorded to the nearest millimeter as fork length, or as total length for species not having a forked caudal fin.

Environmental data

The CBP has collected data biweekly since 1984 on a suite of environmental variables at several stations in the Virginia mainstem Bay and its tributaries (Figure 1). I used only water quality parameters (Table 1) that have been sampled and processed consistently from 1991 to 2003 to evaluate relationships with fish and zooplankton. Freshwater flow is measured in each tributary by the United Stages Geological Survey. Monthly mean flow data from 1991 to 2003 from the most downriver stream-flow gauge locations on the James, Rappahannock, and York Rivers were included in the analyses (USGS

2011). For the lower Chesapeake Bay mainstem, flow data for the James,

Rappahannock, York, Potomac, and Susquehanna Rivers were summed to

approximate freshwater flow to the lower Bay mainstem.

Data analysis

Annual fish community analyses

Annual species diversity and annual species richness (Pielou 1974) were

calculated for the fish community in each system and analyzed for trends using

analysis of covariance (ANCOVA). Catch data from each tributary and the

mainstem lower Bay were analyzed with Principal Components Analysis (PCA).

Species with frequency of occurrence in catches of at least 15% were selected

for these analyses to reduce the number of zero catches in the data. When

possible, length-frequency distributions were used to separate the catch data for

each species into multiple age classes or size classes (Table 2). PCAs were

conducted on annual and seasonal means. Observation data for the tributary

analyses were the $\log_{10}$(mean+1) catches of the selected species at each fixed

station. Observation data for the lower Bay analyses were the $\log_{10}$(mean+1)

catches of the selected species in each geographic stratum (Table 3).

Size spectrum analyses

Dry weight (DW) estimates specific to each zooplankton taxon and life

stage were obtained from the Chesapeake Bay Program or from the literature.

An estimate from a related species was used if a DW estimate for a specific

taxon could not be found. Taxon-specific DW to wet weight (WW) conversions

were used to estimate wet weight size classes. If no taxon-specific conversion

was found, dry weight was assumed to be 15% of wet weight (Jørgensen et al.

1991). The CBP did not measure zooplankton sizes; therefore, the DW

estimates and DW:WW conversions were not size-specific. For example, all

adult *Acartia tonsa* copepods were assigned a dry weight of 12.3 µg (CBP 2007).

Length-weight relationships for each fish species were derived from the literature

to estimate weights of individual fish. When no species-specific relationship

could be found, the length-weight relationship from a related species or similarly

shaped species was used.

Size classes were selected for the analyses based on a plot of the

coefficient of variation (CV) of mean abundance vs. size class. Size classes

exhibiting sudden increases in the CV were assumed to be poorly sampled and

excluded from the analyses. The size classes exhibiting higher CVs occurred at

the extremes of the size distribution and, if they had been included in analyses,

would have had high statistical leverage in the regressions used to quantify the

NBSS parameters. The size range for zooplankton was 0.061 to 3.91 mg (-14 to

-8 in $\log_2$ units). For the fish analyses, only individuals from 0.04 to 2,896 g were

included in the analyses (-4.5 to 11.5 in $\log_2$ units). Normalized biomass size

spectra (NBSS) for zooplankton and fish in each system were then constructed

using the seasonal and annual mean concentration of organisms in each size

class. The seasonal and annual integral spectra were quantified with linear

regression. Following recommendations by Daan et al. (2005), the x-axis (size

class) was centered to reduce the correlation between the intercept and slope

estimates for the zooplankton, fish, and combined zooplankton-fish integral

spectra. Daan et al. (2005) referred to the intercept estimate from the centered

size spectrum as the "height" of the size spectrum. Biomass domes were

quantified using quadratic regression and the following model:

$$y = 0.5c(x - h)^2 + k$$

where y = $\log_2$(number/m^3)
x = the $\log_2$ size classes
c = curvature of the biomass dome or subdome
h = size at peak abundance, i.e. the x-coordinate of the parabola
vertex
k = peak abundance, i.e. the y-coordinate of the parabola vertex

The size at peak abundance is derived for the most common size class, and the

peak abundance is the abundance of that size class (Sprules and Goyke 1994;

Kerr and Dickie 2001; Duplisea and Castonguay 2006). The curvature describes

how broad or narrow the biomass dome is. The curvature parameter is complex

and based on the predator-prey size ratio and production to biomass ratio, which

inhibits simple interpretation without independent estimates of those parameters

(Duplisea and Kerr 1995). Thiebaux and Dickie (1993) stated that curvature of a

biomass dome or subdome is an index of food supply available to a trophic level,

and Sprules and Goyke (1994) proposed that broader curvature indicated greater

ecosystem productivity.

Trends in the seasonal or annual NBSS parameters estimates (curvature, peak abundance, size at peak abundance, integral spectrum slope, and integral spectrum height), mean biomass/m^3, mean individual size (mass) per tow, and mean abundance/m^3 were analyzed with ANCOVA. Quantile-quantile plots (Q-Q plots) were visually inspected to insure that the transformed values and the NBSS parameters met the assumptions of normality for the trend analyses. An α level of 0.10 was used for all analyses. The α = 0.10 level was selected to lower the possibility of making a type II error because failing to recognize an important change in the fish community structure could be detrimental to management efforts (Peterman 1990).

Combined NBSS

Annual zooplankton and fish NBSS were combined, the x-axis centered, and linear regression used to estimate the slope and height parameters of the resulting integral spectra. Trends in the slope and height of the combined zooplankton-fish integral spectrum were analyzed with linear regression. Following from size spectrum theory, the biomass dome parameters (curvature, peak abundance, and size at peak abundance) of one trophic level should be predictable given the parameters of another trophic level because of the predator-prey and allometric relationships upon which size spectrum theory is based (Sprules and Goyke 1994; Kerr and Dickie 2001). Therefore, parameters for the zooplankton and fish biomass domes were detrended to reduce trend-driven correlations and the residuals tested to determine if the zooplankton

biomass dome parameters were correlated with the fish biomass dome
parameters.

<u>Analyses of environmental data</u>

Flow and water quality data were averaged by year and by season for
each year for inclusion in analyses of the annual NBSS parameter estimates for
zooplankton and fish, community metrics (species richness and species
diversity), and metrics based on size and abundance. Seasons were based on
the meteorological convention, i.e. December, January, and February as winter,
March, April, and May as spring, etc. Regression trees (R package "rpart",
Therneau and Atkinson 2002) were used to evaluate relationships among the
environmental data (water quality and freshwater flow data) and the NBSS
parameters and other size and abundance metrics. System (James,
Rappahannock, York, Bay) was entered as a categorical variable to determine if
the NBSS parameters or metrics from the four systems responded differently to
any of the environmental variables. Regression trees, an alternative to traditional
regression techniques for detecting thresholds, have advantages over linear
regression for exploratory analyses, including rapid evaluation of variables from
multivariable datasets, more flexibility in the types of interactions allowed
between predictors, and straightforward interpretations when numeric and
categorical variables are used (Clark and Pregibon 1997). The robustness of
regression trees was examined using 10-fold cross validation (Faraway 2006).
Trees with cross validation relative error estimates greater than 1 or a coefficient

of determination less than 20% were rejected because of low utility as predictive models.

Results

Annual analyses

Fish community analyses

Over the 13-yr survey period, annual species richness declined significantly and at similar rates in each of the tributaries (Table 4; Figure 2A). The trend in annual richness for the lower Bay was not significant. All intercepts of the richness trends differed significantly, with the mainstem lower Bay having the highest richness (mean annual richness = 74 species) and the Rappahannock River having the lowest (mean annual richness = 39 species; Figure 2A). Several species present in the early survey years in the lower Bay and tributaries were absent from tows by the end of the time series, including silver hake (*Merluccius bilinearis*), red hake (*Urophycis chuss*), Atlantic thread herring (*Opisthonema oglinum*), Atlantic herring (*Clupea harengus*), Spanish mackerel (*Scomberomorus maculatus*), and conger eel (*Conger oceanicus*). Depending on the system, these species went missing between 1995 and 2000; furthermore, other species that occurred sporadically throughout the time series occurred more frequently during the first half of the times series.

Annual species diversity increased significantly in the lower Bay and James River over the survey years (Table 4; Figure 2B). Observed annual

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diversity for the Rappahannock and York Rivers also increased but the trends were not significant. The three tributaries were similarly diverse while the lower Bay had the lowest species diversity. Analyses of abundance trends for individual species detected significant declines in 26, 17, 11, and 8 species in the lower Bay, James River, Rappahannock River, and York River, respectively (Table 5). For those systems, only 9, 5, 3, and 7 species exhibited significant increasing trends in abundance. The species with positive trends were primarily alosines, moronids and sciaenids.

Scree plots of the eigenvalues from each of the annual PCAs (Figure S3) depicted 8-10 principal components with eigenvalues greater than one, which indicates that the PC captures as much variance as a single standardized variable (Kaiser 1960). The slopes of the scree plots tended to change after PC2, which indicated that the first two PCs captured the dominant axes of variability (Johnson 1998), and the first two PCs were retained for interpretation. Loadings for the principal components with eigenvalues > 1 are listed in Tables S7-S10.

In a comparison of tributaries, three assemblages were evident in the PCA of the annual mean catch data from the James (Figure 3) and Rappahannock Rivers (Figure 4) corresponding to the oligohaline, mesohaline, and polyhaline regions of each river, and these assemblages ordinated along PC1 (22.5% and 25.7% of the variance, respectively). Two less distinct assemblages in the York

River (Figure 5) ordinated along PC1 (17.8% of the variance) and represented a

combined oligo-mesohaline assemblage and a polyhaline assemblage. The

second PC represented 10.3 - 11.1% of the variance and reflected temporal

changes in each of the assemblages as indicated by the significant correlations

between the PC2 scores for each tributary and year (Table 6; Figures 3-5). The

shift appeared to have occurred between 1995 and 1997 for the assemblages in

the three tributaries based on visual inspection of Figures 3-5. For example, the

prominent species of the oligohaline assemblages in each of the three tributaries

shifted from all sizes of hogchoker (*Trinectes maculatus*), American eel (*Anguilla*

rostrata), all sizes of white catfish (*Ameiurus catus*), and gizzard shad (*Dorosoma*

cepedianum) < 200 mm to all sizes of blue catfish (*Ictalurus furcatus*), age 0

white perch (*Morone americana*), age 0 striped bass (*Morone saxatilis*), and

gizzard shad > 200 mm. The polyhaline assemblages in the tributaries also

shifted in species or age-class composition. The polyhaline assemblages

generally shifted from spot (*Leiostomus xanthrus*), oyster toadfish (*Opsanus tau*),

bay anchovy, and age 0 and 1 summer flounder (*Paralichthys dentatus*) to

kingfishes (*Menticirrhus sp.*), black sea bass (*Centropristus striata*), butterfish

(*Peprilus triacanthus*), age 2+ summer flounder, and age 2+ Atlantic croaker

(*Micropogonias undulatus*). The mesohaline assemblages shifted toward lower

abundance of included species rather than a change in species composition.

In the mainstem lower Bay, multiple patterns were evident in the PCA

biplots (Figures 6A and 6B). PC1 captured 19.8% of the variance and correlated

with depth (r = +0.655, $p < 0.0001$) and bottom temperature (r = -0.525, $p < 0.0001$) measured at the time of collection. The mean bottom temperature of all observations was 16.9°C, and stations with above average bottom temperatures had negative PC1 scores while stations with below average temperatures had positive PC1 scores. Except for kingfishes, striped anchovy (*Anchoa hepsetus*), inshore lizardfish (*Synodus foetens*), and smallmouth flounder (*Etropus microstomus*), remaining species loaded positively on PC1 (Figures 6A and 6B). Station depth provided the most distinct separation of the data (Figure 6A). Stations from the shallow strata (< 9.14 m) scored negatively on PC1, and the stations from the deeper strata (> 9.14 m) had positive scores. PC2 for the lower mainstem Bay captured 11.4% of the variance and was correlated with bottom salinity (r = -0.484, $p < 0.0001$) and bottom dissolved oxygen (r = -0.506, $p < 0.0001$) measured at the time of collection. The data also exhibited a north-south pattern with the northern strata having positive PC2 scores and the southern strata having negative scores (Figure 6B). The PC2 scores of the central strata were between the extremes of the northern and southern strata. The temporal trend for the lower mainstem Bay fish community was distributed across the first two PCs (Table 6; Figure 6) and reflected declining catches of nearly all species and age/size classes included in the analysis.

The long-term temporal patterns in the seasonal PCAs for the Virginia tributaries mirrored those in the annual analyses. PC1 captured 17.5% and 19.9% of the variance in the James and Rappahannock Rivers, respectively, and

represented both the salinity gradient and seasonal differences in the fish community. The oligohaline assemblage had positive scores on PC1 for these two rivers; the polyhaline assemblage had negative scores; and the mesohaline assemblage scores were intermediate. The summer and fall data tended to have primarily negative scores on PC1 while the winter and spring data had mostly positive scores. PC2 captured 11.1% and 12.7% of the variance in the James and Rappahannock Rivers and represented the temporal change in each of the assemblages or overall reduced abundance (Table 7). The York River differed in patterns partitioned on each PC. In the York, the summer and fall data had negative scores on PC1 (17.8% of the variance) while winter and spring had positive scores. The polyhaline data for the York scored positively on PC2 (14.5% of the variance), and the oligohaline data had negative scores. Additionally, PC2 represented the long-term temporal changes in each assemblage in the York River (Table 7).

Based on the correlations between the PC2 scores and year, seasonal changes in species composition for each assemblage were judged to differ among tributaries (Table 7). In the James River, the PC2 scores for the polyhaline assemblage were significantly correlated with year during summer and fall. The PC2 scores for the James River mesohaline assemblage were correlated with year from spring through fall. The PC2 scores for the James River oligohaline assemblage were significantly correlated with year during all seasons. In contrast, the significant correlations between year and PC2 scores

for the Rappahannock River polyhaline assemblage occurred only in winter and only in fall for the mesohaline assemblage. The PC2 scores were significantly correlated with year for all seasons for the Rappahannock River oligohaline assemblage. Significant changes occurred in the species composition of the York River polyhaline assemblage during all seasons, and the York's oligohaline assemblage exhibited significant changes in species composition during all seasons except summer.

The patterns observed in the seasonal PCA for the lower Bay differed from those of the annual PCA. There was no clear separation among the depth strata (< 9.14 m and >9.14 m) across seasons. The data for each of the seasons fell into the different quadrants on the biplot. The winter data had negative scores on PC1 (27.6% of the variance) and on PC2 (13.1% of the variance), and the spring had negative PC1 scores and positive PC2 scores. The data from summer scored positively on both PCs while the fall data scored positively on PC1 and negatively on PC2. The winter assemblage was composed of YOY and age 1+ Atlantic menhaden and blueback herring. Spotted hake (*Urophycis regia*) was the only species included in the analysis that represented the spring lower Bay assemblage. The spring assemblage was composed of age 1 and 2+ summer flounder, age 1 and 2+ Atlantic croaker, age 1+ spot, age 1+ silver perch, scup, butterfish, black seabass, large hogchokers, and age 1+ blackcheek tonguefish. In the fall, YOY spot, weakfish, summer flounder, silver perch, Atlantic croaker, and blackcheek tonguefish were collected most frequently in the

lower Bay as were kingfishes, smallmouth flounder, pigfish, inshore lizardfish, striped anchovy, and bay anchovy. The long-term trends for each seasonal assemblage in the lower Bay were weaker than those for the tributaries, and the pattern was spread across both PC1 and PC2 (Table 7). For the Bay, there were significant correlations between year and the first two PCs in the fall. There was also a significant correlation between year and PC1 for the summer. The summer and fall assemblages were the most well-defined by species included in the analysis, which increased the likelihood of detecting significant changes in the species composition.

Size and abundance metrics: zooplankton

The annual NBSS for zooplankton were variable but generally parabolic (Figure 7). Linear and quadratic regressions were fit to the data. Twenty-four of the 36 centered linear regressions and 27 of 36 quadratic regressions were statistically significant ($p < 0.10$). The significant centered linear regressions explained 19.6 - 62.2% of the variance, while the quadratic regressions often fit better, capturing 30.1 - 80.6% of the variance. Slopes of the significant integral spectra ranged from -1.85 to -0.65 with the mean near -1, the slope predicted by theory. Linear regressions on the abundance of the zooplankton taxa in the lower Bay, James, Rappahannock, and York Rivers detected 14, 21, 12, and 11 taxa with significant negative trends, respectively (Table 8a) and 2, 3, 4, and 5 taxa with positive trends, respectively (Table 8b) .

Many taxa that declined in abundance over the 13-yr survey period were prominent, such as the copepod genera *Acartia*, *Centropages*, *Oithona*, and *Paracalanus*, the cladoceran *Evadne*, and barnacle nauplii. Their declines strongly influenced the size spectrum parameters. Consequently, several NBSS parameters for zooplankton exhibited significant ($p < 0.10$) trends (Table 9). Slopes of the integral spectra became significantly more positive in the Rappahannock and York Rivers (Table 9; Figure 8A) because of the decreased abundance of several taxa in the smaller size classes. Furthermore, mysid shrimp, which occupy the larger zooplankton size classes, became more abundant in the Rappahannock and York, which contributed to the positive trends in the integral spectrum slopes. The heights of the integral spectra declined in all systems except the York River (Table 9; Figure 8B).

Significant trends in biomass dome parameters were detected in all systems; however, the patterns were not always consistent across systems. Peak abundance declined significantly over the 13 years in all systems except the York River (Table 9; Figure 9A). The observed negative trends in the heights of the integral spectra and peak abundance of the biomass domes for all systems except the York River resulted from the decline in numbers of many abundant taxa. The height of the York River integral spectrum for zooplankton and the peak abundance of its biomass domes did not decline over years in the York River because highly abundant taxa did not decline or did not decline as strongly as in the other systems. Size at peak abundance increased significantly in the

York River (Table 9) because several larger taxa in the zooplankton analyses, including dipteran larvae, *Neomysis*, and *Rhithropanopeus* larvae, became more abundant during the study period. The Rappahannock River was the only system with a significant trend in biomass dome curvature, which became broader during the time series (Table 9; Figure 9B).

Due to the parabolic nature of the zooplankton seasonal NBSS, the majority of the linear regressions describing the seasonal integral spectra were not statistically significant and were not analyzed for seasonal trends. The trends that were apparent in the annual zooplankton biomass dome parameters were generally attributable to effects in one or two seasons, which were not always consistent across systems (Tables 10 - 12). The declines in peak abundance in the James River, Rappahannock River, and lower Bay were significant during summer (Table 10). Additionally, peak abundance also declined significantly in the winter in the lower Bay and during the spring in the James River. The declines in peak abundance for these systems resulted from negative trends in abundance of many of the prominent taxa noted earlier. A significant increase in the abundance of mysids in the York River resulted in a significant increase in size at peak abundance during the summer (Table 11) and a significantly broader curvature during the spring (Table 12). An increase in mysid shrimp abundance also contributed to the significant increase in the summer and fall biomass dome curvature in the Rappahannock River (Table 12). The recorded decline in size at peak abundance during fall in the Rappahannock River (Table 11) is believed to

be anomalous, resulting from an anomalously low estimate of size at peak

abundance in fall 2001 attributable to a poor fit of the quadratic regression for the

biomass dome in that year.

There were significant negative trends in annual mean abundance (Figure

10A) and biomass (Figure 10B) of the zooplankton communities in the lower Bay

and its tributaries (Table 13). The slope of the decline in annual mean

abundance of zooplankton in the lower Bay was more negative (ANCOVA, p =

0.005) and the intercept higher (ANCOVA, p = 0.005) than the slope and

intercept for the York River (Figure 10A). The slopes of the negative trends in

zooplankton biomass did not differ among systems, but the intercept for the

Rappahannock River was significantly higher than those for the James or York

Rivers ANCOVA, p = 0.020 and p = 0.026, respectively; Figure 10B). There

were no significant trends in mean mass of an individual zooplankter.

Unlike the NBSS trends over the 13 years in the seasonal biomass dome

parameters for zooplankton, trends in the biomass and abundance metrics were

observed in multiple seasons in each system. Mean zooplankton abundance

trended downward for winter, spring, and summer in the lower Bay,

Rappahannock River, and York River (Table 14). The James River seasonal

zooplankton abundance data were more variable than the other systems, and

there were no seasonal trends. Mean biomass trends were negative for all

seasons in the lower Bay and in winter through summer in the Rappahannock

River (Table 15). The only significant seasonal biomass trend in the York River was for winter. Mean mass of an individual zooplankter decreased in the James River during spring, but there were no other significant seasonal trends in the other systems.

Size and abundance metrics: fish

The fish NBSS were parabolic (Figure 7) and less variable than the zooplankton NBSS. The linear regressions of the NBSS integral spectra explained only 7 - 65% of the variance, but quadratic regressions of the annual fish NBSS biomass domes fit the data well and explained 79 - 96% of the variance. The slopes of the integral spectra were flatter than the -1.0 predicted by theory and ranged from -0.58 to -0.15 with a mean of -0.36. The declining abundances of many species in each system affected the NBSS parameters of the fish communities (Table 16). Specifically, the declining abundance of several highly abundant species, such as bay anchovy and hogchoker, resulted in significant linear trends in the height of the centered integral spectra and both the peak abundance and the curvature of the biomass domes in all four systems (Figures 11 and 12; Table 16).

Only the James and Rappahannock Rivers had significant trends over years in the slope of the integral spectra (Table 16), which increased significantly (became flatter) at a similar rate (Figure 11A). With the exception of the lower

Bay, the height of the centered integral spectra declined at similar rates for all systems (Table 16; Figure 11B). The apparent trend in integral spectrum height for the lower Bay would have been significant if the height estimate for 2003, which was similar in level to estimates at the beginning of the time series, were removed. Peak abundance of the biomass domes declined at similar rates in the tributaries and in the lower Bay (Table 16; Figure 12A). The intercept for the lower Bay peak abundance was significantly lower than the intercepts for the other three systems (Table 16, Tukey multiple comparison, $p < 0.0001$), indicating consistently lower peak abundance in the lower Bay. Additionally, the intercept of the Rappahannock River peak abundance trend was significantly lower than that of the York River (Table 16, Tukey multiple comparison, $p = 0.027$).

The declining abundance of several dominant species over the 13-yr period increased the evenness in abundance of size classes. As a result, the curvature of the biomass domes became broader in all four systems, with no significant differences among systems in the slopes or intercepts of the trends (Tukey multiple comparison $p > 0.10$ Table 16; Figure 12B). Size at peak abundance decreased significantly only in the lower Bay (Table 16) because of strong declines in abundance of several species in the 16-181 g size classes (Table 5), as well as slight increases in abundance of fishes in the 0.04 - 0.06 g size classes.

The parameter estimates of the seasonal integral spectra of the fish communities in the lower Bay and its tributaries were more variable than the annual integral spectra and less suited for fits to linear regression. Over half of the linear regressions for the Rappahannock seasonal integral spectra were not significant; therefore, the Rappahannock integral spectra were excluded from the seasonal analyses. The height estimates declined significantly in the winter in the lower mainstem Bay, the James River, and York River, but trends in other seasons were not consistent across these systems (Table 17). The height declined during all seasons only in the James River. The slope increased significantly only for the James River in winter (Table 17).

Of the trends observed in the annual biomass dome parameters for fish NBSS (Figure 12), only the trend in peak abundance was significant in all seasons in all systems (Table 18). Curvature of the biomass domes became broader in the lower Bay, Rappahannock River, and York River during the fall (Table 19) in response to declining abundance of fish in the 0.5 g to 32 g size range. Additionally, the declining abundance of fish in this size range resulted in the summer biomass dome curvature becoming broader in the Rappahannock River. In contrast to the positive trends in biomass dome curvature observed in the other systems, curvature became narrower in the James River during winter because of strong declines in abundance of the smallest and largest size classes. In the lower Bay, curvature for the spring biomass dome broadened because of increasing abundances in the 256 g to 1024 g size classes of fish

such as kingfish and Atlantic croaker, which also produced a significant positive trend in size at peak abundance during spring (Table 20). Size at peak abundance in the lower Bay decreased in the fall (Table 20) due to declining abundance of 16 g to 256 g fish. In the James River, size at peak abundance increased in both the winter and spring because of large reductions in the abundance of fish in size classes less than 1 g.

The mean fish abundance/m^3 declined significantly in all systems, with no differences among systems in the slopes (ANCOVA, p = 0.64; Table 21; Figure 13A). The intercept of the fish abundance trend was significantly higher in the James River than in the Rappahannock River (Tukey multiple comparison, p = 0.048).   Similarly, mean fish biomass/m^3 declined significantly in all four systems, with no significant differences among slopes (ANCOVA, p = 0.84; Table 21; Figure 13B). Based on Tukey multiple comparisons of the intercept estimates, the York River had the highest biomass/m^3 (p < 0.001), the lower Bay had the lowest (p < 0.005), and James and Rappahannock Rivers had similar biomasses per tow (p = 0.30) that were intermediate to the other two systems. The three tributaries all exhibited significant, positive trends in the mean mass of individual fish collected throughout the year (Table 21; Figure 13C). This result partly derived from declining catches of abundant, small-bodied species such as bay anchovy and hogchoker. There were positive trends in the collection of relatively large blue catfish in the tributaries that also contributed to the positive

trend in mean mass. Additionally, bay anchovy, American eel, hogchoker, summer flounder, oyster toadfish, channel catfish, and white catfish, all of which declined in abundance in more than one system, exhibited significant positive trends in mean size in at least one system (Table 22). Based on visual inspection of length frequency distributions, several of these species exhibited lower abundance of smaller size classes and higher abundance of larger size classes through time. In the lower Bay, there was no trend over years in mean mass of individuals in the survey.

The seasonal trends over the 13 years in mean abundance/m^3 mirrored the declines observed in the annual trends (Table 23). The seasonal trends for mean biomass/m^3 were more variable than the annual trends (Table 24). There were no significant seasonal trends in mean biomass/m^3 in the Rappahannock. The seasonal Rappahannock trends in mean biomass/m^3 were generally negative but the interannual variability was large. There were significant negative trends over years in mean biomass/m^3 during fall in the lower Bay, James, and York Rivers. The James and York also had significant negative trends in biomass for summer, as did the lower Bay and York River in winter. Mean individual mass increased significantly for fish in the three tributaries in spring (Table 25) and in summer for the James and Rappahannock Rivers.

Combined NBSS: zooplankton and fish

Centered linear regressions accounted for 63.3 - 82.3% of the variance in the combined annual zooplankton-fish integral spectra for the 4 systems. The

slopes ranged from -0.92 to -0.68 (Figure 14A). A slope value of -1.0 predicted

by theory was outside the 90% confidence intervals for most slope estimates.

There were significant trends in the slopes (Figure 14A) and heights (Figure 14B)

of the centered NBSS (Table 26). The heights declined significantly in all

systems except the York River, which was consistent with the declines observed

for the peak abundance estimates for the zooplankton and fish biomass domes.

The NBSS slope for combined zooplankton-fish became significantly more

positive (less steep) during the survey period in the mainstem Bay and

Rappahannock River, which had the highest rates of decline in the peak

abundance of the zooplankton biomass domes.

The trend in height of the seasonal zooplankton-fish integral spectrum

declined significantly during spring through fall in the lower Bay (Table 27).

Heights of the summer zooplankton-fish spectra declined over years in the

James and York Rivers. There were no significant declines in height for any

season in the Rappahannock due to high interannual variability for each season.

The slopes of the integral spectra became flatter over years in the lower Bay

during spring and summer (Table 28).

The curvature parameters for the annual biomass domes for zooplankton

were significantly narrower (paired t-test, $p < 0.0001$) than the annual biomass

domes for fish. Contrary to theoretical expectations (Kerr and Dickie 2001), there

were relatively few statistically significant correlations between the detrended

parameter estimates of the annual zooplankton and fish biomass domes. Annual

curvatures of the zooplankton and fish biomass domes were correlated only in

the James River (r = -0.83, p = 0.022). Sizes at peak abundance of the annual

zooplankton and fish biomass domes were not correlated, and peak abundance

of the annual zooplankton and fish domes was correlated only in the James (r =

0.73, p = 0.03) and York Rivers (r = 0.70, p = 0.04).

Environmental analyses: regression trees

Only the regression trees for annual mean biomass/m^3, annual species

richness, and annual species diversity of the fish community had relative errors

and coefficients of determination that met the criteria for retention as informative

models. No zooplankton NBSS parameter regression trees were retained. The

final pruned regression tree for annual mean biomass/m^3 had four nodes, and

accounted for 51.62% of the variance, and captured the negative trend over

years in the analysis of mean biomass/m^3 in each system (Figure 15). For

annual mean fish biomass/m^3, years with high summer pH and high specific

conductance in winter had the lowest biomass/m^3 (mean = 1.09 g/m^3), which

corresponded to data from years after 1995 in the lower Bay and 2002 from the

Rappahannock River. Years with high summer pH and lower specific

conductance had the next lowest biomass/m^3 (mean = 1.54 g/m^3). These

conditions occurred in most years after 1993 in the James River, most years in

the Rappahannock, and years before 1995 in the lower Bay. The years when

summer pH was less than 7.57 and summer ammonium concentrations were

less than 0.045 mg/L had the second highest mean biomass/m^3 (mean = 1.92 g/m^3), which occurred in the York River for most years between 1995 and 2002 and during 1999 in the James River. The highest biomass/m^3 (mean = 2.41 g/m^3) occurred when summer pH was less than 7.57 and summer ammonium concentrations were ≥ 0.045 mg/L, which corresponded to most years before 1996 in the James River, 1991 and 1997 in the Rappahannock River, and 1991-1994, 1998, and 2003 in the York River.

The final pruned regression tree for annual species richness had three nodes, accounted for 81.87% of the variance, and reflected the system-level differences in annual richness but not the negative trends (Figure 16). The highest richness occurred in the lower Bay (mean = 74.38 species per year). The second highest richness occurred in the James River (mean = 54.40 species per year) when annual mean nitrate plus nitrite was greater or equal to 0.19 mg/L, which was the case in all years except 1998, 2000, and 2001. The lowest richness (40.79 species per year) occurred in all years in the Rappahannock and York Rivers, and in the James River during 1998, 2000, and 2001. The annual mean nitrate plus nitrite in these systems during these years was less than 0.19 mg/L.

The final pruned regression tree for annual species diversity separated the lower Bay and several years of low diversity in the James River (1992-1994 and 1998) from the Rappahannock River, York River, and years of higher diversity in the James River (Figure 17). There were only two nodes, and the regression

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tree accounted for only 26.53% of the variance. Low diversity (mean = 1.08) occurred when spring flow was greater than or equal to 315.9 m^3/s. Years and systems with lower spring flow had higher diversity.

Discussion

There were substantial changes in the species composition of fish communities in the lower Chesapeake Bay and its tributaries from 1991 to 2003 detected using traditional community assemblage analyses. The declines in abundance of several fish species in each system indicated lower species richness but increased diversity due to greater evenness in abundances, more even size distributions, lower abundances, and lower biomass in the fish community of each system by the end of the time series. Numerous prominent zooplankton taxa also declined during the same time period. Analyses of NBSS parameters and other metrics, based on size and abundance, quantified the effects of changes in species composition on the size distribution of the fish and zooplankton communities.

The 2-3 fish assemblages in the tributaries of the lower Chesapeake Bay detected by the PCAs corresponding to oligohaline, mesohaline, and polyhaline assemblages were consistent with previous studies of fish species composition along estuarine salinity gradients (Peterson and Ross 1991; Marshall and Elliot 1999; Wagner and Austin 1999; Jung and Houde 2003; Martino and Able 2003). That PC1 reflected the salinity gradient was reflected on PC1 indicates that more

variability in the species composition and abundance was due to salinity than to the temporal trends in each assemblage, which was evident along PC2. The temporal trends in each assemblage resulted from changes in abundance of the individual species within each assemblage rather than a major shift in species composition. The temporal trends in each assemblage in each tributary suggest that the driving factor or factors behind the trends in the fish community are not restricted to individual tributaries or regions within each tributary.

There were multiple ways to delineate assemblages in the lower Chesapeake Bay mainstem as result of multiple spatial gradients in salinity, temperature, dissolved oxygen, and depth. These abiotic factors have been found to structure other estuarine and marine fish communities (Colvocoresses and Musick 1980; Peterson & Ross 1991; Rakocinski et al. 1992; Szedlmayer & Able 1996). However, separating the relative importance of the abiotic factors is difficult given the near perfect collinearity among some of them, such as the east-west and north-south gradients in salinity, depth, and dissolved oxygen. Unlike the tributaries, the temporal trend was correlated with both PC1 and PC2, which suggests that the temporal trend was a larger contributor to the variability of the fish community structure in the lower Bay than in the tributaries.

In the lower Bay and its tributaries, there were significant declines in abundance of nearly all size classes of fishes in the trawl survey data during the 1991-2003 survey period. As a result, the heights of the integral spectra declined significantly in all systems without consistent effects on the slope. The

zooplankton integral spectra behaved in a similar manner. In heavily fished

ecosystems, the slope of the integral spectrum becomes steeper, in part because

of the selective removal of the largest size classes (Haedrich and Barnes 1997;

Bianchi et al. 2000; Kerr and Dickie 2001; Blanchard et al. 2005; Daan et al.

2005) and potential increases in abundance of smaller fishes in response to

lower predation rates or reduced density dependence (Jennings and Blanchard

2004; Blanchard et al. 2005). In the lower Bay and tributaries, the declines in

abundance across all size classes, many of which contained unfished species,

probably were not directly related to fishing.

The annual height estimates for the fish and zooplankton integral spectra

for the lower Bay and its tributaries behaved as an index of abundance as

suggested by Yemane et al. (2008) and had similar declining trends as

abundance/m^3. In many heavily fished systems, such as the North Sea, the

intercept of the integral spectrum increased with increasing fishing pressure in

long-term analyses (Rice and Gislason 1996; Bianchi et al. 2000; Nicholson and

Jennings 2004) and in simulations (Gislason and Rice 1998; Pope et al. 2006).

However, Rice and Gislason (1996) suggested that the small increase in

intercept they observed may have been caused by significant correlation with the

slope estimates, which had become more negative (steeper). Daan et al. (2005)

addressed the correlation between slope and intercept estimates by centering

the x-axis (the size classes), which reduced the correlation between slope and

intercept. The height (centered intercept) of the North Sea integral spectra

declined significantly based on data from three fisheries-independent surveys and despite significant increases in the smallest size classes (Daan et al. 2005), suggesting that fishing reduced the overall abundance of the entire fish community. While the slope and intercept estimates in my study remained correlated after centering the x-axis, the height estimates exhibited similar negative trends with respect to peak abundance of the biomass dome and mean abundance. The similarity of these trends suggests that the height parameter reflects changes in abundance despite its correlation with the slope parameter. Given the statistical complications of analyzing trends in both the slope and intercept of integral spectra, using the height of the centered integral spectrum may be a more reliable indicator for monitoring changes in abundance.

Trends in two of the three biomass dome parameters for the fish communities of the lower Bay and its tributaries contrasted with behavior of trends in biomass dome parameters reported by Duplisea and Castonguay (2006) for the Scotian Shelf and other heavily fished North Atlantic ecosystems. The peak abundance parameter in NBSS declined over the survey years in the lower Bay and its tributaries, resembling results reported by Duplisea and Castonguay (2006) and suggesting that peak abundance is a sensitive indicator of any perturbation that affects abundance of a fish community. Size at peak abundance declined in the lower Bay, but not its tributaries, because of declining abundance of large size classes represented by elasmobranchs and flatfishes, a response similar to that observed in Sydney Bight, the Scotian Shelf, Georges

Bank, and the North Sea (Duplisea and Castonguay 2006). However, no significant changes in size at peak abundance were detected in the lower Chesapeake Bay tributaries despite the declines in abundance of a wide range of sizes. Thus, size at peak abundance appears to be sensitive only to size-selective perturbations rather than those affecting a wide range of sizes.

The curvature of the biomass domes summarized by Duplisea and Castonguay (2006) became narrower as the size range contracted due to removals of the largest size classes by commercial fisheries. The size range of fishes in the biomass domes of the lower Bay and its tributaries remained nearly constant over the survey years, but the curvature broadened significantly because abundances of size classes became more even as the peak abundances declined. Interpreting NBSS biomass dome curvature values is not straightforward because curvature is complex, represented as the ratio of the allometric exponent in the relationships between the biomass density ratio of predators and their prey and the logarithm of the ratio of predator-prey mass (Kerr and Dickie 2001). While the curvature parameter provides a useful visualization of size structure in fish communities, its response to ecological perturbations is not easily predicted from first principles (Duplisea and Castonguay 2006).

Jennings and Blanchard (2004) found that removal of large-bodied fishes in the North Sea resulted in substantial decreases in the turnover time of the fish

community, which could increase interannual variability in biomass and production. In the lower Chesapeake Bay and its tributaries, many of the species declining in abundance were small-bodied, with bay anchovy having a large influence on the trends in abundance and biomass. The broadening curvature of the annual fish domes indicated that size distribution became more even across size classes in the Bay and the three tributaries. Given these results and based on the results of Jennings and Blanchard (2004), the decreased prevalence of small-bodied fishes in the lower Bay and its tributaries suggested that the size distributions of fishes may exhibit less interannual variability as the abundance of small-bodied fishes declined. However, the declining trends in peak abundance and broadening curvature indicated that the size distributions had not stabilized by the end of the time series, which inhibited evaluation of changes in interannual variability.

The negative trends over a 13-yr period observed in metrics based on size and abundance of fish communities in the lower Chesapeake Bay and its tributaries bore general resemblance to long-term trends in large, heavily fished marine ecosystems (Haedrich and Barnes 1997; Jennings and Blanchard 2004; Blanchard et al. 2005; Daan et al. 2005; Piet and Jennings 2005; Duplisea and Castonguay 2006; Blanchard et al. 2010; Bundy et al. 2010). Mean abundance and biomass of fished size classes typically decline with increasing fishing pressure due to removals by the fishery (Rochet et al. 2005; Bundy et al. 2010; Shin et al. 2010). Mean size also declines as large fish are removed from the

community (Overholtz and Tyler 1985; Haedrich and Barnes 1997; Rochet et al. 2005; Blanchard et al. 2010). However, mean size can decline because of increased abundance of small species (Jennings and Blanchard 2004; Blanchard et al. 2005). In Chesapeake Bay, mean size increased in the tributaries of the lower Bay due to the substantial declines in abundance of many unfished species representing the smaller size classes, the most important of which was bay anchovy. This result suggests that mean size might be a more sensitive indicator than size at peak abundance for detecting ecosystem perturbations. The combination of size, abundance, and biomass metrics provides complementary information that can be used to determine where in the size distribution the perturbations occurred and possible causes of the perturbations (Shin et al. 2005). For example, in the tributaries of the lower Bay, the declines in mean abundance and biomass, combined with the increase in mean size, indicated that declines in smaller taxa and size classes (e.g., bay anchovy, hogchoker) were driving the changes in abundance and biomass.

The NBSS parameters for zooplankton and the metrics based on size and abundance detected trends consistent with other long-term analyses of zooplankton in the mesohaline and polyhaline region of Chesapeake Bay (Kimmel et al. 2004; Roman et al. 2005). Kimmel et al. (2004) analyzed the abundance of *Eurytemora affinis* and *Acartia tonsa* in the mainstem of Chesapeake Bay from 1985-2000 using the Chesapeake Bay Program mesozooplankton data. While only a slight negative trend was detected for

Acartia in the mesohaline region (Kimmel et al. 2004), there appeared to be a low-frequency, negative trend in the polyhaline region of the Bay that might have been obscured by a high-frequency seasonality signal. Using an optical plankton counter, Roman et al. (2005) analyzed spatial and temporal variability of zooplankton for the entire mainstem of Chesapeake Bay for four years (1996, 1997, 1999, and 2000). While the emphasis of the Roman et al. study was on seasonal and regional variability, there appeared to be a significant negative bay-wide trend in zooplankton abundance based the data shown in their Table 1, which I analyzed with linear regression (slope = -15.54 mg C m^{-3} yr^{-1}, r^2 = 82.35%, *p* = 0.061; Roman et al. 2005). The trend observed in the data of Roman et al. (2005), which were collected and analyzed using different protocols than the CBP, suggests that my results for the lower Bay and its tributaries are likely not an artifact of the change in CBP zooplankton counting methodology.

In my research on the lower Bay and tributaries, the slopes of the fish integral spectra and the combined zooplankton-fish integral spectra were flatter than predicted by theory (Kerr and Dickie 2001) or observed in the Lakes Ontario and Michigan zooplankton and fish communities (Sprules and Goyke 1994). The flat slopes of the Chesapeake fish integral spectra may have resulted from inclusion of some benthivorous or partially benthivorous fishes, such as Atlantic croaker and spot. This circumstance would flatten the slope because of the greater number of fish occupying the size classes could not have been fully supported by consuming small fish or zooplankton. Jung and Houde (2005)

observed similar results when benthivorous fishes were included in their size spectra for the fish community in the mainstem Chesapeake Bay. In their case, when only piscivorous and zooplanktivorous fishes were included in the spectra, slopes for the integral spectra steepened and were close to -1.

An alternative explanation for the flatter than expected slopes of the combined zooplankton-fish integral spectra is the possible underestimation of abundance of smaller size classes of zooplankton despite adoption of the Hensen-Stempel pipette method that was developed to count zooplankton aliquots (Harris et al. 2000). In another component of my research, the slopes of the zooplankton-fish integral spectra in the Choptank and Patuxent Rivers were closer to -1 (Chapter 3). Those tributaries were sampled using high-frequency acoustics (the Tracor Acoustic Profiling System TAPS) to estimate zooplankton abundance. Microzooplankton, which are largely absent from the CBP mesozooplankton data, are included in the TAPS estimates, thus increasing the abundance of organisms at the small-size end of the spectrum. Another possible explanation for the relatively flat slopes of the zooplankton-fish integral spectra is the relatively steep, declining trend from peak abundance in the zooplankton domes (2 to 5.6 times faster than the trend from peak abundance in the fish biomass domes) in all systems except the York River. Extending the analysis of the zooplankton and fish time series back to the initiation of the CBP monitoring program in 1985 might help to resolve this issue. However, caution is required if such an analysis is undertaken because different trawl doors were used in the

VIMS Trawl Survey prior to 1991 that may have altered the fish abundance estimates.

The biomass dome parameters for the fish and zooplankton communities in the lower Bay and tributaries were less similar than predicted. In theory, the spacing between biomass domes and their curvatures should be similar and consistent among trophic levels (Kerr and Dickie 2001; Sprules and Goyke 1994; Sprules and Stockwell 1995). In addition to effects of including benthivorous fishes and the possible underestimation of small zooplankton mentioned earlier, the fixed sizes assigned to each zooplankton taxon could have contributed to the dissimilarity between the fish and zooplankton biomass domes and to the higher variability of the zooplankton NBSS data. In my zooplankton analysis, each taxon was assigned to a single size class. Consequently, a large catch could result in a high peak for the single size class rather than a lower peak associated with multiple size classes as was the case for the fish data. Variability in the NBSS data depends in part upon how evenly abundances are distributed with respect to the sizes of zooplankton collected at each station.

Seasonal patterns in the NBSS parameters and metrics based on size and abundance generally were not consistent across systems. However, one consistent pattern for both the zooplankton and fish communities were the significant declines in abundance, biomass, the intercept of the integral spectrum, and peak abundance of the biomass domes during summer and, to a

lesser degree, in fall for all systems that had significant interannual trends in these metrics and parameters. Furthermore, the rates of decline during summer and fall were similar to the interannual decline rates. This result suggests that causes of the declines in the aforementioned metrics and parameters are operating during the summer and fall or, alternatively, the cumulative effects of perturbations occurring earlier in the year become strong enough to detect by summer and fall. There were similar trends during other seasons for many of these metrics and parameters but the interannual variability resulted in the slope estimates for the trends having high and non-significant p-values. Data from additional years or more intensive sampling within each season might have provided statistical power required for more precise estimates of the slope of the trends.

The fish species that declined in abundance from 1991-2003, or were no longer represented in the catches in the later years of the VIMS Trawl Survey, were not easily categorized as groups (or guilds) with similar characteristics that might provide insight into the causes of their declines (Table 5). If shifts in spatial distributions of the declining species caused the observed declines, the distributions would have had to shift up-estuary of the salt front in the tributaries and into the Maryland portion of the mainstem Chesapeake Bay, or down-estuary and outside the mouth of the Bay. Up-estuary shifts in the 13-yr period seem unlikely for mesohaline and polyhaline species that are physiologically limited by salinity. Trends in the VIMS Juvenile Striped Bass Seine Survey, which samples

into the tidal freshwater regions of the tributaries 25-30 km beyond the most up-estuary station included in the analyses of the Trawl Survey data, confirmed many of trends observed in the trawl survey data. This result suggests up-estuary shifts in species distribution were unlikely. Possible down-estuary shifts in spatial distributions and movement of species outside the mouth of the Chesapeake Bay cannot be rigorously evaluated with the available data. Northerly shifts on the continental shelf of several marine species that reside in the Chesapeake Bay as juveniles, such as red hake, silver hake, and spotted hake, were documented by Nye et al. (2009). These northerly shifts in the populatons may have reduced the probability of their juveniles entering the Chesapeake. Additionally, climate-related changes in temperature, winds, and circulation patterns on the shelf off the mouth of Chesapeake Bay potentially induced changes in spawning areas and times for coastal-spawning species such as menhaden, Atlantic croaker, summer flounder and scup that could have negatively affected transport of larvae into the Bay (Hare et al. 2005). The only reported long-term shift in the wind field near Chesapeake Bay occurred in 1980 (Scully 2010), well before the beginning of the time series in my analyses.

Many of the species that declined in the lower Bay and tributaries, such as bluefish, scup, Spanish mackerel, spot, and summer flounder, are fished both within the Bay and along the Atlantic Coast and have experienced overfishing at some point during the time period analyzed in this study (41st SAW 2006; NCDMF 2011). The declining abundance of small, unfished species that

complete their life cycle within Chesapeake Bay and its tributaries and feed at relatively low trophic levels, such as bay anchovy, hogchoker, feather blenny, naked goby, and blackcheek tonguefish, suggests a "bottom-up" or "middle-out" change in Bay productivity that lowered the productivity of the fish community. The negative trend in zooplankton abundance in all systems also supports this conjecture.

The regression trees detected few strong relationships between environmental variables and the fish and zooplankton metrics and NBSS parameters that were useful for elucidating possible mechanisms of bottom-up or middle-out effects on the fish and zooplankton communities of the lower Bay and its tributaries. The fish diversity regression tree (Figure 17) likely is strongly leveraged by the abundance of bay anchovy because high abundance of bay anchovy relative to other species reduces diversity by lowering the evenness among species. Similarly, the species richness regression tree (Figure 16) primarily depicted the difference in richness between the mainstem lower Bay and its tributaries.

The regression tree for fish biomass (Figure 15) may be indicative of a positive relationship between primary productivity and fisheries production (Nixon and Buckley 2002) where the pH, conductance, and ammonium variables serve as proxies for productivity. Low summer pH may indicate increased respiration (increased CO_2) in each system resulting from decomposition of higher than

average spring phytoplankton blooms while high summer pH may be associated with higher rates of primary productivity (Soetaert et al. 2007; Yates et al. 2007). On the low biomass side of the regression tree, winter specific conductance may be a proxy for the effects of winter freshwater flow, which was directly included in the analysis but not selected by the algorithm. The importance of ammonium concentrations for the high fish biomass side of the regression tree may reflect remineralization of nitrogen during the summer (Caffrey 1995; Testa and Kemp 2008), with higher ammonium levels associated with higher remineralization from a large spring bloom, as well as excretion from higher trophic levels. However, total nitrogen loads to the Bay declined during the study period (Kemp et al. 2005; Scavia et al. 2006; Langland et al. 2007; Murphy et al. 2011). There is no indication of trends in chlorophyll a or primary production during this time period (Harding et al. 2002; Kemp et al. 2005) to suggest that spring phytoplankton blooms were larger in the early to mid-1990s.

The peak abundance of the fish biomass dome and mean abundance of the fish community exhibited similar trends as mean biomass, but the regression trees for peak abundance and mean abundance were not reliable enough to retain for interpretation. These results suggest that the connection between fish biomass and the variables retained by the regression tree are tenuous. Including measurements of total nitrogen, chlorophyll *a*, and phaeophytin concentrations as well as estimates of primary production may have provided more robust and informative regression trees; however, the CBP has indicated that changes in the

sample processing methodology for these variables during the study period prohibit trend analyses until correction factors can be developed (CBP 2010). Two possibilities for bottom-up or middle-out shifts in the Bay ecosystem that I did not explore due to insufficient data are changes in the timing and extent of hypoxic volume (Murphy et al. 2011) and increases in the abundance of gelatinous zooplankton (Breitburg and Fulford 2006), both of which should be included in future analyses.

An objective of my research was to evaluate the utility of combining traditional, multivariate approaches and NBSS to elucidate understanding trends and status of fish communities. My results indicate that NBSS parameters do have utility for detecting changes and trends in the size structure of the fish community at spatial and temporal scales that are relevant to ecosystem-based management in estuaries. NBSS analyses are an effective method for summarizing large quantities of data and or exploratory analyses of long-term monitoring data, especially when combined with multivariate analyses of species data. The combined approach provided insight into how changes in the species composition of the fish community relate to size-abundance distributions and relationships in Chesapeake Bay. Link et al. (2002, 2010) and Shin et al. (2010) suggested that developing a suite of complementary and contrasting indicators would be more effective for management of large marine ecosystem than relying on a few indicators. The metrics based on size and abundance that were evaluated in my research, in combination with multivariate ordination

approaches, are promising for development of a suite of indicators to be

considered for meeting goals of ecosystem-based management of Chesapeake

Bay.

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Table 1. Water quality variables used in the regression tree analyses.

Variable name	Description	Units
annflo	annual mean flow	m^3/s
chla	chlorophyll a	µg/L
do	dissolved oxygen	mg/L
Kd	light attenuation coefficient	m^{-1}
nh4	ammonium	mg/L
no23	nitrate + nitrite	mg/L
no3	nitrate	mg/L
pH	pH	NA
pheo	pheophytin	µg/L
po4	soluble reactive phosphorus	mg/L
salt	salinity	NA
secchi	Secchi depth	m
si	silica	mg/L
sigma_t	water density	kg/m^3
sp_cond	specific conductance	µmhos/cm at 25° C
temp	water temperature	degrees Celsius
wiflo, spflo, suflo, faflo	mean flow for the season	m^3/s

Table 2. Species, PCA biplot abbreviations, size classes, age groups, and systems used for the annual and seasonal PCAs. System abbreviations: all = Chesapeake Bay, James River, Rappahannock River, and York River; tributaries = James River, Rappahannock River, and York River; Ch = Chesapeake Bay; Ja = James River; Ra = Rappahannock River; Yo = York River.

Scientific name	Common name	Species Abbreviation	Age or size classes	Systems
Alosa aestivalus	blueback herring	bback	age 0	all
Alosa pseudoharengus	alewife	alwf	age 0	tributaries
Ameiurus catus	white catfish	wcat	<150mm, 150-300mm, >300mm	tributaries
Anchoa hepsetus	striped anchovy	stanch	All	Ch, Ja, Yo
Anchoa mitchilli	bay anchovy	banch	All	all
Anguilla rostrata	American eel	eel	All	tributaries
Bairdiella chrysoura	silver perch	silper	age 0, 1+	all
Brevoortia tyrannus	Atlantic menhaden	atmen	age 0, 1+	all
Centropristis striata	black sea bass	seabass	All	Ch, Ja, Yo
Cynoscion regalis	weakfish	weak	age 0, 1+	all
Dorosoma cepedianum	gizzard shad	gshad	<200mm, >200mm	tributaries
Etropus microstomus	smallmouth flounder	smflo	All	Ch, Ja
Gobiesox strumosus	skilletfish	skfsh	All	all
Ictalurus furcatus	blue catfish	bcat	<160mm, 160-330mm, >330mm	tributaries
Ictalurus punctatus	channel catfish	ccat	<130mm, 130-330mm, >330mm	tributaries

Scientific name	Common name	Species Abbreviation	Age or size classes	Systems
Leiostomus xanthurus	spot	spot	age 0, 1+	all
Menticirrhus spp.	kingfishes	kngfsh	age 0	all
Micropogonias undulatus	Atlantic croaker	croak	age 0, 1, 2+	all
Morone americana	white perch	whper	age 0, 1+	tributaries
Morone saxatilis	striped bass	stbass	age 0, 1, 2+	tributaries
Opsanus tau	oyster toadfish	toad	<100mm, 100-225mm, >225mm	all
Orthopristis chrysoptera	pigfish	pgfsh	All	Ch
Paralichthys dentatus	summer flounder	suflo	age 0, 1, 2+	all
Peprilus alepidotus	harvestfish	harfsh	All	all
Peprilus triacanthus	butterfish	butfsh	All	all
Stenotomus chrysops	scup	scup	All	Ch
Symphurus plagiusa	blackcheek tonguefish	tong	age 0, 1+	all
Synodus foetens	inshore lizardfish	inliz	All	all
Trinectes maculatus	hogchoker	hog	<50mm, 50-100mm, >100mm	all
Urophycis regia	spotted hake	sphake	age 0	all

Table 3. Strata used by the VIMS Trawl Survey in the lower mainstem Chesapeake Bay. Southern region corresponds to latitudes < 37°10'N to the Bay mouth; the central region corresponds to 37°10'N – 37°25'N latitude; and the northern region corresponds to 37°25'N – 37°40'N latitude.

Location	Depth	Mean number of stations per year
Southern region, Western shore, shallow	3.7-9.1 m	26
Southern region, Eastern shore, shallow	3.7-9.1 m	26
Southern region, intermediate	9.1-12.8 m	37
Southern region, deep	>12.8 m	29
Central region, Western shore, shallow	3.7-9.1 m	26
Central region, Eastern shore, shallow	3.7-9.1 m	26
Central region, intermediate	9.1-12.8 m	37
Central region, deep	>12.8 m	29
Northern region, Western shore, shallow	3.7-9.1 m	26
Northern region, Eastern shore, shallow	3.7-9.1 m	26
Northern region, intermediate	9.1-12.8 m	37
Northern region, deep	>12.8 m	29

Table 4. Trends in annual species diversity and annual species richness for each system. Standard errors are shown in parentheses. The p-value is for the regression of the trend.

System	Parameter	Slope	Intercept	r^2	p
Bay	diversity	0.04 (0.02)	-86.11 (35.33)	35.59	0.03
James	diversity	0.06 (0.02)	-114.38 (41.81)	41.09	0.02
Rappahannock	diversity	0.02 (0.02)	-41.34 (45.98)	7.36	0.37
York	diversity	0.02 (0.02)	-46.34 (40.70)	11.17	0.26
Bay	richness	-0.43 (0.33)	941.21 (651.06)	13.88	0.21
James	richness	-0.93 (0.30)	1906.97 (592.36)	47.11	0.010
Rappahannock	richness	-0.48 (0.12)	993.15 (243.00)	58.38	0.002
York	richness	-0.64 (0.23)	1325.48 (462.87)	41.15	0.02

Table 5. Fish species exhibiting negative trends in abundance for the lower Chesapeake Bay and its tributaries. Information on residence, spawning area, habitat, salinity preference, diet, and fisheries are from Murdy et al. (1997). System abbreviations are: Ch = lower mainstem Chesapeake Bay, Ja = James River, Ra = Rappahannock River, Yo = York River. Residence abbreviations: resident = present during all seasons, wi = winter, sp = spring, su = summer, fa = fall. Spawning area entries: fresh/oligo = spawns in the freshwater and oligohaline regions, estuarine = spawns within the estuary, coastal = spawns in the nearshore or offshore areas outside of estuaries, Sargasso = spawns in the Sargasso Sea. Diet abbreviations are: b = benthivorous, d = detritivorous, h = herbivorous, i = invertivorous (jellyfish, hydroids, sponges, sea anemones), p = piscivorous, z = zooplanktivorous. Fishery entries: yes = species subjected to directed commercial or recreational fishery in the Bay, no = species not subjected to directed commercial or recreational fishery but may be taken as incidental bycatch.

Scientific name	Common name	Systems w/ decline	Residence	Spawning area	Habitat	Salinity	Diet	Fishery
Ameiurus catus	white catfish	Ja, Ra	Resident	fresh/oligo	demersal	fresh-meso	b, p	yes
Anchoa mitchilli	bay anchovy	Ch, Ja, Ra	Resident	estuarine	pelagic	oligo-poly	z	no
Anguilla rostrata	American eel	Ja, Ra	Resident	Sargasso	benthic	fresh-poly	b, p	yes
Astroscopus guttatus	northern stargazer	Yo	Resident	estuarine	benthic	poly	p	no
Caranx crysos	blue runner	Ch	su, fa	coastal	pelagic	poly	b, p	yes
Chaetodipterus faber	spadefish	Ja	su, fa	coastal	pelagic	poly	i	yes
Clupea harengus	Atlantic herring	Ja	wi, sp	coastal	pelagic	meso-poly	z	yes
Conger oceanicus	conger eel	Ch, Yo		Sargasso	benthic	poly	b, p	no
Cynosion nebulosus	speckled trout	Ch, Yo	sp, su, fa	estuarine/ coastal	demersal/ littoral	meso-poly	p	yes

Scientific name	Common name	Systems w/ decline	Residence	Spawning area	Habitat	Salinity	Diet	Fishery
Cyprinus carpio	common carp	Ja	Resident	fresh/oligo	demersal	fresh-meso	h, b	no
Dorosoma cepedianum	gizzard shad	Ra	Resident	fresh/oligo	demersal	fresh-meso	b	yes
Etropus crossotus	fringed flounder	Ch, Ja	sp, su, fa	estuarine/coastal	benthic	poly	b	no
Etropus microstomus	smallmouth flounder	Ch	resident	estuarine/coastal	benthic	poly	b	no
Gobiesox strumosus	skilletfish	Ch, Ja	resident	estuarine	benthic	oligo-poly	b	no
Gobiosoma bosc	naked goby	Ch	resident	estuarine	benthic	oligo-poly	b	no
Hypsoblennius hentz	feather blenny	Ch, Ja, Ra	resident	estuarine	benthic	meso-poly	b	no
Ictalurus punctatus	channel catfish	Ja, Ra	resident	fresh/oligo	demersal	fresh-meso	b, p	yes
Stenotomus chrysops	scup	Ch, Ja	sp, su, fa	coastal	demersal	poly	b	yes
Leiostomus xanthurus	spot	Ch, Ja, Ra, Yo	sp, su, fa	coastal	demersal	meso-poly	b	yes
Merluccius bilinearis	silver hake	Ch	fa, wi, sp	coastal	demersal	poly	b, p	yes
Ophidion marginatum	striped cusk eel	Ch	sp, su, fa	coastal	benthic	poly	b	no
Opisthonema oglinum	Atlantic thread herring	Ch, Ja	su	coastal	pelagic	poly	z	no
Opsanus tau	oyster toadfish	Ch, Ja, Ra, Yo	resident	estuarine	benthic	meso-poly	b	no

Scientific name	Common name	Systems w/ decline	Residence	Spawning area	Habitat	Salinity	Diet	Fishery
Paralichthys dentatus	summer flounder	Ch, Ra, Yk	sp, su, fa	coastal	benthic	meso-poly	p	yes
Penaeus aztecus	brown shrimp	Ch	su, fa	estuarine/ coastal	benthic	poly	b, d	no
Peprilus alepidotus	harvestfish	Ch	sp, su, fa	coastal	pelagic	meso-poly	b, p	yes
Peprilus triacanthus	butterfish	Ch	sp, su, fa	coastal	pelagic	meso-poly	b, p	yes
Pomatomus saltatrix	bluefish	Ra	sp, su, fa	coastal	pelagic	meso-poly	p	yes
Prionotus tribulus	bighead searobin	Ch	su, fa	estuarine	benthic	meso-poly	b	no
Raja eglanteria	clearnose skate	Ch	su, fa		benthic	poly	b, p	no
Scomberomorus maculatus	Spanish mackerel	Ch, Ja	sp, su, fa	coastal	pelagic	meso-poly	p	yes
Squalus acanthias	spiny dogfish	Ch	fa, wi, sp	coastal	demersal	poly	p	yes
Symphurus plagiusa	blackcheek tonguefish	Ch	resident	estuarine	benthic	meso-poly	b	no
Synodus foetens	inshore lizardfish	Yo	su, fa		benthic	meso-poly	b, p	no
Trinectes maculates	hogchoker	Ch, Ja, Ra, Yo	resident	estuarine	benthic	oligo-poly	b	no
Urophycis regia	spotted hake	Ch, Ja	sp	coastal	demersal	meso-poly	b	yes

Table 6. Correlation coefficients between scores from annual PCAs and year. Bold entries are significant at $p < 0.10$.

System	Assemblage	PC1	PC2
Bay	shallow	**-0.34**	**0.41**
	deep	**-0.58**	**0.25**
	upper	**-0.42**	**0.44**
	central	**-0.33**	**0.35**
	lower	**-0.38**	**0.47**
James	polyhaline	-0.28	**-0.64**
	mesohaline	-0.12	**-0.54**
	oligohaline	**0.33**	**-0.35**
Rappahannock	polyhaline	**-0.36**	**-0.74**
	mesohaline	0.21	**-0.68**
	oligohaline	**0.58**	**-0.80**
York	polyhaline	**-0.32**	**-0.68**
	oligohaline	**-0.31**	**-0.62**

Table 7. Correlations between scores from seasonal PCAs and year by system and assemblage. Bold entries are significant at *p* < 0.10.

System	Stratum	Season	PC1	PC2
Bay	all	winter	-0.29	-0.05
		spring	-0.14	0.05
		summer	**-0.36**	-0.29
		fall	**-0.51**	**-0.68**
James	polyhaline	winter	0.28	-0.37
		spring	-0.13	0.22
		summer	0.22	**0.52**
		fall	**0.56**	0.50
	mesohaline	winter	-0.29	0.17
		spring	-0.12	**0.77**
		summer	**0.48**	**0.60**
		fall	**0.54**	**0.51**
	oligohaline	winter	**-0.77**	**0.83**
		spring	**-0.55**	**0.74**
		summer	-0.32	**0.86**
		fall	-0.05	**0.73**
Rappahannock	polyhaline	winter	-0.22	**0.54**
		spring	-0.04	0.10
		summer	-0.13	-0.12
		fall	**0.73**	-0.39
	mesohaline	winter	0.03	-0.27
		spring	0.09	-0.36
		summer	0.05	-0.42
		fall	**0.50**	**-0.51**
	oligohaline	winter	**-0.74**	**-0.67**
		spring	**-0.51**	**-0.87**
		summer	-0.07	**-0.78**
		fall	-0.02	**-0.70**
York	polyhaline	winter	-0.02	**0.51**
		spring	-0.04	**0.56**
		summer	0.42	**0.69**
		fall	0.14	**0.70**
	oligohaline	winter	0.25	**0.64**
		spring	0.04	**0.54**
		summer	**0.60**	0.14
		fall	0.38	**0.60**

Table 8a. Zooplankton and meroplankton taxa that declined in abundance.
The letters in parentheses indicate the taxonomic group: ba = barnacle larvae, bi
= bivalve larvae, ch = chaetognath, cl = cladoceran, co = copepod, cr = crab
larvae, di = dipteran fly larvae, sh = decapod and mysid shrimp.

Bay	James	Rappahannock	York
Acartia (co)	*Acartia* (co)	*Acartia** (co)	barnacle larvae (ba)
barnacle larvae (ba)	barnacle larvae (ba)	*Alonella* (cl)	*Callinectes* (cr)
Calanus (co)	*Callinectes* (cr)	barnacle larvae (ba)	*Cyclops* (co)
Centropages (co)	*Centropages* (co)	*Cyclops* (co)	*Eurycercus* (cl)
copepoda (co)	copepoda (co)	*Euterpina* (co)	*Labidocera* (co)
Crangon (sh)	*Crangon* (sh)	*Evadne* (co)	*Leptodora* (cl)
Euterpina (co)	*Cyclops* (co)	harpacticoida	*Paralaophonte* (co)
Evadne (co)	*Euterpina* (co)	*Oithona* (co)	*Pinnixa* (cr)
Oithona (co)	*Evadne* (co)	*Podon* (cl)	*Sagitta* (ch)
Ovalipes (cr)	*Hexapanopeus* (cr)	*Sagitta* (ch)	
Paracalanus (co)	*Labidocera* (co)	*Temora* (co)	
Penilia (cl)	*Leptodora* (cl)	*Upogebia* (sh)	
Pinnixa (cr)	*Oithona* (co)		
Sagitta (ch)	*Palaemonetes* (sh)		
	Paracalanus (co)		
	Paralaophonte (co)		
	Podon (cl)		
	Sagitta (ch)		
	Saphirella (co)		
	Temora (co)		
	Upogebia (sh)		

Table 8b. Zooplankton and meroplankton taxa that increased in abundance. The letters in parentheses indicate the taxonomic group: ba = barnacle larvae, bi = bivalve larvae, ch = chaetognath, cl = cladoceran, co = copepod, cr = crab larvae, di = dipteran fly larvae, pc = parasitic copepod, sh = decapod and mysid shrimp.

Bay	James	Rappahannock	York
bivalvia (bi)	*Chydorus* (cl)	Diptera (di)	Diptera (di)
cyclopoida (co)	*Neomysis* (sh)	*Neomysis* (sh)	*Ergasilus* (pc)
	Rhithropanopeus (cr)	*Rhithropanopeus* (cr)	*Neomysis* (sh)
			Rhithropanopeus (cr)

Table 9. Zooplankton. Trends in the annual NBSS parameters. Standard errors are given in parentheses. Parameter abbreviations: slope = slope of the centered integral spectrum, height = y-intercept of the centered integral spectrum, curv = curvature of the biomass dome, sap = size at peak abundance of the biomass dome, pa = peak abundance of the biomass dome. P-values are for the regression, with bold values indicating significant trends with $p < 0.10$.

System	Parameter	Slope of trend	Intercept of trend	r^2 %	p
Bay	slope	0.02 (0.049)	-40.61 (97.61)	2.30	0.70
James	slope	0.06 (0.036)	-121.94 (70.76)	29.38	0.1317
Rappahannock	slope	0.08 (0.036)	-165.79 (72.19)	42.70	**0.06**
York	slope	0.10 (0.029)	-190.58 (57.79)	60.63	**0.01**
Bay	height	-0.40 (0.082)	805.14 (164.29)	79.92	**0.002**
James	height	-0.13 (0.066)	272.67 (132.34)	37.02	**0.08**
Rappahannock	height	-0.17 (0.083)	340.29 (165.51)	37.01	**0.08**
York	height	0.10 (0.087)	-190.72 (172.65)	15.44	0.30
Bay	curv	-0.004 (0.012)	6.90 (24.35)	1.25	0.77
James	curv	0.004 (0.009)	-7.69 (17.02)	2.62	0.68
Rappahannock	curv	0.025 (0.009)	-49.69 (16.93)	54.91	**0.02**
York	curv	0.009 (0.006)	18.23 (11.64)	25.38	0.17
Bay	sap	0.06 (0.10)	-139.17 (204.99)	5.00	0.56
James	sap	0.13 (0.12)	-268.62 (231.70)	14.61	0.31
Rappahannock	sap	-0.06 (0.08)	98.09 (165.05)	6.27	0.52
York	sap	0.18 (0.05)	-385.49 (98.58)	66.92	**0.007**
Bay	pa	-0.45 (0.08)	903.67 (155.64)	82.54	**0.001**
James	pa	-0.31 (0.11)	633.91 (212.25)	55.39	**0.02**
Rappahannock	pa	-0.38 (0.10)	766.80 (189.30)	69.68	**0.005**
York	pa	-0.05 (0.06)	105.17 (126.75)	7.84	0.47

Table 10. Zooplankton biomass domes. Trends in the seasonal peak abundance estimates for the zooplankton biomass domes. Standard errors are given in parentheses. P-values are for the trend regression with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope of trend	Intercept of trend	r^2 %	p
Bay	winter	-0.62 (0.26)	1250.30 (520.76)	44.86	**0.05**
James	winter	-0.26 (0.16)	533.97 (323.23)	27.61	0.15
Rapp	winter	-0.16 (0.18)	326.95 (362.37)	7.98	0.40
York	winter	-0.15 (0.25)	299.52 (501.91)	6.67	0.58
Bay	spring	-0.04 (0.35)	86.68 (696.35)	0.18	0.91
James	spring	-0.29 (0.12)	548.57 (246.26)	43.97	**0.05**
Rapp	spring	-0.12 (0.39)	238.56 (773.04)	0.98	0.77
York	spring	-0.13 (0.13)	252.00 (266.27)	11.63	0.31
Bay	summer	-0.77 (0.12)	1540.82 (245.43)	84.76	**0.0004**
James	summer	-0.33 (0.15)	669.43 (298.73)	44.90	**0.07**
Rapp	summer	-0.34 (0.09)	682.48 (170.77)	63.49	**0.003**
York	summer	-0.12 (0.12)	250.44 (247.20)	12.14	0.36
Bay	fall	-0.22 (0.22)	447.99 (437.52)	12.67	0.35
James	fall	-0.24 (0.16)	495.35 (311.41)	25.98	0.16
Rapp	fall	0.18 (0.18)	-351.56 (349.68)	10.40	0.33
York	fall	0.07 (0.22)	-123.16 (445.12)	1.40	0.78

Table 11. Zooplankton size at peak abundance. Trends in the seasonal size at peak abundance estimates for the zooplankton biomass domes. Standard errors are given in parentheses. P-values are for the trend regression with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope of trend	Intercept of trend	r^2 %	p
Bay	winter	-0.05 (0.17)	83.05 (335.84)	1.22	0.78
James	winter	0.08 (0.12)	-163.71 (248.72)	4.87	0.57
Rapp	winter	0.18 (0.34	-371.23 (678.39)	3.78	0.62
York	winter	0.36 (0.27)	-730.25 (547.94)	19.55	0.23
Bay	spring	-0.37 (0.33)	717.64 (660.67)	14.91	0.30
James	spring	0.11 (0.10)	-226.91 (196.07)	14.29	0.32
Rapp	spring	-0.39 (0.48)	755.79 (964.06)	8.37	0.45
York	spring	0.17 (0.10)	-355.88 (186.27)	32.39	0.11
Bay	summer	0.81 (0.69)	-1624.28 (1372.27)	16.38	0.28
James	summer	0.01 (0.13)	-30.04 (252.19)	0.06	0.95
Rapp	summer	0.15 (0.10)	-307.58 (183.32)	26.78	0.15
York	summer	0.18 (0.07)	-372.56 (154.07)	46.58	**0.04**
Bay	fall	-0.11 (0.06)	208.31 (120.82)	32.67	0.11
James	fall	0.02 (0.07)	-62.68 (131.52)	18.88	0.72
Rapp	fall	-0.57 (0.30)	1131.03 (591.15)	29.49	**0.09**
York	fall	-0.08 (0.11)	142.61 (226.08)	7.45	**0.05**

Table 12. Zooplankton seasonal curvature in biomass domes. Trends in the seasonal curvature for the zooplankton biomass dome parameters. Standard errors are given in parentheses. P-values are for the trend regression with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope of trend	Intercept of trend	r^2 %	p
Bay	winter	0.035 (0.028)	-70.64 (54.41)	19.22	0.24
James	winter	0.020 (0.016)	-36.61 (32.64)	17.17	0.27
Rapp	winter	0.012 (0.021)	-24.32 (42.47)	4.34	0.59
York	winter	0.005 (0.011)	-10.69 (22.40)	3.04	0.65
Bay	spring	0.008 (0.026)	-16.07 (52.10)	1.28	0.77
James	spring	0.012 (0.017)	-24.43 (33.13)	7.02	0.49
Rapp	spring	0.031 (0.036)	-61.24 (72.01)	9.28	0.43
York	spring	0.020 (0.001)	-36.65 (18.31)	39.79	**0.07**
Bay	summer	0.004 (0.019)	-7.38 (37.57)	0.51	0.86
James	summer	-0.001 (0.018)	2.14 (36.36)	0.07	0.95
Rapp	summer	0.029 (0.012)	-58.71 (24.75)	44.31	**0.05**
York	summer	0.019 (0.013)	-38.18 (25.16)	24.47	0.18
Bay	fall	-0.0003 (0.016)	0.25 (32.05)	0.004	0.99
James	fall	0.012 (0.012)	-24.44 (22.88)	13.63	0.33
Rapp	fall	0.022 (0.011)	-43.75 (21.76)	36.35	**0.09**
York	fall	-0.015 (0.025)	30.38 (49.13)	5.29	0.55

Table 13. Zooplankton: Annual trends for mean number/m^3 and mean biomass/m^3 for the zooplankton community in each system. Standard errors are in parentheses, and the listed p-value is that of the regression with bold values indicating significant trends with $p < 0.10$. * excluding 1995, which was a high outlier. ** excluding 1996, which was a high outlier.

System	Parameter	Slope	Intercept	r^2 %	p
Bay	number/m^3	-306.48 (65.40)	613260.05 (130498.35)	75.83	**0.002**
James	number/m^3	-146.45 (64.63)	293976.82 (128975.95)	42.32	**0.058**
Rapp	number/m^3	-135.93 (31.71)	272906.27 (63276.34)	75.38	**0.005***
York	number/m^3	-76.70 (34.48)	154137.44 (68797.28)	41.42	**0.061**
Bay	g/m^3	-0.017 (0.006)	33.73 (11.28)	55.91	**0.021**
James	g/m^3	-0.008 (0.002)	16.06 (44.78)	61.46	**0.012**
Rapp	g/m^3	-0.010 (0.003)	20.22 (6.16)	63.95	**0.017***
York	g/m^3	-0.006 (0.003)	11.33 (5.56)	40.54	**0.090****

Table 14. Zooplankton: Seasonal trends for mean number/m^3 for the zooplankton community in each system. Standard errors are shown in parentheses, and the listed p-value is that of the regression with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope	Intercept	r^2 %	p
Bay	winter	-327.48 (116.43)	654774.58 (232330.62)	53.06	**0.026**
Bay	spring	-298.91 (86.04)	598276.51 (171696.75)	63.29	**0.010**
Bay	summer	-597.72 (150.29)	1195586.48 (299898.66)	69.32	**0.005**
Bay	fall	-76.66 (58.32)	153624.47 (116379.15)	19.79	0.230
James	winter	6.59 (43.16)	-12509.41 (86130.36)	0.33	0.883
James	spring	-34.91 (34.40)	70489.72 (68637.65)	14.65	0.349
James	summer	-536.24 (292.68)	1073607.17 (584036.09)	32.41	0.110
James	fall	-40.43 (86.88)	81855.51 (173367.78)	3.00	0.656
Rapp	winter	-279.70 (64.16)	559835.94 (128018.98)	73.08	**0.003**
Rapp	spring	-174.67 (249.81)	351515.39 (498484.23)	6.53	0.507
Rapp	summer	-177.27 (61.98)	355586.27 (123680.79)	53.89	**0.024**
Rapp	fall	6.58 (30.27)	-12384.70 (60402.39)	0.67	0.834
York	winter	-165.14 (73.64)	330348.83 (146947.70)	41.80	**0.060**
York	spring	-51.13 (21.11)	102881.88 (42122.85)	49.43	**0.052**
York	summer	-103.20 (52.42)	207050.84 (104608.68)	35.63	**0.090**
York	fall	-24.01 (67.40)	49167.00 (134493.47)	1.78	**0.732**

Table 15. Seasonal trends for mean biomass (g)/m^3 zooplankton community in each system. Standard errors are shown in parentheses, and the listed p-value is that of the regression with bold values indicating significant trends with $p <$ 0.10.

System	Season	Slope	Intercept	r^2	p
Bay	winter	-0.021 (0.006)	41.76 (12.82)	60.16	**0.014**
Bay	spring	-0.020 (0.005)	39.04 (10.42)	66.61	**0.007**
Bay	summer	-0.027 (0.011)	54.54 (21.77)	47.09	**0.041**
Bay	fall	-0.013 (0.004)	25.70 (7.47)	66.22	**0.014**
James	winter	0.000 (0.003)	-0.08 (5.04)	0.00	0.983
James	spring	-0.004 (0.005)	8.64 (9.18)	11.09	0.381
James	summer	-0.024 (0.013)	47.63 (26.13)	32.02	0.112
James	fall	-0.005 (0.004)	9.91 (7.59)	19.32	0.237
Rapp	winter	-0.020 (0.006)	39.51 (12.03)	60.51	**0.014**
Rapp	spring	-0.008 (0.014)	16.94 (27.42)	5.07	0.560
Rapp	summer	-0.019 (0.005)	38.02 (10.44)	65.26	**0.008**
Rapp	fall	0.002 (0.003)	-3.28 (5.71)	4.68	0.576
York	winter	-0.006 (0.002)	12.43 (4.54)	51.52	**0.029**
York	spring	-0.003 (0.009)	5.50 (17.02)	1.43	0.760
York	summer	-0.007 (0.006)	14.49 (12.33)	16.28	0.282
York	fall	-0.003 (0.006)	6.81 (12.47)	3.97	0.607

Table 16. Fish. Trends for the annual NBSS integral spectra and biomass dome parameters. Standard errors are given in parentheses. P-values are for the trend regression with bold values indicating significant trends with $p < 0.10$.

System	Parameter	Slope	Intercept	r^2 %	p
Bay	height	-0.068 (0.017)	125.23 (33.99)	61.38	**0.003**
James	height	-0.088 (0.019)	165.66 (38.49)	65.39	**0.0008**
Rapp	height	-0.067 (0.026)	125.61 (51.41)	38.70	**0.023**
York	height	-0.073 (0.026)	137.17 (51.24)	42.68	**0.015**
Bay	slope	-0.001 (0.005)	1.48 (9.11)	0.39	0.839
James	slope	0.010 (0.005)	-19.59 (9.58)	26.66	**0.071**
Rapp	slope	0.015 (0.008)	-29.71 (15.10)	25.62	**0.078**
York	slope	0.006 (0.006)	-11.84 (11.86)	7.91	0.352
Bay	curv	0.003 (0.001)	-5.73 (1.28)	63.63	**0.001**
James	curv	0.003 (0.001)	-5.32 (2.65)	25.99	**0.075**
Rapp	curv	0.002 (0.001)	-3.59 (1.51)	32.36	**0.042**
York	curv	0.003 (0.001)	-5.18 (1.27)	59.10	**0.002**
Bay	spa	-0.069 (0.037)	139.39 (73.48)	24.26	**0.087**
James	spa	-0.005 (0.041)	12.51 (81.11)	0.16	0.896
Rapp	spa	0.026 (0.032)	-49.81 (63.27)	5.75	0.430
York	spa	0.007 (0.023)	-11.68 (46.11)	0.80	0.772
Bay	pa	-0.081 (0.026)	154.54 (51.58)	47.29	**0.009**
James	pa	-0.153 (0.017)	297.96 (33.61)	88.19	**<0.0001**
Rapp	pa	-0.135 (0.027)	262.06 (53.65)	69.59	**0.0004**
York	pa	-0.125 (0.024)	243.84 (47.82)	71.37	**0.0003**

Table 17. Fish. Seasonal trends in the height and slope of the centered integral spectra for the fish community in each system. Standard errors are given in parentheses, and p-values are for the regression of the trend with bold values indicating significant trends with $p < 0.10$. The majority of the regressions quantifying the integral spectra for the Rappahannock River were not significant. Seasonal trends in the height and slope of the Rappahannock integral spectra are listed here for comparison purposes only.

System	Season	Parameter	Slope	Intercept	r^2 %	p
Bay	winter	height	-0.10 (0.04)	185.67 (82.15)	34.28	**0.036**
James	winter	height	-0.14 (0.03)	273.07 (50.32)	74.20	**0.001**
Rapp	winter	height	-0.12 (0.0	229.88 (99.29)	34.63	**0.034**
York	winter	height	-0.05 (0.02)	90.60 (49.64)	27.05	**0.068**
Bay	spring	height	-0.08 (0.04)	151.67 (78.69)	28.15	**0.062**
James	spring	height	-0.10 (0.05)	183.35 (91.91)	28.65	**0.059**
Rapp	spring	height	-0.10 (0.03)	195.27 (58.79)	52.61	**0.005**
York	spring	height	-0.09 (0.05)	166.36 (101.10)	21.57	0.110
Bay	summer	height	-0.04 (0.04)	64.83 (79.02)	7.62	0.361
James	summer	height	-0.11 (0.03)	202.35 (63.25)	50.52	**0.006**
Rapp	summer	height	-0.08 (0.05)	146.70 (96.08)	19.62	0.13
York	summer	height	-0.11 (0.04)	204.64 (75.84)	42.13	**0.016**
Bay	fall	height	-0.04 (0.03)	72.42 (62.16)	13.79	0.212
James	fall	height	-0.16 (0.04)	303.22 (89.26)	52.72	**0.005**
Rapp	fall	height	-0.06 (0.02)	112.01 (47.23)	37.48	**0.027**
York	fall	height	-0.06 (0.04)	113.12 (72.34)	20.61	0.120
Bay	winter	slope	-0.002 (0.01)	3.11 (17.22)	0.40	0.837
James	winter	slope	0.03 (0.01)	-56.44 (22.85)	35.37	**0.032**
Rapp	winter	slope	0.02 (0.01)	-39.42 (23.58)	19.98	0.13
York	winter	slope	0.01 (0.01)	-18.78 (15.67)	11.11	0.266

System	Season	Parameter	Slope	Intercept	r² %	p
Bay	spring	slope	0.01 (0.01)	-11.29 (23.76)	1.98	0.647
James	spring	slope	0.01 (0.01)	-11.85 (22.87)	2.29	0.622
Rapp	spring	slope	0.01 (0.02)	-28.97 (33.28)	6.40	0.404
York	spring	slope	0.02 (0.01)	-31.68 (24.80)	12.80	0.230
Bay	summer	slope	0.01 (0.01)	-17.00 (14.87)	10.29	0.285
James	summer	slope	0.01 (0.01)	-27.75 (21.44)	12.96	0.227
Rapp	summer	slope	-0.01 (0.01)	21.72 (23.32)	7.31	0.372
York	summer	slope	0.003 (0.01)	-7.72 (24.43)	0.91	0.756
Bay	fall	slope	-0.01 (0.01)	24.17 (15.64)	18.32	0.145
James	fall	slope	0.01 (0.01)	-18.61 (22.65)	5.59	0.437
Rapp	fall	slope	0.005 (0.01)	-9.33 (14.30)	3.59	0.535
York	fall	slope	-0.01 (0.01)	23.71 (16.67)	15.80	0.179

Table 18. Fish. Trends for seasonal biomass dome peak abundance estimates.
Standard errors are given in parentheses. P-values are for the trend regression
with bold values indicating significant trends with *p* < 0.10.

System	Season	Slope	Intercept	r^2 %	p
Bay	winter	-0.13 (0.06)	259.42 (116.62)	34.36	**0.04**
James	winter	-0.15 (0.04)	293.75 (78.14)	57.41	**0.003**
Rapp	winter	-0.13 (0.07)	256.18 (145.89)	22.84	**0.10**
York	winter	-0.14 (0.03)	274.07 (54.50)	70.76	**0.0003**
Bay	spring	-0.13 (0.04)	255.77 (79.26)	50.36	**0.007**
James	spring	-0.14 (0.05)	267.19 (97.49)	41.81	**0.02**
Rapp	spring	-0.18 (0.04)	359.34 (86.03)	62.35	**0.001**
York	spring	-0.16 (0.05)	322.51 (96.65)	51.35	**0.006**
Bay	summer	-0.08 (0.04)	144.00 (84.04)	22.84	**0.10**
James	summer	-0.15 (0.03)	294.48 (65.23)	66.06	**0.001**
Rapp	summer	-0.19 (0.07)	369.70 (147.69)	37.35	**0.03**
York	summer	-0.09 (0.05)	177.89 (103.71)	22.53	**0.10**
Bay	fall	-0.05 (0.05)	85.85 (92.02)	8.53	0.33
James	fall	-0.16 (0.05)	313.73 (94.40)	51.18	**0.006**
Rapp	fall	-0.12 (0.03)	230.64 (64.14)	55.51	**0.003**
York	fall	-0.11 (0.04)	203.50 (74.52)	41.92	**0.02**

Table 19. Fish. Trends for seasonal biomass dome curvature estimates. Standard errors are given in parentheses. P-values are for the trend regression with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope	Intercept	r^2 %	p
Bay	winter	0.002 (0.002)	-3.88 (3.33)	10.50	0.28
James	winter	-0.004 (0.002)	7.60 (4.19)	23.62	**0.09**
Rapp	winter	-0.002 (0.002)	4.54 (4.30)	9.68	0.30
York	winter	0.003 (0.002)	-5.68 (3.72)	16.90	0.16
Bay	spring	0.003 (0.001)	-6.68 (2.63)	36.11	**0.03**
James	spring	-0.0001 (0.001)	0.03 (2.26)	0.06	0.94
Rapp	spring	0.002 (0.002)	-3.55 (3.20)	9.38	0.31
York	spring	0.003 (0.002)	-5.81 (3.96)	15.72	0.18
Bay	summer	0.001 (0.001)	-2.67 (2.66)	7.74	0.36
James	summer	0.003 (0.002)	-5.43 (3.46)	17.73	0.15
Rapp	summer	0.006 (0.002)	-12.77 (3.16)	59.35	**0.002**
York	summer	0.001 (0.001)	-1.63 (2.53)	0.031	0.56
Bay	fall	0.003 (0.001)	-5.07 (2.27)	30.47	**0.05**
James	fall	0.002 (0.002)	-4.52 (3.25)	14.28	0.20
Rapp	fall	0.003 (0.001)	-6.37 (2.20)	42.28	**0.02**
York	fall	0.003 (0.001)	-6.81 (2.49)	39.54	**0.02**

Table 20. Fish. Trends for seasonal biomass dome size at peak abundance estimates. Standard errors are given in parentheses. P-values are for the trend regression with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope	Intercept	r^2 %	p
Bay	winter	-0.11 (0.09)	222.53 (173.56)	12.98	0.23
James	winter	0.11 (0.06)	-223.32 (126.58)	22.29	**0.10**
Rapp	winter	0.06 (0.06)	-116.45 (110.10)	9.42	0.31
York	winter	-0.02 (0.06)	46.04 (111.89)	1.46	0.69
Bay	spring	0.06 (0.03)	-116.14 (61.20)	25.67	**0.08**
James	spring	0.09 (0.02)	-173.15 (48.00)	55.01	**0.004**
Rapp	spring	0.10 (0.06)	-193.86 (114.14)	21.30	0.11
York	spring	0.08 (0.06)	-156.83 (117.37)	14.41	0.20
Bay	summer	0.02 (0.05)	-43.35 (105.96)	1.65	0.68
James	summer	-0.02 (0.10)	43.60 (192.48)	0.43	0.83
Rapp	summer	-0.06 (0.06)	123.16 (110.35)	9.72	**0.030**
York	summer	0.07 (0.04)	-129.48 (78.39)	20.62	0.12
Bay	fall	-0.14 (0.06)	275.13 (124.89)	30.41	**0.05**
James	fall	-0.04 (0.07)	77.77 (142.75)	2.53	0.60
Rapp	fall	-0.02 (0.04)	39.08 (71.35)	2.38	0.61
York	fall	-0.04 (0.04)	86.56 (71.16)	11.38	0.26

Table 21. Fish. Annual trends for mean size (g wet weight), mean number/m^3, and mean biomass/m^3 for the fish community in each system. Standard errors are shown in parentheses, and the listed p-value is that of the regression with bold values indicating significant trends with $p < 0.10$.

System	Parameter	Slope	Intercept	r^2 %	p
Bay	mean size	0.37 (0.44)	-702.94 (882.95)	5.98	0.42
James	mean size	1.25 (0.32)	-2466.12 (643.23)	57.68	**0.003**
Rapp	mean size	2.48 (0.59)	-4925.10 (1174.54)	61.84	**0.001**
York	mean size	1.67 (0.60)	-3306.99 (1191.68)	41.59	**0.02**
Bay	number/m^3	-0.05 (0.02)	108.88 (30.19)	53.61	**0.004**
James	number/m^3	-0.08 (0.02)	166.75 (32.88)	69.62	**0.0004**
Rapp	number/m^3	-0.07 (0.03)	134.57 (63.88)	28.21	**0.06**
York	number/m^3	-0.06 (0.03)	123.15 (54.47)	30.95	**0.05**
Bay	g/m^3	-0.013 (0.004)	25.75 (8.47)	45.39	**0.01**
James	g/m^3	-0.020 (0.004)	40.77 (7.82)	71.01	**0.0003**
Rapp	g/m^3	-0.013 (0.004)	25.20 (7.05)	53.50	**0.004**
York	g/m^3	-0.018 (0.008)	36.39 (15.53)	33.10	**0.04**

Table 22. Fish. Trends in mean length for common species that declined in abundance over the survey years. The slope of the trend indicates the rate of change in the mean length in mm/yr. P-values indicate the p-value for the regression with bold values indicating significant trends with *p* < 0.10.

Species	System	Slope (mm/yr)	r^2 %	p
bay anchovy	Bay	0.48	23.00	**0.097**
bay anchovy	James	0.82	34.10	**0.036**
bay anchovy	Rappahannock	0.34	10.36	0.284
bay anchovy	York	0.33	13.35	0.220
channel catfish	James	2.11	4.74	0.475
channel catfish	Rappahannock	2.12	23.21	**0.096**
channel catfish	York	0.86	0.11	0.915
American eel	Bay	2.03	0.31	0.945
American eel	James	5.21	85.17	**<0.0001**
American eel	Rappahannock	4.15	58.84	**0.002**
American eel	York	18.02	79.46	**<0.0001**
hogchoker	Bay	0.19	3.51	0.540
hogchoker	James	0.67	34.58	**0.035**
hogchoker	Rappahannock	-0.02	0.04	0.950
hogchoker	York	0.74	20.74	0.118
summer flounder	Bay	5.83	52.92	**0.005**
summer flounder	James	5.53	70.90	**0.0003**
summer flounder	Rappahannock	4.26	19.52	0.131
summer flounder	York	3.92	30.49	**0.050**
oyster toadfish	Bay	2.91	16.61	0.167
oyster toadfish	James	3.24	72.41	**0.0002**
oyster toadfish	Rappahannock	-2.05	9.74	0.324
oyster toadfish	York	-1.31	18.51	0.142
white catfish	James	2.31	9.94	0.294
white catfish	Rappahannock	4.47	52.49	0.005
white catfish	York	-0.23	0.07	0.931

Table 23. Fish. Seasonal trends for mean number/m^3 for the fish community in each system. Standard errors are in parentheses, and the listed p-value is that of the regression with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope	Intercept	r^2 %	p
Bay	winter	-0.034 (0.014)	68.57 (27.30)	36.28	**0.03**
Bay	spring	-0.010 (0.004)	20.03 (7.33)	40.26	**0.02**
Bay	summer	-0.008 (0.003)	15.69 (5.00)	46.81	**0.01**
Bay	fall	-0.008 (0.007)	16.72 (14.25)	10.92	0.27
James	winter	-0.030 (0.011)	59.05 (22.45)	38.46	**0.02**
James	spring	-0.020 (0.010)	40.85 (20.83)	25.73	**0.08**
James	summer	-0.016 (0.007)	32.13 (11.22)	42.50	**0.02**
James	fall	-0.014 (0.006)	27.22 (11.99)	31.60	**0.05**
Rappahannock	winter	-0.022 (0.010)	44.38 (20.22)	30.25	**0.05**
Rappahannock	spring	-0.011 (0.004)	21.65 (8.81)	35.24	**0.03**
Rappahannock	summer	-0.005 (0.002)	9.71 (4.28)	31.68	**0.05**
Rappahannock	fall	-0.013 (0.003)	25.97 (6.48)	59.08	**0.002**
York	winter	-0.034 (0.016)	68.49 (31.58)	29.82	**0.05**
York	spring	-0.020 (0.008)	39.37 (15.72)	36.17	**0.03**
York	summer	-0.006 (0.003)	11.66 (5.84)	26.33	**0.07**
York	fall	-0.012 (0.009)	24.67 (17.54)	15.04	0.19

Table 24. Fish. Seasonal trends for mean biomass/m^3 for the fish community in each system. Standard errors are in parentheses, and the listed p-value is that of the regression with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope	Intercept	r^2 %	p
Bay	winter	-0.065 (0.022)	129.51 (44.34)	43.49	**0.01**
Bay	spring	0.003 (0.013)	-6.23 (25.73)	0.66	0.79
Bay	summer	-0.037 (0.045)	75.31 (88.83)	5.88	0.42
Bay	fall	-0.130 (0.025)	260.12 (50.68)	70.29	**0.0003**
James	winter	-0.035 (0.038)	70.33 (76.73)	6.90	0.39
James	spring	-0.029 (0.022)	60.75 (42.99)	14.53	0.20
James	summer	-0.111 (0.032)	223.50 (62.92)	52.97	**0.005**
James	fall	-0.131 (0.032)	263.28 (62.83)	61.19	**0.002**
Rappahannock	winter	-0.096 (0.068)	194.14 (134.88)	15.62	0.18
Rappahannock	spring	0.070 (0.010)	-137.97 (198.50)	4.36	0.49
Rappahannock	summer	-0.057 (0.090)	115.05 (179.94)	3.48	0.54
Rappahannock	fall	-0.050 (0.096)	102.19 (192.34)	2.35	0.62
York	winter	-0.061 (0.014)	122.13 (27.80)	63.40	**0.001**
York	spring	-0.032 (0.080)	66.71 (158.77)	1.44	0.70
York	summer	-0.076 (0.040)	153.88 (79.54)	24.79	**0.08**
York	fall	-0.099 (0.042)	199.91 (82.81)	34.07	**0.04**

Table 25. Fish. Seasonal trends for mean size (g wet weight) for individuals in the fish community in each system. Standard errors are shown in parentheses, and the listed p-value is that of the regression with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope	Intercept	r^2 %	p
Bay	winter	-0.64 (0.43)	1291.96 (864.08)	16.65	0.17
Bay	spring	2.16 (1.38)	-4277.41 (2758.82)	18.24	0.15
Bay	summer	1.17 (0.82)	-2278.58 (1627.47)	15.67	0.18
Bay	fall	-1.11 (0.68)	2244.03 (1367.17)	19.25	0.13
James	winter	1.16 (0.80)	-2294.31 (1601.92)	15.88	0.18
James	spring	1.64 (0.85)	-3250.18 (1700.67)	25.24	**0.08**
James	summer	1.64 (0.38)	-3238.00 (758.32)	62.83	**0.001**
James	fall	0.70 (0.68)	-1367.40 (1367.00)	8.60	0.33
Rappahannock	winter	0.23 (0.30)	-447.80 (590.96)	5.18	0.45
Rappahannock	spring	4.11 (0.95)	-8162.18 (1905.34)	62.76	**0.001**
Rappahannock	summer	4.99 (1.68)	-9912.04 (3358.73)	44.48	**0.01**
Rappahannock	fall	0.54 (0.51)	-1057.56 (1020.27)	9.34	0.31
York	winter	0.08 (0.17)	-151.70 (334.01)	2.06	0.64
York	spring	4.02 (1.21)	-7988.71 (2419.37)	50.02	**0.007**
York	summer	2.26 (1.30)	-4480.45 (2603.14)	21.53	0.11
York	fall	0.10 (0.34)	-180.65 (673.58)	0.82	0.77

Table 26. Combined zooplankton and fish. Trends in the annual combined zooplankton-fish NBSS integral spectrum parameters. Standard errors are shown in parentheses. P-values are for the regression for each trend with bold values indicating significant trends with $p < 0.10$.

System	Parameter	Slope	Intercept	r^2 %	p
Bay	height	-0.18 (0.02)	360.93 (40.72)	91.99	**<0.0001**
James	height	-0.15 (0.03)	292.95 (54.01)	81.21	**0.001**
Rapp	height	-0.13 (0.03)	262.67 (61.93)	72.62	**0.004**
York	height	-0.04 (0.04)	71.32 (71.59)	13.62	0.33
Bay	slope	0.02 (0.002)	-32.19 (3.97)	89.89	**0.0001**
James	slope	0.01 (0.005)	-13.01 (9.38)	19.50	0.23
Rapp	slope	0.01 (0.005)	-22.26 (8.90)	45.39	**0.05**
York	slope	-0.01 (0.005)	1.36 (9.35)	0.73	0.83

Table 27. Combined zooplankton and fish. Trends in the height of the centered seasonal combined zooplankton-fish NBSS integral spectrum parameters. Standard errors are shown in parentheses. P-values are for the regression for each trend with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope	Intercept	r^2 %	p
Bay	winter	-0.14 (0.08)	278.86 (159.48)	31.19	0.12
Bay	spring	-0.23 (0.04)	45.19 (84.24)	81.22	**0.001**
Bay	summer	-0.17 (0.04)	342.90 (68.76)	78.45	**0.002**
Bay	fall	-0.16 (0.07)	317.04 (136.81)	44.09	**0.05**
James	winter	-0.08 (0.06)	154.05 (121.18)	18.11	0.25
James	spring	-0.13 (0.09)	250.01 (173.29)	23.52	0.19
James	summer	-0.12 (0.04)	239.49 (77.93)	58.15	**0.02**
James	fall	-0.19 (0.11)	370.64 (219.10)	29.46	0.13
Rapp	winter	-0.09 (0.07)	178.47 (141.77)	19.23	0.24
Rapp	spring	-0.08 (0.09)	145.87 (178.11)	9.17	0.43
Rapp	summer	-0.05 (0.08)	96.65 (762.49)	5.27	0.55
Rapp	fall	-0.06 (0.08)	113.70 (157.19)	7.48	0.48
York	winter	0.21 (0.05)	-47.51 (92.09)	2.98	0.66
York	spring	-0.05 (0.07)	96.08 (128.94)	7.94	0.46
York	summer	-0.95 (0.05)	185.98 (97.44)	35.20	**0.09**
York	fall	-0.04 (0.05)	72.48 (105.70)	6.97	0.49

Table 28. Combined zooplankton and fish. Trends in the slope of the centered seasonal combined zooplankton-fish NBSS integral spectrum parameters. Standard errors are shown in paretheses. P-values are for the regression for each trend with bold values indicating significant trends with $p < 0.10$.

System	Season	Slope	Intercept	r^2 %	p
Bay	winter	0.02 (0.01)	-30.15 (22.49)	19.54	0.23
Bay	spring	0.02 (0.01)	-31.65 (10.45)	55.41	**0.02**
Bay	summer	0.02 (0.01)	-40.45 (10.97)	65.06	**0.01**
Bay	fall	0.01 (0.01)	-12.76 (15.52)	7.84	0.47
James	winter	0.001 (0.01)	-2.64 (13.84)	0.28	0.89
James	spring	0.006 (0.01)	-13.06 (10.33)	16.87	0.27
James	summer	0.006 (0.01)	-12.06 (13.36)	9.18	0.42
James	fall	0.0001 (0.01)	-0.93 (16.08)	0.002	0.99
Rapp	winter	-0.001 (0.01)	0.42 (14.80)	0.09	0.94
Rapp	spring	0.008 (0.01)	-15.73 (15.47)	11.75	0.37
Rapp	summer	0.003 (0.01)	-7.43 (9.99)	5.98	0.52
Rapp	fall	0.0003 (0.01)	-1.20 (16.67)	0.02	0.97
York	winter	-0.004 (0.01)	6.74 (18.12)	2.36	0.69
York	spring	0.00 (0.01)	-0.69 (6.91)	0.00	1.00
York	summer	0.002 (0.01)	-4.61 (10.40)	1.94	0.72
York	fall	-0.007 (0.01)	13.92 (10.58)	21.55	0.21

Figure 1. Sampling locations for the VIMS Trawl Survey, CBP Mesozooplankton Monitoring Survey, and CBP Water Quality Monitoring Survey. The VIMS Trawl Survey stations in the tributaries are fixed, but the stations in the mainstem Bay are selected each month using a random-stratified design. The VIMS Trawl Survey stations shown here are for July 1995. The Water Quality Monitoring Survey stations and Mesozooplankton Monitoring Survey stations are fixed.

Figure 2. Fish. Trends in (A) annual richness as number of species and (B) annual diversity in the lower Chesapeake Bay and its tributaries. Dashed lines indicate the regression was not significant.

Figure 3. Annual PCA biplot for the James River. Each observation is the score for one of the fixed stations for each year. Observation labels are the last two digits of the year. Stations are color-coded by salinity region. Fish species abbreviations are listed in Table 2.
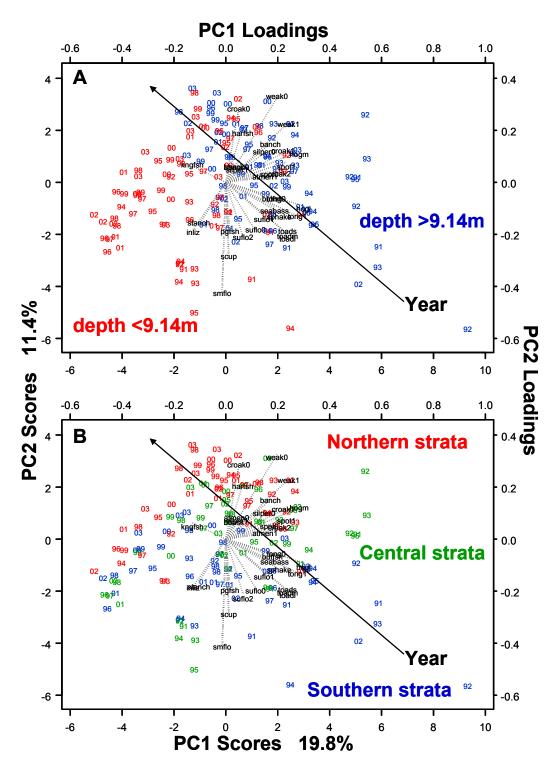
Figure 4. Annual PCA biplot for the Rappahannock River. Each observation is the score for one of the fixed stations for each year. Observation labels are the last two digits of the year. Stations are color-coded by salinity region. Fish species abbreviations are listed in Table 2

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Figure 5. Annual PCA biplot for the York River. Each observation is the score for one of the fixed stations for each year. Observation labels are the last two digits of the year. Stations are color-coded by salinity region. Fish species abbreviations are listed in Table 2.

Figure 6. Annual PCA biplot for the lower Chesapeake Bay. Each observation is the score for one of the fixed stations for each year. Observation labels are the last two digits of the year. Stations are color-coded by depth (A) and latitudinal strata (B). The black arrow indicates the temporal trend. Fish species abbreviations are listed in Table 2.

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Figure 7. Zooplankton and fish. Example NBSS biomass domes from (A) the lower Chesapeake Bay, (B) the James River, (C) the Rappahannock River, and (D) the York River for three years. The dotted lines in A and C indicate the regression was not significant.

Figure 8. Zooplankton. Trends in the (A) slope and (B) height of the centered annual zooplankton integral spectra. Dashed lines indicate the regression was not significant.

Figure 9. Zooplankton. Trends in the (A) peak abundance and (B) curvature of the annual zooplankton biomass domes. Dashed lines indicate the regression was not significant.

Figure 10. Zooplankton. Trends in (A) the annual mean abundance and (B) annual mean biomass of the zooplankton community in each system.
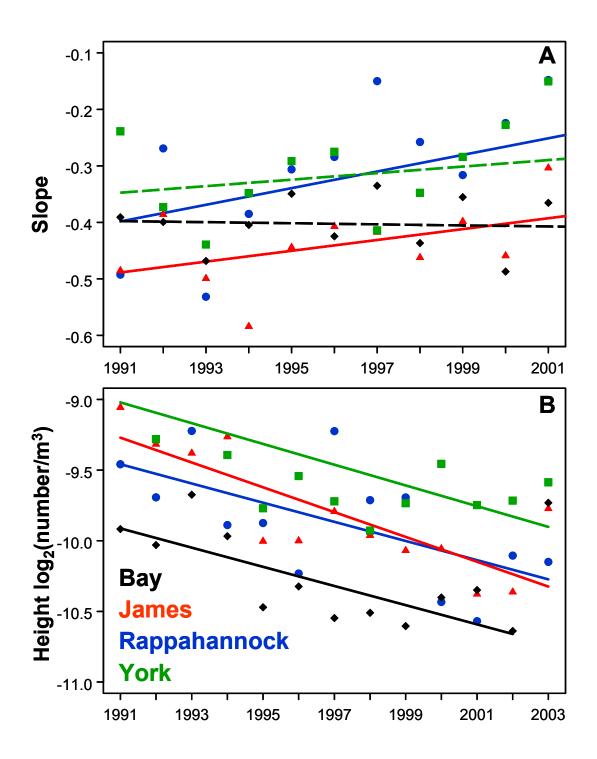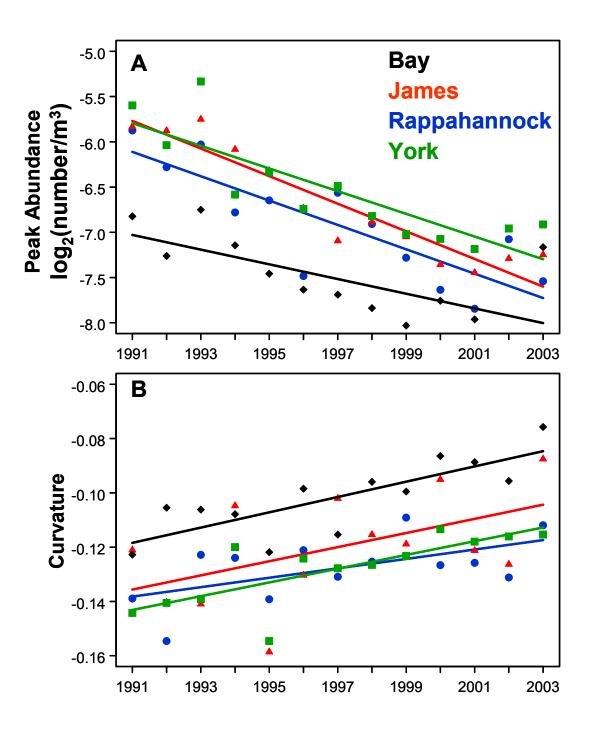
Figure 11. Fish. Trends in the (A) slope and (B) height of the centered annual fish integral spectra. Dashed lines indicate the regression was not significant.

Figure 12. Fish. Trends in the (A) peak abundance and (B) curvature of the annual fish biomass domes.
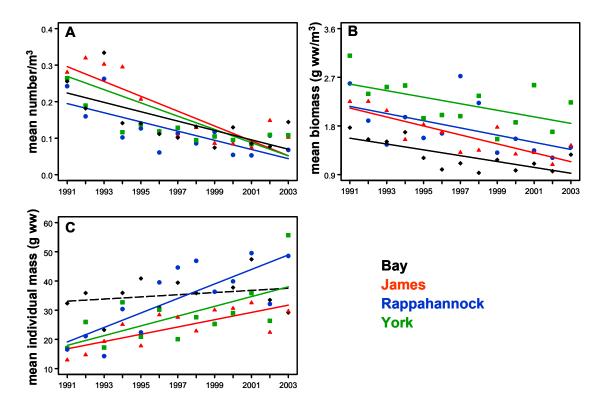
Figure 13. Fish. Trends in the (A) annual mean abundance, (B) annual mean biomass, and (C) annual mean individual mass for the fish community in each system. Dashed lines indicate a regression was not significant.
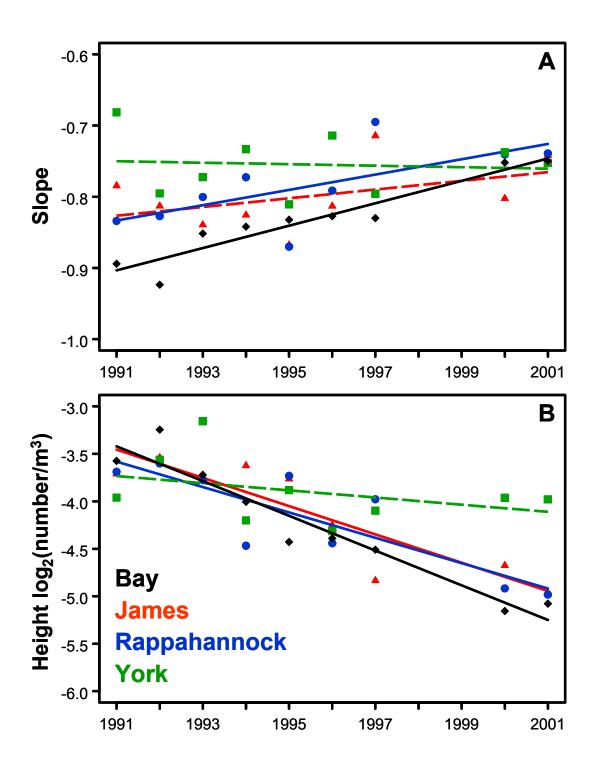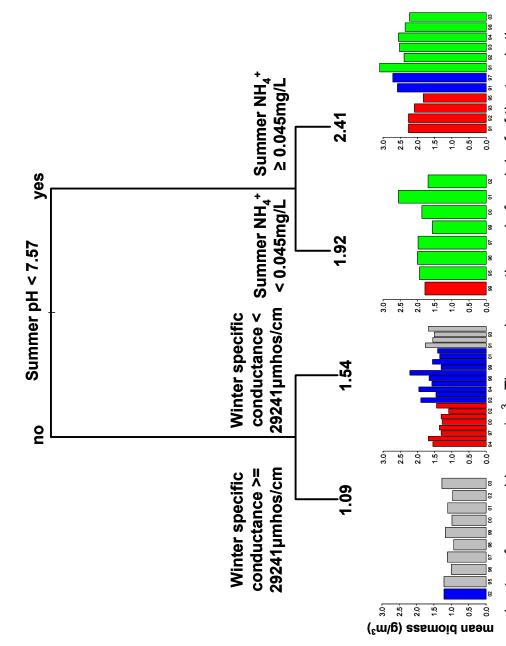
Figure 14. Combined zooplankton and fish. Trends in the (A) slope and (B) height of the centered annual combined zooplankton-fish integral spectra. Dashed lines indicate the regression was not significant.

Figure 15. Regression tree for mean biomass/m³. The number on the end of each leaf of the tree is the mean fish biomass in g/m³ for that leaf. The bar plots below each leaf show the mean biomass for each year in each system associated with that leaf. Gray bars = lower Chesapeake Bay, red bars = James River, blue bars = Rappahannock River, and green bars = York River.
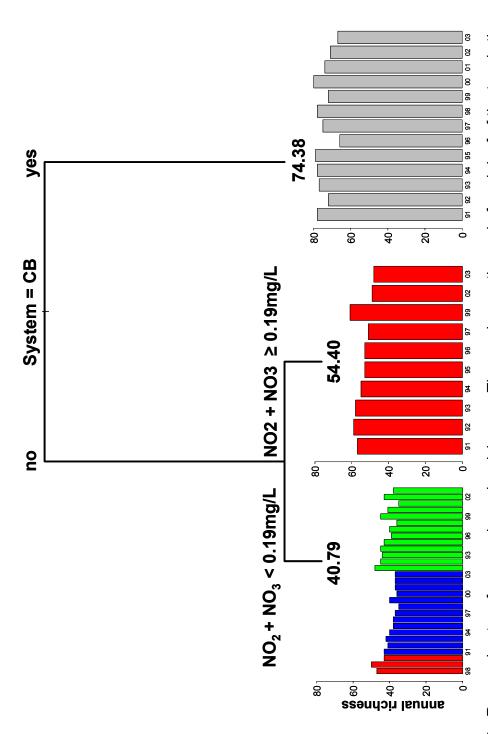
Figure 16. Regression tree for annual species richness. The number on the end of each leaf of the tree is the mean annual species richness for that leaf. The bar plots below each leaf show the annual richness for each year in each system associated with that leaf. Gray bars = lower Chesapeake Bay, red bars = James River, blue bars = Rappahannock River, and green bars = York River.
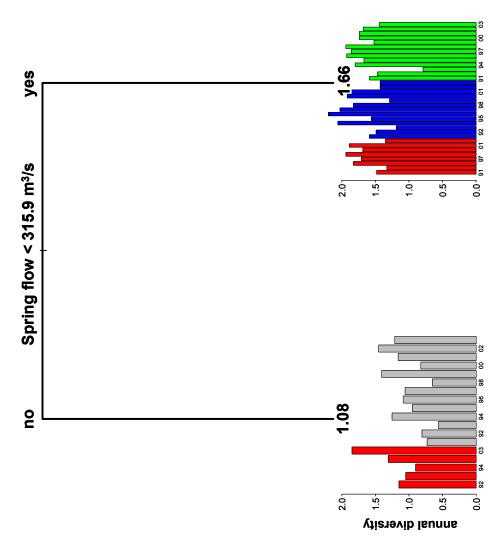
Figure 17. Regression tree for annual species diversity. The number on the end of each leaf of the tree is the mean diversity for that leaf. The bar plots below each leaf show the annual diversity for each year in each system associated with that leaf. Gray bars = lower Chesapeake Bay, red bars = James River, blue bars = Rappahannock River, and green bars = York River.

CHAPTER 5

Decadal-scale variability in the species composition and size structure of fish and crustacean communities in Pamlico Sound and its tributaries

Abstract

Variability and trends in the size structure and abundance of the fish and macro-crustacean communities in Pamlico Sound, North Carolina, and its tributaries were investigated for the period 1992 - 2003. Shifts in size structure and species composition of fish, crabs, and shrimp attributable to human-induced stresses and climate change have implications for ecosystem-based fisheries management in coastal ecosystems but few metrics or indicators are available to describe effects of perturbations at the community level. Here, metrics derived from size-spectra analysis and multivariate ordination are obtained to evaluate their potential to characterize communities and detect changes in them. Normalized biomass size spectrum (NBSS) parameters, mean abundance, mean biomass, and mean size of the fish and crustacean communities were estimated using fisheries-independent monitoring data. Principle component analysis (PCA) of abundance data for ecologically and economically important species was conducted to track temporal changes in species composition in relation to observed patterns in the size and abundance metrics. The NBSS parameters, and size and abundance metrics, were relatively stable over the 12-yr time period. Species richness increased significantly in Pamlico Sound and its

tributaries based on the June surveys while species diversity increased in the Pamlico and Pungo Rivers. No trends in diversity or richness were observed in the September data. From two to four temporal assemblages were detected by PCA in all systems. Older (and larger) Atlantic croaker, spot, and southern flounder declined in abundance near the end of the time series while pinfish, bluefish, bay whiff, and brown shrimp became more common. Combining multivariate and NBSS analyses quantified and provided insights into shifts in size and taxonomic structure of the fish-macroinvertebrate communities that were not fully evident in either analysis alone.

Introduction

Fish and crustacean communities vary spatially and temporally in species composition, and in size and age structure. Gradients in hydrographic and environmental factors shape the spatial structure of fish communities (Peterson and Ross 1991; Wagner and Austin 1999; Martino and Able 2003), while temporal variability in communities results from the cumulative effect of short-term (seasonal and annual) and longer-term (decadal) responses to natural and anthropogenic influences on the ecosystem (Methratta and Link 2006, 2007; Nye et al. 2009). The effects of temporal and spatial variability in species composition and size distribution on standing stock and productivity of fish communities are important to consider when developing spatially-explicit, ecosystem-based fisheries management plans (Link 2010). Integrated indicators of the state of communities, in addition to status of individual species, will be important to

assess the effectiveness of proposed management actions. To be effective,

simple or aggregate indicators must detect and quantify status and changes in

the fish community. Such indicators should track changes through time and

provide information on sources of variability (Rochet and Trenkel 2003; Jennings

2005; Shin et al. 2005). Evaluating and comparing spatial and temporal changes

in fish communities in large coastal or estuarine systems is difficult because of

costs and the need for repeated sampling over long periods of time. However,

long-term data from fishery-independent monitoring surveys are available that

can be analyzed to gain insights into shifts or changes in communities that may

have occurred.

Metrics based on size and abundance from fisheries-independent

monitoring surveys have been demonstrated to be sensitive indicators of effects

of fishing intensity based on long-term analyses of survey data in large marine

ecosystems (Haedrich and Barnes 1997; Bianchi et al. 2000; Blanchard et al.

2005; Duplisea and Castonguay 2006). Normalized biomass size spectra

(NBSS) constitute one family of size and abundance metrics that depict the

decline in abundance with increasing size for aquatic organisms. NBSS

parameters describe and represent predator-prey size ratios and changes in

metabolism and turn-over rates with size (Kerr and Dickie 2001; see Figure 1 in

Chapter 1). The slope and intercept of the linear relationship between

abundance and body size, referred to as the integral spectrum, are the most

thoroughly evaluated NBSS parameters and have been shown to be sensitive to

the effects of fishing in large marine ecosystems (Rice and Gislason 1996;

Bianchi et al. 2000; Jennings et al. 2002; Daan et al. 2005). However, parabolic

deviations from the integral spectrum, referred to as biomass domes, often

characterize marine and freshwater ecosystems (see Figure 1 in Chapter 4;

Boudreau and Dickie 1992; Sprules and Goyke 1994; Kerr and Dickie 2001;

Duplisea and Castonguay 2006). The additional parameters in NBSS that

describe the shape and location of a biomass dome with respect to abundance

and size provide information about the size distribution and have characteristics

that offer statistical advantages, including resistance to high-leverage data points

and effects on size distributions of changes in sampling gear, while still remaining

sensitive to ecosystem perturbations (Duplisea and Castonguay 2006).

In an analysis of the fish community from lower Chesapeake Bay, I

demonstrated that metrics based on size and abundance can effectively

characterize fish and decapod crustacean communities at spatial scales relevant

for management of resources in estuarine ecosystems (Chapter 4). In lower

Chesapeake Bay and its tributaries I detected long-term trends in fish and

crustacean community size structure using size and abundance-based metrics.

Additionally, changes in the species composition of the fish assemblages were

detected using principal component analyses (PCA). In the lower Chesapeake

Bay analysis, causes of trends in the NBSS parameters and other metrics

derived from size and abundance data did not appear to be directly related to

fishing but may have been responsive to biotic and abiotic changes within the ecosystem.

In this chapter, I evaluate size- and abundance-based metrics for an estuarine ecosystem that is subject to a suite of natural and anthropogenic perturbations different from those in Chesapeake Bay. The Albemarle-Pamlico Sound Estuarine System (APES) is the second largest estuary in the United States. Unlike Chesapeake Bay, which is a drowned river valley, APES is a shallow lagoonal estuary (mean depth = 3 m, maximum depth = 8 m (Paerl et al. 2001)). Compared to Chesapeake Bay, APES has 1) a smaller watershed and open-water surface area, 77,700 km^2 and 7,840 km^2, respectively (USFWS 2006), 2) a smaller tidal range (< 0.5 m) (Ramus et al. 2003), and 3) a smaller salinity gradient (0 - 20, with higher salinities near the ocean inlets). Despite being substantially smaller than Chesapeake Bay, residence time of water in APES is ~11-12 months because connections to the Atlantic Ocean are restricted to 4 small inlets (Joyeux 1998; Paerl et al. 2001). Additionally, the seasonal and annual climate of APES is considerably less variable than that of Chesapeake Bay (SCONC 2006b), but the number and strength of coastal storms, including hurricanes, impacting the APES is relatively high and varies annually.

This chapter analyzes data from Pamlico Sound, which constitutes the southern portion of APES (Figure 4.1). Pamlico Sound supports numerous fish and decapod crustacean species, many of which also are common in

Chesapeake Bay and experiences anthropogenic stresses similar to coastal and estuarine ecosystems worldwide, e.g., eutrophication, hypoxic and anoxic events, and fishing (Paerl et al. 2006). The Sound and its tributaries are important for commercial fishing in North Carolina, with approximately 50% of the state's commercial landings and landed value taken from the Sound and its tributaries (Diaby 2001). There is evidence that overfishing of some fish species may have occurred during the past two decades (Smith and Scharf 2010; NCDMF 2011). Hypoxic and anoxic events lasting from hours to weeks occur regularly in the tributaries of Pamlico Sound and can alter the species composition, spatial distribution, and growth rates of fishes near the hypoxic areas (Eby and Crowder 2004; Eby et al. 2005). Stresses and their effects on the Sound and tributaries can be exacerbated by extreme meteorological events such as the frequent hurricanes in the mid to late 1990s (Adams et al. 2003; Paerl et al. 2001, 2006).

My objectives were to analyze a 12-year, fishery-independent data set to 1) describe the status and identify changes in species composition and size distribution of the fish and crustacean community in Pamlico Sound and its tributaries and 2) identify or explain potential causes of shifts in species composition. The analyses provide an evaluation of the combined approach of using NBSS and multivariate analyses as a potential assessment methodology. Additionally, the analyses provide insight into and a comparison of patterns in the

fish community of the Pamlico systems and those of the adjacent lower

Chesapeake Bay.

Methods

Data collection

Data on fishes and macroinvertebrates were provided by the North

Carolina Department of Marine Fisheries (NCDMF) Pamlico Sound Survey

(Moore 2000, Figure 1). The survey collects fishery-independent data on 1)

species composition and its temporal and spatial variability, 2) relative

abundances, and 3) spatial distribution of the fish and decapod crustacean

community in Pamlico Sound and its tributaries. The survey has been conducted

since 1987, and sampling protocols have remained consistent since 1992. My

analysis was confined to years 1992 - 2003 when sampling protocols remained

consistent.

Sampling was conducted during the first and second weeks of June and

the second and third weeks of September, except for 1999 when vessel

malfunctions in June delayed the survey until the second and third weeks of July,

and hurricanes during September extended sampling into October. Five sites,

randomly selected by NCDMF were sampled in the Pamlico and Neuse Rivers,

and three random sites were sampled in the Pungo River during each survey.

No stratification scheme was used for sampling within the tributaries. The

NCDMF stratified Pamlico Sound by depth (< 3.7 m or > 3.7 m) and geography

(East and West) for a total of four strata. The number of sampling sites per

stratum in Pamlico Sound was allocated based on previous surveys using the

following formula (Moore 2000):

$$N_s = N_t(\frac{F_s}{F_t})$$

where N_s = the number of stations in the stratum
N_t = the total number of stations
F_s = the area of the stratum
F_t = the total survey area.

A minimum of three sites per stratum and a total of 51 - 54 sites per survey were

sampled (Moore 2000).

Two demersal mongoose trawls (9.1-m headrope, 1.0 m X 0.6 m doors,

2.2-cm bar mesh body, 1.9-cm bar mesh cod end, and a 100-mesh tailbag

extension) were towed simultaneously at each station by the R/V *Carolina Coast*

for 20 minutes at 2.5 knots (Moore 2000). The catch from both nets was

combined and sorted by species. A total count and weight for each species was

recorded, a random subsample of 30-60 individuals of each target species was

measured to the nearest millimeter total length, and the subsample was weighed.

Depth as well as bottom and surface salinity and temperature were recorded at

each sampling site.

Size spectrum analyses

Normalized biomass size spectrum (NBSS) analyses followed

methodology described in previous chapters of the dissertation. Length-weight

relationships from published literature were used to estimate weights of individual fish. The relationship between the coefficient of variation (CV) of abundance and weight class was U-shaped. The CVs of size classes between 1 g and 1024 g inclusive ranged from 100-500%, but the CVs of the size classes < 1 g and > 1024 g increased dramatically. Therefore, only the weight classes with a CV of 500% or less (1-1024 g) were included in the analyses. Because the NBSS data relating log abundance to log weight were strongly parabolic, only parameters describing the parabolic biomass domes were analyzed for trends. Biomass dome parameters, mean abundance, mean biomass, and mean size were estimated for each system based on the June cruises, the September cruises, and the June and September cruises combined. Trends over years were compared across the sampled systems using Analysis of Covariance (ANCOVA). An alpha level of 0.10 was used to judge significance in statistical analyses. The α = 0.10 level was selected to lower the possibility of making a type II error because failing to recognize an important change in the fish community structure could be detrimental to management efforts (Peterman 1990). Quantile-quantile plots (Q-Q plots) were used to determine if data used in the trend regressions met the assumptions of normality.

Community analyses

 Species richness (number of species) and Shannon diversity (Pielou 1974) in each system were analyzed for trends. Principal components analysis (PCA) was conducted to identify temporal patterns in the sampled fish-

macroinvertebrate community of Pamlico Sound and each tributary. The

analyses were conducted across years by season (June and September) for

each system. Species were selected for inclusion in the PCA based on a

frequency of occurrence during the time series and their presence in all four

systems. Based on a plot of species ranked by their frequency of occurrence, a

frequency of occurrence of ≥10% was chosen to exclude rarely collected

species. When possible, the data for each species were assigned to age classes

based on modes in the length-frequency distributions. Eighteen fish species and

four crustacean species were selected for PCA. Not every species occurred in

every system during each season (Tables 1 and 2). The species were the

variables in the PCA. Observations were the log-transformed ($\log_{10}$(catch+1))

number per tow of each species collected at each sampled site. Spatial or

temporal assemblages were delineated based on the grouping of observations in

the resulting biplots.

Once assemblages were identified based on PCA, salinity and

temperature data from the survey were analyzed across assemblages using a

Student's t-test or one-way ANOVA to determine if the temporal assemblages

were associated with specific environmental conditions. For each assemblage

detected by the PCAs, the NBSS biomass dome parameters were compared

using a Student's t-test or one-way ANOVA to evaluate the variability of the

NBSS parameters with respect to the fish-macroinvertebrate community in each

system. Similar to the the trend analyses, Q-Q plots were used to determine if the data used in the ANOVAs and t-tests met the assumptions of normality.

Results

The NCDMF Pamlico Sound Survey sampled 1265 stations in the years 1992 to 2003. Bottom-water temperature ranged from 17.5°C to 30.8°C and bottom salinity ranged from 0.1 to 29.1 with no significant trends (Figure 2). The survey collected 1,495,094 fish and crustaceans ranging in weight from 15 mg to 16 kg.   Mean weight was 22.31 g in the tributaries and 37.64 g in Pamlico Sound. Spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) dominated the fish communities in all four systems. These two species constituted 82 - 83% of the total catch by numbers in the tributaries and 68% in the Sound. Other prevalent species included Atlantic menhaden (*Brevoortia tyrannus*), pinfish (*Lagodon rhomboides*), weakfish (*Cynoscion regalis*), silver perch (*Bairdiella chrysoura*), and blue crab (*Callinectes sapidus*). The rank abundance of these species differed by system.

Community metrics

Based on the June survey data, species richness increased significantly in all four systems over the 12-yr time series (Figure 3A). For the September data, there were no significant trends in richness or diversity. Pamlico Sound was more speciose than the tributaries. The Pamlico and Pungo Rivers consistently had fewer species than the Neuse River. The increasing trend in June species

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richness for the Pungo River was significant only through 2001. The increases in

June richness during the time series were driven by the addition of a few

individuals of previously unrepresented species. These species included alewife

(*Alosa pseudoharengus*), hickory shad (*Alosa mediocris*), fringed flounder

(*Etropus crossotus*), longnose gar (*Lepisosteus osseus*), striped mullet (*Mugil

cephalus*), and banded drum (*Larimus fasciatus*), which occurred in more than

one of the systems toward the end of the time series, but were not represented in

earlier years. Two species, pinfish and bay whiff (*Citharichthys spilopterus*),

which were collected primarily near the end of the time series (late 1990s to

2003), became quite common. Overall, there were several species in each

system with significant positive trends in abundance, but fewer species with

negative trends (Table 3). Most species that exhibited significant trends made

only minor contributions to the overall abundance of the fish-macroinvertebrate

community of each system. The positive trends in diversity for the Pamlico and

Pungo Rivers during the June survey (Figure 3B) were responses to declining

catches of age-1 Atlantic croaker near the end of the time series, which

increased the evenness of the community.

Community analyses

The first two PCs of the June and September PCAs captured between

23.5% and 39.0% of the variance in each system. Scree plots of the eigenvalues

from each of the annual PCAs (Figures S4 and S5) depicted 8-10 principal

components with eigenvalues greater than one, which indicates that the PC

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captures as much variance as a single standardized variable (Kaiser 1960). The slopes of the scree plots tended to change after PC2 for the majority of the PCAs, which indicated that the first two PCs captured the dominant axes of variability (Johnson 1998), and the first two PCs were retained for interpretation. Loadings for the principal components with eigenvalues > 1 are listed in Tables S11-18.

The PCA biplots of the June and September data indicated presence of two to four assemblages for each system. These assemblages were groups of species and age classes that exhibited similar patterns in abundance for multiple years during the 12-year survey rather than in space and will be referred to as "temporal assemblages". The number of temporal assemblages and species membership in each assemblage differed between the two survey months for each system. However, there were some broadly consistent patterns across systems and in the two survey months. Fish-macroinvertebrate communities in Pamlico Sound and the Pamlico River were similar, with each exhibiting two to three temporal assemblages. However, in the Neuse and Pungo Rivers, three to four temporal assemblages were observed.

There were two primary temporal assemblages detected in the June PCAs of all four systems (Figures 4-7). These two primary assemblages separated along PC2 in Pamlico Sound and the Pamlico River, separated along PC1 in the Pungo River, and were split across the first two PCs in the Neuse River. The two

assemblages represented temporal shifts in species composition and age distribution of the fish and macroinvertebrate communities, with the shift occurring between 1996 and 1999. While species membership of the two primary assemblages differed among systems, there were some consistent patterns. The older age classes of spot, Atlantic croaker, and southern flounder were more abundant during the early-years assemblages in the four systems while bluefish, pinfish, and brown shrimp were more prevalent in the later-years assemblages. The later-years assemblage in the Neuse River departed slightly from this pattern because of overall reduced abundance of most species in the analysis.

In the June PCAs, there were assemblages in addition to the two primary temporal assemblages in Pamlico Sound, the Pungo River, and the Neuse River, but only in isolated years (Figures 4-7). The data from 1999, when the survey was conducted in July rather than June, partitioned separately from the other years in these three systems. Large catches of YOY weakfish, bluefish, and brown shrimp distinguished 1999 from other years in these systems. In addition to 1999, data from 2000 and 2002 grouped separately in the Pungo River and Neuse River, respectively. Age-1 weakfish was one of the species that defined the 2000 assemblage in the Pungo River. The 2002 assemblage in the Neuse River resulted from high catches of blue crab, age 1+ southern flounder, YOY spot, and pinfish.

In the September PCAs, the behavior of the temporal assemblages was more variable across systems than in June (Figures 4-7). Similar to June, a temporal shift in species composition was evident in the September PCAs for the Pamlico Sound and Pamlico River fish-macroinvertebrate communities, but a slightly different suite of species was involved. A shift point between the two assemblages in each system occurred in 2001 and 1999 in the Sound and the Pamlico River, respectively. In the Pungo River, three fish-macroinvertebrate assemblages were defined in September. Unlike other analyses, the September Pungo River assemblages did not persist for consecutive years but rather represented oscillations among different species groups. The temporal assemblages in the September PCA for the Neuse River indicated a cyclical pattern, with reduced abundance of most species at the beginning and end of the series of survey years, but a transitional assemblage with higher abundance for most species during the middle survey years.

The temporal patterns for several species in Pamlico Sound, the Pamlico River, and the Neuse River differed between June and September. For example, pigfish in Pamlico Sound were more abundant in the early-years assemblage in the June PCA but were more common in the later-years assemblage in the September analysis. The age-1+ classes of spot and Atlantic menhaden exhibited similar behavior in the Pamlico River as did age-1+ spot, hogchokers, and YOY summer flounder in the Neuse River. These shifts suggested either a change in timing of residence in these systems or changes in their growth rates.

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Size and abundance metrics

There were no significant trends over the 12-yr survey period in annual mean abundance per tow, mean biomass per tow, or mean size. However, the means for these variables did differ significantly among the four systems (Table 4). Annual mean abundance per tow was significantly higher in the Pungo River than in the Pamlico River or Pamlico Sound (Tukey HSD test, $p < 0.10$, Table 4) because of higher catches of spot, Atlantic menhaden, and Atlantic croaker. Annual mean biomass per tow was significantly higher in the Pungo River than in the Pamlico River (Tukey HSD test, $p < 0.10$, Table 4). Annual mean weight was significantly heavier in Pamlico Sound than in any of the tributaries (Tukey HSD test, $p < 0.10$, Table 3) due to higher occurrences of large rays, e.g., smooth butterfly rays (*Gymnura micrura*), cownose rays (*Rhinoptera bonasus*), and Atlantic stingrays (*Dasyatis sabina*).

The size and abundance metrics (Table 5) exhibited several significant trends over the 12-yr period in some systems when collections for June and September were examined separately. Mean size of fish and crustaceans collected during June in the Neuse River followed a parabolic trend, with the smallest mean sizes observed in 1997 and 1998 (Figure 8A), primarily due to high catches of age-1 Atlantic croaker and low catches of other species, especially in the larger size classes. There were no significant trends in mean biomass per tow for the June data, and there were no significant trends in mean size for the September data. However, mean biomass per tow in September

increased significantly in the Pamlico River over the 12-yr survey period because of increases in numbers of fish weighing 16 - 64 g. A parabolic trend in biomass per tow was observed during September in the Neuse River, with highest biomass observed in the mid to late-1990s (Figure 8B) because of increases in catches of fish in the 32 - 256 g size classes. There were no significant trends in mean abundance per tow in either June or September. However, mean abundance per tow was higher in September than in June (ANOVA, $p = 0.004$). Mean abundance was higher in the Pungo River than in the other systems, and was significantly higher in the Neuse River than in Pamlico Sound (Tukey HSD, $p < 0.10$, Table 5).

The NBSS biomass domes for the fish-macroinvertebrate community in each system for combined June-September data were described well by quadratic regression (Figure 9). The 48 quadratic regressions (12 years X 4 systems) explained 53-95% of the variance. No significant trends in these annual biomass dome parameters were detected for any of the systems over the 12-yr survey. The mean curvature parameter of these annual biomass domes did not differ among the four systems (Table 6). For the combined June-September data, size at peak abundance (g, wet wt) was heavier in Pamlico Sound than in the Pamlico River (Tukey HSD test, $p < 0.10$, Table 6). Peak abundance ($\log_2$-transformed number per trawl tow) in Pamlico Sound was substantially lower than in the Neuse and Pungo Rivers (Tukey HSD test, $p < 0.10$, Table 6).

The quadratic regressions fit separately to the June and September data (12 years X 2 months X 4 systems) also defined biomass domes described well by quadratic regressions that explained 33-97% of the variance. Mean values for curvature, size at peak abundance, and abundance are summarized in Table 7. There were two significant trends over the 12-yr period in the June biomass dome parameters, but no significant trends in the September data. Size at peak abundance in June declined significantly over the survey years in Pamlico Sound (Figure 10) because abundance of relatively small 0.5 to 2.0 g bay anchovy (*Anchoa mitchilli*), weakfish, and brown shrimp (*Farfantepenaeus aztecus*) increased in the Sound from 1999 through 2003. In contrast, the size at peak abundance in June increased significantly in the Pamlico River (Figure 10) where abundance of the 1.4 to 4.0 g size classes declined while abundance of the 22.6 to 32.0 g size classes increased. Although peak abundance did not differ significantly between June and September in any system, the peak abundances did differ among systems (ANOVA, $p = 0.040$), with peak abundance in the Pungo River significantly higher than in Pamlico Sound (Tukey HSD test, $p < 0.10$, Table 7). There was a significant interaction between system and survey month in the mean curvature parameter (ANOVA, $p = 0.005$) because the Pamlico and Pungo Rivers had the broadest mean curvature in June but the narrowest in September while Pamlico Sound exhibited the opposite behavior (Table 7).

Effects of species shifts on NBSS parameters

The observed changes in species composition in each system had an effect on the NBSS biomass dome parameters, although changes were not consistent among systems or across the June and September analyses (Table 8). For June, size at peak abundance was larger in the later-years assemblages in the Pamlico and Pungo Rivers but smaller in the later-years assemblage in Pamlico Sound. Peak abundance was significantly higher in the 1999 assemblages in Pamlico Sound and the Neuse River. Lastly, there were significant differences in biomass dome curvature among the June assemblages in the Pamlico and Pungo Rivers.

In September, peak abundance was the only biomass dome parameter that differed significantly among assemblages in every system (Table 8). Peak abundance for the later-years assemblages was significantly higher than that of the early-years assemblages in both the Pamlico and Neuse Rivers. In contrast, the peak abundance of the later-years assemblage in Pamlico Sound was significantly lower than that of the early-years assemblage despite sharing many of the same taxa as the Pamlico River. In the Pungo River, the two assemblages of the fish-macroinvertebrate community which had oscillated between the positive PC2 assemblage and the negative PC2 assemblage had similar peak abundances and these were significantly higher than peak abundance of the negative PC1 assemblage. The curvature in the later-years Pamlico River assemblage was significantly narrower than in the early-years assemblage,

suggesting that size classes responsible for the increase in peak abundance were near the size at peak abundance rather than a uniform increase in abundance of all size classes.

Environmental variables and assemblages

There were significant differences in bottom water temperature and bottom salinity for the assemblages delineated by the June and September PCAs (Table 8), but some of the temperature or salinity differences among assemblages were driven by one or two anomalous years, usually 1997 when temperatures were far below average in June and/or 2003 when salinities were below average in June and September. In the June assemblage analysis, water temperature during the survey period was warmest in 1999, probably because sampling was delayed until July. June water temperatures were generally higher during surveys representing the later-years assemblages although this trend was not apparent in September. Salinity was lower for the September assemblages in the mid to late 1990s than in the early and late years of the surveys due to increased hurricane activity and freshwater input.

Discussion

The size distribution and species composition of the fish-macroinvertebrate communities in Pamlico Sound and its tributaries underwent substantial change from 1992 to 2003. Two or more assemblages defined by their temporal occurrence were identified in the Sound and in each of the three

tributaries. One notable conclusion of the assemblage analyses was that the oldest age classes of several sciaenid and flatfish species were less abundant by the end of the time series in all four systems (Figures 11A and 11B) or experienced shifts in the time of the year when they were most abundant. In contrast, other taxa, including pinfish, bluefish, bay whiff, and brown shrimp, had become more abundant by the end of the time series (Figures 11C and 11D), but the community remained dominated by spot and Atlantic croaker. Despite the reduced abundance of older age classes, there were few decadal-scale trends judged to be significant in the size distributions of the fish-macroinvertebrate communities. However, there were significant differences in NBSS biomass dome parameters that described the abundance-size structure of the four systems.

At the outset of this study, I had anticipated that hurricane activity would have a substantial effect on the fish-macroinvertebrate communities of the Pamlico Sound and tributaries. The increase in hurricane activity during the late-1990s strongly affected the physicochemical characteristics of Pamlico Sound and its tributaries (Bales and Childress 1996; Paerl et al. 2001; Bale 2003; Burkholder et al. 2006; Paerl et al. 2006a), and temporally altered the spatial distribution of the fish community (Paerl et al. 2001). The flooding caused by hurricane Fran in September 1996 altered the salinity gradient for an extended period, and produced complete anoxia in parts of the Neuse River estuary resulting in large fish kills (Burkholder et al. 2006; Paerl et al. 2006a; Paerl et al.

2008). Hurricanes Dennis and Floyd, which hit in September 1999, were more extreme events that caused 500-year floods in nearly all North Carolina rivers (Bales 2003). Salinity at the mouths of the Neuse and Pamlico Rivers in September 1999 was reduced to oligohaline levels and declined by more than 50% in Pamlico Sound (Paerl et al. 2001). Hypoxia persisted in the Sound for three weeks until winds from hurricane Irene in October 1999 destratified and aerated the water column. The subsequent areal extent and frequency of hypoxic events from June to October 2000 exceeded those during the 1994-1999 period (Paerl et al. 2001).

The changes in the species composition and age structure of the fish and macroinvertebrate communities observed in my research may reflect the cumulative effect of the changes in the physico-chemical conditions within Pamlico Sound and its tributaries. Multiple fish kills were coincident with hypoxic events in the Neuse River following the 1999 hurricanes (Paerl et al. 2008) and potentially could have altered the fish community structure. The change in the salinity gradient following hurricane Floyd in 1999 reduced the abundance of Atlantic croaker, spot, bay anchovy, shrimp, and other species by 50% in the Neuse River based on sampling conducted in October 1999 (Paerl et al. 2001). However, Paerl et al. (2001) found that the abundance of finfish and crabs in Pamlico Sound itself increased 3-5 fold during the month after the hurricane, suggesting that fish and macroinvertebrates were displaced from the Neuse River into Pamlico Sound. Salinity and dissolved oxygen began returning to pre-

hurricane levels by mid-2000 (Paerl et al. 2001; Peierls et al. 2003), and surveys in August-October 2000 revealed that the abundance of most collected species in the Neuse River had rebounded to, or exceeded, abundance in 1998 (Paerl et al. 2006a). However, abundance of fish and crustaceans remained low in Pamlico Sound through 2001 (Paerl et al. 2006a), indicating that the increase in abundance in the Sound observed by Paerl et al. (2001) immediately following the 1999 hurricanes was short lived.

Shifting environmental conditions resulting from increased hurricane activity within Pamlico Sound and its tributaries in the late-1990s may have affected the species composition of temporal assemblages defined by my PCAs. The change point between assemblages, i.e. the year when the fish community shifted from one assemblage to another in all systems except for the September community in the Pungo River was nearly coincident with the period of high hurricane activity between 1996 and 1999, and the resulting assemblages generally persisted for several years until the end of the survey time series in 2003. In contrast to the Pamlico Sound and tributaries, effects of strong hurricanes that altered the salinity gradient in other North American estuarine ecosystems appeared to have only one or two month impacts on fish communities. For example, tropical storm Agnes struck the Chesapeake Bay in June 1972, displacing the mesohaline and polyhaline fish communities 13 - 23 km down-estuary or caused fish to shift their distribution from shallow areas where salinity was reduced to deeper areas with higher salinity, but fish returned

to their pre-storm spatial distributions in approximately two months (Hoagman and Wilson 1977; Ritchie 1977). A similar outcome was observed in Charlotte Harbor, Florida, following the heavy rainfall in hurricane Charley in 2004 (Greenwood et al. 2006; Stevens et al. 2006). Hurricanes with large storm surges but only moderate rainfall in Chesapeake Bay, such as hurricane Isabel in September 2003, are associated with notable increases in abundance of larval and juvenile Atlantic croaker, apparently a result of wind-driven influx and transport (Houde et al. 2005; Montane and Austin 2005). Noting the relatively fast and brief responses to hurricanes of the fish communities in Chesapeake Bay and Charlotte Harbor, it is probable that the long residence time of water in Pamlico Sound and its tributaries magnified the severity and duration of effects on the fish community associated with high rainfall hurricanes in 1996 and 1999 (Paerl et al. 2001).

While significant variability in salinity, temperature, or both variables was detected among the temporal assemblages, the environmental conditions experienced by the different assemblages were not outside of ranges encountered by the same species in other estuaries such as Chesapeake Bay. The observed increases in the frequency, duration, and areal extent of hypoxic events in Pamlico Sound and its tributaries (Paerl et al. 2001; 2006a) had measurable effects on individual growth rates and population growth rates of fish species in Pamlico Sound and its tributaries (Eby et al. 2005). In experiments and field collections of juvenile Atlantic croaker in the Neuse River conducted

from 1998 to 2000, Eby et al. (2005) found that intermittent hypoxic events affected growth of juveniles of demersal fishes by restricting them to shallower water where fewer prey are available, causing density-dependent reductions in growth because of crowding, and reductions in prey densities in deeper waters. In my analysis, silver perch, weakfish, Atlantic menhaden, bluefish, pinfish, and brown shrimp were more common in the later-years assemblages of all four systems when hypoxia had become more common. The shifts in environmental conditions that followed the strong hurricane seasons may have been factors contributing to increased abundance of these species which may be better able to occupy shallow waters or, for some taxa, to live in the pelagic zone above hypoxic waters.

The significant differences in NBSS dome parameters detected within each of the Pamlico systems indicated that the size structure of the fish communities was altered with changes in species composition. However, the differences in NBSS parameters among assemblages were not always intuitive given the patterns observed in the PCAs. For example, despite a reduction in abundance of older age classes of Atlantic croaker, spot, and southern flounder in the later years of the survey, size at peak abundance of the community in the Pamlico and Pungo Rivers increased. The older age classes of the aforementioned species were a relatively small fraction of the catch in these systems, averaging 10s-100s per tow whereas catches of the younger age classes averaged 1000s per tow. Consequently, the lower abundance of the

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older age classes in later-years assemblages had relatively little effect on size at peak abundance. Furthermore, in the later years, abundance of the smallest size classes also decreased while abundance of intermediate sizes increased, which tended to increase the size at peak abundance.

In six heavily fished North Atlantic shelf ecosystems, Duplisea and Castonguay (2006) found that direct removals of large fish reduced the size at peak abundance of the fish biomass domes. Other studies of heavily fished large marine ecosystems also found negative trends in metrics representing the mean size of the fish community (Haedrich and Barnes 1997; Bianchi et al. 2000; Jennings and Blanchard 2004; Blanchard et al. 2005; Daan et al. 2005). The changes in size at peak abundance observed in my research resulted from variability in abundance and sizes of the smaller size classes. The increased abundance of smaller size classes in Pamlico Sound and the reduced abundance of smaller size classes in the tributaries may have been caused by environmental conditions less favorable for transport of larvae through the Sound into the tributaries or conditions less favorable for survival of smaller fish in the tributaries.

The shifts in peak abundance observed over the 12 years of the survey in the September assemblages suggested a shift in the spatial distribution of the fish community in Pamlico Sound and its tributaries. Peak abundances of early-years assemblages were lower in the tributaries than in the Sound, but the

reverse was true for later-years assemblages. Given that most species comprising the assemblages in later years occurred in all four systems, the pattern in peak abundance indicates that the shift in spatial distribution from the Sound to the tributaries of the September fish community that Paerl et al. (2006a) observed through 2001 persisted through 2003 and was accompanied by a change in species composition.

The reduced abundances of older age classes of spot, Atlantic croaker, and southern flounder occurring at the end of the 1992-2003 series for several PCAs suggest selective mortality, reduced recruitment, or altered migration patterns of those age classes. Evaluating the possibility of a change in size-selective mortality over the survey years is not possible with the data at hand. Lower recruitment rates are unlikely to have caused the observed patterns because the abundance of the youngest age classes of these taxa remained unchanged or increased. Given the patterns observed in the PCAs, any environmental factor that resulted in emigration would have had to affect the older age classes of spot, Atlantic croaker, and southern flounder disproportionally and caused them to abandon the area sampled by the NCDMF Pamlico Sound Survey. These species may have experienced a shift in the time period or duration of their occupancy of the Sound and its tributaries, as indicated by differences between the June and September PCAs, but no explanation for the possible altered phenology was apparent based on observations of variability in temperature and salinity.

The changes in age structure observed for Atlantic croaker, spot, and southern flounder might have resulted from removals by commercial and recreational fisheries, which may have effectively truncated their age distributions during the 12-yr period of my analysis. Fisheries-independent analyses of these species conducted by NCDMF, Atlantic States Marine Fisheries Commission (ASMFC), and Smith and Scharf (2010) produced results that are largely consistent with the patterns observed in my study. A large fraction of the YOY and age-1 southern flounder stock is harvested by the commercial fishery (Smith and Scharf 2010), and this species was listed as a stock of concern or overfished by NCDMF from 1999 to the present (NCDMF 2011). Similarly, NCDMF listed Atlantic croaker as a species of concern, indicating that a stock assessment was unavailable and incomplete, but the fishery had experienced increased effort and landings (ASMFC 2003; NCDMF 2011). The age distribution of the croaker population within Pamlico Sound and its tributaries may have been truncated by selective removal of larger and older fish by commercial and recreational fisheries. In the Mid-Atlantic as a whole, the Atlantic croaker stock was not considered to be overfished or experiencing overfishing during the period of my study (ASMFC 2004). There is no stock assessment for spot. Its commercial landings in the Mid-Atlantic have declined steadily since the mid-1990s (ASMFC 2011), which is consistent with the patterns for the Pamlico systems observed in my PCAs.   Additionally, spot declined in abundance in the lower Chesapeake Bay and its tributaries.

The size structure and species composition of the fish communities of Pamlico Sound, the lower Chesapeake Bay (see Chapter 4), and their respective tributaries exhibited some notable changes from the 1990s to the early 2000s (Table 9). However, the patterns in each estuary were different despite the commonality of species in both systems. The metrics based on size and abundance and the community analyses indicated substantial overall declining trends in abundance and biomass of fishes in the lower Chesapeake Bay systems. PCAs of the communities in each of the Chesapeake subsystems indicated shifts in species composition and age structure during the 1990s. In contrast, the community analyses for the Pamlico systems in the same period indicated a shift in species composition that was the driver of the size distribution. Unlike the Chesapeake Bay where many species declined in abundance, there were more species that increased in abundance than decreased in the Pamlico Sound systems. The comparison of Chesapeake Bay and Pamlico Sound systems is constrained, however, because many species that declined in abundance in the lower Chesapeake Bay systems were small-bodied taxa that were not fully retained by the larger codend meshes of the NCDMF Pamlico Sound Survey trawl. An additional difference between the two estuaries was that the lower Chesapeake Bay and its tributaries were relatively unaffected by the strong hurricanes that perturbed the Pamlico Sound systems (Montane and Austin 2005; Paerl et al. 2006). Lastly, the patterns in the community metrics and metrics based on size and abundance were similar in all four systems analyzed for the lower Chesapeake Bay while the Pamlico Sound systems were

not so synchronized. The synchrony of the Chesapeake Bay subsystems and the lack of synchrony in the Pamlico Sound systems might be related to the number of openings and inlets to the Atlantic Ocean. The wide mouth of the Chesapeake Bay is the primary pathway for entry of larvae of coastal-spawning species to the lower Bay and its tributaries. In contrast, there are four small inlets to Pamlico Sound (Joyeux 1998), and the recruitment of coastal-spawning species to the Sound and its tributaries may depend upon temporal variability in the inflow dynamics at each inlet and the proximity of each tributary to the inlets.

The combination of multivariate and NBSS analyses detected patterns in the structure of the fish communities of Pamlico Sound and its tributaries that were not fully evident in either analysis alone (Table 9). The result contrasts with the trends and changes observed in the fish community of the lower Chesapeake Bay and its tributaries (Chapter 4), which were driven by long-term declines in abundance of several dominant species that were detected by both the PCA and NBSS analyses. Shifts in the fish communities of Pamlico Sound and its tributaries were not as clear or dramatic, but the combined NBSS and PCA approach provided sufficient sensitivity to detect changes in the species composition of the fish communities and quantify effects of those changes on the size distributions. Other research on changes in the size distribution of fish communities in large marine ecosystems relied on regression or smoothing techniques to detect trends in NBSS parameters (Bianchi et al. 2000; Blanchard et al. 2005; Daan et al. 2005; Duplisea and Castonguay 2006). However,

important changes in the species composition and size distribution of fish communities can occur that are not quantified easily by regression or smoothing techniques, or described fully by NBSS alone, as observed in my research. Combining size-based approaches with traditional community analyses permits detection of changes in ecosystem status and facilitates identification of species that contribute most to the observed variability. The complementary nature of the two analytical approaches deserves consideration for inclusion in developing indicators for ecosystem-based management in estuaries.

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Table 1. Age classes of fish and crustacean species and age classes included from each system in the June principal components analysis (PCA). "All" indicates all age classes were combined. "NA" indicates that the species was not included in the PCA for that system.

Scientific Name	Common Name	Pamlico Sound	Pamlico River	Pungo River	Neuse River
Anchoa mitchilli	bay anchovy	All	All	All	All
Bairdiella chrysoura	silver perch	1, 2+	1, 2+	1, 2+	1, 2+
Brevoortia tyrannus	Atlantic menhaden	0, 1+	0, 1+	0, 1+	0, 1+
Callinectes sapidus	blue crab	All	All	All	All
Chaetodipterus faber	Spadefish	1+	NA	NA	NA
Citharichthys spilopterus	bay whiff	All	All	All	All
Cynoscion regalis	Weakfish	0, 1+	0, 1+	0, 1+	0, 1+
Farfantepenaeus aztecus	brown shrimp	All	All	All	All
Farfantepenaeus duorarum	pink shrimp	All	All	All	All
Lagodon rhomboides	Pinfish	All	All	All	All
Leiostomus xanthurus	Spot	0, 1+	0, 1+	0, 1+	0, 1+
Menticirrhus americanus	southern kingfish	0, 1+	NA	NA	NA
Micropogonias undulatus	Atlantic croaker	1, 2+	1, 2+	1, 2+	1, 2+
Orthopristis chrysoptera	Pigfish	All	NA	NA	NA
Paralichthys dentatus	summer flounder	0, 1, 2+	0	0	0
Paralichthys lethostigma	southern flounder	0, 1, 2+	0, 1, 2+	0, 1, 2+	0, 1, 2+
Penaeus setiferus	white shrimp	All	All	All	NA
Peprilus alepidotus	harvestfish	All	NA	NA	NA
Peprilus triacanthus	Butterfish	All	All	All	All
Pomatomus saltatrix	Bluefish	All	All	All	All
Synodus foetens	inshore lizardfish	All	NA	NA	NA
Trinectes maculatus	hogchoker	All	All	All	All

Table 2. Fish and crustacean species and age classes included from each system in the September PCA. "All" indicates all age classes were combined. "NA" indicates that the species was not included in the PCA for that system.

Scientific Name	Common Name	Pamlico Sound	Pamlico River	Pungo River	Neuse River
Anchoa mitchilli	bay anchovy	all	all	all	all
Bairdiella chrysoura	silver perch	0, 1	0, 1	0, 1	0, 1
Brevoortia tyrannus	Atlantic menhaden	0, 1+	0, 1+	0, 1+	0, 1+
Callinectes sapidus	blue crab	all	all	all	all
Chaetodipterus faber	Spadefish	0, 1	NA	NA	NA
Citharichthys spilopterus	bay whiff	all	all	all	all
Cynoscion regalis	Weakfish	0, 1+	0, 1+	0, 1+	0, 1+
Farfantepenaeus aztecus	brown shrimp	all	all	all	all
Farfantepenaeus duorarum	pink shrimp	all	all	all	all
Lagodon rhomboides	Pinfish	all	all	all	all
Leiostomus xanthurus	Spot	0, 1+	0, 1+	0, 1+	0, 1+
Menticirrhus americanus	southern kingfish	0, 1+	NA	NA	NA
Micropogonias undulatus	Atlantic croaker	1, 2+	1, 2+	1, 2+	1, 2+
Orthopristis chrysoptera	Pigfish	all	all	NA	all
Paralichthys dentatus	summer flounder	0, 1	0	0, 1	0, 1
Paralichthys lethostigma	southern flounder	0, 1	0, 1	0, 1	0, 1
Penaeus setiferus	white shrimp	all	all	all	all
Peprilus alepidotus	harvestfish	all	all	all	all
Peprilus triacanthus	Butterfish	all	all	NA	all
Pomatomus saltatrix	Bluefish	all	all	all	all
Synodus foetens	inshore lizardfish	all	all	all	all
Trinectes maculatus	hogchoker	all	all	all	all

Table 3. Fish and invertebrates exhibiting significant positive or negative linear trends in abundance by system. + indicates a positive trend, and – indicates a negative trend. System abbreviations: PAS = Pamlico Sound, PAR = Pamlico River, PUR = Pungo River, NER = Neuse River, ALL = all four systems.

Scientific name	Common name	Trend	Systems
Aluterus schoepfi	orange filefish	-	PAS
Archosargus probatocephalus	sheepshead	+	PAS
Caranx hippos	crevalle jack	-	PAR[†], PUR
Chloroscombrus chrysurus	Atlantic bumper	-	PAS
Citharichthys spilopterus	bay whiff	+	PAR
Dasyatis Sabina	Atlantic stingray	+	PAS
Dorosoma cepedianum	gizzard shad	+	PAR
Gymnura altavela	spiny butterfly ray	-	PAS
Gymnura micrura	smooth butterfly ray	+	PAS
Lagodon rhomboids	pinfish	+	ALL
Lepisosteus osseus	longnose gar	+	NER[†]
Loligo sp.	Loligo squid	+	PAS[†]
Menippe mercenaria	Florida stone crab	+	PAS[†]
Monacanthus hispidus	planehead filefish	-	NER
Palaemonetes pugio	grass shrimp	+	PA[†]
Paralichthys lethostigma	southern flounder	-	PAS, PAR
Penaeus aztecus	brown shrimp	+	PUR[†]
Peprilus alepidotus	harvestfish	-	PAS, PAR
Pomatomus saltatrix	bluefish	+	NER, PAS*, PAR*,
Prionotus carolinus	northern searobin	-	PAS
Prionotus tribulus	bighead searobin	-	PAS
Rhinoptera bonasus	cownose ray	+	PAS
Scomberomorus maculatus	Spanish mackerel	-	NER, PUR
Synodus foetens	Inshore lizardfish	-	NER*
Trachinotus carolinus	Florida pompano	+	PAS[†]
Urophycis regia	Spotted hake	+	NER

Table 4. Mean values for the annual abundance, biomass, and size metrics. Standard errors are shown in parentheses. Entries with different superscripted letters indicate differences detected by a Tukey HSD multiple comparison test with α = 0.10.

System	Abundance (no./tow)	Biomass (kg wet weight/tow)	Size (g wet weight)
Pamlico Sound	992.24 (87.78)^{b}	37.77 (2.35)^{ab}	43.05 (1.72)^{a}
Neuse River	1609.94 (190.46)^{ab}	36.07 (3.71)^{ab}	23.33 (1.09)^{b}
Pamlico River	1550.08 (217.04)^{b}	31.07 (4.63)^{b}	24.67 (2.62)^{b}
Pungo River	2198.01 (226.05)^{a}	44.86 (4.07)^{a}	21.66 (1.36)^{b}

Table 5. Mean values for the June and September abundance, biomass, and size metrics. Standard errors are shown in parentheses.

System	Cruise	Abundance (no./tow)	Biomass (kg/tow)	Size (g wet weight)
Pamlico Sound	June	988.64 (133.64)	37.27 (3.45)	40.82 (3.74)
Neuse River	June	1399.44 (269.55)	24.75 (4.99)	28.03 (2.23)
Pamlico River	June	1121.61 (121.74)	18.34 (1.34)	28.15 (5.59)
Pungo River	June	1821.33 (290.64)	29.07 (2.80)	24.41 (2.57)
Pamlico Sound	September	993.03 (78.68)	38.17 (3.63)	45.70 (1.85)
Neuse River	September	1820.44 (181.33)	47.40 (4.82)	20.01 (1.70)
Pamlico River	September	1980.11 (400.89)	43.78 (8.47)	23.07 (4.05)
Pungo River	September	2572.35 (296.50)	60.29 (6.59)	19.17 (1.36)

Table 6. Mean values for the annual NBSS biomass dome parameters. Standard errors are shown in parentheses. Entries with different superscripted letters indicate differences detected by a Tukey HSD multiple comparison test with α = 0.10.

System	Curvature	Size at Peak Abundance (g wet weight)	Peak Abundance (no./tow)
Pamlico Sound	-0.37 (0.01)[a]	21.16 (1.05)[a]	96.67 (1.10)[a]
Neuse River	-0.39 (0.02)[a]	17.30 (1.08)[ab]	142.20 (1.10)[b]
Pamlico River	-0.38 (0.03)[a]	15.18 (1.10)[bc]	131.39 (1.13)[ab]
Pungo River	-0.40 (0.02)[a]	18.41 (1.09)[ab]	190.06 (1.14)[b]

Table 7. Mean values for the June and September NBSS biomass dome parameters. Standard errors are shown in parentheses.

System	Cruise	Curvature	Size at Peak Abundance (g wet weight)	Peak Abundance (no./tow)
Pamlico Sound	June	-0.42 (0.02)	23.71 (0.37)	104.39 (0.42)
Neuse River	June	-0.37 (0.02)	15.19 (0.41)	94.59 (0.45)
Pamlico River	June	-0.33 (0.02)	13.22 (0.42)	86.03 (0.41)
Pungo River	June	-0.33 (0.02)	14.63 (0.42)	116.02 (0.46)
Pamlico Sound	September	-0.35 (0.01)	21.50 (0.37)	70.82 (0.42)
Neuse River	September	-0.41 (0.04)	19.40 (0.44)	109.14 (0.48)
Pamlico River	September	-0.46 (0.05)	20.82 (0.43)	107.37 (0.68)
Pungo River	September	-0.43 (0.04)	22.86 (0.43)	149.88 (0.51)

Table 8. Representative species and age classes and mean bottom temperature, mean bottom salinity, and mean NBSS biomass dome parameter estimates for the June and September assemblages in each system. Salinity, temperature, and NBSS parameter estimates were compared only among the assemblages from each PCA and not across months or systems. Results of the Tukey HSD multiple comparison test or Student's t-test are indicated by superscripted letters. Different superscripted letters indicate a significant difference with $p < 0.10$. Column abbreviations: Sys. = system, Mo. = month, Temp. = Temperature, SPA = size at peak abundance, PA = peak abundance, Curv. = biomass dome curvature. System abbreviations: PAS = Pamlico Sound, PAR = Pamlico River, PUR = Pungo River, NER = Neuse River. Month abbreviations: Sept. = September. Assemblage names are shown on the biplots (Figures 7-10). Assemblage abbreviations: 2nd quad. = second quadrant, pos. PC1 = positive PC1, neg. PC1 = negative PC1, 4th quad. = fourth quadrant. Representative species codes: The first two letters are the species abbreviations, and the numbers represent age class (0 = YOY, 1 = age 1 or age 1+, 2 = age 2+). Species abbreviations: am = Atlantic menhaden, ba = bay anchovy, bc = blue crab, bf = bluefish, bs = brown shrimp, bu = butterfish, bw = bay whiff, cr = Atlantic croaker, hc = hogchoker, hf = harvestfish, lf = inshore lizardfish, pf = pinfish, pg = pigfish, ps = pink shrimp, sf = spadefish, sk = southern kingfish, si = silver perch, so = southern flounder, sp = spot, su = summer flounder, wf = weakfish, ws = white shrimp. * difference between assemblages driven isolated anomalous years.

Sys.	Mo.	Assemblage Name	Representative Species	Temp. °C	Salinity PSU	SPA g wet wt.	PA no./tow	Curv.
PAS	June	Late	am1, bf, bw, cr1, hf, lf, sp0	25.2^b	18.3^b	20.40^b	100.71^a	-0.39^a
PAS	June	1999	ba, bs, wf0	28.0^c	21.9^c	14.69^b	251.98^b	-0.39^a
PAS	Sept.	Early	ba, bs, bw, hf, wf0, wf1	24.6^a	20.7^{a*}	19.97^a	81.62^a	-0.35^a
PAS	Sept.	Late	am0, am1, pf, pg	24.2^a	19.2^{b*}	26.82^a	46.27^b	-0.36^a
PAR	June	Early	am1, cr2, so2, sp1	24.4^{a*}	8.9^a	9.89^a	97.43^a	-0.27^a
PAR	June	Late	am0, bf, bs, bu, bw, pf, wf0, wf1, ws	26.3^{b*}	10.0^a	16.27^b	78.71^a	-0.36^b
PAR	Sept.	Early	am0, bu, cr1, pf, si0, sp0, wf0	25.0^a	13.9^{a*}	19.75^a	73.72^a	-0.40^a
PAR	Sept.	Late	bf, lf, su0, bs, ps, so0, ws	23.2^b	10.5^{b*}	23.13^a	227.76^b	-0.59^b

Sys.	Mo.	Assemblage Name	Representative Species	Temp. °C	Salinity PSU	SPA g wet wt.	PA no./tow	Curv.
PUR	June	2nd quad.	am1, cr1, cr2, ps, si1, sp1	24.5[a]	10.4[a]	18.47[ab]	145.71[a]	-0.39[a]
PUR	June	1999	am0, bf, wf0	28.0[b]	13.9[a]	19.60[a]	181.14[a]	-0.42[b]
PUR	June	2000	ba, bu, hc, so0, wf1	22.7[a]	12.33[a]	14.58[ab]	73.11[a]	-0.31[c]
PUR	June	pos. PC1	am0, bf, bs, bw, pf, si2, so2, sp0, su0, wf0, ws	26.2[b]	7.94[a]	18.89[ac]	105.05[a]	-0.36[d]
PUR	Sept.	neg. PC1	ba, bf, bw, pf, su0	25.1[a]	15.6[a]	18.84[a]	60.51[a]	-0.35[a]
PUR	Sept.	pos. PC2	am0, bc, hc, si0, so0, so1, sp0	23.5[a]	10.9[a]	29.06[a]	177.84[b]	-0.50[a]
PUR	Sept.	neg. PC2	bs, cr1, hf, lf, ps, sp1, wf0, wf1, ws	24.8[a]	14.4[a]	19.41[a]	181.58[b]	-0.40[a]
NER	June	4th quad.	bu, cr2, hc, si1, si2, so0, so2, sp1, su0, wf1	23.7[a]	12.5[a]	15.93[a]	99.11[ab]	-0.36[a]
NER	June	neg. PC1	am0, am1	24.9[b]	10.0[a]	12.84[a]	69.02[a]	-0.38[a]
NER	June	1999	bf, bw, wf0	26.2[c]	18.4[b]	18.62[a]	194.41[b]	-0.30[a]
NER	June	2002	bc, pf, so1, sp0	25.6[bc]	19.2[b]	22.62[a]	177.11[b]	-0.40[a]
NER	Sept.	early	bu cr2, hf, so1	24.7[a*]	20.53[a]	17.02[a]	65.91[a]	-0.38[a]
NER	Sept.	transition	bc, cr1, hc, wf0, wf1, ws	25.3[ab*]	9.30[b]	23.13[a]	116.37[b]	-0.36[a]
NER	Sept.	late	am0, am1, bf, pf, pg, si0, si1, sp0	26.0[b*]	14.32[c]	18.56[a]	169.50[b]	-0.40[a]

Table 9. Comparison of characteristics of fish and macro-crustacean communities of the lower Chesapeake Bay and Pamlico Sound, and their respective tributary systems. Data from the Chesapeake systems were analyzed for the period 1991-2003; data for the Pamlico systems were analyzed for 1992-2003. "Synchrony" refers to the degree to which the different systems within each estuary exhibited similar patterns with regard to the NBSS parameters and size and abundance metrics.

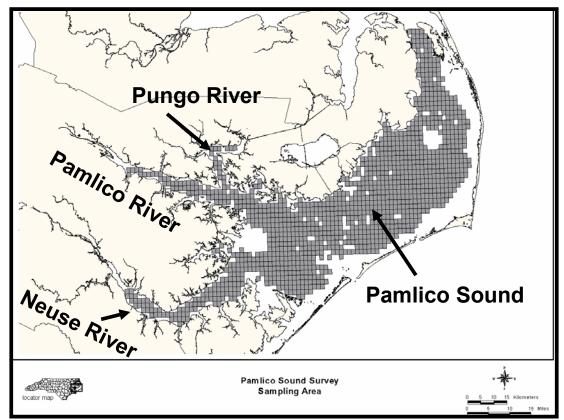| Estuary	Synchrony of patterns among systems	Richness and diversity	PCA results	Size/abundance metrics	NBSS parameters	Hurricane effects on fish community
Lower Chesapeake Bay and its tributaries	high	richness decreased diversity increased	2-3 assemblages along physical gradients temporal changes in species composition in each assemblage	negative trends in mean abundance and biomass positive trend in mean size in tributaries	negative trends in peak abundance positive trends in curvature negative trend in size at peak abundance in mainstem Bay	weak
Pamlico Sound and its tributaries	low	richness increased diversity increased in two systems	2-4 temporal assemblages in each system reflecting changes in the age structure and species composition through time	no trends in mean abundance trends in mean size and biomass in the Neuse R. mean biomass increased in Pamlico R. in Sept.	significant differences in NBSS parameters among temporal assemblages within each system	strong

Figure 1. Map of the area sampled by the North Carolina Department of Marine Fisheries Pamlico Sound Survey (from Moore 2000). The gray grid squares are selected randomly for sampling before each cruise. See text for more information.
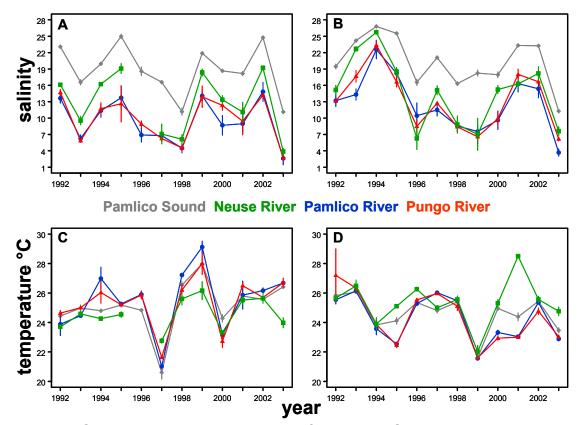
Figure 2. Salinity and temperature trends for Pamlico Sound and its tributaries. A) June salinity, B) September salinity, C) June temperature, and D) September temperature. Error bars are +/- 1 standard error.
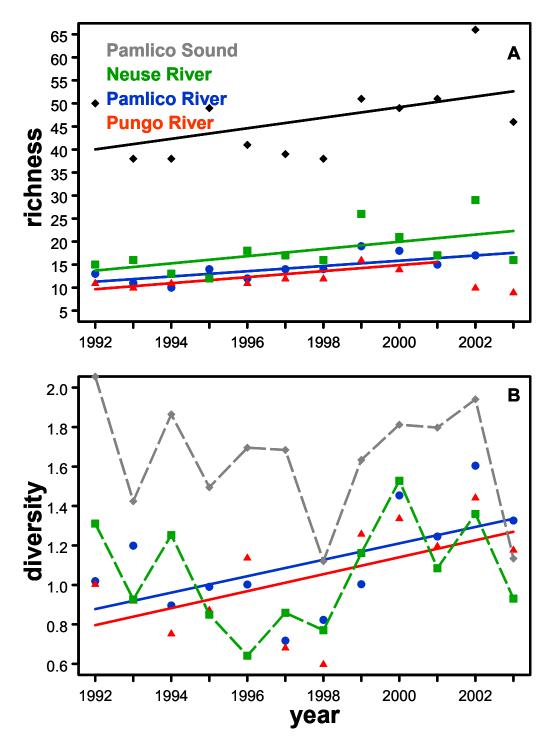
Figure 3. June survey data: (A) species richness and (B) diversity by year for the Pamlico Sound and its tributaries. Solid lines indicate significant trend, and dashed lines indicate no trend. The data points for 2002 and 2003 were excluded from the Pungo River richness analysis.
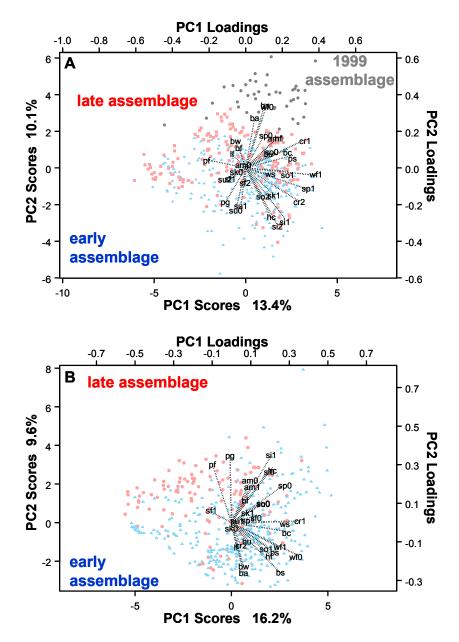
Figure 4. (A) June and (B) September PCA biplots for the Pamlico Sound. The data from 1992-1998 are shown in blue, the 1999 data are in green, and the 2000-2003 data are in red. The percentage following each axis label is the percent of the variance represented by each PC. The variable label format is sp.age where "sp" is the species abbreviation and "age" is the numeric age estimate based on visual inspection of annual length histograms. The possible ages are blank (all ages combined), 0, 1, or 2. Species abbreviations are am = Atlantic menhaden, ba = bay anchovy, bc = blue crab, bf = bluefish, bs = brown shrimp, bu = butterfish, bw = bay whiff, cr = Atlantic croaker, hc = hogchoker, hf = harvestfish, lf = lizardfish, pf = pinfish, pg = pigfish, ps = pink shrimp, sf = spadefish, sk = southern kingfish, si = silver perch, so = southern flounder, sp = spot, su = summer flounder, wf = weakfish, ws = white shrimp.
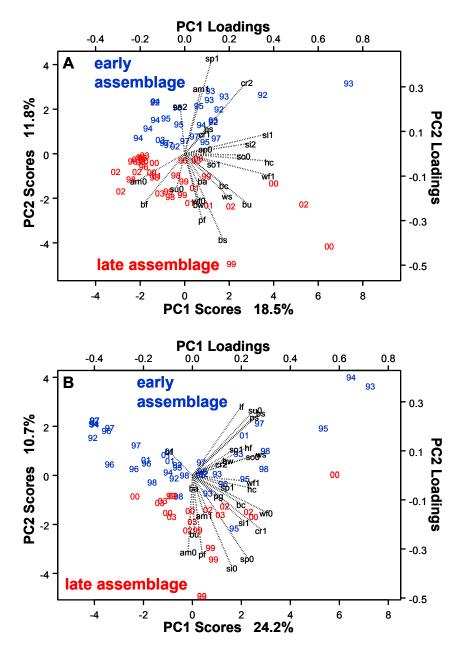
Figure 5. (A) June and (B) September PCA biplots for the Pamlico River. The data from 1992-1995 and 1997 are shown in blue, and the 1996 and 1998-2003 data are in red. The percentage following each axis label is the percent of the variance represented by each PC. The variable label format is sp.age where "sp" is the species abbreviation and "age" is the numeric age estimate based on visual inspection of annual length histograms. The possible ages are blank (all ages combined), 0, 1, or 2. Species abbreviations are am = Atlantic menhaden, ba = bay anchovy, bc = blue crab, bs = brown shrimp, bu = butterfish, bw = bay whiff, cr = Atlantic croaker, hc = hogchoker, hf = harvestfish, lf = lizardfish, pf = pinfish, pg = pigfish, ps = pink shrimp, si = silver perch, so = southern flounder, sp = spot, su = summer flounder, wf = weakfish, ws = white shrimp.
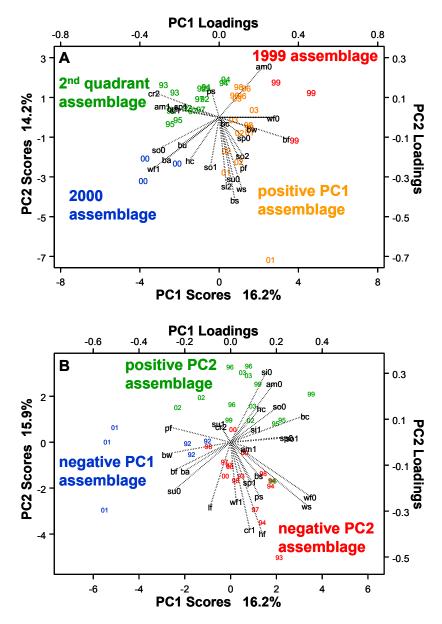
Figure 6. (A) June and (B) September PCA biplots for the Pungo River. The data from 1992-1995 and 1997 are shown in green, the data from 1996, 1998, and 2001-2003 are shown in orange, the 1999 data are shown in red, and the 2000 data are shown in blue. The percentage following each axis label is the percent of the variance represented by each PC. The variable label format is sp.age where "sp" is the species abbreviation and "age" is the numeric age estimate based on visual inspection of annual length histograms. The possible ages are blank (all ages combined), 0, 1, or 2. Species abbreviations are am = Atlantic menhaden, ba = bay anchovy, bc = blue crab, bf = bluefish, bs = brown shrimp, bu = butterfish, bw = bay whiff, cr = Atlantic croaker, hc = hogchoker, hf = harvestfish, lf = lizardfish, pf = pinfish, ps = pink shrimp, si = silver perch, so = southern flounder, sp = spot, su = summer flounder, wf = weakfish, ws = white shrimp.
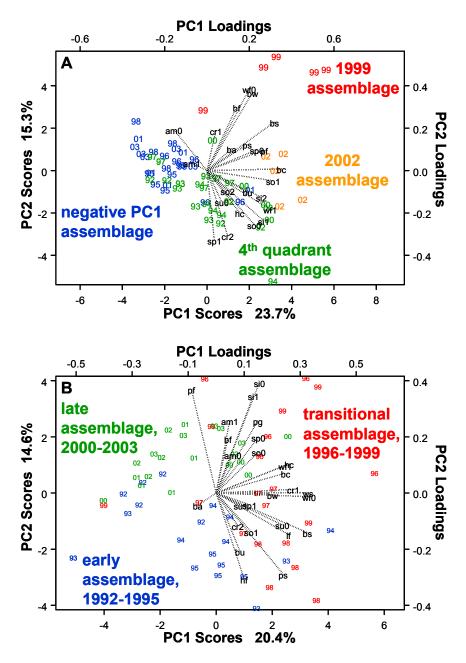
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Figure 7. (A) June and (B) September PCA biplots for the Neuse River. Assemblages discussed in the text are labeled here. The percentage following each axis label is the percent of the variance represented by each PC. The variable label format is sp.age where "sp" is the species abbreviation and "age" is the numeric age estimate based on visual inspection of annual length histograms. The possible ages are blank (all ages combined), 0, 1, or 2. Species abbreviations are am = Atlantic menhaden, ba = bay anchovy, bc = blue crab, bf = bluefish, bs = brown shrimp, bu = butterfish, bw = bay whiff, cr = Atlantic croaker, hc = hogchoker, hf = harvestfish, lf = lizardfish, pf = pinfish, pg = pigfish, ps = pink shrimp, si = silver perch, so = southern flounder, sp = spot, su = summer flounder, wf = weakfish, ws = white shrimp.
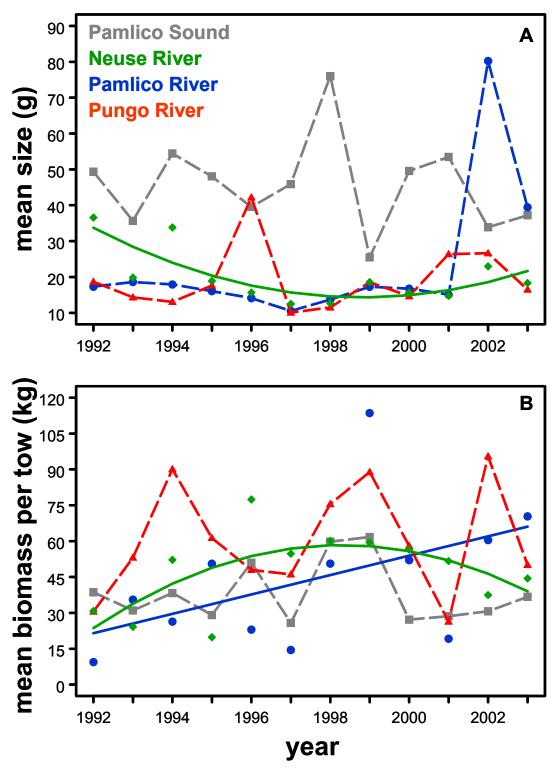
Figure 8. (A) Mean size June and (B) mean biomass September per tow. Solid lines indicate significant trend, and dashed lines indicate no trend.
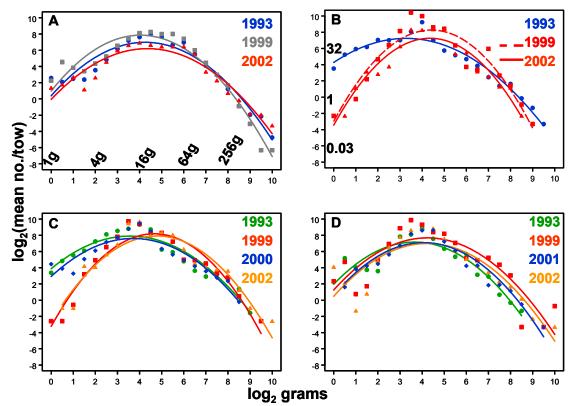
Figure 9. Examples of June NBSS biomass domes from (A) Pamlico Sound, (B) the Pamlico River, (C) the Pungo River, and (D) the Neuse River. The years shown for each system were selected from each of the temporal assemblages defined by the June PCAs and shown in Figures 7-10 and are color-coded accordingly. The numbers shown witin the axes of A and B are the nontransformed values for the size classes and number per tow, respectively.
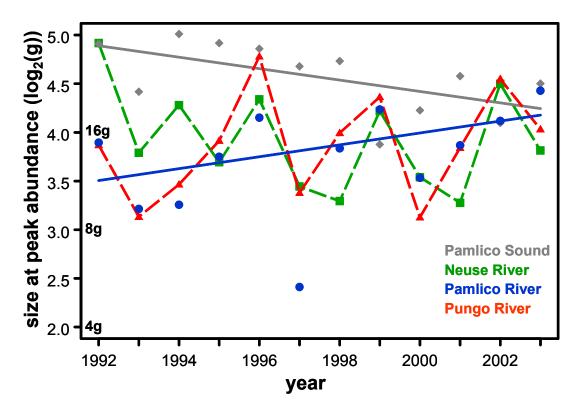
Figure 10. June survey data: NBSS biomass dome estimated size at peak abundance by year. Solid lines indicate significant trend, and dashed lines indicate no trend. The Pamlico River trend represents the regression with the 1997 data point estimate excluded as an outlier.
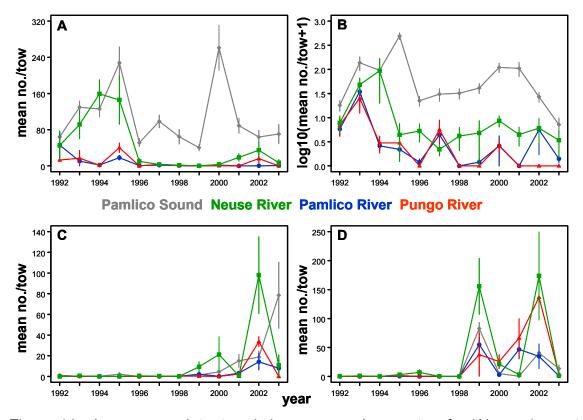
Figure 11. June survey data: trends in mean number per tow for (A) age 1+ spot, (B) age 2+ Atlantic croaker, (C) pinfish, and (D) brown shrimp. Note that the y-axis scales of each plot differ and that the y-axis for Atlantic croaker (B) is in $\log_{10}$ units. Error bars are +/- 1 standard error.

CHAPTER 6

Conclusions and Synthesis

Overall conclusions

A combination of size and abundance metrics and multivariate analyses were successful in describing and quantifying the seasonal, annual, and decadal variability in species composition and size distribution of fish communities in Chesapeake Bay and Pamlico Sound at spatial scales ranging from 50 - 100 km. Spatial and temporal shifts in species composition, detected in principal components analysis (PCA), provided insight into sources of variability expressed in normalized biomass size spectrum (NBSS) parameters. Metrics based on size and abundance exhibited behavior consistent with the patterns observed in the PCAs and NBSS parameters. Not surprisingly, the NBSS parameters were most sensitive to variability of numerically dominant species in the survey catches, for example bay anchovy in Chesapeake Bay and Atlantic croaker and spot in Pamlico Sound.

At seasonal and annual time scales and at spatial scales < 50 km, PCA indicated that fluctuations in recruitment of young-of-the-year (YOY) anadromous fish species drove the variability in species composition of fish communities in the upper Chesapeake Bay estuarine transition zone (ETZ), the Choptank River, and the Patuxent River (Chapters 2 and 3). Recruitment variability of the YOY anadromous fish strongly influenced parameters of the normalized biomass size

spectrum (NBSS) in the Patuxent and Choptank Rivers, and the effects of poor

recruitment in 2002 on the NBSS were projected and still detectable in the

NBSS in the following year (Chapter 3). In the ETZ of upper Chesapeake Bay,

recruitment variability of YOY anadromous fish and of the abundant bay anchovy

strongly affected NBSS parameters (Chapter 2). Within the ETZ, poor fits of

NBSS models for 18-km segments discouraged meaningful analysis and

interpretation of fish size distributions at these smaller spatial scales despite

sampling at high spatial resolution within each segment (Chapter 2). Overall,

results from the small spatial scale analyses suggested that an NBSS approach

was sufficient to parameterize and describe the size structure of fish communities

at spatial scales of 30 – 50 km, but not at smaller scales.

        At larger spatial scales (> 50 km) in long-term fisheries surveys of the

lower Chesapeake Bay and its tributaries (13-year time series, Chapter 4) and

Pamlico Sound and its tributaries (12-year time series, Chapter 5), composition

and trends in species and size distribution were investigated. Long-term

changes in the fish community of the lower Chesapeake Bay and its tributaries

were detected and explained by PCA and NBSS analyses, and metrics of size

and abundance. Persistent declines in abundance of several prominent species,

including bay anchovy, hogchoker, and spot resulted not only in negative trends

in mean abundance and mean biomass but also in NBSS parameters related to

abundance. In lower Chesapeake Bay, the long-term decline in abundance of

small-bodied species such as bay anchovy resulted in significant positive trends

in mean size of fish in the tributaries. Two to three assemblages were defined by the PCAs on the lower Bay tributaries. Species composition of these assemblages shifted during the 13-yr time series. In contrast, in Pamlico Sound and its tributaries, there were few long-term trends in the NBSS parameters or metrics based on size and abundance, and fish assemblages delineated in the PCAs were not strongly responsive to gradients in environmental conditions. However, there were substantial shifts in the species composition of the fish and macroinvertebrate community in each of the Pamlico Sound systems that occurred between 1996 and 1999, possibly driven by effects of frequent hurricane events. In this transition period, significant differences in the size distribution were detected in the NBSS parameters, which demonstrated the strength of the combined PCA and NBSS approach to quantify and describe fish communities.

Despite the consistency and persistence of the trends identified in Chesapeake Bay and Pamlico Sound, identifying causes of observed trends in each estuary based on environmental data proved elusive. In the Pamlico Sound systems, the observed shifts in the species composition and size distribution may have been related to fishing pressure and/or alterations in water quality resulting from the frequent hurricanes impacting the Sound from 1996-1999. In the Chesapeake Bay systems, several of the prominent fish species that declined in abundance were unfished, resident species that occupied relatively low trophic levels. These observations, combined with the declines in zooplankton

abundance in lower Chesapeake Bay, suggest that the trends in the fish communities may have resulted from bottom-up or middle-out changes in the Chesapeake ecosystem. However, attempts to link the trends in NBSS parameters and size and abundance metrics of the fish and zooplankton communities to environmental variables were not successful, indicating that additional environmental variables and further analysis are needed to explain the changes that occurred. Two variables not evaluated, changes in hypoxic volume and increases in gelatinous zooplankton, are possible causes of trends in the fish and zooplankton communities, but the available data were insufficient for rigorous evaluation.

NBSS also quantified the temporal variability of the phytoplankton and zooplankton size distributions in the Choptank and Patuxent Rivers (Chapter 3) and zooplankton size distributions in the lower Chesapeake Bay and its tributaries (Chapter 4). The NBSS of these groups varied seasonally and annually. However, the NBSS of the plankton communities in the rivers did not indicate decreased productivity in response to lower freshwater flow in 2002 or increased productivity resulting from high freshwater flow in 2003, as had been expected. The slope values of the integral spectrum, including the combined phytoplankton, zooplankton, ichthyoplankton, and fish data from the Choptank and Patuxent Rivers were near the expected theoretical value of -1 and were remarkably consistent across seasons and years despite the observed variability of NBSS parameters for the individual trophic groups. In the lower Bay and its

tributaries, the NBSS parameters of the zooplankton communities exhibited long-term declining trends as had been observed for the fish communities in those systems. For zooplankton, there were declines in abundance of several prominent taxa, including *Acartia* sp. copepods and barnacle nauplii and cypris larvae (Chapter 4). In both the upper Bay and lower Bay systems, NBSS parameters for the fish community and zooplankton or phytoplankton communities generally were uncorrelated. The lack of correlation was unexpected based on NBSS theory and may have resulted from assigning fixed body sizes to the phytoplankton taxa in the upper Bay and tributaries and to zooplankton in the lower Bay and tributaries. Direct measurements of phytoplankton cell sizes and zooplankton body sizes would have greatly improved the accuracy and precision of NBSS parameter estimates for these trophic levels.

Approach and recommendations

The first step in my approach to describe and evaluate fish communities was to use PCA to identify temporal and spatial patterns of species occurrences that can strongly affect the size distributions and structure of communities. The PCAs were successful in accomplishing this objective. In the analyses on the upper Bay (Chapter 2) and the Choptank and Patuxent Rivers (Chapter 3) the PCAs indicated effects of variability in freshwater flow on the species composition of the fish communities, especially the results of recruitment differences in YOY anadromous fishes and bay anchovy. Temporal changes in

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species composition in the lower Chespeake Bay and Pamlico Sound, and their tributaries, were similarly detected. The second step in the approach was to estimate NBSS parameters and to identify sizes classes exhibiting strong seasonal or annual variability. These size classes were then cross-referenced with the influential species identified in the PCA to determine what species contributed strongly to the variability in NBSS parameters. While this overall approach succeeded in identifying and quantifying changes in the fish community structure, the approach can be improved and simplified.

Based on outcomes of my analyses, estimating NBSS parameters and size and abundance metrics on annual time scales was found to provide nearly as much information about fish communities as the seasonal analyses. For the phytoplankton and zooplankton communities, sampling at the appropriate temporal resolution is important to define the NBSS parameters. Ideally, the temporal sampling frequency for these groups should consider the turnover times such that the phytoplankton and zooplankton communities are sampled more frequently than the fish community. Scaling temporal sampling to turnover time in future investigations may facilitate detecting responses of the phytoplankton and zooplankton communities to environmental variability. As such, data should be collected to insure that seasonal variability is represented, but analysis on data aggregated at the annual time scale will provide reliable estimates of the parameters and metrics, and interannual variability.

An objective of the approach was to determine if NBSS could effectively characterize structure of communities as small spatial scales. Estimating NBSS parameters and also size and abundance metrics at spatial scales ≥ 30 km was more effective than at the 18 km scale as indicated by results of small-scale analysis in the upper Chesapeake Bay (Chapter 2). Moreover, results of the PCAs on data from the Choptank and Patuxent Rivers (Chapter 3) suggested that intensive sampling would be required to more accurately represent the fish assemblages in the downriver portions of the tributaries. Simulation studies could be effective to determine the sampling resolution required at these spatial scales. It is possible that the appropriate sampling resolution depends on the sampling gear as well as the spatial variability of the fish and communities in terms of abundance, size, and species composition.

The PCAs effectively identified temporal and spatial patterns in the fish communities. They portrayed seasonal patterns, as was noted in the long-term surveys in lower Chesapeake Bay, in which seasons contributed to annual patterns in the PCA and served to indicate in what seasons variability in the annual NBSS occurs. However, presenting the large quantity of results in the PCAs is challenging. A direct gradient analysis, such as canonical correspondence analysis or redundancy analysis, including month and year variables as well as environmental variables, might portray results more efficiently. Additionally, a direct gradient analysis could help to identify environmental variables associated with changes in species composition that

then could be used to predict NBSS parameters and size and abundance
metrics.

Statistical considerations

Several statistical considerations with respect to the regression techniques
used to estimate NBSS parameters have not been considered or discussed in
the size spectrum literature. First, the ordinary least squares (OLS) regressions
assume that there is no measurement error in the independent variable, which is
size in the NBSS analyses. Error in the measurement of length or weight of
individuals, and bias can be introduced when adopting length-weight regressions
rather than obtaining weights directly (Kimmerer et al. 2005). Such
measurement errors and bias in assigning sizes to organisms are small relative
to errors in abundance estimation (Kimmerer et al. 2005), especially since the
weight classes in NBSS are expressed in $\log_2$ units.

Another assumption of OLS regression that can be violated in NBSS
analyses is the assumption of a normal error structure. Fisheries catch data are
often lognormally distributed (Haddon 2000). Therefore, it is likely that the
abundance of organisms in each designated size class also is lognormally
distributed. The $\log_2$ transformation of the abundance data used in NBSS
analyses likely reduces this bias.

Daan et al. (2005) advocated centering the x-axis of an NBSS as a means to reduce the correlation between the slope of the integral spectrum and the intercept. However, the slope and intercept of a linear regression will always be correlated because of the statistical calculations required to estimate each parameter. One positive result of centering the x-axis is that it facilitates comparisons of vertical locations of plankton NBSS, which sit on the far negative side of the x-axis. Small differences in slope result in large differences in the intercept when the x-axis is not centered for plankton NBSS because of the "distance" between the plankton size range and the y-axis. Centering eliminates this effect and facilitates comparison of the vertical location of the NBSS. Although the correlated nature of the slope and intercept is problematic, the peak abundances of biomass domes can be used as alternative measures of vertical location of the NBSS.

Regression trees were selected to evaluate relationships between environmental variables and the NBSS parameters and size and abundance metrics because they are not affected by collinearity in the independent variables, allow for straightforward interpretation when either numeric or categorical variables are used, work well for detecting thresholds, and can detect interactions that are more complex than those expressed in linear regression (Clark and Pregibon 1997). Other analytical tools, such as canonical correspondence analysis or a neural network approach, might have provided more insight. Canonical correspondence analysis would allow for simultaneous

analysis of the environmental relationships between NBSS parameters and size and abundance metrics, and plotting the observation scores may have provided insight into possible temporal lags. Interpreting interactions among the environmental variables in a correspondence analysis would be problematic. Neural networks were effective in estimating primary production in Chesapeake Bay for primary productivity and water quality data collected from 1982 to 1996 (Scardi and Harding 1999). A similar approach may be informative to detect relationships between environmental variables and NBSS parameters and size and abundance metrics.

The reliability of NBSS parameters and survey data required to effectively evaluate NBSS as an approach to describe community structure could be tested in simulation modeling. Simulations could be conducted to evaluate the sensitivity of NBSS parameters and size and abundance metrics by determining the minimum magnitude of perturbations required to produce detectable trends in the metrics and parameters. For example, abundance trends of the prominent species that contributed to the trends observed in the lower Chesapeake Bay and its tributaries could be used as an upper limit in the simulations. The slopes of the trends for species that declined in abundance could be reduced incrementally until the NBSS parameters and other metrics no longer responded. Similarly, a bootstrapping approach could be used to determine the minimum number of sampling sites required in each of the lower Bay systems to detect the observed trends by testing the effect of increasing or decreasing the number of

stations relative to current sampling protocol on the precision of the parameter estimates and metrics.

Management considerations

The research was planned in part to investigate potential for development of indicators that could have utility in ecosystem-based fisheries management. To be effective, such indicators must 1) have a theoretical or "common sense" basis, 2) be measurable and compatible with fish-survey designs, 3) be sensitive to measured levels of perturbations, 4) facilitate the establishment of reference points or reference directions, and 5) be easily explainable to stakeholders (Rochet and Trenkel 2003; Jennings 2005; Rice and Rochet 2005; Rochet and Rice 2005; Shin et al. 2005). NBSS parameters and metrics based on size and abundance have been demonstrated to meet criteria 1, 3 and 4 (Bianchi et al. 2000; Rochet and Trenkel 2003; Jennings 2005). With respect to criterion 2, the data and measurements required to estimate NBSS parameters and metrics based on size and abundance are simple, if costly, to collect, but changes in the fish community may not be detectable on the time scales required by fisheries management agencies. Based on an analysis of the North Sea International Bottom Trawl Survey (IBTS) data collected between 1982 and 2000, Nicholson and Jennings (2004) found that the power of monitoring surveys to detect trends in the slope of the integral spectrum was low if there are fewer than 10 years of data. However, the IBTS covers a very large spatial area sampled by agencies from several nations over several months, which likely elevates effects of spatial

and temporal heterogeneity and reduces efficacy of estimating NBSS parameters. The fish monitoring surveys in Chesapeake Bay and Pamlico Sound sample at much higher temporal and spatial resolution. The trends in NBSS detected in the lower Bay and its tributaries were apparent within the first few years of the time series.

During my research, two constraints were recognized in considering how NBSS parameters could be used in fisheries management. One minor constraint is that the theory underpinning use of NBSS parameters as indicators can be difficult to explain to stakeholders (criterion 5 above, Shin et al. 2010), which could reduce support of their use and acceptance (Rice and Rochet 2005). The second constraint, perhaps more important, is NBSS parameters require statistical fitting with linear or quadratic models. High variability in abundances among size classes can confound obtaining precise estimates of the parameters, as was observed in the analyses of the lower Bay zooplankton data or the fish data in the 18-km segments of the upper Chesapeake Bay. While parameters from a poorly fitting regression are the best linear, unbiased estimates of the integral spectra, poor regression fits to NBSS biomass domes or subdomes can produce estimates that are not biologically meaningful, e.g. size at peak abundance estimates for fish data that fall into the zooplankton size range. Despite drawbacks, NBSS parameters are powerful tools for summarizing large quantities of complex size and abundance data and for visualizing structure and

trends in the temporal and spatial variability of fish and plankton size distributions.

Application of the indicators

Since data from unperturbed fish and plankton communities are unavailable, NBSS parameters and size and abundance metrics used in an indicator framework are best analyzed for trends with respect to "reference directions" rather than reference points (Trenkel and Rochet 2003; Jennings and Dulvy 2005; Shin et al. 2005; Blanchard et al. 2010; Shin et al. 2010). In this approach, trends persisting for a number of years or representing a relative decrease in indicator values would trigger management actions. Simultaneous trends in multiple indicators could elicit more rigorous management actions. Since NBSS parameters and size and abundance metrics exhibit negative trends from effects of fishing pressure (Trenkel and Rochet 2003; Jennings and Dulvy 2005; Shin et al. 2005; Blanchard et al. 2010; Shin et al. 2010), lack of trend in the indicators may be considered as a threshold reference scenario for maintaining the status quo. Positive trends in NBSS and size indicators may define target reference criteria for rebuilding an overfished community. Reference directions could be established for trophic levels other than fish, for example the phytoplankton community and its response to nutrient management.

NBSS approaches could be applied in unique and interesting ways to help understand the Chesapeake Bay ecosystem. Jennings and Blanchard (2004)

conducted a unique analysis based on NBSS theory, stable isotope data, and

estimates of trophic transfer efficiency that allowed them to reconstruct the

characteristics of the North Sea fish community in an unfished state. Based on

their analysis, the current biomass of the North Sea fish community is 38% of

that in the unfished community; turnover time of the current fish community is

twice as fast; and, 70% less primary production is required to support the current

fish community. The extensive data available for Chesapeake Bay and Pamlico

Sound could be analyzed in a similar manner to reconstruct past histories of

community structure and productivity. Threshold, target, and trigger reference

points might then be identified based on relative biomass or abundance

compared to the unfished community.

Future research

In my research causes of trends in the fish and zooplankton communities

in the lower Chesapeake Bay and its tributaries were not determined. Measures

of total nitrogen and primary productivity were not included in the regression

trees because the sample processing protocol in the Chesapeake Bay Program

changed for these variables during the study period, precluding trend analyses

(CBP 2010). If correction factors could be developed for these variables,

including them in a regression tree analysis that also included measures of

hypoxic volume may provide insights into the causes or correlates of the

observed trends. Additionally, incorporating explicit, size-specific estimates of

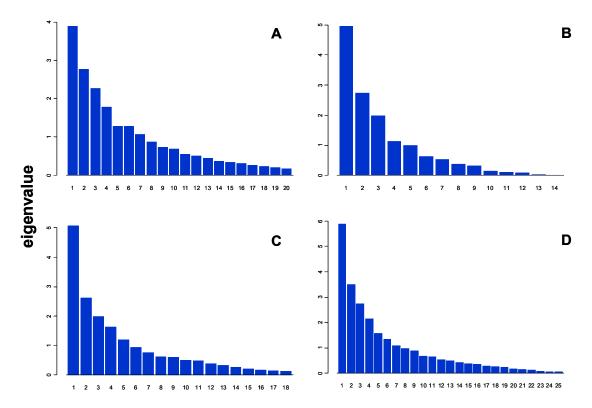abundance for the phytoplankton and zooplankton communities would greatly

improve precision and accuracy of NBSS parameter estimates for those trophic

groups. In this regard, it may be possible to analyze archived samples using flow

cytometry and optical particle counting to determine size distributions for the

phytoplankton and zooplankton communities, respectively. Theory and

observation indicate that the biomass domes of phytoplankton, zooplankton, and

fish are similarly shaped and consistently spaced (Kerr and Dickie 2001). Thus,

knowledge of the shape and location of two of the trophic levels permits

prediction of the shape and location of the third (Sprules and Goyke 1994).

Obtaining more precise NBSS parameter estimates for the phytoplankton and

zooplankton communities would, in theory, allow improved prediction of NBSS

parameters for the fish community in Chesapeake Bay.

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eigenvalue

principal component number

Figure S1. Scree plots for the principal components analyses based on (A) data from all cruises, (B) data from May cruises, (C) data from July cruises, and (D) data from October cruises. The slope of the curve represents the decline in the amount of variance explained by each additional PC. The point at which the slope begins to level off represents the boundary between the dominant signals and noise.
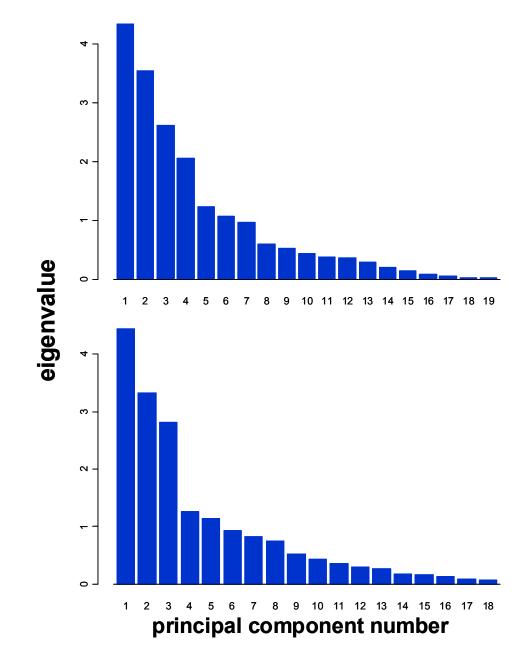
Figure S2. Scree plots for the principal components analyses based on (A) data from the summer cruises and (B) data from all cruises in 2003 and 2004. The slope of the curve represents the decline in the amount of variance explained by each additional PC. The point at which the slope begins to level off represents the boundary between the dominant signals and noise. In these plots, the dominant signals are represented by the first 3-4 PCs.

Figure S3. Scree plots for the annual principal components analyses for (A) the lower Chesapeake Bay mainstem, (B) the James River, (C) the Rappahannock River, and (D) the York River. The slope of the curve represents the decline in the amount of variance explained by each additional PC. The point at which the slope begins to level off represents the boundary between the dominant signals and noise. In these plots, the dominant signals are represented by the first two PCs.
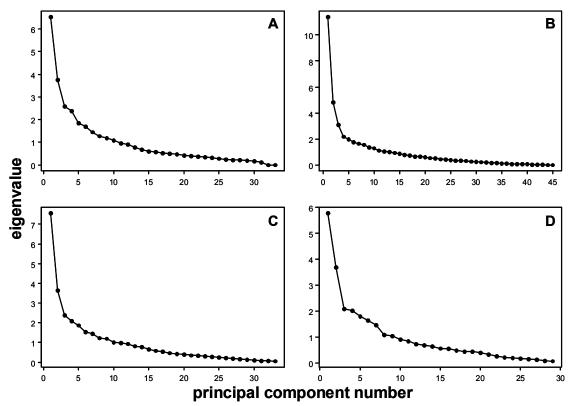
Figure S4. Scree plots for the June principal components analyses for (A) Pamlico Sound, (B) the Pamlico River, (C) the Pungo River, and (D) the Neuse River. The slope of the curve represents the decline in the amount of variance explained by each additional PC. The point at which the slope begins to level off represents the boundary between the dominant signals and noise. In these plots, the dominant signals are represented by the first two PCs.

Figure S5. Scree plots for the September principal components analyses for (A) Pamlico Sound, (B) the Pamlico River, (C) the Pungo River, and (D) the Neuse River. The slope of the curve represents the decline in the amount of variance explained by each additional PC. The point at which the slope begins to level off represents the boundary between the dominant signals and noise. In these plots, the dominant signals are represented by the first 2-4 PCs.
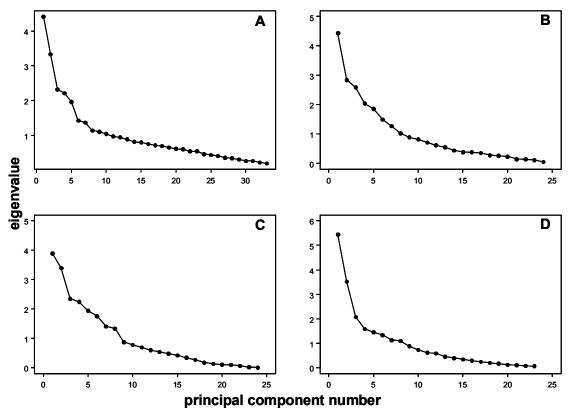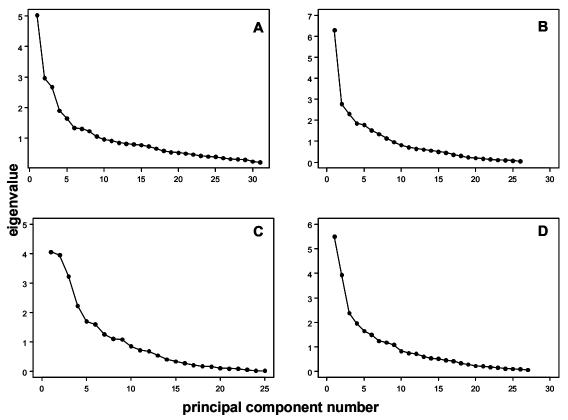
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SUPPLEMENTARY TABLES

Table S1. Loadings for the principal components with eigenvalues > 1 for the PCA that includes fish data from May, July, and October in the Chesapeake Bay ETZ. The percentage of the variance represented by each PC is shown under each PC number.

Taxon, size class	PC1 19.5%	PC2 13.8%	PC3 11.3%	PC4 8.9%	PC5 6.4%	PC6 5.4%	PC7 4.3%
alewife, small	-0.41	-0.07	-0.18	-0.16	0.20	0.09	-0.03
American eel, all	-0.31	0.23	0.15	0.27	-0.19	-0.04	-0.05
Atlantic croaker, large	0.07	-0.19	-0.06	0.63	0.05	0.03	0.00
Atlantic croaker, small	-0.07	0.39	0.16	0.15	0.33	-0.11	0.18
Atlantic menhaden, large	0.16	0.26	-0.22	0.08	-0.08	0.01	-0.07
Atlantic menhaden, med	0.01	-0.29	-0.14	0.45	0.13	0.13	0.03
Atlantic menhaden, small	0.05	0.01	0.40	-0.05	0.36	-0.35	0.25
bay anchovy, large	0.21	0.29	-0.31	0.13	0.25	0.06	-0.22
bay anchovy, small	-0.03	0.03	-0.45	-0.04	0.36	-0.23	-0.17
blue crab, all	-0.01	0.20	-0.06	0.16	0.21	0.39	0.49
blueback herring, small	-0.34	-0.02	-0.27	-0.14	0.00	0.06	-0.15
channel catfish, all	-0.17	0.18	0.30	0.11	-0.23	0.10	-0.36
gizzard shad, all	0.01	0.28	0.03	-0.02	0.13	0.57	-0.09
hogchoker, all	-0.18	0.38	0.00	0.22	-0.33	-0.11	0.08
striped bass, large	-0.05	0.01	0.26	0.14	0.40	-0.08	-0.58
striped bass, medium	-0.18	-0.33	-0.10	0.29	-0.16	-0.03	-0.03
striped bass, small	-0.39	-0.05	-0.18	-0.05	0.06	0.01	0.21
weakfish, all	0.02	0.33	-0.33	0.05	-0.17	-0.39	0.00
white perch, large	-0.33	0.01	0.06	0.17	0.15	-0.29	0.16
white perch, small	-0.42	0.02	0.08	-0.10	0.11	0.16	-0.07

Table S2. Loadings for the principal components with eigenvalues > 1 for the May PCA of the Chesapeake Bay ETZ fish data. The percentage of the variance represented by each PC is shown under each PC number.

Taxon, size class	PC1 24.8%	PC2 13.7%	PC3 9.9%	PC4 5.6%
American eel, large	0.28	-0.13	0.34	-0.16
American eel, small	0.34	-0.14	-0.03	-0.22
Atlantic croaker, small	0.09	0.48	0.24	-0.01
Atlantic menhaden, large	-0.19	-0.19	0.24	-0.37
Atlantic menhaden, small	-0.11	0.53	0.21	0.07
bay anchovy, large	-0.13	0.46	0.30	0.12
channel catfish, large	0.37	0.10	-0.18	0.21
channel catfish, medium	0.38	0.04	-0.17	0.10
hogchoker, large	0.05	-0.25	0.56	0.23
hogchoker, medium	0.30	-0.18	0.31	0.28
hogchoker, small	0.35	0.05	-0.07	0.43
striped bass, large	0.19	0.25	-0.33	-0.18
white perch, large	0.33	0.09	0.21	-0.23
white perch, small	0.30	0.14	0.09	-0.56

Table S3. Loadings for the principal components with eigenvalues > 1 for the July PCA of the Chesapeake Bay ETZ fish data. The percentage of the variance represented by each PC is shown under each PC number.

Taxon, size class	PC1 25.4%	PC2 13.1%	PC3 9.9%	PC4 8.2%	PC5 6.0%
alewife, small	0.33	-0.22	0.01	0.23	-0.10
American eel, large	0.15	0.20	0.44	0.17	0.10
American eel, small	0.26	0.23	0.28	0.00	0.02
Atlantic croaker, large	-0.21	0.35	0.26	0.21	0.06
Atlantic menhaden, large	-0.12	0.09	0.22	-0.31	-0.66
Atlantic menhaden, medium	-0.26	0.24	0.28	-0.09	-0.03
bay anchovy, large	-0.35	0.02	0.06	0.14	-0.21
bay anchovy, small	-0.10	-0.43	0.06	0.30	-0.17
blueback herring, small	0.34	-0.05	0.07	-0.26	-0.19
bluefish, small	0.00	-0.30	0.45	-0.25	-0.11
hogchoker, medium	0.22	0.26	-0.01	-0.25	0.08
hogchoker, small	0.28	0.26	-0.05	-0.09	0.12
striped bass, large	-0.15	0.06	0.07	0.38	-0.26
striped bass, medium	0.08	0.37	0.03	0.16	-0.21
striped bass, small	0.31	-0.05	-0.05	0.12	-0.33
weakfish, small	0.11	-0.34	0.46	-0.13	0.21
white perch, large	0.21	-0.02	0.27	0.47	0.17
white perch, small	0.34	0.05	-0.16	0.17	-0.34

Table S4. Loadings for the principal components with eigenvalues > 1 for the October PCA of the Chesapeake Bay ETZ fish data. The percentage of the variance represented by each PC is shown under each PC number..

Taxon, size class	PC1 23.6%	PC2 13.9%	PC3 11.0%	PC4 8.5%	PC5 6.2%	PC6 5.4%	PC7 4.3%
alewife, small	0.31	0.22	-0.02	-0.07	0.29	-0.04	0.1
American eel, large	0.36	0	-0.05	0.12	-0.12	0.1	0.16
American eel, small	0.3	-0.09	-0.01	0.07	-0.3	0.05	0.22
Atlantic croaker, large	-0.04	-0.18	-0.19	0.38	0.11	-0.11	-0.25
Atlantic croaker, small	0.28	-0.05	0.19	-0.07	0.1	0.12	-0.24
Atlantic menhaden, large	-0.04	-0.26	0.16	-0.07	0.21	-0.06	0.48
Atlantic menhaden, medium	0.11	-0.09	0.4	0.13	0.26	-0.02	-0.13
bay anchovy, large	0.02	-0.2	0.06	-0.44	-0.1	0.05	0.15
bay anchovy, small	0.07	-0.21	0.03	-0.44	0.07	-0.26	-0.31
blue crab, large	0.1	0.09	-0.08	-0.1	0.03	0.66	-0.12
blue crab, small	0	-0.16	0.36	0.18	-0.02	0.15	0.25
blueback herring, small	0.27	0.1	0.06	-0.35	-0.02	-0.26	0.01
channel catfish, medium	0.15	-0.1	0.06	-0.05	-0.51	-0.19	-0.06
gizzard shad, large	0.18	0.29	0.17	0.23	0.05	-0.19	-0.15
gizzard shad, small	0	0.07	0.43	0.26	-0.11	-0.16	-0.02
hogchoker, large	0.24	-0.13	-0.26	0.2	-0.32	0.07	-0.02
hogchoker, medium	0.25	-0.32	0.06	0.14	-0.19	0	-0.01
hogchoker, small	0.11	-0.28	0.29	0.01	0.19	0.06	0.1
striped bass, large	0.15	0.22	-0.17	-0.06	0.03	-0.32	0.31
striped bass, medium	0.06	-0.11	-0.35	0.24	0.31	-0.14	0.24
striped bass, small	0.3	0.01	-0.06	-0.09	0.18	0.33	0
weakfish, large	0.04	-0.32	-0.21	-0.01	0.13	-0.05	0.16
weakfish, small	0.07	-0.42	-0.13	0.06	0.13	-0.1	-0.32
white perch, large	0.3	-0.06	-0.08	-0.01	0.16	-0.11	-0.17
white perch, small	0.32	0.26	-0.01	0.06	0.09	-0.05	0.01

Table S5. Loadings for principal components with eigenvalues >1 for summer PCA of the Patuxent and Choptank River fish data. The percentage of the variance captured by each PC is shown under each PC number.

Taxon, size class	PC1 22.8%	PC2 18.7%	PC3 13.8%	PC4 10.8%	PC5 6.5%	PC6 5.6%
alewife, large	-0.33	-0.20	-0.11	-0.13	-0.14	0.21
alewife, small	-0.28	-0.12	0.32	0.23	0.03	0.03
Atlantic menhaden, large	-0.28	-0.09	-0.04	-0.46	-0.15	0.20
Atlantic menhaden, small	-0.26	-0.23	0.03	0.36	0.11	-0.18
bay anchovy, large	-0.20	-0.05	0.28	-0.43	0.07	0.14
bay anchovy, medium	-0.05	0.04	0.29	-0.41	0.08	-0.25
bay anchovy, small	-0.06	-0.18	0.18	-0.19	0.46	-0.50
blue crab, large	-0.20	0.34	-0.12	0.00	-0.16	-0.45
blue crab, medium	-0.15	0.30	0.32	0.17	0.00	-0.27
blue crab, small	-0.21	0.19	-0.29	-0.21	-0.04	-0.07
blueback herring, medium	-0.33	-0.27	0.02	0.28	-0.09	-0.02
channel catfish medium	-0.12	0.32	-0.26	0.06	0.20	0.15
channel catfish, large	0.04	0.20	0.40	0.08	-0.11	0.18
hogchoker, medium	-0.17	0.38	-0.17	0.03	0.25	0.03
striped bass, small	-0.38	-0.17	0.07	-0.01	-0.07	0.07
white catfish, large	0.04	0.12	0.13	-0.02	-0.75	-0.24
white perch, large	-0.01	0.22	0.42	0.14	0.10	0.36
white perch, medium	-0.24	0.40	0.08	-0.02	0.06	0.14
white perch, small	-0.39	0.02	-0.18	0.14	-0.04	-0.04

Table S6. Loadings for principal components with eigenvalues >1 for seasonal PCA of the 2003 and 2004 fish data from the Choptank and Patuxent Rivers. The percentage of the variance captured by each PC is shown under each PC number.

Taxon, size class	PC1 24.7%	PC2 18.5%	PC3 15.6%	PC4 7.0%	PC5 6.3%
alewife, large	-0.27	-0.22	0.11	-0.03	-0.26
alewife, small	-0.26	-0.39	0.05	-0.16	0.05
Atlantic menhaden, large	-0.21	0.15	0.37	-0.19	-0.19
bay anchovy, large	-0.19	0.16	0.23	-0.28	-0.31
bay anchovy, medium	-0.21	0.28	0.18	-0.01	-0.14
bay anchovy, small	-0.34	0.18	0.19	-0.10	-0.12
blue crab, large	-0.10	0.11	0.16	0.43	0.29
blue crab, medium	-0.09	0.01	0.35	0.52	0.17
blue crab, small	0.04	0.09	0.21	-0.45	0.47
blueback herring, medium	-0.27	-0.38	0.04	0.03	0.14
hogchoker, large	0.33	-0.19	0.22	0.04	-0.21
hogchoker, medium	0.35	-0.21	0.13	-0.12	-0.13
striped bass, large	0.23	-0.08	0.14	-0.36	0.26
striped bass, medium	0.01	0.19	0.36	-0.04	0.42
striped bass, small	-0.27	-0.37	0.10	-0.03	0.00
white perch, large	0.32	-0.15	0.32	0.01	-0.11
white perch, medium	0.22	-0.09	0.43	0.18	-0.23
white perch, small	-0.11	-0.43	0.06	0.03	0.20

Table S7. Loadings for lower Chesapeake Bay annual principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance captured by each PC is shown under each PC number.

Taxon abbrev.	Taxon, size/age	PC1 19.8%	PC2 11.4%	PC3 7.8%	PC4 7.2%	PC5 5.6%	PC6 5.1%	PC7 4.4%	PC8 3.9%	PC9 3.6%	PC10 3.3%
atmen0	Atlantic menhaden, age 0	0.04	0.07	0.20	0.05	-0.01	-0.22	0.46	-0.08	0.22	-0.33
atmen1	Atlantic menhaden, age 1+	0.15	0.02	-0.06	0.18	0.13	0.24	0.07	0.25	-0.12	0.22
banch	bay anchovy, all	0.17	0.15	-0.10	0.04	0.28	0.18	0.19	0.14	0.27	0.08
bback	blueback herring, age 0	0.03	0.07	0.04	-0.02	-0.18	-0.08	0.35	0.41	-0.37	-0.11
butfsh	butterfish, all	0.18	-0.06	0.10	0.30	0.25	-0.14	0.03	0.13	0.25	0.00
croak0	Atlantic croaker, age 0	0.05	0.28	0.23	0.01	0.02	-0.18	0.09	-0.01	0.03	-0.31
croak1	Atlantic croaker, age 1	0.22	0.11	-0.04	0.12	0.12	-0.28	-0.03	-0.09	-0.15	0.19
croak2	Atlantic croaker, age 2+	0.21	0.04	-0.13	-0.09	-0.32	0.25	-0.02	0.27	0.13	-0.18
harfsh	harvestfish, all	0.06	0.21	-0.16	-0.13	0.11	0.21	0.24	-0.30	0.10	0.25
hogl	hogchoker, large	0.30	-0.09	0.09	0.07	-0.14	-0.03	-0.08	0.08	-0.20	-0.18
hogm	hogchoker, medium	0.28	0.12	-0.14	-0.06	-0.15	-0.03	-0.11	-0.08	-0.12	0.01
inliz	inshore lizardfish, all	-0.13	-0.18	-0.38	0.05	0.13	-0.10	-0.02	-0.26	-0.21	-0.03
kngfsh	kingfish species, all	-0.13	0.06	0.41	0.00	-0.01	-0.06	-0.20	0.07	-0.12	0.15
pgfsh	pigfish, all	0.02	-0.20	-0.16	-0.21	-0.32	-0.21	0.07	0.25	0.29	0.22
scup	scup, all	0.01	-0.29	-0.02	0.22	0.13	0.03	0.17	0.01	0.32	0.07
seabass	black sea bass, all	0.19	-0.09	0.11	0.01	-0.29	-0.08	0.29	-0.21	0.09	0.07
silper0	silver perch, age 0	0.15	0.11	0.22	0.10	-0.08	-0.27	0.01	-0.22	0.00	0.34
silper1	silver perch, age 1+	0.04	0.06	0.07	-0.24	0.02	-0.09	-0.22	-0.03	0.11	0.14
smflo	smallmouth flounder, all	-0.01	-0.42	0.15	0.14	-0.08	-0.05	0.08	0.02	-0.01	0.00
sphake	spotted hake, age 0	0.21	-0.12	0.16	0.16	0.23	0.29	-0.07	0.12	-0.02	0.02
spot0	spot, age 0	0.17	0.04	-0.29	0.13	0.14	-0.33	-0.07	0.31	0.11	0.15
spot1	spot, age 1+	0.23	0.08	-0.20	-0.02	-0.21	0.12	0.04	-0.28	0.04	-0.09
stanch	striped anchovy, all	-0.10	-0.17	0.17	-0.13	-0.21	-0.01	0.16	0.04	0.02	0.48
suflo0	summer flounder, age 0	0.11	-0.19	-0.27	0.12	-0.13	-0.25	-0.11	-0.08	0.08	-0.15
suflo1	summer flounder, age 1	0.15	-0.13	0.19	0.07	-0.18	0.40	-0.08	-0.19	0.20	-0.02
suflo2	summer flounder, age 2+	0.07	-0.21	0.13	0.16	-0.10	-0.06	-0.44	-0.01	0.13	-0.11

Taxon abbrev.	Taxon, size/age	PC1 19.8%	PC2 11.4%	PC3 7.8%	PC4 7.2%	PC5 5.6%	PC6 5.1%	PC7 4.4%	PC8 3.9%	PC9 3.6%	PC10 3.3%
toadl	oyster toadfish, large	0.24	-0.20	0.08	-0.39	0.21	-0.04	0.01	0.00	-0.06	-0.05
toadm	oyster toadfish, medium	0.24	-0.20	0.08	-0.39	0.21	-0.04	0.01	0.00	-0.06	-0.05
toads	oyster toadfish, small	0.24	-0.20	0.08	-0.39	0.21	-0.04	0.01	0.00	-0.06	-0.05
tong0	blackcheek tonguefish, age 0	0.19	-0.06	-0.01	0.17	-0.15	0.14	0.08	0.08	-0.35	0.18
tong1	blackcheek tonguefish, age 1+	0.28	-0.13	0.00	0.22	0.05	-0.03	0.10	-0.25	-0.23	0.00
weak0	weakfish, age 0	0.20	0.32	0.21	0.04	0.00	-0.10	-0.13	-0.04	0.07	0.09
weak1	weakfish, age 1+	0.24	0.23	-0.09	-0.05	-0.16	0.02	-0.21	0.09	0.16	0.02

Table S8. Loadings for James River annual principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance captured by each PC is shown under each PC number.

Taxon abbrev.	Taxon, size/age	PC1 25.3%	PC2 10.7%	PC3 6.9%	PC4 4.8%	PC5 4.4%	PC6 3.9%	PC7 3.7%	PC8 3.5%	PC9 3.0%	PC10 2.9%
alwf0	alewife, age 0	-0.08	-0.01	-0.03	0.01	-0.13	-0.36	-0.11	0.17	0.18	-0.09
alwf1	alewife, age 1+	-0.01	0.13	-0.17	-0.16	-0.39	-0.19	-0.09	0.13	0.23	0.04
atmen0	Atlantic menhaden, age 0	0.03	-0.14	-0.01	0.19	0.07	-0.18	-0.26	0.07	0.05	-0.27
atmen1	Atlantic menhaden, age 1+	-0.01	0.19	0.08	-0.18	0.15	-0.39	0.00	0.03	0.31	-0.14
banch	bay anchovy, all	0.22	0.05	0.02	-0.26	0.18	-0.04	-0.02	0.08	-0.01	0.05
bback	blueback herring, age 0	0.03	0.01	-0.08	-0.23	-0.41	0.06	0.15	0.28	-0.21	-0.21
bcat	blue catfish, all	-0.17	-0.13	0.04	0.10	-0.08	0.10	0.12	0.20	0.28	-0.07
butfsh	butterfish, all	0.17	-0.13	0.07	0.10	-0.01	0.02	-0.16	0.02	-0.15	-0.32
ccatlm	channel catfish, med. & large	-0.17	-0.06	0.25	-0.17	0.09	0.10	-0.02	0.00	0.00	-0.03
ccats	channel catfish, small	-0.08	-0.10	0.03	0.12	-0.01	0.22	0.31	0.17	0.45	-0.08
croak0	Atlantic croaker, age 0	-0.16	-0.06	0.24	0.20	-0.02	0.01	0.02	-0.06	0.06	0.15
croak1	Atlantic croaker, age 1	-0.11	0.21	0.33	-0.18	0.06	-0.07	-0.09	0.05	-0.09	0.06
croak2	Atlantic croaker, age 2+	0.04	0.18	-0.15	0.05	-0.03	0.22	-0.30	0.03	0.08	0.47
eel	American eel, all	-0.22	0.01	0.02	-0.24	0.05	0.15	-0.11	-0.03	-0.25	-0.03
gshad	gizzard shad, all	-0.22	-0.02	0.15	-0.09	-0.03	0.03	0.01	0.08	0.08	0.08
harfsh	harvestfish, all	0.05	0.08	0.05	-0.29	0.05	-0.05	0.09	-0.47	0.28	-0.02
hogl	hogchoker, large	-0.13	0.23	0.15	0.18	-0.14	0.19	0.05	-0.02	0.10	0.03
hogm	hogchoker, medium	-0.25	0.18	0.11	-0.02	-0.07	0.06	-0.03	-0.01	-0.03	-0.04
hogs	hogchoker, small	-0.24	0.03	0.23	-0.02	0.09	0.05	0.03	-0.01	-0.02	-0.04
inliz	inshore lizardfish, all	0.17	0.02	0.18	-0.09	-0.25	0.16	0.15	-0.04	-0.07	-0.20
kngfsh	kingfish species, all	0.14	-0.10	0.22	0.19	-0.16	-0.10	-0.10	-0.24	-0.15	-0.19
seabass	black sea bass, all	0.21	-0.17	0.09	-0.04	-0.01	0.04	0.06	-0.02	0.07	0.21
silper0	silver perch, age 0	-0.01	0.24	-0.10	0.09	-0.04	0.14	0.08	-0.34	0.14	-0.32
silper1	silver perch, age 1+	0.06	0.12	-0.20	-0.15	-0.02	0.34	-0.10	-0.18	0.01	-0.12
skfsh	skilletfish, all	0.08	0.14	0.12	0.00	-0.11	0.07	-0.01	0.29	-0.10	0.10
smflo	smallmouth flounder, all	0.21	-0.13	0.20	-0.04	-0.25	0.08	0.08	-0.14	0.00	-0.04

Taxon abbrev.	Taxon, size/age	PC1 25.3%	PC2 10.7%	PC3 6.9%	PC4 4.8%	PC5 4.4%	PC6 3.9%	PC7 3.7%	PC8 3.5%	PC9 3.0%	PC10 2.9%
sphake	spotted hake, age 0	0.06	0.31	-0.04	0.19	0.23	-0.09	0.04	0.04	0.02	-0.09
spot0	spot, age 0	0.09	0.14	0.26	-0.02	-0.22	-0.15	0.12	0.09	-0.07	0.11
spot1	spot, age 1+	0.16	0.26	0.09	-0.06	-0.04	0.14	-0.02	0.02	0.09	0.12
stanch	striped anchovy, all	0.17	-0.20	-0.01	-0.11	0.04	-0.04	0.09	-0.22	0.09	0.24
stbass0	striped bass, age 0	-0.08	-0.02	-0.08	0.29	-0.07	-0.13	0.23	-0.20	-0.32	0.21
stbass1	striped bass, age 1	-0.16	0.12	-0.20	0.00	-0.19	-0.12	0.02	-0.11	-0.09	0.15
stbass2	striped bass, age 2+	-0.16	0.01	-0.03	0.14	0.01	-0.07	0.19	-0.05	-0.01	0.07
suflo01	summer flounder, age 0 &1	0.23	0.06	0.21	0.05	-0.16	-0.05	0.00	-0.02	0.11	0.13
suflo2	summer flounder, age 2+	0.20	-0.13	0.12	0.02	-0.11	0.10	-0.15	-0.01	0.13	0.13
toadl	oyster toadfish, large	0.17	0.15	0.04	0.11	0.20	-0.04	0.27	0.09	-0.03	0.01
toadm	oyster toadfish, medium	0.10	0.30	-0.15	-0.02	0.03	0.10	0.27	-0.02	-0.11	-0.11
toads	oyster toadfish, small	0.14	0.02	-0.03	-0.14	0.23	-0.10	0.33	0.23	-0.16	0.05
tong0	blackcheek tonguefish, age 0	-0.11	0.04	0.28	-0.03	0.08	-0.11	-0.01	-0.20	-0.05	0.05
tong1	blackcheek tonguefish, age 1	0.10	0.27	0.22	0.10	0.01	-0.03	0.07	0.00	-0.02	-0.05
tong2	blackcheek tonguefish, age 2+	0.09	0.18	0.08	0.23	0.16	0.27	-0.29	0.17	0.04	-0.07
wcat	white catfish, all	-0.23	-0.07	0.15	-0.22	0.04	0.11	-0.09	0.03	-0.14	-0.04
weak	weakfish, all	0.02	0.23	0.01	0.16	-0.18	-0.22	-0.19	-0.08	-0.07	0.03
whper0	white perch, age 0	-0.15	-0.09	0.05	0.21	-0.08	0.05	0.21	0.02	0.01	0.05
whper1	white perch, age 1+	-0.24	0.09	-0.17	-0.06	-0.17	-0.02	0.04	-0.08	0.02	0.00

Table S9. Loadings for Rappahannock River annual principal components analysis for the first 10 PCs. The first 13 PCs had eigenvalues > 1. The percentage of the variance captured by each PC is shown under each PC number.

Taxon abbrev.	Taxon, size/age	PC1 22.9%	PC2 11.1%	PC3 7.2%	PC4 6.3%	PC5 5.7%	PC6 4.7%	PC7 4.4%	PC8 3.7%	PC9 3.6%	PC10 3.1%
alwf0	alewife, age 0	-0.06	0.15	0.05	0.01	-0.06	0.36	-0.03	0.32	0.11	0.32
alwf1	alewife, age 1+	0.01	0.06	0.05	-0.41	0.17	-0.03	0.13	-0.23	-0.31	0.23
atmen0	Atlantic menhaden, age 0	-0.05	0.00	-0.10	-0.30	0.17	-0.20	-0.28	0.29	0.21	0.01
atmen1	Atlantic menhaden, age 1+	0.03	0.28	-0.19	-0.31	0.00	-0.03	0.03	0.12	-0.04	-0.05
banch	bay anchovy, all	0.13	0.33	0.16	-0.08	0.08	-0.05	0.16	0.21	0.02	0.00
bback	blueback herring, age 0	0.11	0.02	0.00	-0.27	0.18	-0.21	-0.22	0.03	-0.48	0.05
bcatl	blue catfish, large	-0.16	-0.16	-0.22	-0.17	0.05	-0.33	-0.09	-0.13	0.20	-0.10
bcatm	blue catfish, medium	-0.26	-0.13	-0.09	0.10	0.17	-0.01	-0.16	-0.07	-0.12	-0.28
bcats	blue catfish, small	-0.18	-0.03	0.01	0.22	0.24	0.16	-0.20	0.09	-0.39	-0.20
ccat	channel catfish, all	-0.26	0.13	0.13	0.17	0.22	-0.02	0.05	0.22	-0.03	-0.04
croak0	Atlantic croaker, age 0	0.12	0.02	-0.08	-0.04	0.18	-0.03	-0.46	0.30	0.12	-0.13
croak1	Atlantic croaker, age 1	-0.06	0.31	0.25	-0.17	0.00	0.06	-0.09	-0.04	0.24	-0.18
croak2	Atlantic croaker, age 2+	0.14	-0.16	0.33	0.00	-0.22	-0.11	-0.23	0.06	-0.03	0.07
gshadl	gizzard shad, large	-0.20	-0.02	-0.09	-0.04	-0.13	-0.36	0.06	-0.01	0.22	0.19
gshads	gizzard shad, small	-0.21	0.27	0.20	-0.05	0.06	0.07	0.07	0.03	0.04	0.14
hogl	hogchoker, large	-0.22	0.22	0.07	0.11	0.02	-0.30	-0.08	0.13	0.03	0.24
hogm	hogchoker, medium	-0.29	0.16	0.08	0.08	-0.04	-0.22	0.04	-0.09	-0.03	0.05
hogs	hogchoker, small	-0.30	0.03	0.01	0.12	0.20	-0.07	0.16	0.02	0.03	-0.08
silper0	silver perch, age 0	0.15	-0.13	0.26	0.23	-0.07	-0.31	0.04	0.25	-0.09	0.22
silper1	silver perch, age 1+	0.01	-0.04	0.31	0.07	-0.15	-0.25	-0.33	-0.33	0.06	0.01
sphake	spotted hake, age 0	0.27	0.08	-0.04	0.08	0.11	-0.01	-0.16	0.02	0.19	-0.05
spot	spot, all	0.12	0.30	0.19	0.07	-0.06	0.16	-0.14	-0.20	0.13	-0.18
stbass	striped bass, all	-0.16	0.03	0.25	-0.13	-0.12	0.25	-0.37	-0.21	-0.09	0.05
suflo	summer flounder, all	0.16	0.21	0.04	0.17	0.29	-0.14	0.03	-0.22	0.11	-0.18
toadl	oyster toadfish, large	-0.04	0.29	-0.19	0.02	-0.45	-0.07	-0.04	0.05	-0.16	-0.18
toadm	oyster toadfish, medium	0.10	0.31	-0.27	0.13	-0.07	-0.10	-0.19	-0.14	-0.11	0.20
toads	oyster toadfish, small	0.02	0.22	-0.18	0.08	-0.37	-0.14	0.05	0.11	-0.25	-0.30
tong0	blackcheek tonguefish, age 0	0.08	0.07	0.29	-0.28	0.09	-0.11	0.15	0.08	-0.19	-0.16

Taxon abbrev.	Taxon, size/age	PC1 22.9%	PC2 11.1%	PC3 7.2%	PC4 6.3%	PC5 5.7%	PC6 4.7%	PC7 4.4%	PC8 3.7%	PC9 3.6%	PC10 3.1%
tong1	blackcheek tonguefish, age 1	0.16	0.21	-0.19	0.07	0.28	-0.02	0.05	-0.33	0.10	0.13
tong2	blackcheek tonguefish, age 2+	0.06	0.12	-0.19	0.25	0.10	0.07	-0.23	-0.02	-0.18	0.43
wcat	white catfish, all	-0.30	0.08	0.02	0.13	0.05	0.00	-0.10	0.04	0.01	-0.07
weak	weakfish, all	0.20	0.05	0.21	0.25	0.13	-0.21	0.16	-0.02	-0.14	-0.08
whper	white perch, all	-0.31	0.01	0.03	-0.13	-0.07	0.05	0.01	-0.21	-0.07	0.12

Table S10. Loadings for the York River annual principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance captured by each PC is shown under each PC number.

Taxon abbrev.	Taxon, size/age	PC1 19.9%	PC2 12.7%	PC3 7.2%	PC4 7.0%	PC5 6.2%	PC6 5.6%	PC7 5.1%	PC8 3.8%	PC9 3.6%
alwf0	alewife, age 0	-0.07	-0.16	-0.12	0.00	-0.11	0.43	-0.18	-0.01	0.41
alwf1	alewife, age 1+	0.02	0.14	0.26	0.17	-0.02	0.34	0.25	-0.35	-0.21
atmen0	Atlantic menhaden, age 0	-0.26	-0.12	-0.07	0.19	0.01	0.08	0.03	0.03	0.37
atmen1	Atlantic menhaden, age 1+	0.05	0.18	-0.19	0.08	-0.17	0.18	-0.46	-0.12	-0.08
banch	bay anchovy, all	0.25	0.02	-0.32	0.06	-0.23	0.14	-0.18	-0.01	-0.09
bback	blueback herring, age 0	0.11	-0.20	-0.06	0.33	-0.27	-0.13	0.15	-0.11	-0.19
bcat	blue catfish, all	-0.18	-0.09	-0.02	0.28	0.09	0.32	-0.09	0.40	-0.01
ccatm	channel catfish, medium	-0.16	-0.07	-0.13	-0.38	-0.33	0.13	0.16	-0.13	-0.04
croak0	Atlantic croaker, age 0	-0.19	-0.17	0.17	0.22	-0.01	0.03	0.26	-0.02	0.18
croak1	Atlantic croaker, age 1	0.07	0.40	-0.04	0.07	-0.13	-0.08	-0.24	0.12	-0.03
croak2	Atlantic croaker, age 2+	0.06	-0.31	0.12	0.06	-0.10	0.18	-0.19	-0.28	-0.03
gshadl	gizzard shad, large	-0.26	-0.06	-0.08	-0.03	0.23	-0.01	-0.13	0.03	-0.34
gshads	gizzard shad, small	-0.18	0.16	-0.05	0.17	0.01	0.18	-0.06	0.28	0.19
hog	hogchoker, all	-0.22	0.28	0.01	-0.09	-0.10	-0.01	-0.01	-0.23	0.11
silper0	silver perch, age 0	0.18	-0.04	0.11	-0.41	0.25	0.05	-0.09	0.23	0.19
silper1	silver perch, age 1+	0.10	0.11	0.42	-0.11	0.02	0.17	-0.28	-0.16	0.02
sphake	spotted hake, age 0	-0.06	-0.02	-0.38	-0.24	0.21	0.07	0.01	-0.42	0.21
spot	spot, all	0.28	0.08	-0.15	0.14	-0.24	0.15	0.21	0.13	0.00
stbass0	striped bass, age 0	-0.22	-0.16	-0.11	-0.02	0.18	0.19	-0.07	0.12	-0.43
stbass12	striped bass, age 1 & 2+	-0.20	0.16	0.30	0.11	-0.17	-0.01	-0.06	-0.07	0.01
suflo01	summer flounder, age 0 &1	0.21	0.16	-0.07	0.00	0.09	0.36	0.36	0.06	-0.06
suflo2	summer flounder, age 2+	0.15	-0.02	0.32	-0.21	0.10	0.30	0.18	0.06	0.00
toad	oyster toadfish, all	-0.07	0.38	-0.10	0.08	0.12	0.21	0.08	-0.15	0.00
tong	blackcheek tonguefish, all	0.04	0.31	-0.28	0.03	0.28	-0.05	0.24	0.05	0.02
wcat	white catfish medium & large	-0.30	0.17	0.01	-0.13	-0.25	-0.02	0.11	0.05	-0.08
wcats	white catfish, small	-0.16	0.01	-0.03	-0.24	-0.42	-0.09	0.21	0.19	0.11
weak	weakfish, all	0.18	0.06	0.09	-0.23	-0.22	0.14	-0.07	0.29	-0.13

Taxon abbrev.	Taxon, size/age	PC1 19.9%	PC2 12.7%	PC3 7.2%	PC4 7.0%	PC5 6.2%	PC6 5.6%	PC7 5.1%	PC8 3.8%	PC9 3.6%
whper0	white perch, age 0	-0.29	-0.15	-0.15	-0.21	-0.05	0.22	0.04	0.02	-0.29
whper1	white perch, age 1+	-0.29	0.28	0.16	-0.02	0.02	-0.05	-0.07	0.04	-0.04

Table S11. Loadings for the Pamlico Sound June principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance represented by each PC is shown under each PC number.

Taxon abbreviation	Taxon, age	PC1 13.4%	PC2 10.1%	PC3 7.0%	PC4 6.7%	PC5 5.9%	PC6 4.3%	PC7 4.1%	PC8 3.4%	PC9 3.3%	PC10 3.2%
am0	Atlantic menhaden, 0	-0.01	0.03	0.01	-0.12	-0.11	-0.01	0.04	0.56	-0.10	0.30
am1	Atlantic menhaden, 1+	0.16	0.16	0.02	0.04	-0.21	0.08	0.02	-0.23	-0.36	0.31
ba	bay anchovy	0.05	0.27	-0.04	0.26	0.01	0.07	0.09	-0.04	0.04	0.22
bc	blue crab	0.23	0.10	0.19	-0.31	0.08	0.06	0.07	0.02	-0.20	-0.04
bf	bluefish	-0.04	0.12	0.24	0.12	-0.31	0.15	-0.17	0.14	-0.25	0.14
bs	brown shrimp	0.11	0.35	0.22	0.12	0.18	0.19	0.09	0.07	0.06	0.07
bu	butterfish	0.12	0.09	-0.13	0.17	-0.05	0.05	0.09	-0.07	0.05	-0.42
bw	bay whiff	-0.06	0.15	0.17	-0.02	0.37	-0.09	-0.17	-0.18	-0.05	-0.10
cr1	Atlantic croaker, 1	0.32	0.15	0.20	-0.04	-0.06	-0.04	0.10	0.11	0.01	0.10
cr2	Atlantic croaker, 2+	0.29	-0.18	-0.20	0.15	0.09	-0.06	0.01	0.25	-0.07	0.00
hc	hogchoker	0.14	-0.27	0.26	-0.10	0.17	0.03	0.17	0.07	0.04	0.00
hf	harvestfish	0.18	0.17	-0.10	0.26	0.15	0.04	0.01	-0.04	0.20	-0.03
lf	inshore lizardfish	-0.07	0.08	0.12	0.09	0.20	-0.52	0.04	-0.16	-0.14	0.10
pf	pinfish	-0.21	0.05	0.21	0.26	-0.04	-0.12	-0.16	0.14	-0.26	-0.08
pg	pigfish	-0.11	-0.19	0.18	0.33	0.15	-0.14	0.03	0.15	-0.07	-0.05
ps	pink shrimp	0.26	0.07	-0.15	-0.02	0.35	-0.01	-0.16	0.12	-0.18	0.05
sf1	spadefish, 1	-0.08	-0.06	0.13	0.30	0.07	0.13	-0.38	0.13	-0.02	-0.13
sf2	spadefish, 2+	0.00	-0.09	-0.04	0.18	0.02	0.09	-0.17	-0.05	0.46	0.57
si1	silver perch, 1	0.21	-0.28	0.19	0.18	-0.23	-0.01	0.08	-0.10	0.09	-0.08
si2	silver perch, 2+	0.17	-0.31	0.12	0.19	-0.11	-0.02	0.09	-0.03	0.19	-0.01
sk0	southern kingfish, 0	-0.05	-0.03	0.03	0.16	0.07	-0.54	0.22	-0.09	-0.05	0.25
sk1	southern kingfish, 1+	0.16	-0.15	0.13	0.18	0.02	0.13	-0.09	-0.25	-0.26	-0.05
so0	southern flounder, 0	0.14	0.08	0.29	-0.20	-0.18	-0.23	-0.34	-0.13	0.24	-0.10
so1	southern flounder, 1	0.23	-0.02	0.16	-0.27	-0.02	-0.17	-0.40	-0.11	0.09	0.08
so2	southern flounder, 2+	0.09	-0.16	0.15	-0.22	0.18	0.01	0.07	0.18	0.10	0.09
sp0	spot, 0	0.11	0.19	0.29	0.16	-0.26	0.00	0.14	0.05	0.00	-0.06

Taxon abbreviation	Taxon, age	PC1 13.4%	PC2 10.1%	PC3 7.0%	PC4 6.7%	PC5 5.9%	PC6 4.3%	PC7 4.1%	PC8 3.4%	PC9 3.3%	PC10 3.2%
sp1	spot, 1+	0.34	-0.12	-0.19	0.13	-0.03	-0.08	-0.03	-0.02	-0.12	0.03
su0	summer flounder, 0	-0.05	-0.23	0.37	0.02	0.19	0.16	0.08	0.16	0.07	-0.05
su1	summer flounder, 1	-0.03	-0.21	0.04	-0.06	0.29	0.27	0.07	-0.21	-0.32	0.19
su2	summer flounder, 2+	-0.11	-0.06	0.05	0.08	0.09	0.25	-0.23	-0.27	0.06	0.17
wf0	weakfish, 0	0.12	0.35	0.11	0.10	0.29	0.07	0.10	0.08	0.22	-0.09
wf1	weakfish, 1+	0.38	-0.04	-0.10	0.06	-0.01	0.00	0.02	-0.10	-0.06	-0.02
ws	white shrimp	0.13	-0.04	-0.19	0.08	0.07	-0.11	-0.45	0.28	-0.09	-0.04

Table S12. Loadings for the Pamlico River June principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance represented by each PC is shown under each PC number.

Taxon abbreviation	Taxon, age	PC1 18.5%	PC2 11.8%	PC 3 10.8%	PC4 8.5%	PC5 7.7%	PC6 6.2%	PC7 5.3%	PC8 4.3%
am0	Atlantic menhaden, 0	-0.21	-0.12	0.04	-0.41	0.11	-0.01	0.13	0.16
am1	Atlantic menhaden, 1+	0.07	0.30	0.21	-0.18	-0.25	0.01	0.20	-0.09
ba	bay anchovy	0.08	-0.12	-0.42	0.12	-0.06	0.28	-0.02	0.08
bc	blue crab	0.18	-0.14	0.15	0.20	0.29	0.07	-0.24	-0.37
bf	bluefish	-0.18	-0.22	0.02	-0.39	0.16	0.04	0.01	0.13
bs	brown shrimp	0.17	-0.38	0.20	0.04	-0.19	-0.14	0.04	0.05
bu	butterfish	0.28	-0.22	-0.30	0.01	0.08	-0.15	0.27	-0.04
bw	bay whiff	0.06	-0.22	0.19	0.19	-0.24	-0.16	-0.26	0.16
cr1	Atlantic croaker, 1	0.09	0.09	0.25	0.21	0.04	0.18	0.47	-0.04
cr2	Atlantic croaker, 2+	0.28	0.32	0.03	-0.13	-0.10	-0.07	-0.04	-0.09
hc	hogchoker	0.38	-0.03	0.05	0.06	0.05	0.03	-0.22	-0.10
pf	pinfish	0.08	-0.29	0.15	-0.29	0.00	-0.34	-0.09	0.05
ps	pink shrimp	0.11	0.12	0.04	0.19	0.41	-0.20	-0.20	0.50
si1	silver perch, 1	0.37	0.09	-0.12	-0.28	-0.09	-0.03	0.00	-0.11
si2	silver perch, 2+	0.30	0.05	0.01	-0.37	-0.06	-0.11	-0.14	-0.23
so0	southern flounder, 0	0.26	-0.01	0.26	-0.02	0.02	0.45	0.01	0.05
so1	southern flounder, 1	0.13	-0.04	0.26	-0.16	0.31	0.28	0.07	0.28
so2	southern flounder, 2+	-0.02	0.21	-0.02	0.23	0.21	-0.53	0.13	-0.15
sp0	spot, 0	0.09	0.02	0.31	0.00	0.08	-0.25	0.46	0.08
sp1	spot, 1+	0.12	0.43	0.01	0.00	0.05	0.04	-0.15	0.30
su0	summer flounder, 0	-0.04	-0.15	0.16	0.03	0.47	0.10	-0.02	-0.39
wf0	weakfish, 0	0.06	-0.21	0.28	0.26	-0.37	0.02	-0.01	0.12
wf1	weakfish, 1+	0.38	-0.10	-0.16	-0.02	0.09	-0.08	0.03	0.26
ws	white shrimp	0.19	-0.19	-0.35	0.10	0.04	0.07	0.38	0.06

Table S13. Loadings for the Pungo River June principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance represented by each PC is shown under each PC number.

Taxon abbreviation	Taxon, age	PC1 16.2%	PC2 14.2%	PC 3 9.8%	PC4 9.4%	PC5 8.1%	PC6 7.3%	PC7 5.9%	PC8 5.6%
am0	Atlantic menhaden, 0	0.23	0.26	-0.22	0.03	0.08	0.33	0.09	-0.21
am1	Atlantic menhaden, 1+	-0.29	0.06	0.20	0.33	-0.07	0.03	-0.17	-0.23
ba	bay anchovy	-0.26	-0.21	0.09	-0.32	0.13	0.16	-0.18	-0.22
bc	blue crab	0.03	-0.03	0.35	-0.03	0.29	0.18	0.23	-0.23
bf	bluefish	0.34	-0.11	0.02	-0.03	0.06	-0.12	-0.06	-0.27
bs	brown shrimp	0.08	-0.41	0.28	0.12	-0.05	0.08	-0.15	0.13
bu	butterfish	-0.19	-0.13	0.00	-0.32	0.01	0.25	-0.26	0.03
bw	bay whiff	0.16	-0.05	0.40	-0.20	-0.19	-0.06	0.30	0.27
cr1	Atlantic croaker, 1	-0.23	0.05	0.01	0.13	0.16	0.00	0.51	-0.10
cr2	Atlantic croaker, 2+	-0.33	0.13	-0.05	0.06	-0.35	-0.14	0.16	0.06
hc	hogchoker	-0.15	-0.21	-0.28	-0.11	-0.32	0.17	0.05	0.34
pf	pinfish	0.12	-0.25	0.19	0.40	0.06	-0.06	-0.26	0.15
ps	pink shrimp	-0.04	0.14	-0.09	-0.07	0.09	-0.33	-0.04	0.34
si1	silver perch, 1	-0.22	0.04	0.05	0.26	-0.48	0.10	0.08	-0.19
si2	silver perch, 2+	0.04	-0.34	-0.20	-0.06	0.02	-0.29	-0.06	-0.21
so0	southern flounder, 0	-0.31	-0.16	0.19	-0.06	0.20	-0.26	0.27	-0.03
so1	southern flounder, 1	-0.04	-0.24	-0.04	0.27	0.21	0.32	0.20	0.27
so2	southern flounder, 2+	0.12	-0.19	-0.18	0.24	0.11	0.30	0.19	0.21
sp0	spot, 0	0.12	-0.10	0.20	0.19	-0.37	0.08	-0.04	-0.25
sp1	spot, 1+	-0.19	0.06	0.13	0.25	0.25	-0.31	-0.14	0.14
su0	summer flounder, 0	0.07	-0.30	-0.20	-0.02	-0.04	-0.14	0.34	-0.26
wf0	weakfish, 0	0.27	0.00	0.37	-0.27	-0.22	-0.05	0.17	0.12
wf1	weakfish, 1+	-0.33	-0.26	0.04	-0.24	0.03	0.16	-0.04	-0.05
ws	white shrimp	0.11	-0.36	-0.27	0.04	-0.10	-0.28	0.05	-0.11

Table S14. Loadings for the Neuse River June principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance represented by each PC is shown under each PC number.

Taxon abbreviation	Taxon, age	PC1 23.7%	PC2 15.3%	PC 3 9.0%	PC4 6.9%	PC5 6.3%	PC6 5.8%	PC7 4.9%	PC8 4.8%
am0	Atlantic menhaden, 0	-0.16	0.19	0.04	0.08	0.07	0.55	0.25	0.00
am1	Atlantic menhaden, 1+	-0.07	0.04	-0.06	-0.07	-0.45	0.26	0.32	0.41
ba	bay anchovy	0.12	0.10	-0.25	0.30	-0.34	0.25	-0.20	-0.10
bc	blue crab	0.35	0.01	-0.18	-0.08	0.17	-0.22	-0.06	0.03
bf	bluefish	0.14	0.30	0.01	-0.10	0.18	0.31	0.29	0.09
bs	brown shrimp	0.32	0.23	0.01	-0.13	-0.09	0.05	-0.24	-0.02
bu	butterfish	0.19	-0.10	0.32	0.32	-0.24	0.13	-0.08	-0.07
bw	bay whiff	0.21	0.37	0.03	0.24	0.04	-0.14	0.03	0.08
cr1	Atlantic croaker, 1	0.04	0.19	-0.21	-0.19	-0.27	-0.24	0.40	-0.32
cr2	Atlantic croaker, 2+	0.10	-0.31	0.17	0.30	-0.16	-0.09	0.23	0.03
hc	hogchoker	0.15	-0.20	-0.42	0.24	0.16	0.11	-0.01	0.05
pf	pinfish	0.27	0.10	0.13	-0.35	0.00	0.12	-0.09	-0.13
ps	pink shrimp	0.19	0.12	0.12	0.34	0.28	-0.25	0.37	0.26
si1	silver perch, 1	0.27	-0.24	0.27	-0.17	0.02	0.18	0.07	0.10
si2	silver perch, 2+	0.26	-0.13	0.38	-0.18	0.20	0.17	0.01	-0.02
so0	southern flounder, 0	0.22	-0.26	-0.27	-0.01	-0.18	0.03	0.04	-0.15
so1	southern flounder, 1	0.31	-0.05	-0.20	-0.17	0.01	0.02	-0.11	0.20
so2	southern flounder, 2+	0.10	-0.09	-0.38	-0.18	0.13	0.06	0.12	0.42
sp0	spot, 0	0.24	0.10	0.05	-0.20	-0.33	-0.10	0.24	-0.19
sp1	spot, 1+	0.03	-0.33	0.12	-0.08	-0.14	-0.26	0.24	0.16
su0	summer flounder, 0	0.07	-0.15	-0.16	0.08	0.33	0.16	0.36	-0.55
wf0	weakfish, 0	0.20	0.39	0.06	0.23	-0.04	-0.15	-0.02	0.03
wf1	weakfish, 1+	0.30	-0.18	-0.03	0.25	-0.06	0.18	-0.07	-0.03

Table S15. Loadings for the Pamlico Sound September principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance represented by each PC is shown under each PC number.

Taxon abbrev.	Taxon, age	PC1 16.2%	PC2 9.6%	PC3 8.6%	PC4 6.1%	PC5 5.3%	PC6 4.3%	PC7 4.2%	PC8 4.0%	PC9 3.4%
am0	Atlantic menhaden, 0	0.10	0.22	0.28	-0.07	0.14	0.14	-0.11	0.39	0.03
am1	Atlantic menhaden, 1+	0.11	0.20	0.23	-0.16	0.14	0.02	-0.03	0.23	0.05
ba	Bay anchovy	0.06	-0.26	0.09	-0.28	-0.06	0.06	0.02	0.32	0.06
bc	blue crab	0.29	-0.05	0.06	0.21	-0.35	-0.06	-0.04	0.13	0.04
bf	bluefish	0.07	0.11	0.19	0.11	0.23	0.04	0.11	0.30	-0.01
bs	brown shrimp	0.25	-0.26	-0.06	-0.10	-0.01	-0.20	0.25	-0.03	0.01
bu	butterfish	0.08	-0.10	-0.10	0.00	0.14	0.50	0.32	-0.24	-0.02
bw	Bay whiff	0.06	-0.23	-0.10	-0.17	0.35	-0.29	0.11	0.14	-0.12
cr1	Atlantic croaker, 1	0.36	0.01	-0.04	0.09	0.14	0.16	-0.04	-0.14	-0.03
cr2	Atlantic croaker, 2+	0.05	-0.12	-0.08	-0.16	0.15	0.00	-0.49	0.00	0.03
hc	hogchoker	0.21	0.28	-0.13	0.20	-0.29	-0.08	-0.08	-0.01	-0.02
hf	harvestfish	0.20	-0.16	0.12	0.11	0.06	0.30	-0.19	0.24	-0.03
lf	inshore lizardfish	0.02	-0.11	-0.39	0.16	0.29	0.02	0.03	0.22	0.00
pf	pinfish	-0.10	0.30	-0.06	-0.26	0.38	0.01	0.05	-0.03	-0.03
pg	pigfish	-0.01	0.35	-0.32	-0.03	-0.05	0.08	0.02	0.00	0.03
ps	pink shrimp	0.22	-0.15	-0.15	-0.14	-0.13	-0.01	0.21	0.01	-0.08
sf0	spadefish, 0	0.13	0.04	-0.33	-0.11	-0.10	0.05	-0.27	0.30	0.05
sf1	spadefish, 1+	-0.10	0.06	-0.08	0.08	0.10	-0.16	0.05	0.09	0.41
si0	silver perch, 1	0.20	0.28	0.11	-0.31	-0.13	-0.05	0.17	-0.05	-0.14
si1	silver perch, 2+	0.21	0.35	0.00	-0.07	-0.06	0.03	0.14	0.04	0.10
sk0	southern kingfish, 0	0.00	-0.02	-0.23	-0.44	-0.17	-0.09	0.15	0.18	-0.06
sk1	southern kingfish, 1+	0.08	0.05	-0.27	0.04	-0.06	0.10	-0.33	0.02	-0.07
so0	southern flounder, 0	0.17	0.11	0.14	0.22	0.13	-0.46	-0.01	-0.07	-0.24
so1	southern flounder, 1	0.18	-0.12	-0.07	0.28	0.18	-0.12	-0.02	0.08	-0.35
sp0	spot, 0	0.28	0.20	-0.01	0.03	0.32	0.09	0.03	-0.21	-0.04
sp1	spot, 1+	0.09	0.02	-0.18	-0.28	0.11	-0.12	-0.33	-0.32	-0.08
su0	summer flounder, 0	0.17	0.10	-0.33	0.20	0.01	-0.04	0.23	0.20	0.10

Taxon abbrev.	Taxon, age	PC1 16.2%	PC2 9.6%	PC3 8.6%	PC4 6.1%	PC5 5.3%	PC6 4.3%	PC7 4.2%	PC8 4.0%	PC9 3.4%
su1	summer flounder, 1+	0.03	0.01	-0.05	0.07	0.14	-0.28	0.03	-0.06	0.64
wf0	weakfish, 0	0.33	-0.16	0.07	-0.14	-0.07	0.04	0.11	-0.08	0.13
wf1	weakfish, 1+	0.25	-0.13	0.09	0.01	0.08	0.19	-0.11	-0.19	0.37
ws	white shrimp	0.28	0.00	0.19	-0.14	-0.04	-0.23	-0.17	-0.10	0.07

Table S16. Loadings for the Pamlico River September principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance represented by each PC is shown under each PC number.

Taxon abbreviation	Taxon, age	PC1 24.2%	PC2 10.7%	PC3 8.9%	PC4 7.1%	PC5 6.8%	PC6 5.8%	PC7 5.2%	PC8 4.4%
am0	Atlantic menhaden, 0	-0.02	-0.31	0.18	0.24	-0.18	0.25	-0.07	-0.32
am1	Atlantic menhaden, 1+	0.05	-0.16	-0.41	0.02	0.12	-0.29	0.04	-0.11
ba	bay anchovy	0.01	-0.05	0.10	-0.03	0.43	0.49	0.08	0.04
bc	blue crab	0.20	-0.11	0.08	0.42	0.03	-0.16	-0.12	-0.22
bf	bluefish	-0.10	0.10	-0.03	0.05	0.48	-0.01	-0.14	-0.21
bs	brown shrimp	0.28	0.26	0.15	0.00	-0.07	-0.06	-0.02	-0.08
bu	butterfish	0.01	-0.24	0.04	-0.01	-0.25	0.22	-0.25	0.36
bw	bay whiff	0.14	0.06	0.28	-0.03	0.27	-0.17	0.13	0.45
cr1	Atlantic croaker, 1	0.28	-0.22	-0.12	0.01	0.24	0.21	0.13	0.04
cr2	Atlantic croaker, 2+	0.12	0.05	0.26	0.34	0.19	-0.24	-0.05	0.27
hc	hogchoker	0.24	-0.05	0.20	-0.08	-0.09	0.08	-0.44	0.08
hf	harvestfish	0.23	0.12	-0.22	-0.03	0.25	0.13	-0.07	-0.21
lf	inshore lizardfish	0.20	0.28	-0.01	-0.21	-0.11	0.26	0.11	0.13
pf	pinfish	0.04	-0.32	0.24	-0.44	0.12	-0.02	0.14	0.01
pg	pigfish	0.11	-0.08	0.34	-0.24	0.18	-0.21	-0.38	-0.28
ps	pink shrimp	0.25	0.24	-0.01	0.11	-0.31	0.12	0.05	-0.15
si0	silver perch, 0	0.16	-0.37	-0.18	-0.02	-0.11	-0.18	-0.05	0.21
si1	silver perch, 1+	0.21	-0.19	-0.01	-0.38	-0.09	-0.20	-0.10	-0.21
so0	southern flounder, 0	0.25	0.08	-0.28	-0.03	-0.04	-0.11	-0.25	0.25
so1	southern flounder, 1	0.18	0.11	-0.35	-0.17	0.07	-0.08	0.02	-0.01
sp0	spot, 0	0.22	-0.34	-0.14	0.05	0.08	0.13	0.22	0.05
sp1	spot, 1+	0.14	-0.05	0.21	0.12	-0.05	-0.30	0.45	0.01
su0	summer flounder, 0	0.26	0.27	0.14	-0.21	-0.04	0.06	0.07	-0.04
wf0	weakfish, 0	0.30	-0.15	0.04	0.20	-0.04	0.24	0.00	0.00
wf1	weakfish, 1+	0.25	-0.03	0.10	-0.03	-0.12	-0.05	0.36	-0.24
ws	white shrimp	0.28	0.09	-0.09	0.23	0.14	-0.03	-0.16	0.04

Table S17. Loadings for the Pungo River September principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance represented by each PC is shown under each PC number.

Taxon abbreviation	Taxon, age	PC1 16.2%	PC2 15.9%	PC3 12.9%	PC4 8.9%	PC5 6.8%	PC6 6.4%	PC7 5.1%	PC8 4.4%	PC9 4.3%
am0	Atlantic menhaden, 0	0.19	0.26	0.16	-0.18	-0.23	-0.27	-0.14	0.07	0.18
am1	Atlantic menhaden, 1+	0.08	-0.02	-0.11	0.15	-0.54	-0.16	-0.26	-0.08	-0.16
ba	bay anchovy	-0.20	-0.12	0.20	-0.08	-0.39	-0.23	0.16	0.12	0.09
bc	blue crab	0.32	0.12	0.18	-0.18	-0.13	0.01	0.16	-0.19	-0.15
bf	bluefish	-0.25	-0.12	0.08	0.10	0.09	-0.16	-0.29	-0.36	-0.09
bs	brown shrimp	0.12	-0.14	-0.04	-0.14	-0.20	0.36	-0.35	0.32	-0.20
bw	bay whiff	-0.28	-0.05	-0.30	-0.10	-0.03	0.11	0.36	-0.22	0.10
cr1	Atlantic croaker, 1	0.08	-0.38	-0.11	0.22	-0.19	-0.11	0.23	0.06	-0.05
cr2	Atlantic croaker, 2+	-0.04	0.07	-0.12	-0.51	-0.13	0.00	-0.21	-0.18	0.31
hc	hogchoker	0.13	0.15	-0.36	-0.07	-0.07	-0.27	0.21	0.03	-0.36
hf	harvestfish	0.14	-0.40	0.05	0.11	-0.10	0.05	0.09	0.04	0.09
lf	inshore lizardfish	-0.09	-0.28	-0.27	-0.33	0.04	0.04	-0.05	-0.03	0.15
pf	pinfish	-0.27	0.07	-0.30	0.18	-0.27	0.02	0.10	0.12	-0.13
ps	pink shrimp	0.12	-0.23	-0.08	-0.27	0.10	-0.17	-0.11	0.20	-0.31
si0	silver perch, 0	0.16	0.31	-0.25	0.12	-0.06	0.08	-0.05	-0.10	-0.14
si1	silver perch, 1+	0.11	0.06	0.11	0.02	-0.31	0.55	-0.11	-0.23	-0.09
so0	southern flounder, 0	0.21	0.16	-0.28	-0.13	0.10	0.01	0.09	-0.15	-0.22
so1	southern flounder, 1	0.27	0.02	-0.29	0.06	0.31	0.04	-0.15	0.01	0.17
sp0	spot, 0	0.24	0.02	-0.23	-0.01	-0.26	-0.16	0.12	-0.11	0.48
sp1	spot, 1+	0.08	-0.17	0.19	-0.01	0.04	-0.29	-0.13	-0.58	-0.21
su0	summer flounder, 0	-0.25	-0.21	-0.17	-0.35	-0.03	-0.06	-0.19	0.03	-0.18
su1	summer flounder, 1	-0.05	0.08	-0.21	0.32	0.04	-0.23	-0.48	0.14	0.20
wf0	weakfish, 0	0.35	-0.23	0.06	-0.09	0.04	0.08	0.05	0.04	0.14
wf1	weakfish, 1+	0.02	-0.26	-0.24	0.22	-0.03	0.23	-0.09	-0.33	0.09
ws	white shrimp	0.33	-0.27	-0.04	0.11	0.09	-0.15	0.01	0.09	-0.02

Table S18. Loadings for the Neuse River September principal components analysis for the PCs with eigenvalues > 1. The percentage of the variance represented by each PC is shown under each PC number.

Taxon abbreviation	Taxon, age	PC1 20.4%	PC2 14.6%	PC3 8.8%	PC4 7.2%	PC5 6.1%	PC6 5.5%	PC7 4.6%	PC8 4.4%	PC9 4.0%
am0	Atlantic menhaden, 0	0.06	0.14	0.29	-0.11	-0.30	-0.06	0.26	-0.09	0.33
am1	Atlantic menhaden, 1+	0.05	0.26	0.20	-0.08	0.17	-0.36	-0.02	0.16	0.11
ba	bay anchovy	-0.07	-0.04	0.20	-0.39	-0.15	0.28	-0.21	-0.35	-0.01
bc	blue crab	0.25	0.07	0.41	0.04	0.02	0.09	-0.06	-0.14	-0.04
bf	bluefish	0.04	0.19	-0.14	-0.16	-0.32	0.15	0.09	0.03	-0.38
bs	brown shrimp	0.33	-0.14	-0.08	0.10	0.07	0.03	-0.07	0.17	-0.11
bu	butterfish	0.08	-0.21	-0.13	0.08	-0.11	-0.40	0.19	-0.15	0.03
bw	bay whiff	0.20	-0.01	-0.24	0.25	-0.19	-0.13	-0.28	-0.01	-0.07
cr1	Atlantic croaker, 1	0.28	0.01	-0.11	-0.20	-0.31	-0.17	-0.12	0.01	0.15
cr2	Atlantic croaker, 2+	0.08	-0.12	0.24	-0.10	-0.15	0.25	-0.31	0.34	0.14
hc	hogchoker	0.26	0.10	-0.04	0.27	0.26	0.13	-0.04	-0.07	0.24
hf	harvestfish	0.10	-0.31	0.00	-0.31	0.17	-0.07	0.29	-0.14	-0.11
lf	inshore lizardfish	0.26	-0.15	-0.21	0.03	-0.05	0.20	0.07	-0.18	-0.08
pf	pinfish	-0.09	0.37	-0.17	-0.01	-0.05	-0.06	-0.16	-0.27	0.06
pg	pigfish	0.15	0.26	0.25	0.07	0.11	-0.14	0.16	-0.34	-0.22
ps	pink shrimp	0.24	-0.29	0.24	0.03	0.04	-0.07	-0.10	-0.10	0.14
si0	silver perch, 0	0.15	0.39	0.11	0.07	0.04	-0.04	-0.02	-0.19	-0.07
si1	silver perch, 1+	0.13	0.35	-0.25	-0.11	0.07	0.24	0.17	0.08	-0.07
so0	southern flounder, 0	0.15	0.15	0.18	0.30	-0.01	0.37	0.09	0.24	-0.10
so1	southern flounder, 1	0.13	-0.14	0.10	0.06	-0.49	0.11	0.29	-0.06	-0.20
sp0	spot, 0	0.15	0.20	-0.13	-0.07	-0.36	-0.15	-0.11	0.17	0.32
sp1	spot, 1+	0.12	-0.04	-0.27	-0.22	0.18	0.31	-0.20	-0.33	0.24
su0	summer flounder, 0	0.24	-0.11	-0.07	0.29	-0.08	-0.12	-0.26	-0.22	-0.22
su1	summer flounder, 1	0.09	-0.04	-0.14	0.22	-0.03	0.20	0.45	-0.10	0.49
wf0	weakfish, 0	0.33	-0.01	0.07	-0.17	0.17	-0.03	0.17	0.24	-0.10
wf1	weakfish, 1+	0.25	0.10	-0.24	-0.34	0.14	-0.09	0.11	0.20	-0.10
ws	white shrimp	0.33	0.00	0.11	-0.22	0.11	-0.07	-0.13	0.00	0.06

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