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Climatologically forced coherence between diverse juvenile populations in the Virginia tributaries to the Chesapeake Bay

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**Climatologically forced coherence between diverse juvenile populations
in the Virginia tributaries to the Chesapeake Bay**

A Dissertation

Presented to

**The Faculty of the School of Marine Science
The College of William and Mary in Virginia**

In Partial Fulfillment

of the Requirements for the Degree of

Doctor of Philosophy

by

Thomas C. Mosca III

August, 1997

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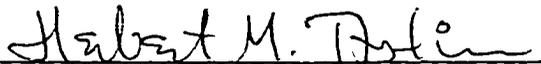
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the requirements for the degree of
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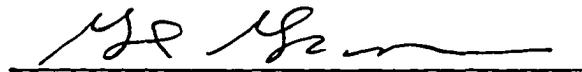

Gregory Garman
Virginia Commonwealth University

Table of Contents

	Page
Dedication	iv
Acknowledgements	v
List of Tables	vi
List of Figures	ix
Abstract	xiii
Introduction	1
Materials and Methods	6
Results	21
Discussion	55
Conclusions	65
Appendix	66
References	84
Vita	109

Dedication

This dissertation is dedicated to my Mother, and the memory of my Father.

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List of Tables

	Page
Table 2.1.	7
Configurations of the various trawl survey gears, by gear code. All gears except 035 are 30 feet nets; gear 035 is 16 feet. The metal China-V otter board doors are thought to be equivalent to the 54" x 24" wooden doors.	
Table 2.2.	9
The weights used in construction of the trawl survey indices. All weights are based upon the number of trawlable 1/4 square mile quadrants within each stratum.	
Table 2.3.	10
List of species by VIMS species code, common name, and scientific name. The letters accompanying the species code indicate the species is collected in the t-trawl survey and s-beach seine survey.	
Table 2.4.	12
Months and strata used in trawl survey indices, by species.	
Table 2.5.	13
Gear types used to construct juvenile indices from the trawl survey data, by VIMS species codes and year. For all years before 1972 gear type 10 was used for all species, from 1981 until 1990 gear type 70 was used, and from 1991 until 1995 gear type 108 was used for all species.	
Table 2.6.	15
Pearson correlation coefficients between individual oyster rocks. Rocks are identified by Fall Oyster Survey station number, which are as follows: S123-Point of Shoals on James River, S175-Wreck Shoals, offshore on James River, S001-Aberdeen Rock on York River, S067-Hog House Bar on Rappahannock River, S180-Morattico Bar on Rappahannock River,	

and S181-Drumming Ground on Rappahannock River. The notation * indicates $p < 0.05$, and ** indicates $p < 0.01$.

Table 2.7. 20

Long term (1965 - 1995) mean water temperature by month, as measured off the VIMS pier, and the difference between each month and the previous month (ΔT).

Table 3.1. 37

Principal component analyses on the 16 trawl survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/16 of total (0.0625) are considered insignificant and are not presented.

Table 3.2. 38

Principal component analyses on the 17 beach seine survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/16 of total (0.0588) are considered insignificant and are not presented.

Table 3.3. 39

Principal component analyses on the residuals of the 16 loess-smoothed trawl survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/16 of total (0.0625) are considered insignificant and are not presented.

Table 3.4. 40

Principal component analyses on the residuals of the 17 beach seine survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/16 of total (0.0588) are considered insignificant and are not presented.

Table 3.5.	41
<p>Principal component analyses on the 16 loess-smoothed trawl survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/16 of total (0.0625) are considered insignificant and are not presented.</p>	
Table 3.6.	42
<p>Principal component analyses on the residuals of the 17 beach seine survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/16 of total (0.0588) are considered insignificant and are not presented.</p>	
Table 3.7.	48
<p>Pearson correlations of PC#1 on the loess-smoothed indices for each of the three river and both surveys. The coded variables are t-trawl survey, s-beach seine survey, followed by j-James River, y-York River, and r-Rappahannock River.</p>	
Table 3.8.	49
<p>Correlations (Pearson) between the loess-smoothed biological indices vs. the loess-smoothed January-February temperature index.</p>	
Table 3.9.	50
<p>Correlations (Pearson) between the loess smoothed biological indices vs. the loess smoothed January-February temperature index. The biological indices are given by species codes (see Table 2.3).</p>	

List of Figures

Figure 2.1.	19
Long term (1965 - 1995) monthly mean water temperatures, measured at the VIMS pier. The months are in chronological order beginning with January, and January and February are repeated at the end for reasons of symmetry.	
Figures 3.1, 3.2.	22
Juvenile indices for Atlantic croaker and spot in the James, York and Rappahannock Rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.	
Figures 3.3, 3.4.	23
Juvenile indices for summer flounder and weakfish in the James, York and Rappahannock Rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.	
Figures 3.5, 3.6.	24
Juvenile indices for white catfish and channel catfish in the James, York and Rappahannock Rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.	
Figures 3.7, 3.8.	25
Juvenile indices for alewife and blueback herring in the James, York and Rappahannock Rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.	
Figures 3.9, 3.10.	26
Juvenile indices for striped bass and white perch in the James, York and Rappahannock Rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.	
Figures 3.11, 3.12.	27
Juvenile indices for blackcheek tonguefish and silver tonguefish in the James, York and Rappahannock Rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.	

Figures 3.13, 3.14.	28
<p>Juvenile indices for hogchoker and bay anchovy in the James, York and Rappahannock Rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.</p>	
Figures 3.15, 3.16.	29
<p>Juvenile indices for bluecrab from data collected by the VIMS trawl survey, and oyster from data collected by the VIMS fall dredge survey, in the James, York and Rappahannock Rivers. Each index is smoothed by loess.</p>	
Figures 3.17, 3.18.	30
<p>Juvenile indices for Atlantic croaker and spot in the James, York and Rappahannock Rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.</p>	
Figures 3.19, 3.20.	31
<p>Juvenile indices for striped bass and white perch in the James, York and Rappahannock Rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.</p>	
Figures 3.21, 3.22.	32
<p>Juvenile indices for Atlantic menhaden and gizzard shad in the James, York and Rappahannock Rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.</p>	
Figures 3.23, 3.24.	33
<p>Juvenile indices for hogchoker and channel catfish in the James, York and Rappahannock Rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.</p>	
Figures 3.25, 3.26, 3.27.	34
<p>Juvenile indices for banded killifish, mummichog and eastern silvery minnow in the James, York and Rappahannock Rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.</p>	

Figures 3.28, 3.29, 3.30.	35
<p>Juvenile indices for satinf shiner, spottail shiner and tessellated darter in the James, York and Rappahannock Rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.</p>	
Figures 3.31, 3.32, 3.33.	36
<p>Juvenile indices for inland silverside, Atlantic silverside and bay anchovy in the James, York and Rappahannock Rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.</p>	
Figure 3.34.	43
<p>Coefficients of principal component analyses for loess-smoothed indices from the trawl survey data. Species are identified by species codes in Table 2.1.</p>	
Figure 3.35.	44
<p>Coefficients of principal component analyses for loess-smoothed indices from the summer beach seine survey data. Species are identified by species codes in Table 2.1.</p>	
Figure 3.36.	45
<p>The first three principal components of the PCA analyses on the loess-smoothed indices for the trawl survey and summer beach seine survey data, for each of the Virginia rivers. Only the first PC (shown in red) is used in this study.</p>	
Figure 3.37.	47
<p>The annual indices of seasonal water temperature constructed from the VIMS pier temperatures. Each index is smoothed by loess at the $k = 0.4$ and $k = 0.5$ levels.</p>	
Figure 3.38.	51
<p>Scatterplots of loess-smoothed winter temperature vs. PC's#1 on the loess-smoothed biological indices, for trawl survey and summer beach seine survey data from each of the Virginia rivers.</p>	

Figure 3.39.

52

Cross correlations on the loess-smoothed trawl survey PC's#1 vs. loess-smoothed winter water temperature.

Figure 3.40.

53

Cross correlations on a subset of the data in Figure 3.39, the years of anomalous temperatures. The period 1969 - 1982 was chosen to span the anomalous years.

Abstract

Long term trends in juvenile recruitment of oyster, bluecrab, and 24 species of finfish in a large temperate estuary (lower Chesapeake Bay, USA) are coherent across the three major tributaries (the Virginia rivers James, York, and Rappahannock). The driving force for these long term trends is geographically large in scale. Anomalous winters in the mid 1970's, with the warmest years on record followed immediately by the coldest, caused a severe perturbation in population dynamics. The extreme conditions caused the system to shift, with recruitment patterns following temperatures by a one year lag. Following this anomalous episode, smoothed mean winter water temperatures have increased steadily from 1979 until 1995 (3.9 - 5.7°C, long-term $\bar{T} = 4.6^\circ\text{C}$), closely followed (with zero lag) by the first principal component (PC) from each set of smoothed biological indices.

Annual indices of juvenile abundance (means of log-transformed catch per unit effort) were calculated by river for the James, York and Rappahannock Rivers. Two collections of different temporal lengths are analysed, oyster, bluecrab and 14 species of finfish (1965 - 1995) and 17 species of finfish (1980 - 1995), with an overlap of seven species of finfish. The indices are smoothed by loess (locally weighted scatterplot smoother), and analyses are performed on the indices, the loess-smoothed indices, and the residuals.

Principal components analysis (PCA) on the indices indicates coherence in the population fluctuations by a relatively small number of PC's. Weak relationships are found in the unsmoothed indices and the residuals. Smoothed long-term trends eliminate much of the noise, thus exposing the underlying behavior of populations. PCA on the loess-smoothed indices were remarkably cohesive, with only three or four PC's significant in each of the six treatments, accounting for 93 to 98% of total variance, with 44 to 70% in PC#1. Correlations on the first PC's of the loess-smoothed indices, between rivers, within and between surveys, yielded 87 - 99% agreement; such coherence indicates the underlying causal factor is geographically broad. Cross correlations and scatterplots of smoothed winter water temperature and PC#1 identify the lag during the perturbation years.

Introduction

“Climate plays an important part in determining the average number of a species, and periodical seasons of extreme cold or drought seem to be the most effective of all checks. I estimated (chiefly from the greatly reduced numbers of nests in the spring) that the winter of 1854-55 destroyed four-fifths of the birds in my own grounds; and this is a tremendous destruction, when we remember that ten per cent. is an extraordinarily severe mortality from epidemics with man” (Darwin 1859).

Most ecologists agree that the physical environment (*e.g.*, temperature, freshwater discharge), its inhabitants, their interactions, and inter- and intraspecific interactions (*e.g.*, competition and predation) collectively should be thought of as a system. It is often not difficult to discover some connection between a physical parameter and the population dynamics of a single species (*e.g.*, salinity and the oyster disease MSX, Abbe 1992). Many predator/prey (*e.g.*, white perch/bay anchovy, Luo 1991) and competition (*e.g.*, resource partitioning among species of mummichogs, Weisberg 1986) relationships have been demonstrated. However, because of the immense complexity of the biosphere, a unifying theory has not been established.

An important step towards a conceptual understanding of ecosystems is to understand the broader system of species-environment relationships. This can be accomplished in the Chesapeake Bay by considering juvenile recruitment of a large group of species in conjunction with characteristics of the environment they inhabit.

The debate over the relative importance of density-dependent (*e.g.*, disease, parasitism, parent stock size, malnutrition and predation) and density-independent (*e.g.*, temperature, salinity) (Ricker 1954) factors to juvenile recruitment and mortality is longstanding and unresolved. For example, for many species juvenile recruitment is normally independent of spawning stock size (Walters and Ludwig 1981).

The distinction between density-dependent and density-independent factors affecting juvenile stock size is often blurred. Climate sometimes indirectly controls juvenile recruitment through a less direct biological intermediate stage. For example, Merriman (1941) noted that striped bass recruitment was often greatest following cold winters. Detritivore copepod population size in April and May depends upon very harsh (cold, with high precipitation) winters, so that detritus in the salt marshes is ground up by shifting ice, and the subsequent high volume of fresh water discharge moves the material out into the rivers (Heinle *et al.* 1976). Abundance of copepods as a food supply contributes directly to survival of larval striped bass. Climate has been demonstrated to exert direct control over plankton production (Colebrook 1978, 1982, Chelton *et al.* 1982, Koslow 1983), which in turn regulates larval fish recruitment (Cushing 1980, 1982, Smith and Eppley, 1982). Therefore, climatic control of one species may be reflected in the population abundance of another.

Many direct physical controls of juvenile abundance of marine species have been demonstrated. For example, croaker and spot spawn in the Atlantic Ocean and recruitment to the juvenile stock in Chesapeake Bay depends on the timing, duration and velocity of wind driven currents (Norcross 1983, Bodolus 1993). Similarly, an eleven year cycle in the strength of westerly winds off Australia may control recruitment cycles of fish, lobsters and scallops (Thresher 1994). Locally, northward wind controls recruitment of Chesapeake Bay bluecrabs. When winds are favorable bluecrab larvae are positioned in the northeastward quadrant of the Chesapeake Bight of the western North Atlantic. This location is advantageous for surface currents to later return larvae to Chesapeake Bay (Johnson 1995), with June through September wind patterns accounting for about 36% of harvest variation in subsequent years (Johnson 1989).

Changes in the Gulf stream may have profound effects on recruitment of certain marine-estuarine species of the North Atlantic. For instance, in the 1980's a reduction in American and European eel recruitment may have been related to weakening of the Gulf Stream (Castonguay *et al.* 1994). Changes in the oceanic environment sometimes can have large effects on recruitment, as

happened in the late 60's and 70's when a body of cold water migrated from Greenland to Labrador to Newfoundland, and then down to the Gulf Stream, and affected stock recruitment everywhere it went (Blindheim 1993).

Environmental factors, including stream flow and temperature explain 80-90% of the variation in American shad recruitment in the Connecticut River (Crecco *et al.* 1986) and survival of larvae of several species of salmon depends on fall and winter stream flow (Kocik and Taylor 1987). Recruitment of juveniles of the Indian oil-sardine is thought to depend on the intensity of the southwest monsoon (Raja 1973).

An unusually favorable physical condition may have a beneficial effect on recruitment, while moderate to poor expressions of the same factor may not necessarily depress recruitment. Some years multiple cohorts of juvenile dungeness crabs have been observed in Puget Sound (Dinnel *et al.* 1993). Multiple cohorts of juvenile striped bass, as evidenced by size\frequency analysis, were observed in Chesapeake Bay in the summer of 1993 (Herbert Austin, VIMS, pers. comm.). Perhaps some favorable environmental factor induced spawners to remain on or return to the spawning grounds for a second (or even third, in Puget Sound, 1988) spawning event, or perhaps some unfavorable event interrupted spawning, as has been reported for striped bass (Rutherford 1992).

Biological effects, particularly predation and prey abundance, often affect recruitment. Turbidity, has been shown to be more important than temperature or salinity in the recruitment of many species of South African fishes, because it reduces predation (Blaber and Blaber 1980). Predation by epibenthic fauna has been demonstrated to be the most important source of mortality of juvenile starfish (Keesing and Halford 1992). Recruitment of barnacle larvae from kelp forests to rocky intertidal habitat can be 50 times higher if predation by juvenile rockfish is absent (Gaines and Roughgarden 1987). In the rocky intertidal, predation by birds may control recruitment of juvenile mussels (Marsh 1986). The presence of mussel beds may control recruitment of sea anemones, which when mature will prey upon dislodged mussels (Sebens 1981, 1982).

The relationship between the timing of the spring phytoplankton bloom and the abundance of bay anchovies in the Maryland half of Chesapeake Bay was evaluated by linear regression (Mosca, T.C. III, unpublished data). About 83% of the variation in the anchovy juvenile index computed by Maryland Department of Natural Resources could be accounted for by the difference between the annual date and the mean date of the phytoplankton spring bloom. The absolute difference between the dates was found to have an insignificant effect. This combination of results and the negative regression coefficient of the signed differences indicates that a late spring bloom had a deleterious effect on recruitment, while an earlier bloom may have enhanced survival.

Each of the studies discussed above focused on single species relationships. Recruitment patterns of many species across a broad geographical region are evidence that geographically large-scale environmental forcing functions are in partial control (*e.g.*, ENSO and recruitment of rock lobster, Pearse and Phillips 1988). The existence of such patterns can be demonstrated by using multivariate analysis tools, such as principal component analysis (PCA). Patterns in recruitment were found in the time series of 14 northwest Atlantic fish stocks, including cod, haddock and herring. A similarly positive correlation was found in another group, including cod, haddock and redfish. Further, a negative relationship was identified between offshore spawners and inshore spawners. These patterns were identified using PCA (Koslow 1984).

What controls interannual variation in juvenile population abundances? Do fluctuations of one species, bluecrabs, for example, occur in synchrony with others, like oyster or flounder? It is obvious that the size of parent stocks influences reproduction, but it is also clear that extrinsic effects cause changes in juvenile abundance. Which climatic variables are responsible? Which fluctuations are measurable across the Chesapeake Bay basin, and which are river-specific?

In this paper I investigated coherence in the annual abundances of juvenile fishes, oysters, and bluecrabs within the Virginia portion of the Chesapeake Bay that are well represented in the trawl, beach seine, and fall dredge surveys. The list of species is given in Table 1. These are the species for

which we have sufficient data from which to construct meaningful, long-term indices (C. Bonzek, pers. comm.).

The hypothesis tested is twofold; 1) that recruitment of the different species for which the Bay system is nursery ground is not random, and the "non-randomness" of recruitment can be detected as coherence between species population fluctuations, and 2) that the environment at least partially controls the recruitment process, and through coherence with physical parameters we can detect this control.

The biological data used here are indices of annual juvenile abundance for oyster (VIMS fall oyster dredge survey, 1965 - 1995), bluecrab and 14 species of finfish (VIMS otter trawl survey, 1965 - 1995), and 17 species of finfish (VIMS beach seine survey, 1980 - 1995). Seven species of finfish are collected in both the trawl and beach seine surveys.

Species that fluctuate in synchrony (in phase or out of phase) do so because of an extrinsic reason, which was the object of this search. Is there some broad-scale environmental control of juvenile abundance in the Virginia half of Chesapeake Bay? If there is coherence within rivers, but not between rivers, a local control is implicated, such as freshwater discharge or summertime dissolved oxygen, which vary widely between the very different watersheds and basins. At the same time, if there is coherence in population abundance fluctuations within and between rivers, local signals are not in control, and a geographically broad forcing function, such as drought or regional temperature, probably regulates recruitment.

The interspecies component of this study is unique. There is great diversity in the life histories of the selected species. Some have an offshore component in the juvenile or larval stage, such as menhaden, croaker, spot and bluecrab. Others reproduce entirely within the Chesapeake Bay, such as the catfish, striped bass, white perch and oysters. Some are restricted to the upper reaches of rivers where salinity is very low, including white perch, the minnows, shiners and darters, while others like the weakfish, hogchoker, silversides, anchovies and silver perch are found farther downstream.

Materials and Methods

In this chapter the relationship between the environment and biota will be examined by comparing indices of abundance of juvenile finfish, the decapod crustacean, bluecrab and the bivalve mollusc, oyster, and indices of seasonal temperature. The individual species used in the study are profiled in the appendix.

The Juvenile Indices

The data used to construct annual indices of abundance are time series of juvenile abundance for oyster spat collected year-round in the VIMS fall oyster dredge survey (1965 - 1995), bluecrab and 14 species of finfish collected by the VIMS trawl survey (1965 - 1995) and 17 species of finfish collected in the VIMS summer beach seine survey (1980 - 1995). Seven species of finfish are collected in both the trawl and beach seine surveys, providing redundant estimates of juvenile abundance at two temporal and spatial locations (Table 2.1). Species are frequently identified in this study by VIMS species codes (Table 2.1). Because the time series were temporally coincident, the oyster data were grouped with the trawl survey data. Indices of annual abundance of each species within each Virginia river were constructed.

The indices were annual means of log-transformed catch per unit effort, by river for the three principal Virginia Chesapeake Bay tributaries, the James, York, and Rappahannock rivers. The indices were smoothed by loess (locally weighted scatterplot smoother, Cleveland 1979), and analyses were performed on the indices, the loess-smoothed indices, and the residuals. Two data sets were employed and treated separately: the beach seine indices, and the trawl survey indices. Because the oyster data have the same period of record, oyster indices were grouped with the trawl survey data.

Eighteen sets of data resulted: the trawl survey and beach seine indices for each of three rivers, the six sets of loess smoothed indices, and six sets of residuals of the smoothed indices. Each set was be

Gear code	Lined	Tickler chain	Bridle	Otter boards
010	No	No	30'	48" x 22"
033	Yes	No	30'	48" x 22"
043	No	Yes	30'	54" x 24"
068	Yes	Yes	30'	54" x 24"
070	Yes	Yes	60'	54" x 24"
108	Yes	Yes	60'	China-V
035	Yes	No	23'	24" x 12"

Table 2.1. Configurations of the various trawl survey gears, by gear code. All gears except 035 are 30 feet nets; gear 035 is 16 feet. The metal China-V otter board doors are thought to be equivalent to the 54" x 24" wooden doors.

examined for temporal coincidence. Principal components analysis (PCA) of a set of indices was used to indicate coherence in population fluctuations by a relatively small number of significant components. Comparisons were made within rivers using PCA to detect coherence between species. The results of PCA were compared across the three rivers to determine the scale of the effect.

Trawl survey data

VIMS conducts a year-long otter trawl survey of the lower portion of the Chesapeake Bay and the major Virginia tributaries. Sites in the James, York, and Rappahannock rivers, and the Bay proper, were visited monthly and sampled with a 10 m semi-balloon otter trawl (Bonzek *et al.* 1993). The survey was designed "to produce annual indices of juvenile (young-of-year) abundance of commercially, recreationally and ecologically important marine and estuarine finfish and crustaceans" (Bonzek *et al.* 1993). While the VIMS trawl survey program was not designed to sample adult populations, in some cases it does so very well (*e.g.* white perch).

The trawl survey provides a nearly continuous record from 1955 to the present, though some changes have been made over the years in gear and methodology (Table 2.2). In 1965 the survey was expanded from the York River to include the James and Rappahannock rivers; this is the date at which the data become useful for inter-river comparisons. The changes in gear (boats and nets) and methodology have been documented (Geer and Austin 1995, Geer *et al.* 1995).

To produce a meaningful time series, the effects of different gear types must be removed. For some years data from more than one gear type exist. Only data for one gear type were used for any particular year (Table 2.3). The subsets of the data set by gear type were standardized to zero mean and unit variance. Since indices for the different species were derived from data collected during different months, and gear changes occurred in midyears, it was necessary to segregate the data by gear type and decide which gear type to use for a particular year. The decision was made based on number

River	Stratum I	Stratum II
James	≤ 17	$> 17 \leq 42$
York	≤ 15	$> 15 \leq 42$
Rappahannock	≤ 20	$> 20 \leq 42$

Table 2.2a. River miles of strata on the three Virginia rivers.

River	Stratum I	Stratum II
James	687 (.654)	364 (.346)
York	372 (.669)	184 (.331)
Rappahannock	283 (.598)	190 (.402)

Table 2.2b. The number of 1/4 square mile, trawlable, quadrants per stratum and the weight assigned to each stratum for use in indices for species for which both up and down river strata are used.

Tables 2.2. The weights used in construction of the trawl survey indices. All weights are based upon the number of trawlable 1/4 square mile quadrants within each stratum.

Species code	Common name	Scientific name
	oyster	<i>Crassostrea virginica</i>
3 t	summer flounder	<i>Paralichthys dentatus</i>
5 ts	Atlantic croaker	<i>Micropogonias undulatus</i>
7 t	weakfish	<i>Cynoscion regalis</i>
26 t	alewife herring	<i>Alosa pseudoharengus</i>
27 t	blueback herring	<i>Alosa aestivalis</i>
31 ts	striped bass	<i>Morone saxatilis</i>
32 ts	white perch	<i>Morone americana</i>
33 ts	spot	<i>Leiostomus xanthurus</i>
37 s	Atlantic menhaden	<i>Brevoortia tyrannus</i>
39 t	white catfish	<i>Ictalurus catus</i>
40 ts	channel catfish	<i>Ictalurus punctatus</i>
51 s	gizzard shad	<i>Dorosoma cepedianum</i>
89 s	tssellated darter	<i>Etheostoma olmstedii</i>
103 ts	bay anchovy	<i>Anchoa mitchilli</i>
107 s	eastern silvery minnow	<i>Hybognathus regius</i>
109 s	satinfin shiner	<i>Cyprinella analostanas</i>
110 s	spottail shiner	<i>Notropis hudsonius</i>
121 s	banded killifish	<i>Fundulus diaphanus</i>
122 s	mummichog	<i>Fundulus heteroclitus</i>
149 s	inland silverside	<i>Menidia beryllina</i>
150 s	Atlantic silverside	<i>Menidia menidia</i>
151 ts	hogchoker	<i>Trinectes maculatus</i>
152 t	blackcheek tonguefish	<i>Symphurus plagiusa</i>
213 t	silver perch	<i>Bairdiella chrysoura</i>
614 t	bluecrab	<i>Callinectes sapidus</i>

Table 2.3. List of species by VIMS species code, common name, and scientific name. The letters accompanying the species code indicate the species is collected in the t-trawl survey and s-beach seine survey.

of observations by gear type and year, and continuity of gear type across years. Three gear types (68, 70 and 108) were used from 1980 to 1995, but they were sufficiently similar that they were grouped together. Also, it was necessary in a few cases to group gear types 33 and 35; these were both lined nets, but 35 is smaller, has a shorter bridle, and lacks a tickler chain. However, in no case was more than one year of gear type 35 included, and it was felt that the inclusion of a dissimilar gear type was preferable to missing a year of data.

The young-of-the-year counts for each species were log-transformed ($\log[x+1]$), and annual means were calculated for each river. The rivers were divided into two strata each, with the division based upon trawlable surface area (Table 2.4a, b). Each river was divided into two equal strata (Geer *et al.* 1995) The data from upper strata, lower strata, or both strata for each river were used, depending on the habits of the fish. Data from the months of greatest availability for a particular species were used to construct the indices for that species (Table 2.5). The sums of the weighted strata means make the index. The weights depend upon the trawlable stations per stratum (Table 2.4). In all cases appropriate weights have unit sums; for within river indices in which only one stratum was used, unit weight was assigned.

Beach Seine Data

VIMS conducts a summer beach seine survey to evaluate the abundance of young-of-the-year (YOY) striped bass (Colvocoresses 1984). The beach seine survey was conducted from 1967 to 1973, and from 1980 to the present. Observations were made monthly at several locations on each of the Virginia rivers from July through September (Austin *et al.* 1993). Counts and lengths on all species in the seine were recorded.

The abundance data (counts per haul) were log-transformed, and within-river means were calculated. Data were segregated according to the station type (primary or auxiliary) and tow. Only primary stations were used, and because the first and second tows were not independent, only the first

Species	Data months	Strata used
summer flounder	Sept. - Nov.	lower
Atlantic croaker	Oct. - Dec.	both
weakfish	Aug. - Oct.	both
alewife herring	Dec. - Mar.	upper
blueback herring	Dec. - Mar.	upper
striped bass	Dec. - Feb.	upper
white perch	Dec. - Feb.	upper
spot	Jul. - Oct.	both
white catfish	Jan. - Apr.	upper
channel catfish	Jan. - Apr.	upper
bay anchovy	Jul. - Dec.	both
hogchoker	May - Jul.	both
blackcheek tonguefish	Apr. - Jun.	both
silver perch	Aug. - Nov.	both
bluecrab	Aug. - Nov.	both

Table 2.4. Months and strata used in trawl survey indices, by species.

Yr	3	5	7	26	27	31	32	33	39	40	103	151	152	213	614
72	10	10	10	10	10	10	10	10	10	10	10	10	10	10	43
73	43	43	43	35	35	35	35	43	35	35	43	43	43	43	43
74	43	43	43	33	33	33	33	43	33	33	43	43	43	43	43
75	43	43	43	33	33	33	33	43	33	33	43	43	43	43	43
76	43	43	43	33	33	33	33	43	33	33	43	43	43	43	43
77	43	43	43	33	33	33	33	43	33	33	43	43	43	43	43
78	43	43	43	33	33	33	33	43	33	33	43	43	43	43	43
79	68	68	68	33	33	33	33	68	33	33	68	68	68	68	68
80	70	70	70	33	33	33	33	70	33	33	70	70	70	70	70

Table 2.5. Gear types used to construct juvenile indices from the trawl survey data, by VIMS species codes and year. For all years before 1972 gear type 10 was used for all species, from 1981 until 1990 gear type 70 was used, and from 1991 until 1995 gear type 108 was used for all species.

tow was used (Rago *et al.* 1995). Because of the considerable temporal gap and moderate changes in gear, only the 1980 - 1995 data were used.

Fall oyster survey

Each fall, the VIMS oyster dredge survey samples the public oyster "rocks" (or "reefs"), known as Baylor Grounds, with a standard dredge (Morales-Alamo and Mann 1997). In the past, one bushel of "clutch" (mixed grab of oysters and empty oyster shells) was examined, and the number of recently attached spat, yearling, sub-market sized (usually < 2 y old), market sized oysters (usually > 2 y old) and two categories of "boxes" (recently killed and oysters dead for a longer time) were recorded. In more recent years, the sample size was reduced to $\frac{1}{2}$ bushel, and the yearling category was dropped (yearlings and sub-markets are now grouped together as sub-markets). Doubling recent data adjusts for the change in sample size.

Within the three Virginia rivers 35 stations have been visited over the interval 1965 - 1995. However, only six of these have been sampled with sufficient regularity to be useful in this study. These stations were missed by the survey some years, but the number of missing observations was small (16 of 186, 8.6%) and only twice were consecutive years missed. Two stations were on James River (Wreck Shoal Offshore, and Point of Shoals), three were on the Rappahannock (Morattico Bar, Hog House Bar, and Drumming Ground), and one was on the York River (Aberdeen Rock).

Indices of juvenile (spat-on-shell) abundance were constructed for each Baylor Ground, and consist of the means of the log-transformed counts per bushel. Correlations between oyster rocks within each river and the location of the oyster rock in the river were used to determine which data should be included in the index for James and Rappahannock rivers. Wreck Shoal and Point of Shoals are geographically close, and are relatively far upriver, but are in sections of the James River that have different circulation patterns (Haven and Fritz 1985). Hog House Bar and Drumming Ground on the Rappahannock are near each other, but Morattico Bar is much farther upriver.

Correlations of oysters within rivers (Table 2.6) indicated that the two James River stations

Station	S175	S001	S067	S180	S181
S123	.44*	ns	.52**	ns	.44*
S175		ns	.41*	ns	ns
S001			ns	ns	ns
S067				ns	.51**
S180					ns

Table 2.6. Pearson correlation coefficients between individual oyster rocks. Rocks are identified by Fall Oyster Survey station number, which are as follows: S123-Point of Shoals on James River, S175-Wreck Shoals, offshore on James River, S001-Aberdeen Rock on York River, S067-Hog House Bar on Rappahannock River, S180-Morattico Bar on Rappahannock River, and S181-Drumming Ground on Rappahannock River. The notation * indicates $p < 0.05$, and ** indicates $p < 0.01$.

and two of the Rappahannock River stations were coherent. The third station on the Rappahannock was Morattico, which is also geographically distant from the others. Based on proximity and correlations, the two stations on the James River (Point of Shoals and the Offshore Wreck Shoals bars) and two of the stations on the Rappahannock River (Drumming Ground and Hog House Bar) were combined to produce James and Rappahannock River oyster indices. York River was represented by a single station (Aberdeen Rock). The means of the log-transformed spat per bushel (standardized, as above) for the appropriately pooled data comprise the index for each river. Because these indices span the period 1965 - 1995, they were grouped and analysed with the trawl survey indices.

Loess

Each of the indices used in the study was smoothed by the loess (locally weighted scatterplot smoother) method (Cleveland 1979). Loess calculates a new smoothed y' -value for each (x, y) pair, and plots the (x, y') pairs with a connecting curve. The loess smooth reveals the long-term trend in data. A parameter was set between zero and one to determine the degree of flexibility of the smooth; a medium flexibility was chosen ($k = 0.5$).

At the $k = 0.5$ level, loess uses 50% (or whatever $k\%$ is chosen) of the data to calculate each new smoothed value. The data that were used were weighted by

$$w = \left[1 - \left(\frac{D}{\max D} \right)^3 \right]^3$$

where D was the distance along the x -axis from the selected point to each point in the weighting group. Weighted linear regression was then performed on the selected points. The y -value of the regression line corresponding to the x -value of the original point becomes the new y' . To reduce the influence of outliers, the process was repeated twice, this time using

$$w = \left[1 - \left(\frac{r}{6 \bullet \text{median } |r|} \right)^2 \right]^2$$

where r is the value of each respective residual from the previous step.

Principal component analysis

The major thrust of this project was to identify possible coherent fluctuations in the magnitude of juvenile populations of finfish, bluecrab and oyster. Principal component analysis (PCA) calculates the ranked eigenvectors (eigenvector bases and eigenvalues) of the square matrix of correlations or covariances of the time series. The correlation method was used here. The method summarizes a multivariate dataset using the minimum number components, by finding a quantitative association between the variables, and partitions the variance of the data set.

The data were linearly transformed from the original variables $X_j \rightarrow \Gamma_j$, the eigenvectors. The Γ_j have variance λ_j , the respective eigenvalues ranked from largest to smallest. The relative magnitudes of the λ_j describe the degree to which the data are coherent. If the first few λ_i are "large" and $\lambda_{i+1} \dots \lambda_n$ are relatively small, then the data are very coherent. If the variance is more or less evenly distributed among the λ_i , then the data are uncorrelated.

Correlations were performed on the first PC's of each index within the two sets of loess smooths for trawl and beach seine surveys, and between surveys.

Water temperature

Water temperature is perhaps the most often cited physical causal factor in the regulation of Chesapeake Bay populations (*e.g.*, Ford 1996, Shaih 1994, Cargo 1990, Coutant and Benson 1990, Van Engel 1987, Norcross 1983, Cook 1981). Temperature controls the metabolic rates of cold-blooded animals. An expression of this control is Van't Hoff's equation, which indicates that change in metabolic rate (given as Q_{10}) in poikilotherms will increase or decrease by a factor of two to three for each 10°C increase or decrease in ambient temperature, respectively. A Q_{10} value outside of the range of two to three indicates some other process is in control (Vernberg and Vernberg 1972). The animals considered in this study are all cold-blooded, so water temperature was selected for comparison with

trends in overall population abundance, as identified through PCA.

Indices of seasonal mean water temperature were chosen as the variables. The VIMS pier temperatures were chosen for index construction, as they are long-term data that span the periods of interest with relatively few, short-term interruptions (usually due to equipment failures (Gary Anderson, VIMS, pers. comm.). Although frequency of sampling has increased over the years (2/d to 240/d), seasonal means can be constructed over the period of record. The VIMS pier temperatures (York River) were considered to be an adequate surrogate for water temperatures on the James and Rappahannock rivers (*e.g.*, Austin *et al.* 1995).

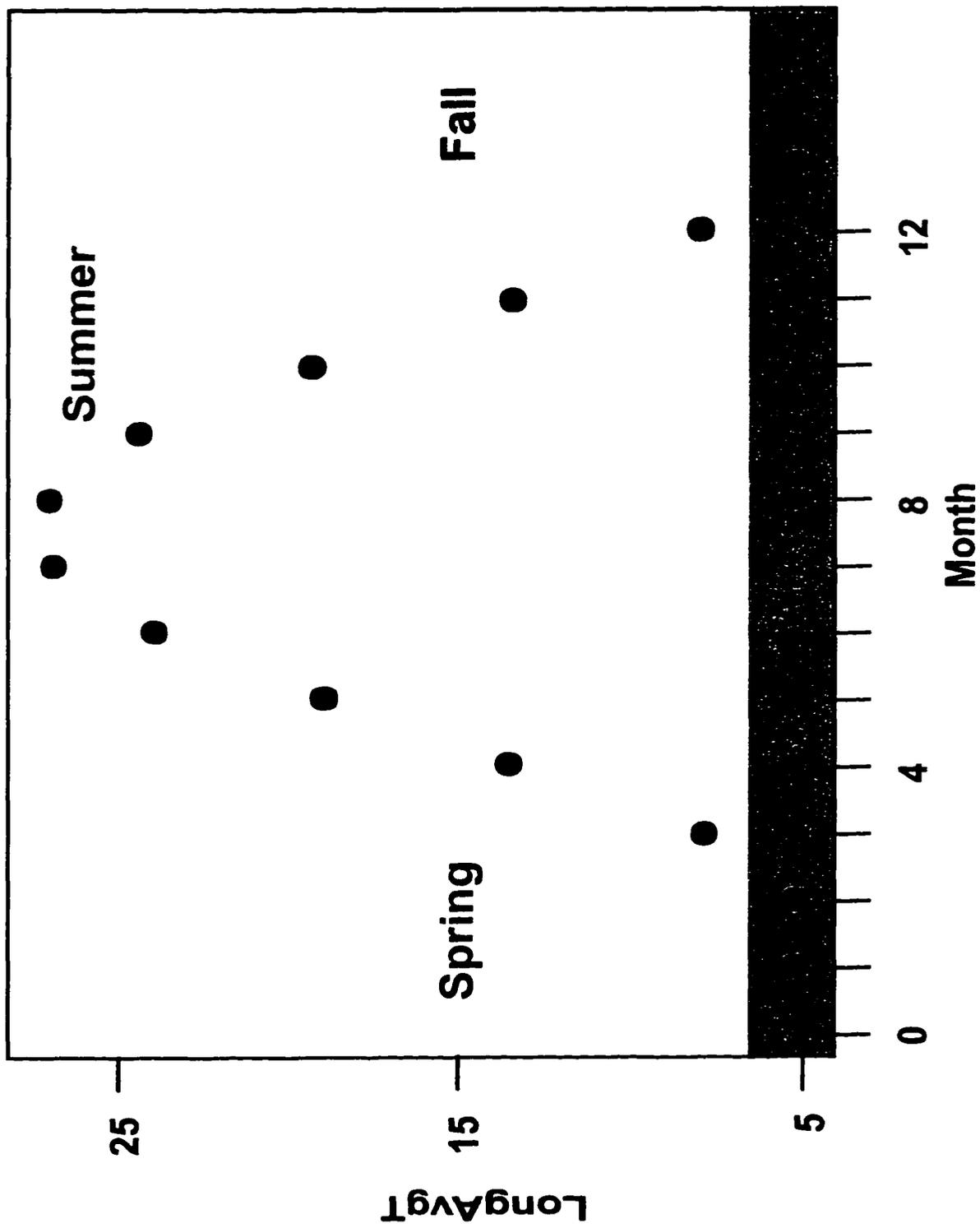
To decide which months to include in the index for each season, long-term (1965 - 1995) monthly means (Figure 2.1), and the differences (ΔT) between the monthly means were calculated (Table 2.7). In Figure 2.1 the months January and February appear twice, at the beginning and end, for reasons of symmetry.

Based on the decision above, indices of seasonal mean water temperature for the period 1965 - 1995 were constructed. The temperature indices were smoothed by loess at the $k = 0.5$ and $k = 0.4$ levels.

Scatterplots were constructed of winter water temperature loess vs. PC#1. Based on the appearance of these, cross correlations were performed on winter water temperature loess vs. trawl survey PC#1. Another set of cross correlations were performed on a subset of these data (1969 - 1982).

As an aid in interpreting each species contribution to the smoothed indices PCA and the relationship with winter water temperature, correlations were performed between each smoothed biological index and the smoothed winter temperature index.

Figure 2.1. Long-term (1965 - 1995) monthly mean water temperatures, measured at the VIMS pier. The months are in chronological order beginning with January, and January and February are repeated at the end for reasons of symmetry.



Month	\bar{T}	ΔT
1	5.2	
2	5.2	0
3	7.9	2.7
4	13.6	5.7
5	19.0	5.4
6	24.0	5.0
7	27.1	3.1
8	27.2	0.1
9	24.5	2.7
10	19.3	5.2
11	13.5	6.8
12	8.0	5.5
1	5.2	2.8

Table 2.7. Long-term (1965 - 1995) mean water temperature by month, as measured off the VIMS pier, and the difference between each month and the previous month (ΔT).

Results

Indices of 16 species in the trawl survey group and 17 species in the beach seine group were constructed for each of the three Virginia rivers. Each index was smoothed by loess (Figures 3.1a, b, c - 3.33a, b, c).

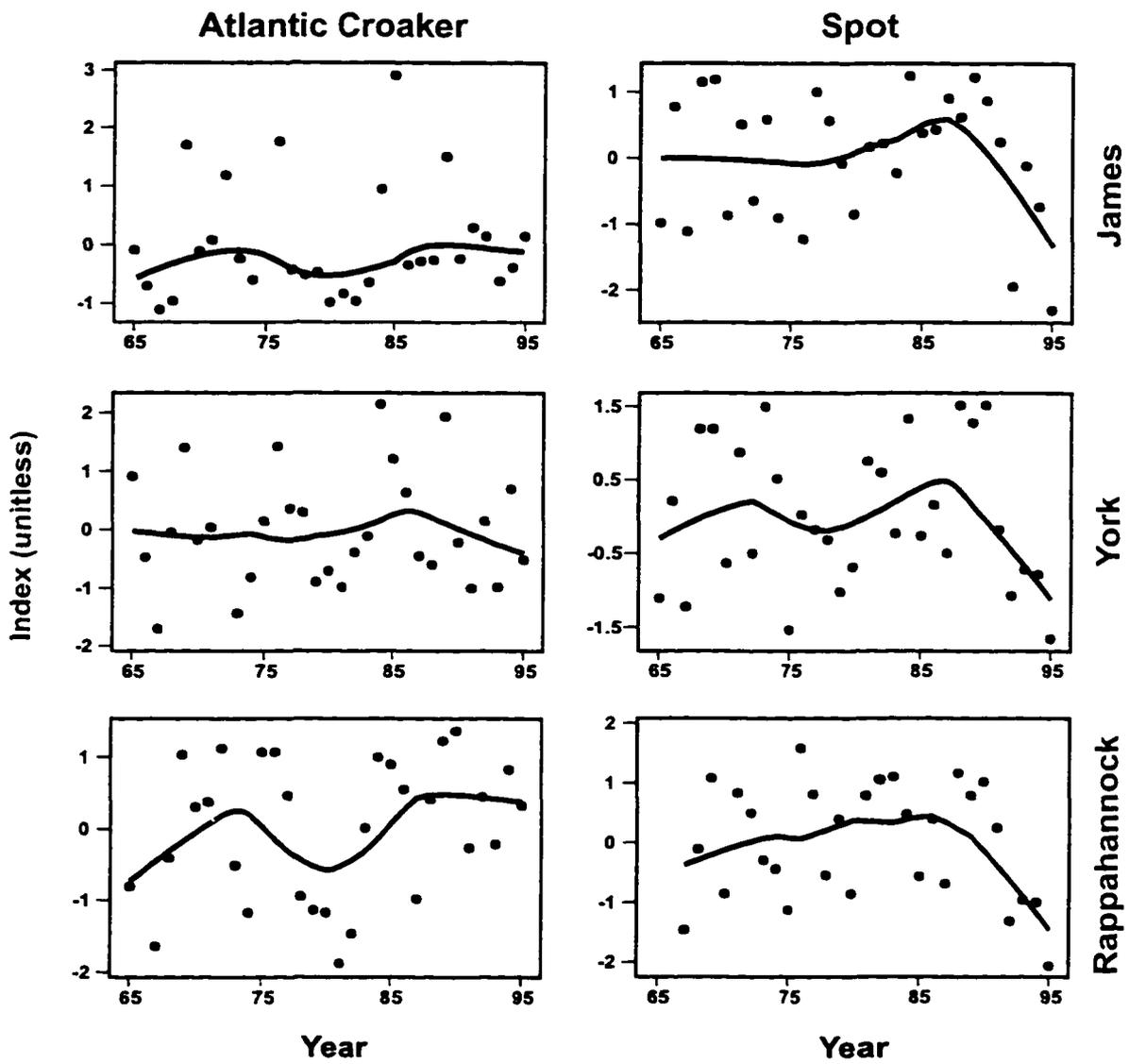
Principal component analysis

The 18 groups of data, consisting of indices, residuals, and loess trends for each of three rivers, from two survey data sets (oyster indices were grouped with trawl survey indices) were partitioned by PCA. The eigenvalues, proportion of variation for each, and cumulative proportions of variation were given in Tables 3.1 - 3.6. The coefficients by which the loess smooths on the indices were transformed into new variates are given graphically in Figures 3.34 - 3.35. The first three scores (the transformed variables) for the loess smoothed indices contain almost all of the variance (Figure 3.36), of which the first PC (PC#1) is used in these analyses.

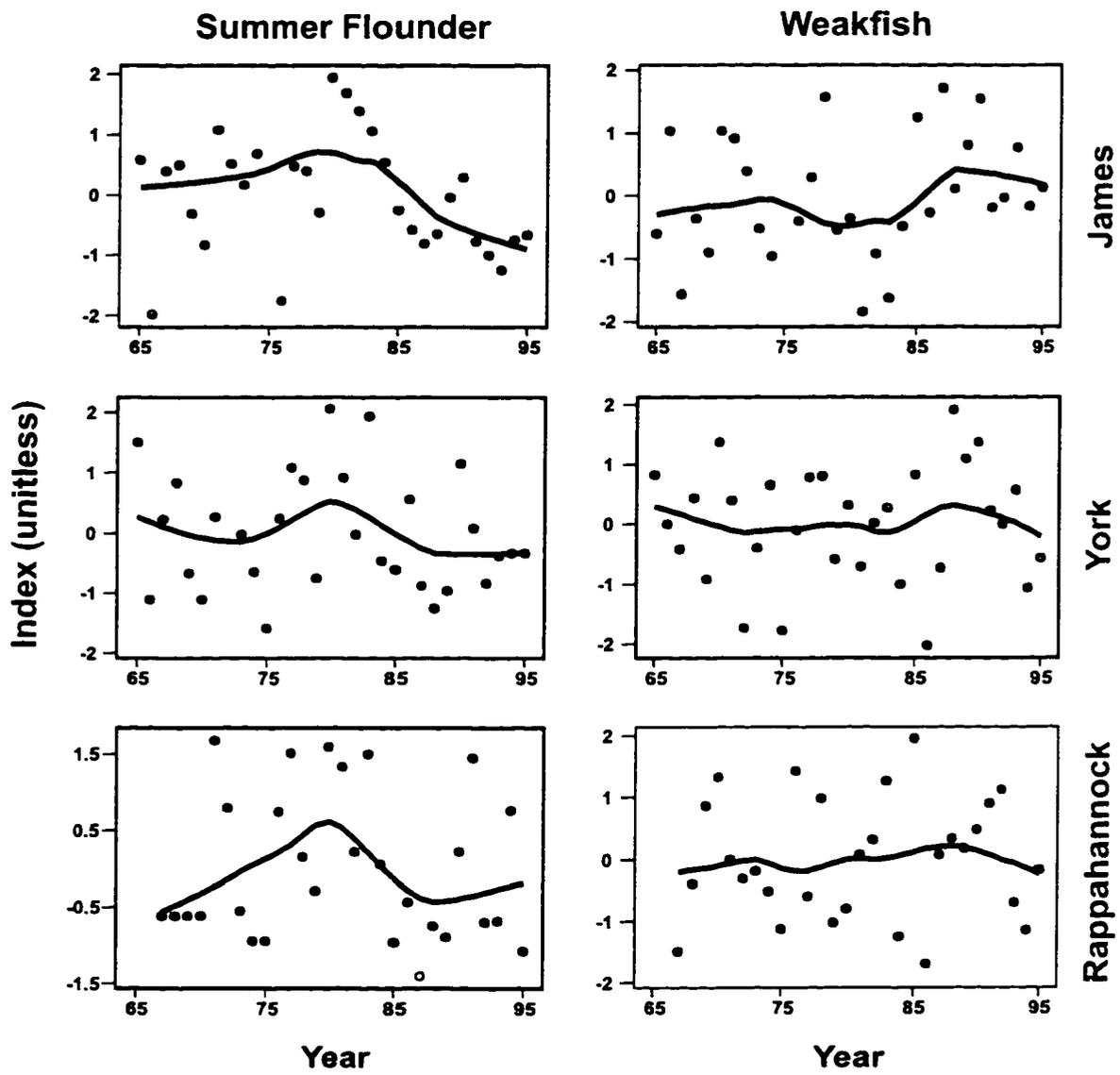
Given N variates, a principal component (PC) is considered significant if N^{-1} of the variance is contained in that PC. Thus, for the 16 trawl survey indices, any PC with variance ≥ 0.0625 of total variance is significant (for beach seine survey $N = 17$, with significance level ≥ 0.0588). Alternately, with the correlation method of PCA used here, one can consider the eigenvalues themselves. If the eigenvalue is ≥ 1 , the PC is significant.

Weak but significant relationships were found in the unsmoothed indices (Table 3.1) In the trawl survey indices less than half (six or seven of 16) of the PC's were significant for any river, explaining up to 84% of variance. The analysis on the beach seine indices indicated even stronger relationships (Table 3.2), with about one-third of the PC significant, accounting for 82 to 86% of total variance. PC#1 accounted for about one-fifth of variance in the trawl survey indices, and one third in the beach seine indices. PCA on the residuals were similar in magnitude (Table 3.3, 3.4).

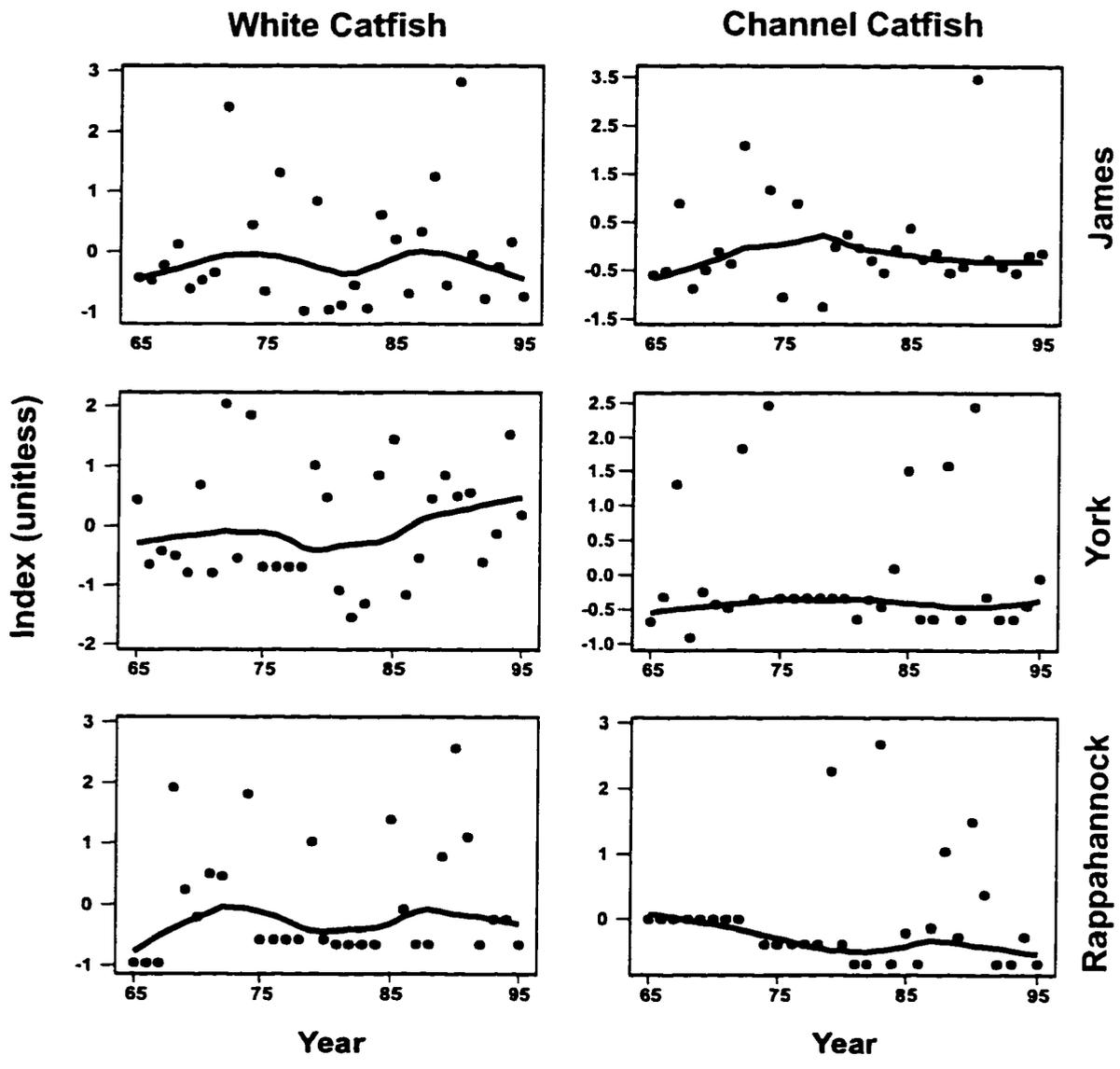
Figures 3.1, 3.2. Juvenile indices for Atlantic croaker and spot in the James, York and Rappahannock rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.



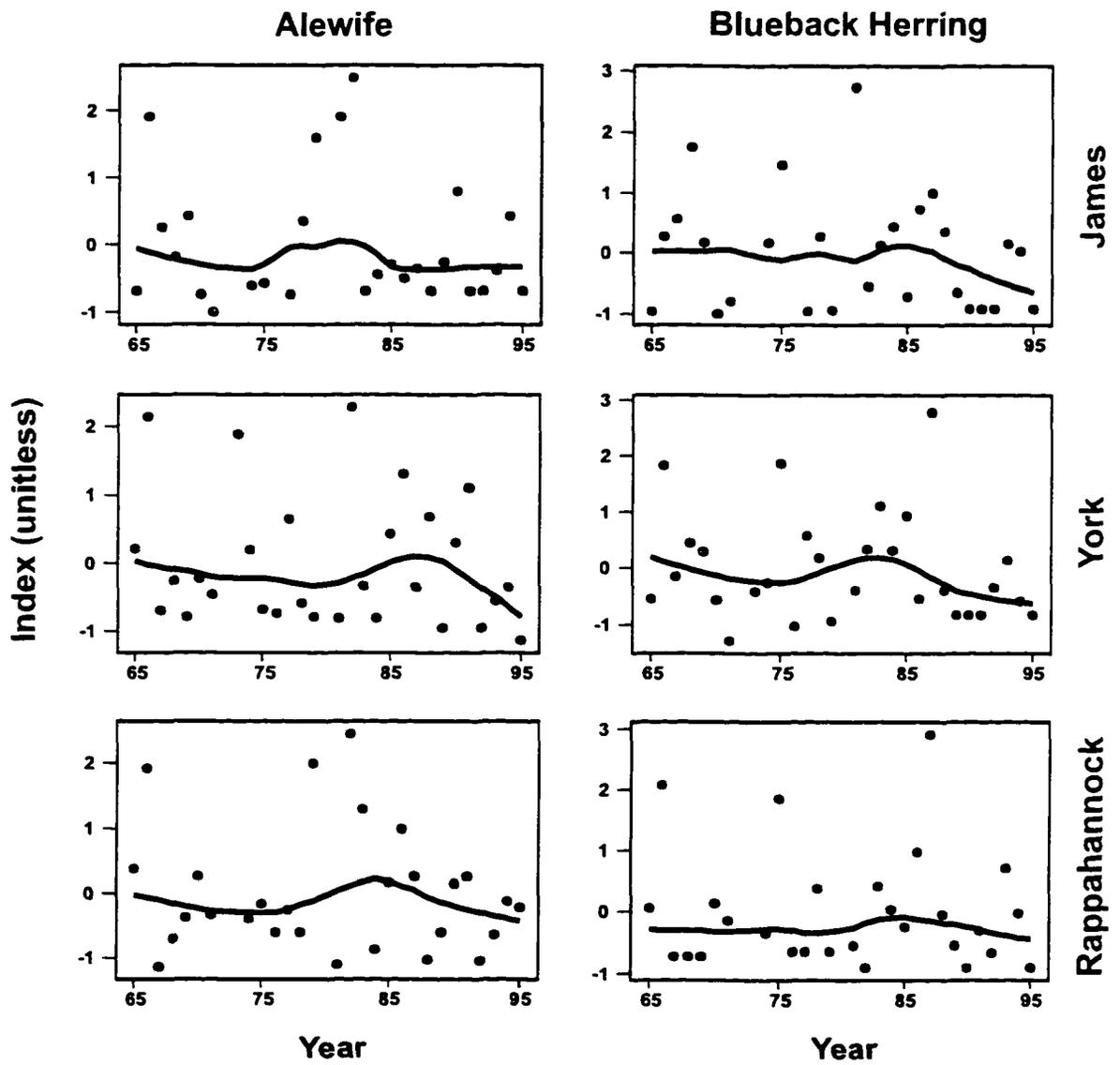
Figures 3.3, 3.4. Juvenile indices for summer flounder and weakfish in the James, York and Rappahannock rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.



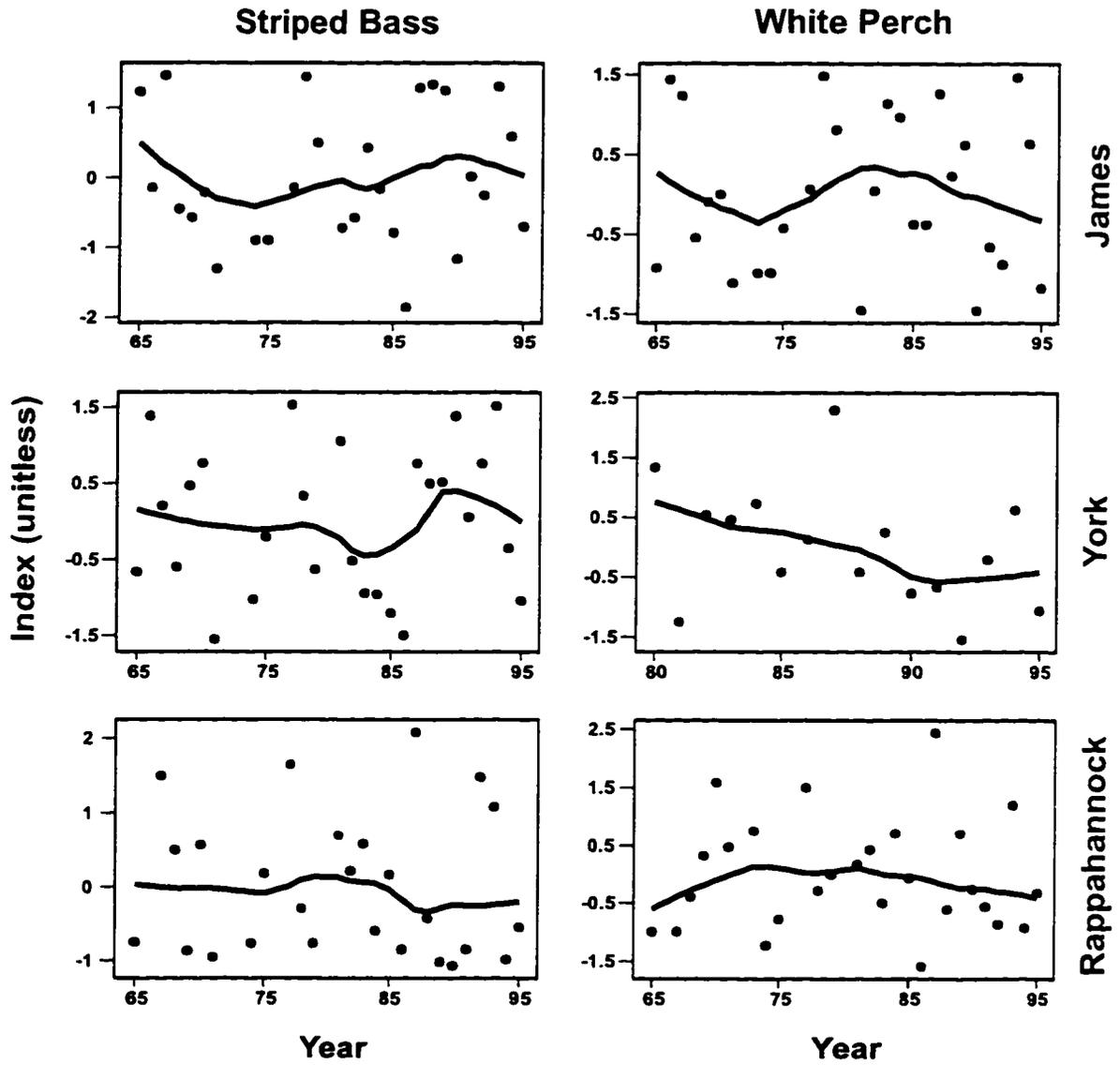
Figures 3.5, 3.6. Juvenile indices for white catfish and channel catfish in the James, York and Rappahannock rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.



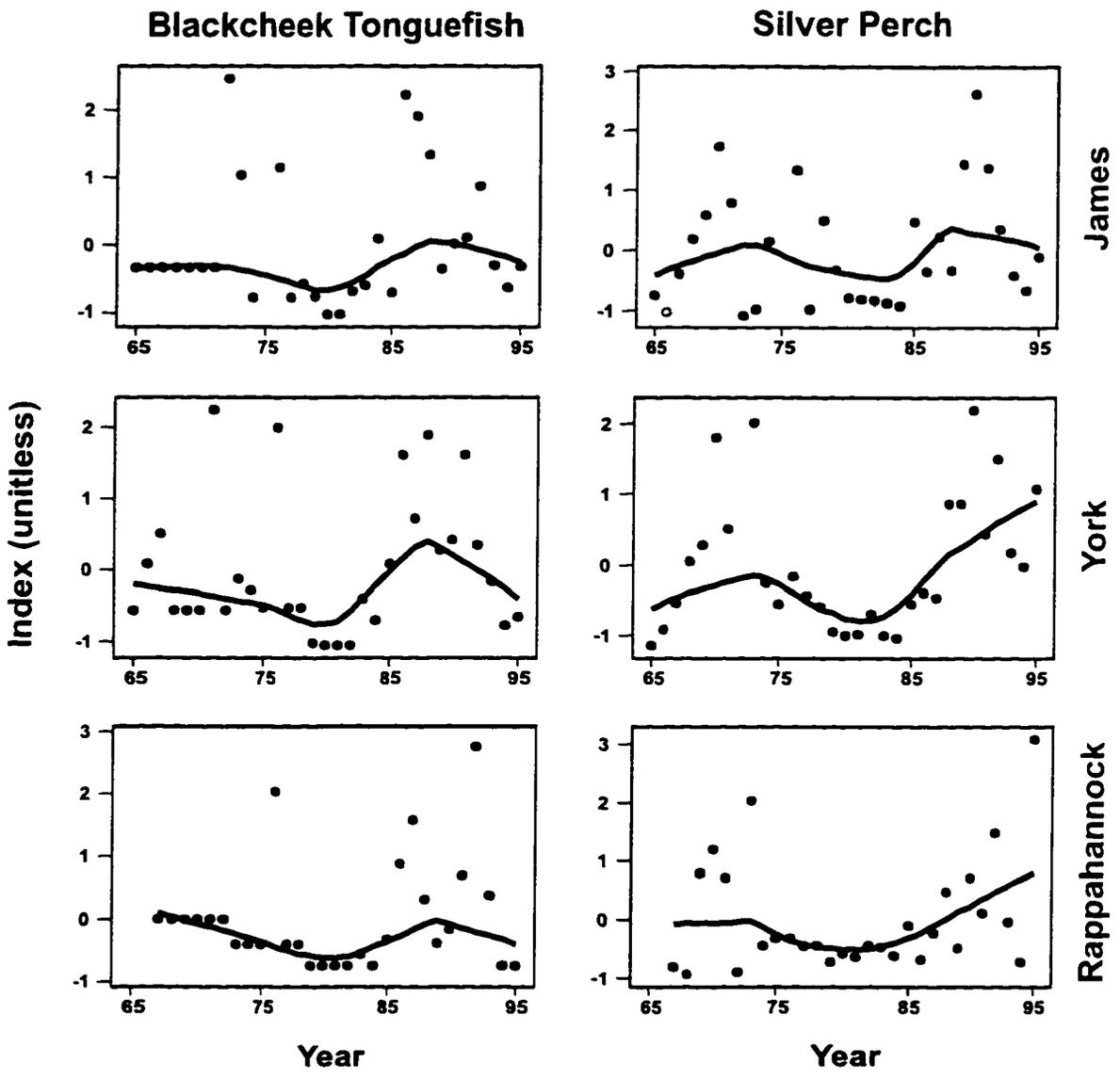
Figures 3.7, 3.8. Juvenile indices for alewife and blueback herring in the James, York and Rappahannock rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.



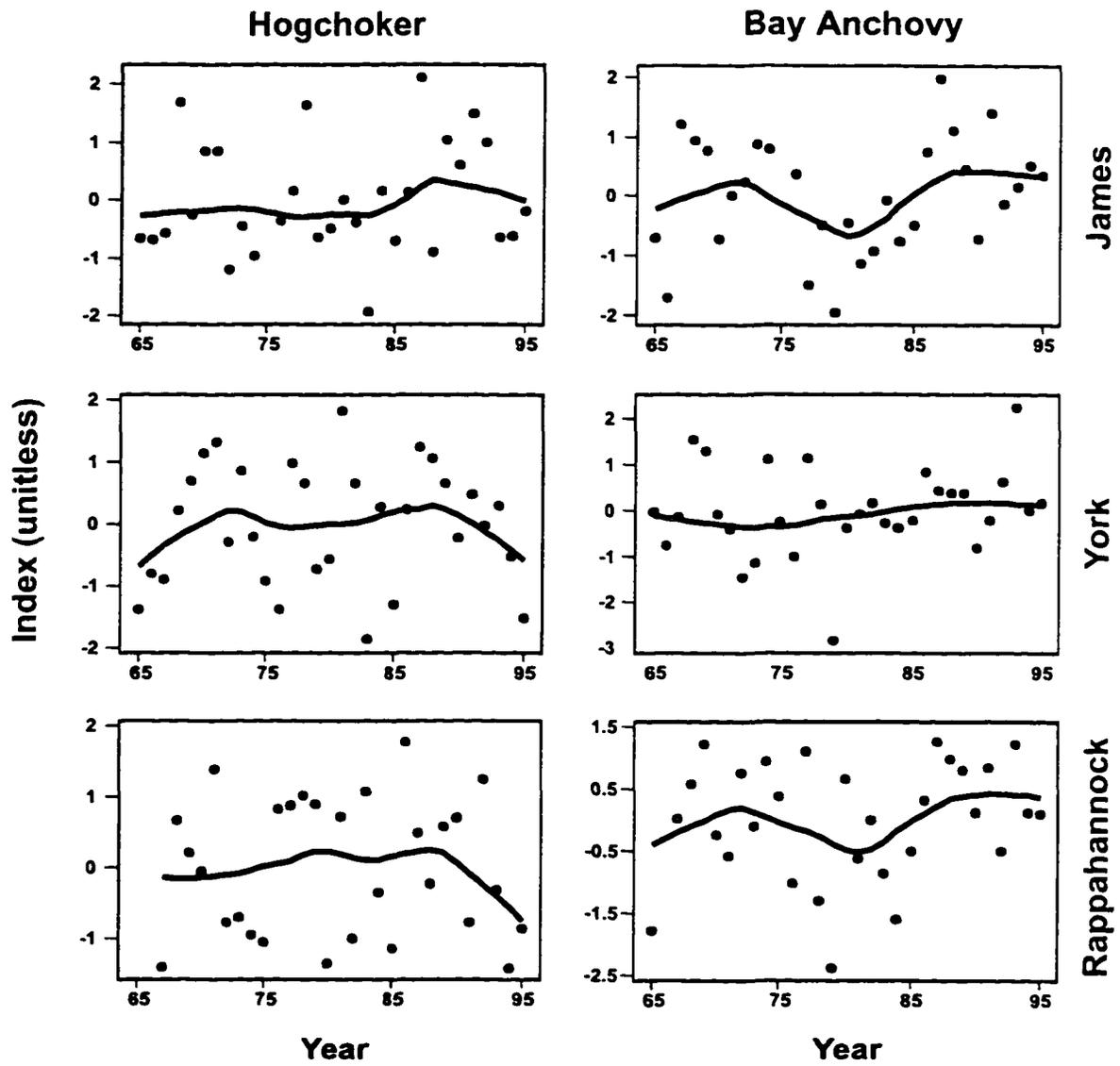
Figures 3.9, 3.10. Juvenile indices for striped bass and white perch in the James, York and Rappahannock rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.



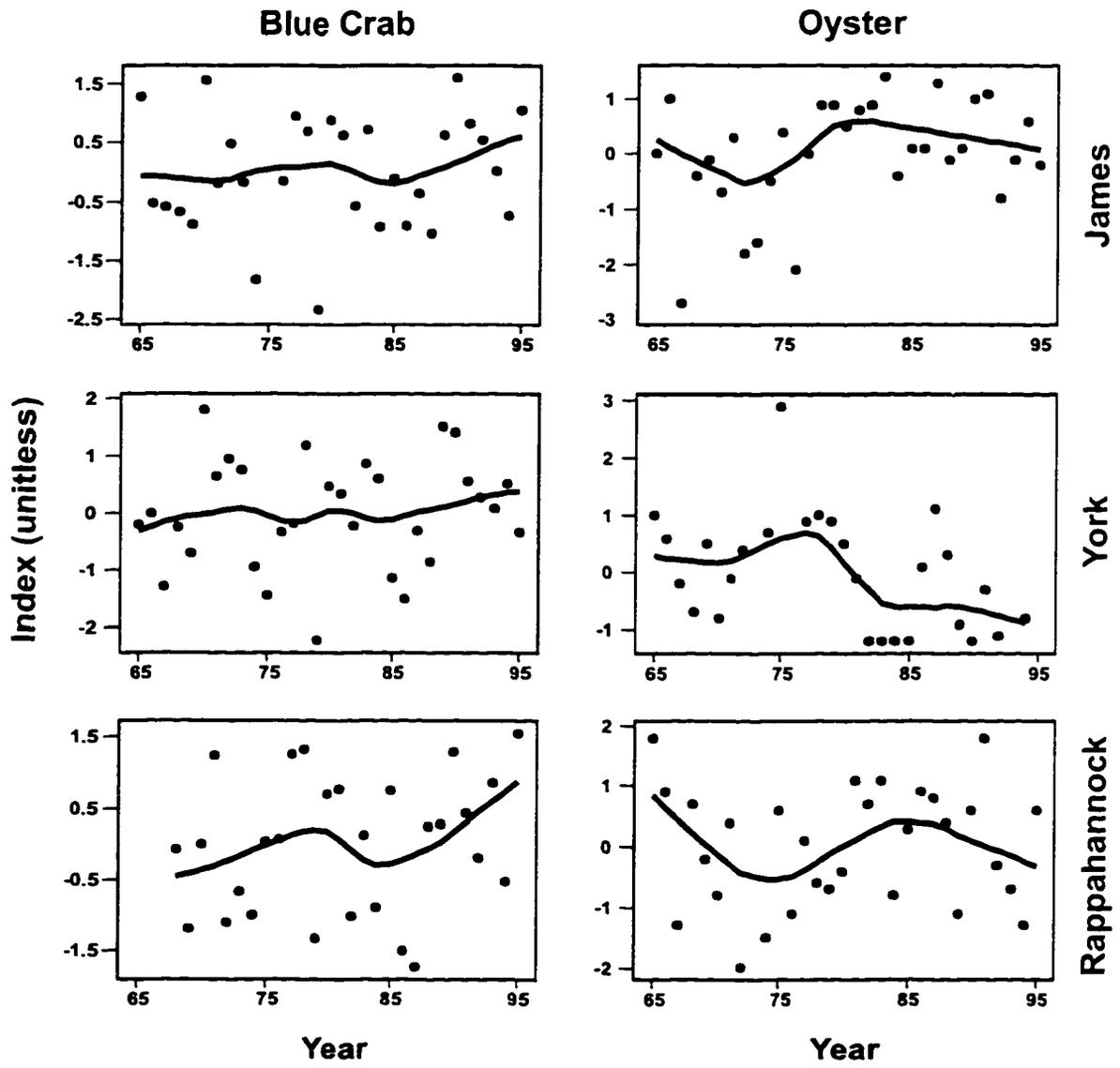
Figures 3.11, 3.12. Juvenile indices for blackcheek tonguefish and silver tonguefish in the James, York and Rappahannock rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.



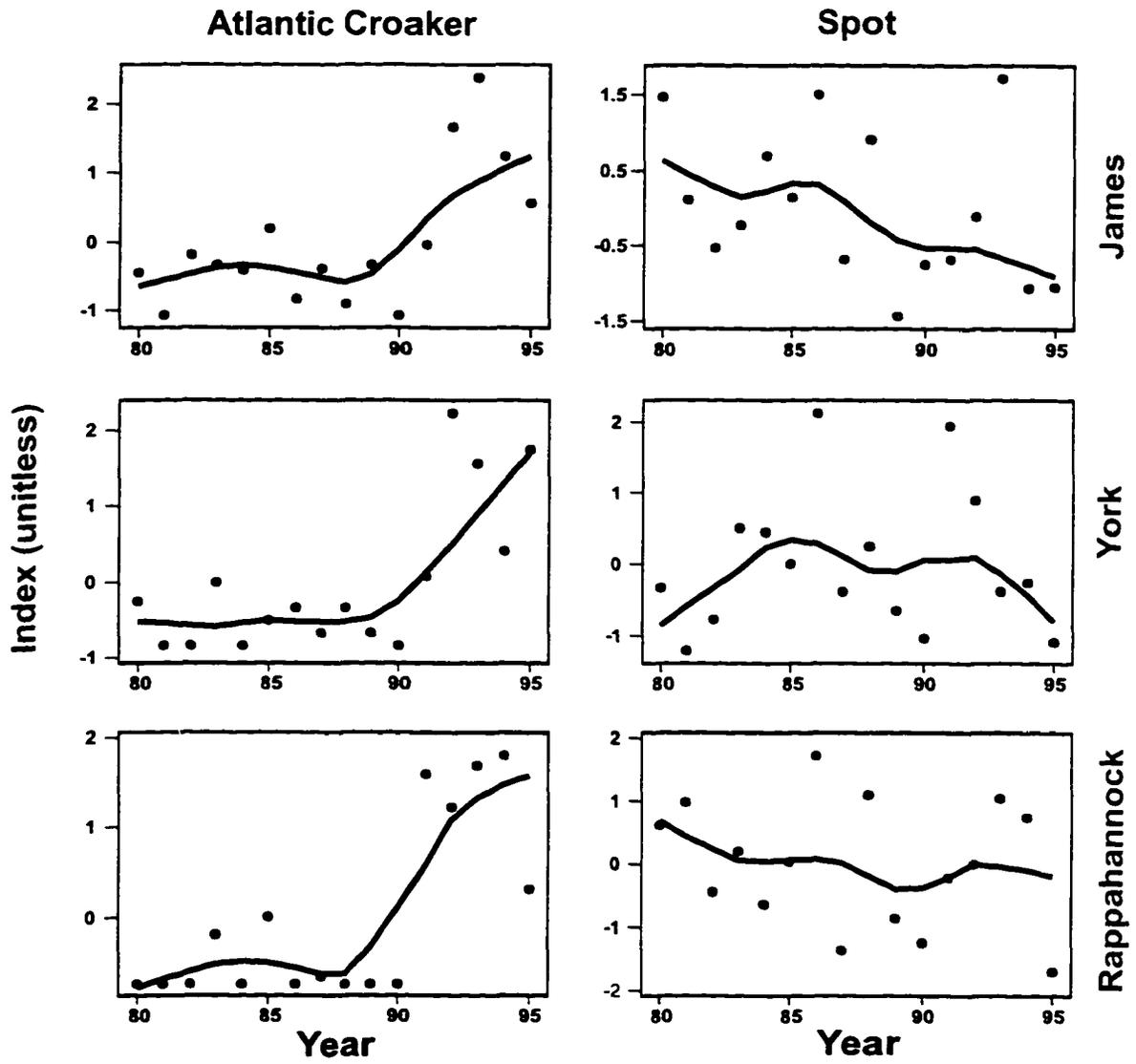
Figures 3.13, 3.14. Juvenile indices for hogchoker and bay anchovy in the James, York and Rappahannock rivers, from data collected by the VIMS trawl survey. Each index is smoothed by loess.



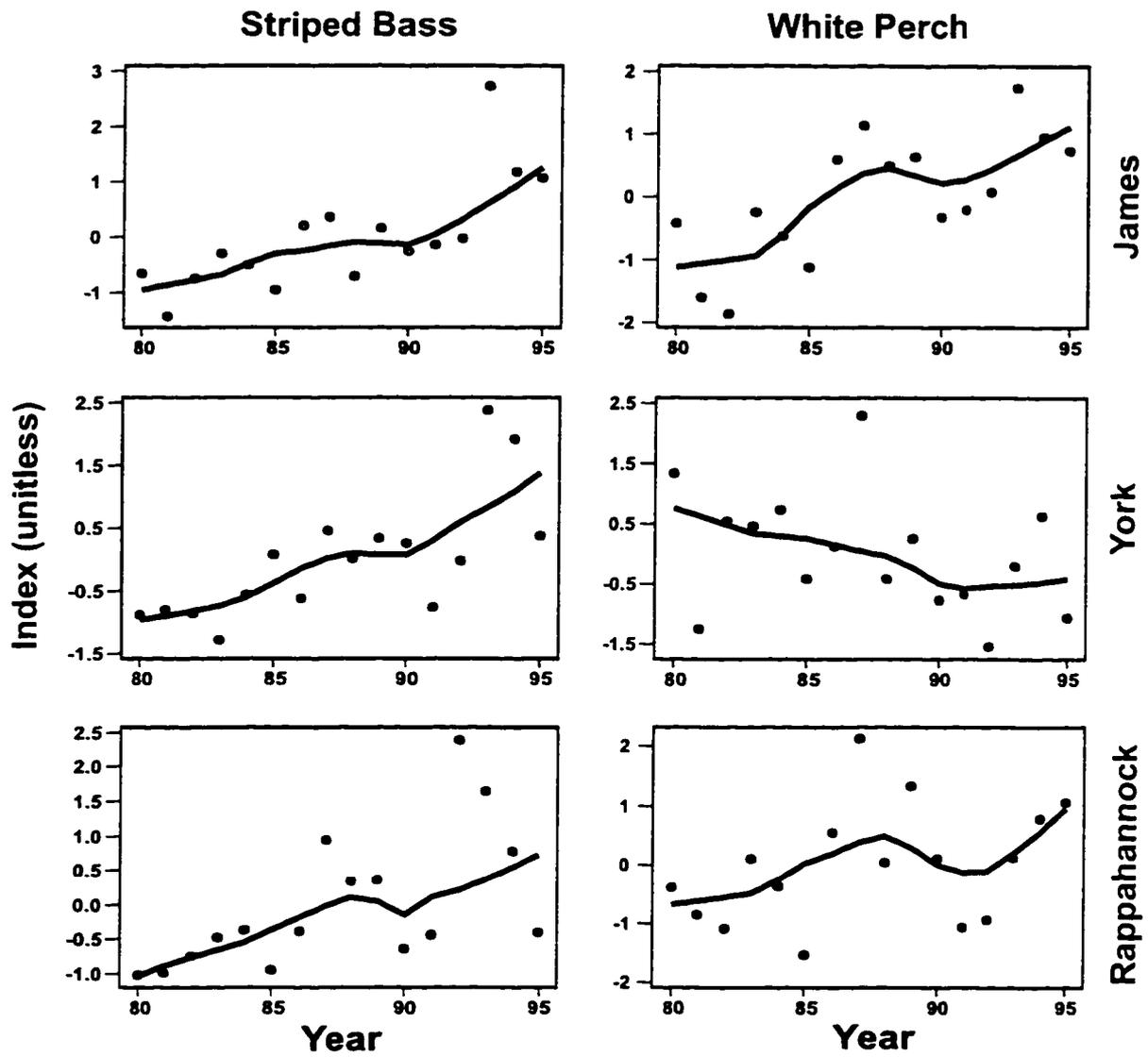
Figures 3.15, 3.16. Juvenile indices for bluecrab from data collected by the VIMS trawl survey, and oyster from data collected by the VIMS fall dredge survey, in the James, York and Rappahannock rivers. Each index is smoothed by loess.



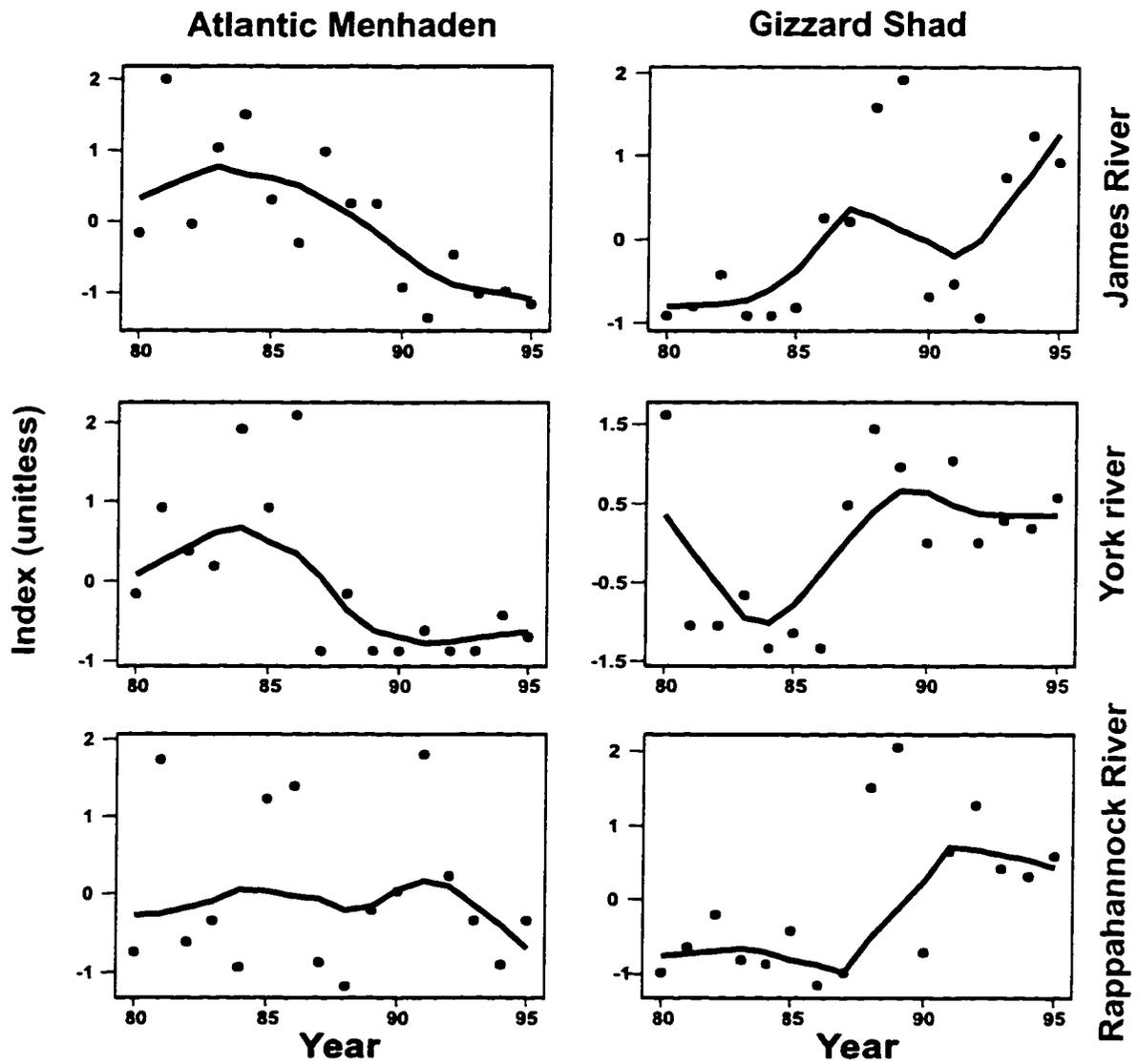
Figures 3.17, 3.18. Juvenile indices for Atlantic croaker and spot in the James, York and Rappahannock rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.



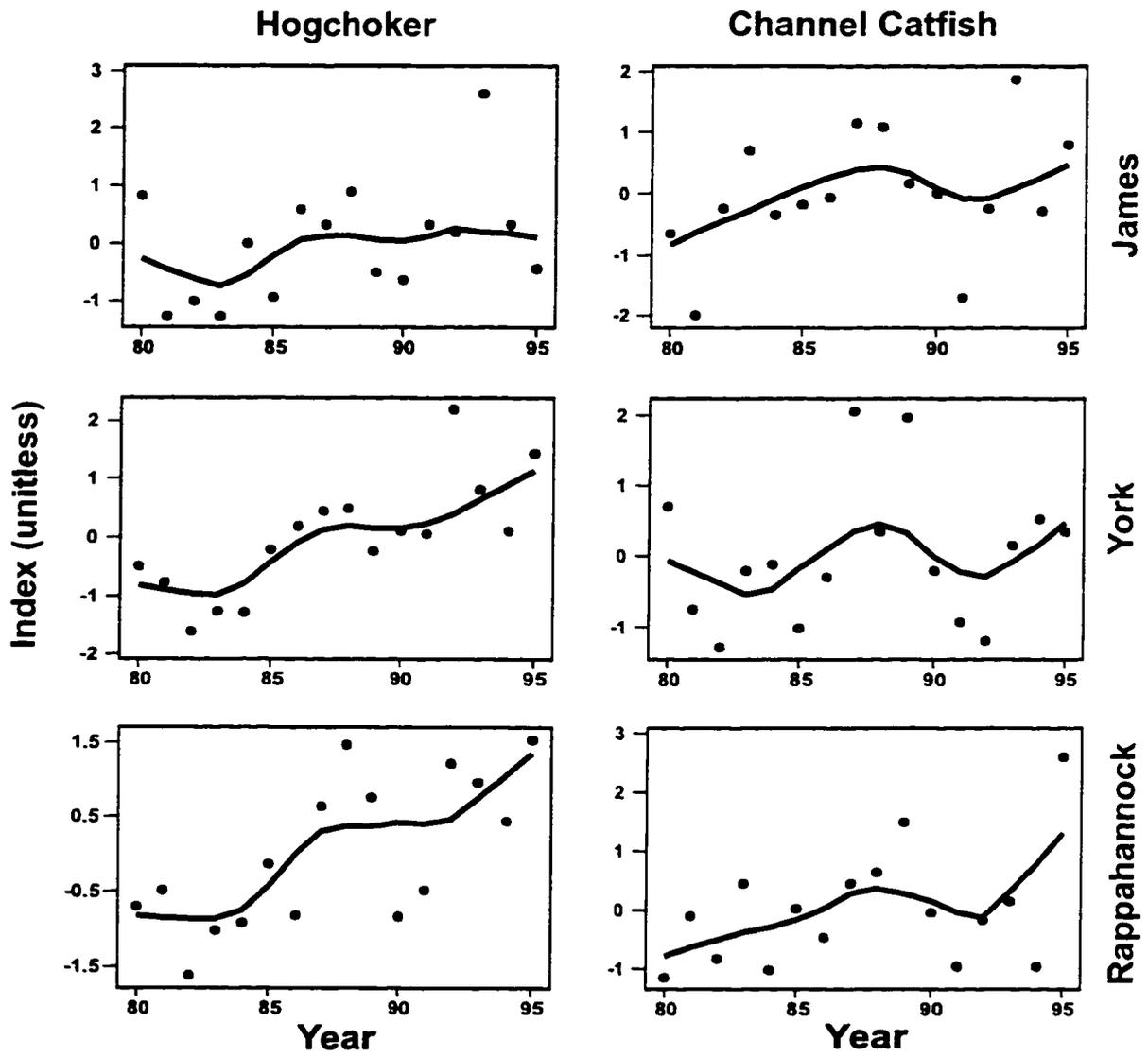
Figures 3.19, 3.20. Juvenile indices for striped bass and white perch in the James, York and Rappahannock rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.



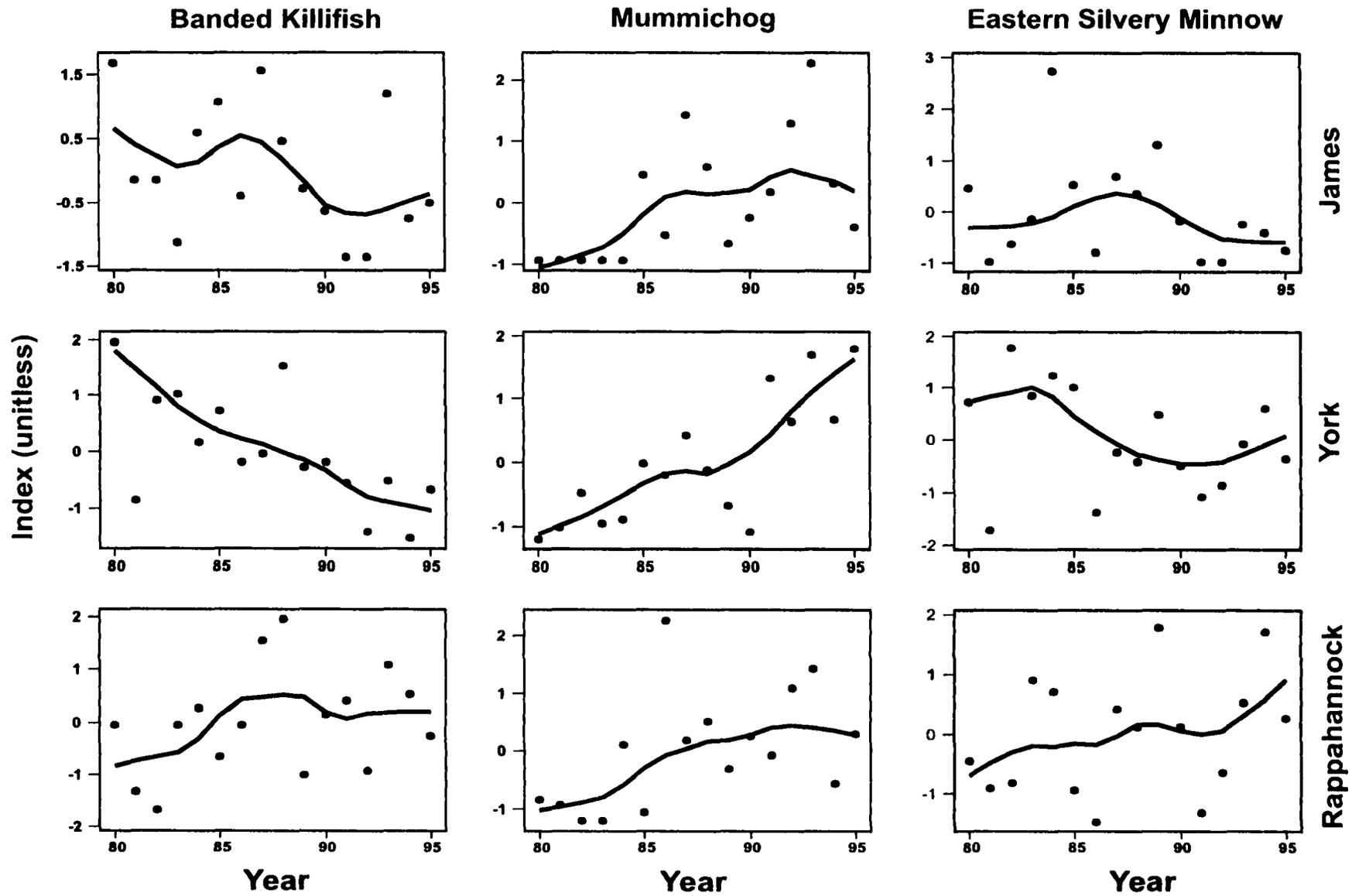
Figures 3.21, 3.22. Juvenile indices for Atlantic menhaden and gizzard shad in the James, York and Rappahannock rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.



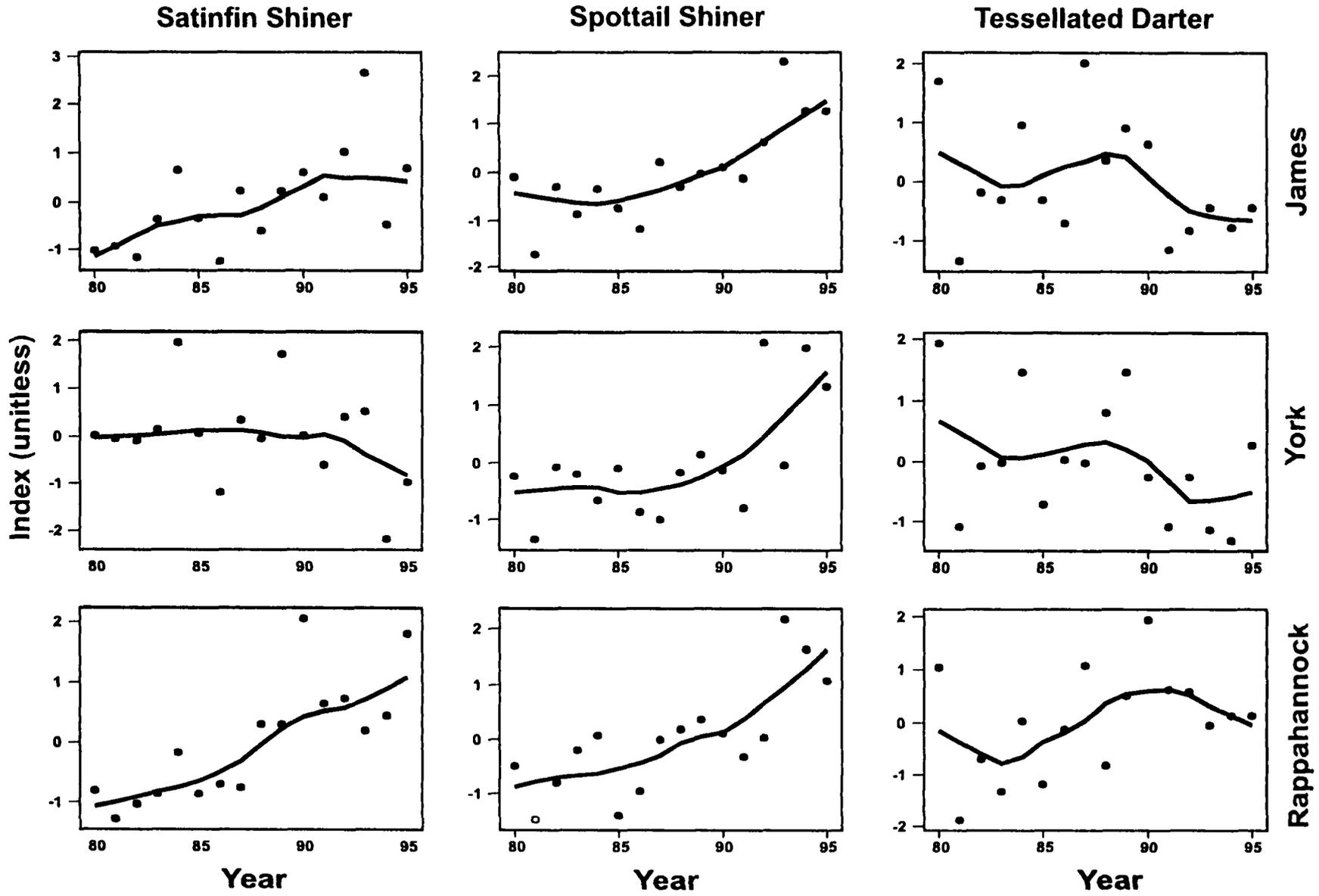
Figures 3.23, 3.24. Juvenile indices for hogchoker and channel catfish in the James, York and Rappahannock rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.



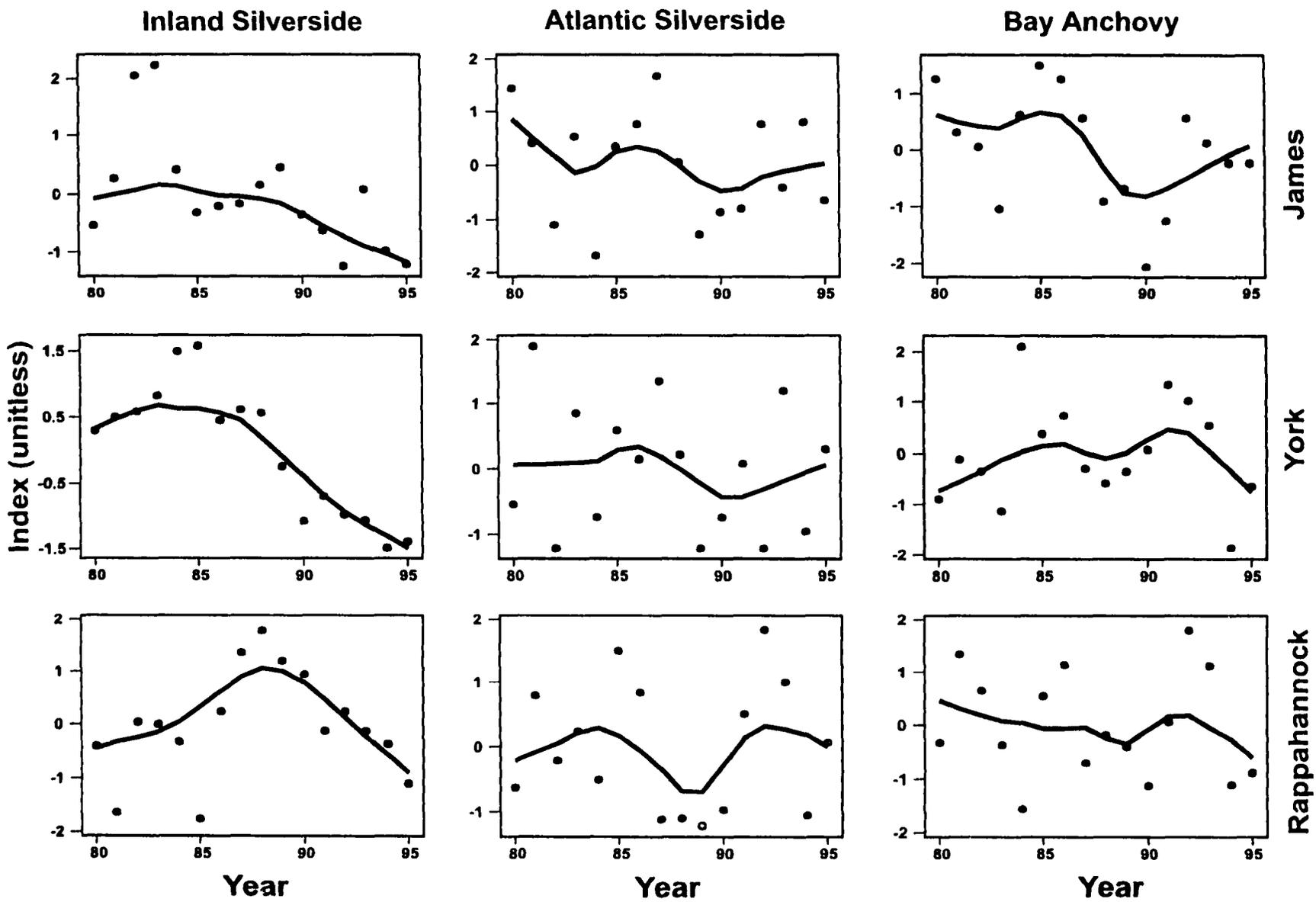
Figures 3.25, 3.26, 3.27. Juvenile indices for banded killifish, mummichog and eastern silvery minnow in the James, York and Rappahannock rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.



Figures 3.28, 3.29, 3.30. Juvenile indices for satinfish shiner, spottail shiner and tessellated darter in the James, York and Rappahannock rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.



Figures 3.31, 3.32, 3.33. Juvenile indices for inland silverside, Atlantic silverside and bay anchovy in the James, York and Rappahannock rivers, from data collected by the VIMS summer beach seine survey. Each index is smoothed by loess.



Eigenvalue	3.2784	2.5426	2.0875	1.7762	1.5431
Proportion	0.205	0.159	0.130	0.111	0.096
Cumulative	0.205	0.364	0.494	0.605	0.702

Eigenvalue	1.1675	1.0095
Proportion	0.073	0.063
Cumulative	0.775	0.838

Table 3.1a. James River, 25 cases used, 6 cases contained missing values.

Eigenvalue	3.6149	2.5430	1.9541	1.6054	1.3945
Proportion	0.226	0.159	0.122	0.100	0.087
Cumulative	0.226	0.385	0.507	0.607	0.694

Eigenvalue	1.1165
Proportion	0.070
Cumulative	0.764

Table 3.1b York River, 23 cases used, 8 cases contained missing values.

Eigenvalue	2.9755	2.3331	2.0913	1.4696	1.2858
Proportion	0.186	0.146	0.131	0.092	0.080
Cumulative	0.186	0.332	0.462	0.554	0.635

Eigenvalue	1.1367	1.0750
Proportion	0.071	0.067
Cumulative	0.706	0.773

Table 3.1c Rappahannock River 24 cases used, 7 cases contained missing values.

Table 3.1. Principal component analyses on the 16 trawl survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/16 of total (0.0625) are considered insignificant and are not presented.

Eigenvalue	6.2018	3.1331	2.2068	1.2879	1.0386
Proportion	0.365	0.184	0.130	0.076	0.061
Cumulative	0.365	0.549	0.679	0.755	0.816

Table 3.2a. James River,

Eigenvalue	5.6620	3.1867	1.8139	1.6623	1.2124
Proportion	0.333	0.187	0.107	0.098	0.071
Cumulative	0.333	0.521	0.627	0.725	0.796

Eigenvalue	1.1004
Proportion	0.065
Cumulative	0.861

Table 3.2b. York River.

Eigenvalue	5.8011	3.3383	1.8205	1.5283	1.4144
Proportion	0.341	0.196	0.107	0.090	0.083
Cumulative	0.341	0.538	0.645	0.735	0.818

Table 3.2c. Rappahannock River

Table 3.2. Principal component analyses on the 17 beach seine survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/17 of total (0.0588) are considered insignificant and are not presented.

Eigenvalue	3.3922	2.7725	2.0321	1.5575	1.4898
Proportion	0.212	0.173	0.127	0.097	0.093
Cumulative	0.212	0.385	0.512	0.610	0.703

Eigenvalue	1.2925
Proportion	0.081
Cumulative	0.784

Table 3.3a. James River, raw, 25 cases used, 6 cases contained missing values.

Eigenvalue	3.3137	2.3288	1.9468	1.7310
Proportion	0.207	0.146	0.122	0.108
Cumulative	0.207	0.353	0.474	0.583

Eigenvalue	1.1990	1.1280
Proportion	0.075	0.071
Cumulative	0.657	0.728

Table 3.3b. York River, raw, 25 cases used, 6 cases contained missing values.

Eigenvalue	3.2503	2.3821	1.7616	1.6122	1.3434
Proportion	0.203	0.149	0.110	0.101	0.084
Cumulative	0.203	0.352	0.462	0.563	0.647

Eigenvalue	1.1328	1.0184
Proportion	0.071	0.064
Cumulative	0.718	0.781

Table 3.3c. Rappahannock River, 24 cases used, 7 cases contained missing values.

Table 3.3. Principal component analyses on residuals of the 16 loess smoothed trawl survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/16 of total (0.0625) are considered insignificant and are not presented.

Eigenvalue	6.4416	2.3909	1.9627	1.3410	1.261
Proportion	0.379	0.141	0.115	0.079	0.074
Cumulative	0.379	0.520	0.635	0.714	0.788

Eigenvalue	1.1328
Proportion	0.067
Cumulative	0.855

Table 3.4a. James River.

Eigenvalue	3.9656	2.6926	2.3574	2.0262	1.6964
Proportion	0.233	0.158	0.139	0.119	0.100
Cumulative	0.233	0.392	0.530	0.650	0.749

Eigenvalue	1.3583	0.9948
Proportion	0.080	0.059
Cumulative	0.829	0.888

Table 3.4b. York River.

Eigenvalue	5.3151	3.1408	2.5122	1.7150	1.0332
Proportion	0.313	0.185	0.148	0.101	0.061
Cumulative	0.313	0.497	0.645	0.746	0.807

Table 3.4c. Rappahannock River.

Table 3.4. Principal component analyses on residuals of the 17 loess smoothed beach seine survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/17 of total (0.0588) are considered insignificant and are not presented.

Eigenvalue	8.7622	3.1327	2.1894	1.5912
Proportion	0.548	0.196	0.137	0.099
Cumulative	0.548	0.743	0.880	0.980

Table 3.5a. James River, 25 cases used, 6 cases contained missing values.

Eigenvalue	6.9573	4.7253	2.6328	1.0168
Proportion	0.435	0.295	0.165	0.064
Cumulative	0.435	0.730	0.895	0.958

Table 3.5b. York River, 25 cases used, 6 cases contained missing values.

Eigenvalue	7.6473	4.3673	2.1683	1.3806
Proportion	0.478	0.273	0.136	0.086
Cumulative	0.478	0.751	0.886	0.973

Table 3.5c. Rappahannock River, 24 cases used, 7 cases contained missing values.

Table 3.5. Principal component analyses on the 16 loess smoothed trawl survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/16 of total (0.0625) are considered insignificant and are not presented.

Eigenvalue	11.911	2.539	1.579
Proportion	0.701	0.149	0.093
Cumulative	0.701	0.850	0.943

Table 3.6a. James River.

Eigenvalue	10.147	3.080	1.747	1.250
Proportion	0.597	0.181	0.103	0.074
Cumulative	0.597	0.778	0.881	0.954

Table 3.6b. York River.

Eigenvalue	10.817	3.146	1.824
Proportion	0.636	0.185	0.107
Cumulative	0.636	0.821	0.929

Table 3.6c. Rappahannock River.

Table 3.6. Principal component analyses on the 17 loess smoothed beach seine survey indices, Eigenanalysis of the Correlation Matrix, given in descending order of the eigenvalues. Components containing a proportion of variance less than 1/17 of total (0.0588) are considered insignificant and are not presented.

Figure 3.34. Coefficients of principal component analyses for loess-smoothed indices from the trawl survey data. Species are identified by species codes in Table 2.1.

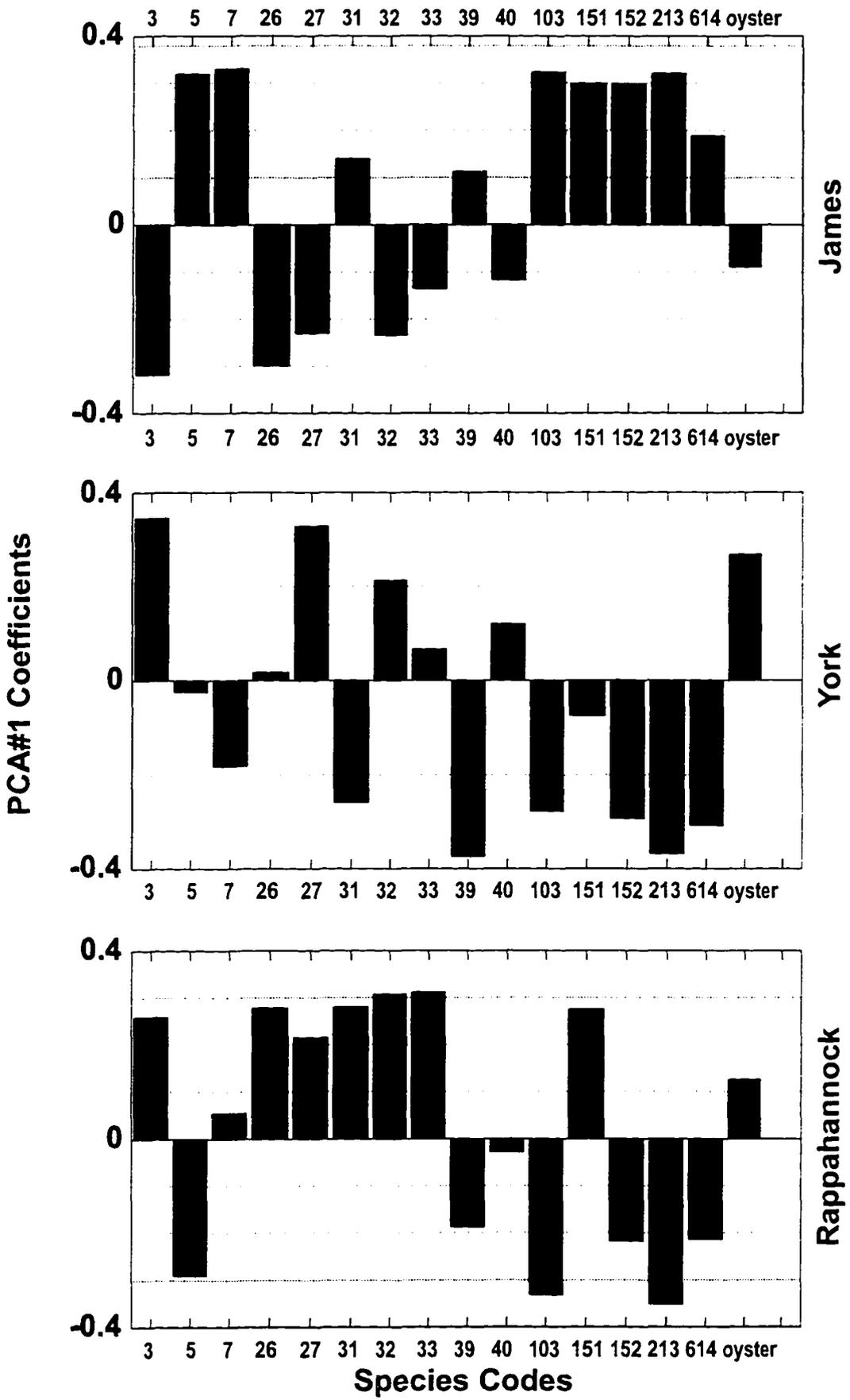


Figure 3.35. Coefficients of principal component analyses for loess-smoothed indices from the summer beach seine survey data. Species are identified by species codes in Table 2.1.

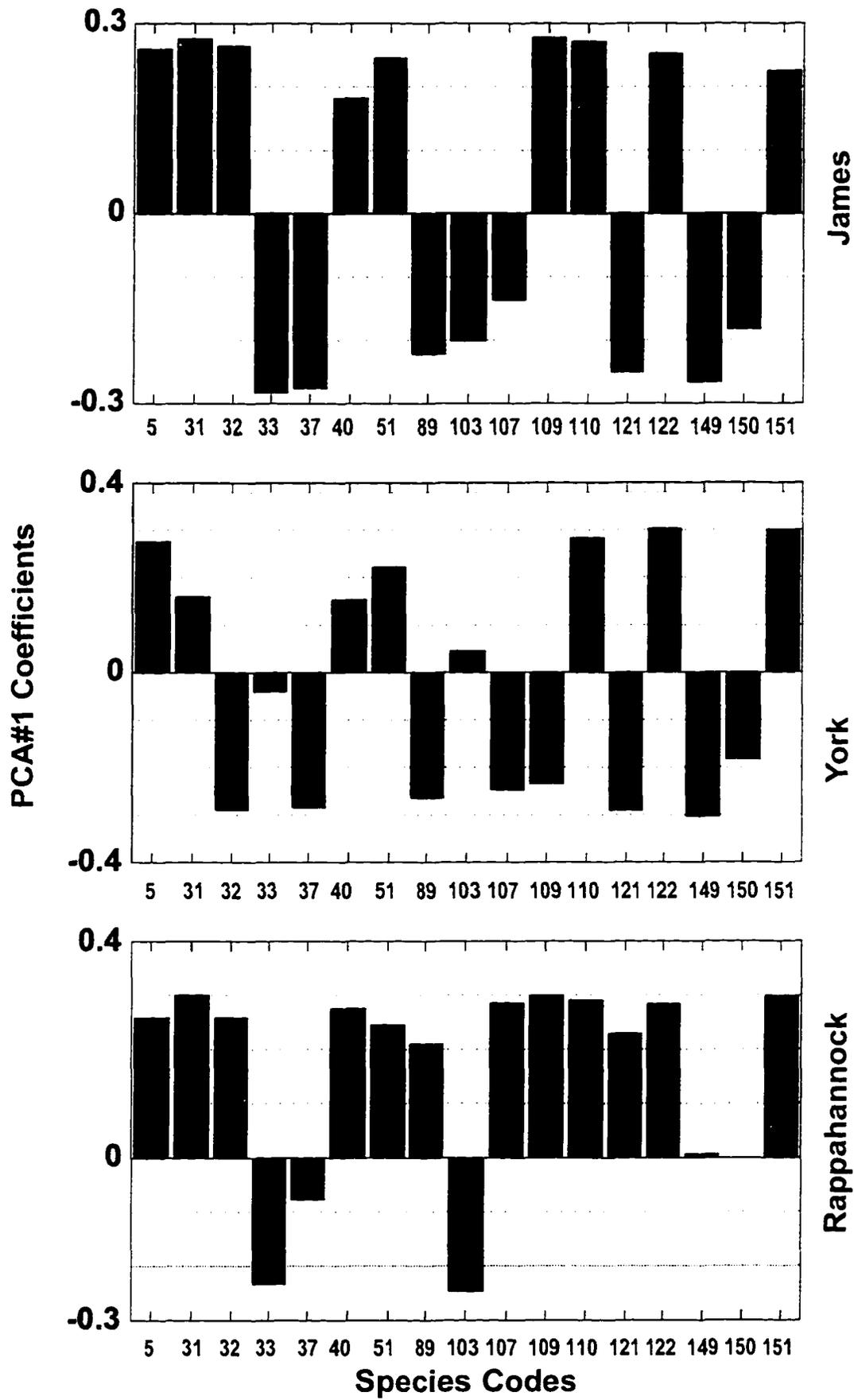
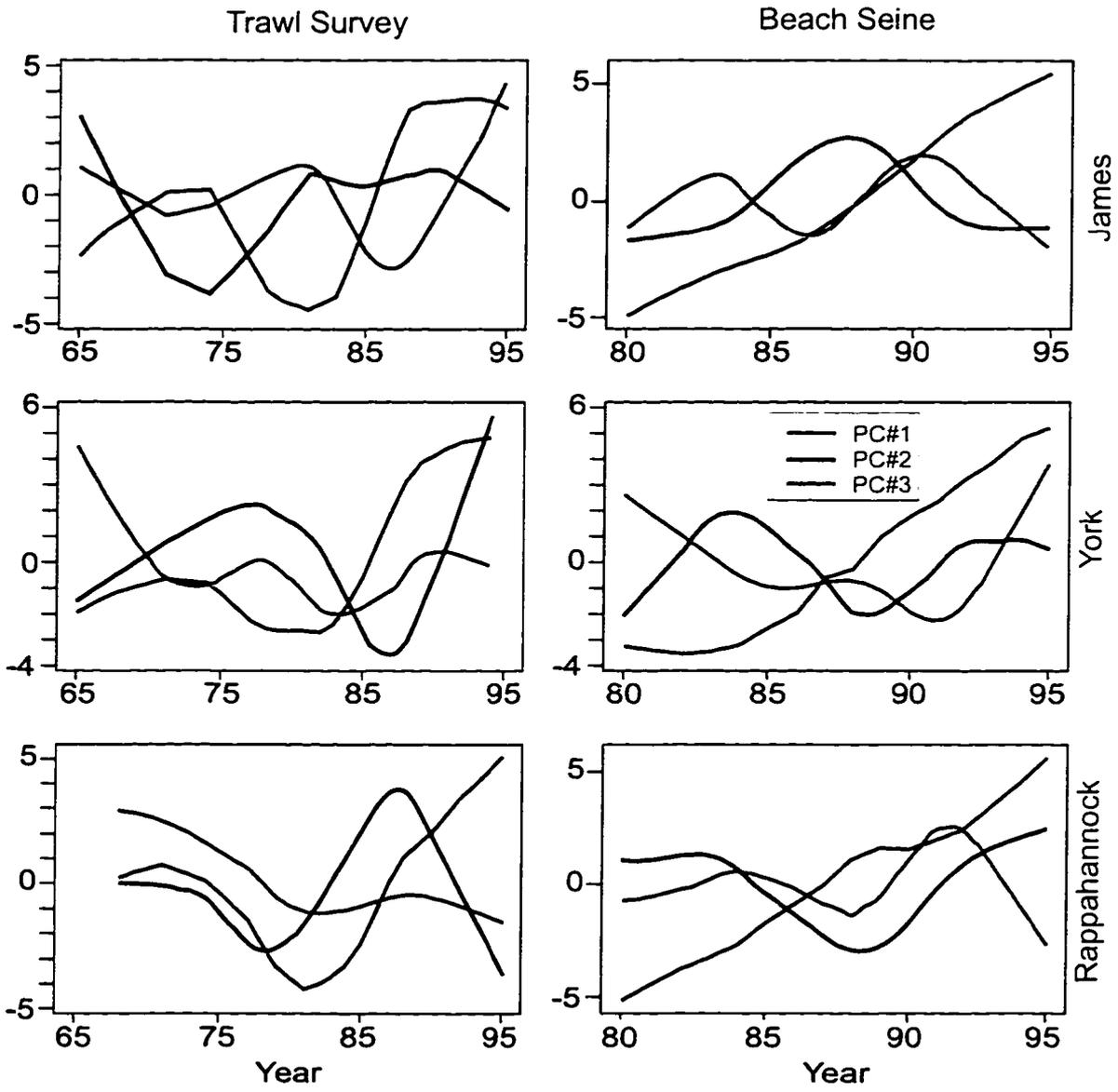


Figure 3.36. The first three principal components of the PCA analyses on the loess-smoothed indices for the trawl survey and summer beach seine survey data, for each of the Virginia rivers. Only the first PC (shown in red) is used in this study.



PCA on the loess smoothed indices were remarkably cohesive. Only three or four PC's were significant in any analysis, explaining up to 98% of total variance (Tables 3.5, 3.6). In the trawl survey, up to 55% of variance is contained in PC#1, and PC#1 accounts for up to 70% total beach seine variance.

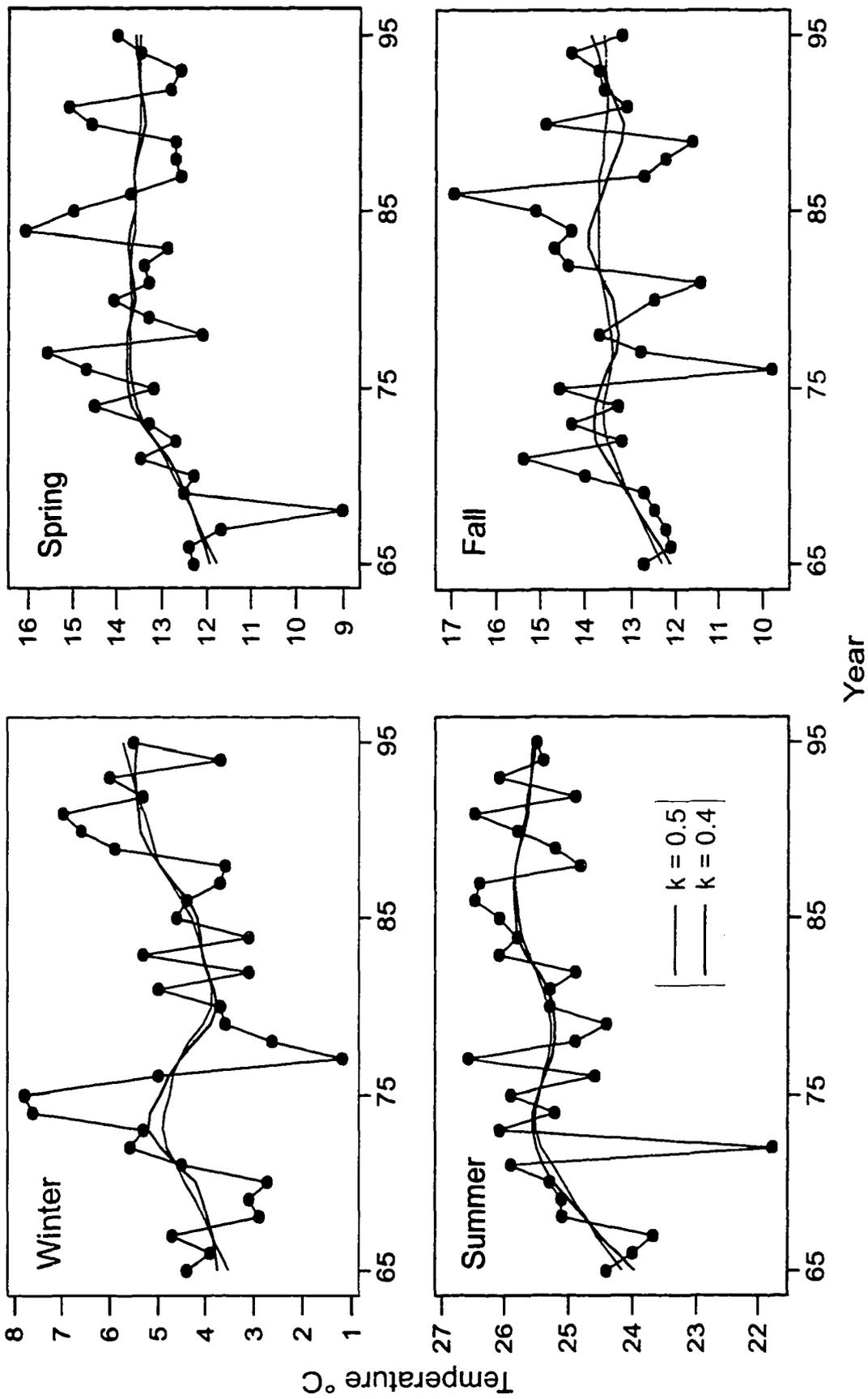
Correlations between the first PC's of the loess smooths are given in Table 3.7. Correlations between rivers, within surveys, yielded 87 - 96% correlations for trawl survey, and 96 - 99% correlations for the beach seine survey. Between river, between survey correlations varied from 87 - 99%.

Temperature

As can be seen in Figure 2.1, January and February were uniformly cold, and were chosen as the months that constitute winter (Figure 3.37). March, April and May were transition months during which the temperature is rising rapidly (Table 2.7); this transition was chosen to represent spring (Figure 3.37). The months June, July, August and September were uniformly hot, and include the peak of summer water temperature, with little change (Figure 2.1, Table 2.7); these were determined to be summer (Figure 3.37). October, November and December were clearly transition months (Figure 2.1, Table 2.7), showing the change from summer to winter temperatures; they were determined to be the fall season (Figure 3.37). Each of the seasonal temperature indices is smoothed by loess (Figure 3.37).

Correlations between the mean seasonal water temperatures, loess smooth at $k = 0.5$, and loess smooth at $k = 0.4$ and the first PC on the biological indices were calculated (Table 3.8). Only one index of water temperature shows a significant relationship to the first principal component (PC#1) of all six groups of biological indices. The winter loess smooth at $k = 0.5$ correlates from 0.89 (trawl survey, James River) to 0.99 (beach seine survey, James and Rappahannock rivers). The winter loess smooth at $k = 0.4$ also significantly correlates with PC#1 of the biological indices, with coefficients ranging from 0.86 (trawl survey, York River) to 0.96 (beach seine survey, James and Rappahannock

Figure 3.37. The annual indices of seasonal water temperature constructed from the VIMS pier temperatures. Each index is smoothed by loess at the $k = 0.4$ and $k = 0.5$ levels.



	tj-pca1	ty-pca1	tr-pca1	sj-pca1	sy-pca1
ty-pca1	0.963				
tr-pca1	0.919	0.865			
sj-pca1	0.867	0.943	0.984		
sy-pca1	0.869	0.946	0.987	0.988	
sr-pca1	0.914	0.975	0.989	0.979	0.964

Table 3.7. Pearson correlations of PC#1 on the loess smoothed indices for each of the three river and both surveys. The coded variables are t-trawl survey, s-beach seine survey, followed by j-James River, y-York River, and r-Rappahannock River.

	tjpcal	typcal	trpcal	sjpcal	sypcal	srpcal
TW	0.461	0.360	0.344	0.497	0.491	0.441
TS	0.125	0.117	-0.097	-0.137	-0.175	-0.169
TU	0.344	0.219	0.070	0.017	-0.034	0.029
TF	-0.002	0.020	-0.111	-0.007	-0.095	-0.014
TW.5	0.890	0.870	0.925	0.986	0.983	0.987
TS.5	0.160	0.204	-0.249	-0.946	-0.923	-0.918
TU.5	0.416	0.479	0.094	0.139	0.045	0.263
TF.5	0.249	0.295	-0.187	-0.626	-0.702	-0.546
TW.4	0.900	0.855	0.867	0.963	0.954	0.957
TS.4	0.126	0.153	-0.251	-0.612	-0.643	-0.592
TU.4	0.420	0.460	0.134	0.166	0.059	0.290
TF.4	0.113	0.091	-0.200	-0.144	-0.217	-0.162

Table 3.8. Correlations (Pearson) between the trawl survey (t) and beach seine (s) survey PC's#1 for James (j), York (y) and Rappahannock (r) rivers vs. indices of seasonal water temperature (T). The indices of water temperature are by season (W-winter, S-spring, U-summer, and F-fall). Smoothed indices are indicated by the appended k-value of the loess smooth (k = .4 or .5).

Trawl survey

	3	5	7	26	27	31	32	33
James	-0.799	0.885	0.819	-0.716	-0.830	0.084	-0.727	-0.573
York	-0.840	-0.335	-0.088	-0.531	-0.970	0.498	-0.833	-0.418
Rapp	-0.457	0.889	0.048	-0.652	-0.373	-0.800	-0.250	-0.696
	39	40	103	151	152	213	614	oyster
James	0.283	0.016	0.754	0.722	0.601	0.833	0.692	-0.256
York	0.915	0.113	0.422	0.092	0.393	0.933	0.863	-0.462
Rapp	0.702	-0.420	0.905	-0.608	0.293	0.878	0.662	-0.527

Beach seine survey

	5	31	32	33	37	40	51	89
James	0.817	0.927	0.944	-0.961	-0.938	0.684	0.868	-0.652
York	0.801	0.474	-0.959	0.018	-0.901	0.534	0.695	-0.815
Rapp	0.861	0.961	0.777	-0.733	-0.187	0.839	0.861	0.772
	103	107	109	110	121	122	149	150
James	-0.742	-0.351	0.951	0.898	-0.821	0.912	-0.878	-0.618
York	0.269	-0.859	-0.643	0.829	-0.964	0.948	-0.909	-0.582
Rapp	-0.815	0.880	0.993	0.946	0.722	0.948	0.041	0.000
	151							
James	0.852							
York	0.969							
Rapp	0.972							

Table 3.9. Correlations (Pearson) between the loess smoothed biological indices vs. the loess smoothed January-February temperature index. The biological indices are given by species codes (see Table 2.3).

ivers). There were three other significant correlations, the loess smooth of the springtime temperature index at $k = 0.5$ on the three PC#1's of the beach seine survey, ranging from -0.92 (York and Rappahannock rivers) to -0.95 (James River). Correlations between winter temperature loess at $k = 0.4$ ranged from 0.86 (trawl survey, York River) to 0.96 (beach seine, James and Rappahannock rivers).

Scatterplots of winter water temperature loess vs. PC#1 were constructed for all six PC's#1 (Figure 3.38). The scatterplots for the trawl survey PC's#1 reveal an unusual behavior (best seen in York River) during the mid to late 1970's.

This behavior prompted further investigation, in the form of cross correlations. Scatterplots for the beach seine PC's#1 were obviously not lagged, so no cross correlations were performed. Winter water temperature loess vs. trawl survey PC#1 were cross correlated and a lag of zero was identified as most important in each case (Figure 3.39). Cross correlations on a subset of these data, the "perturbation years," revealed that PC#1 for York and Rappahannock rivers lagged winter temperature loess by one year (Figure 3.40), with both having correlation coefficient 0.87. James River showed the highest correlation coefficient at lag 0 (0.85) but the lag 1 coefficient was very close at 0.82.

Most of the correlations between smoothed winter water temperature and smoothed biological indices were significant (Table 3.9). A value of $r \geq 0.70$ was somewhat arbitrarily chosen to be significant. For more than half of the species (58%) correlations for two out of three rivers were significant and agree in sign, while the third either agrees in sign or is not significant. In addition, for six more species (cumulatively 76%), there was a significant correlation for one river and no disagreement in another river. In only four species was there a conflicting result, with significant correlations of opposite sign, leaving four species for which no correlations were significant.

Figure 3.38. Scatterplots of loess smoothed winter temperature vs. PC's#1 on the loess smoothed biological indices, for trawl survey and summer beach seine survey data from each of the Virginia rivers.

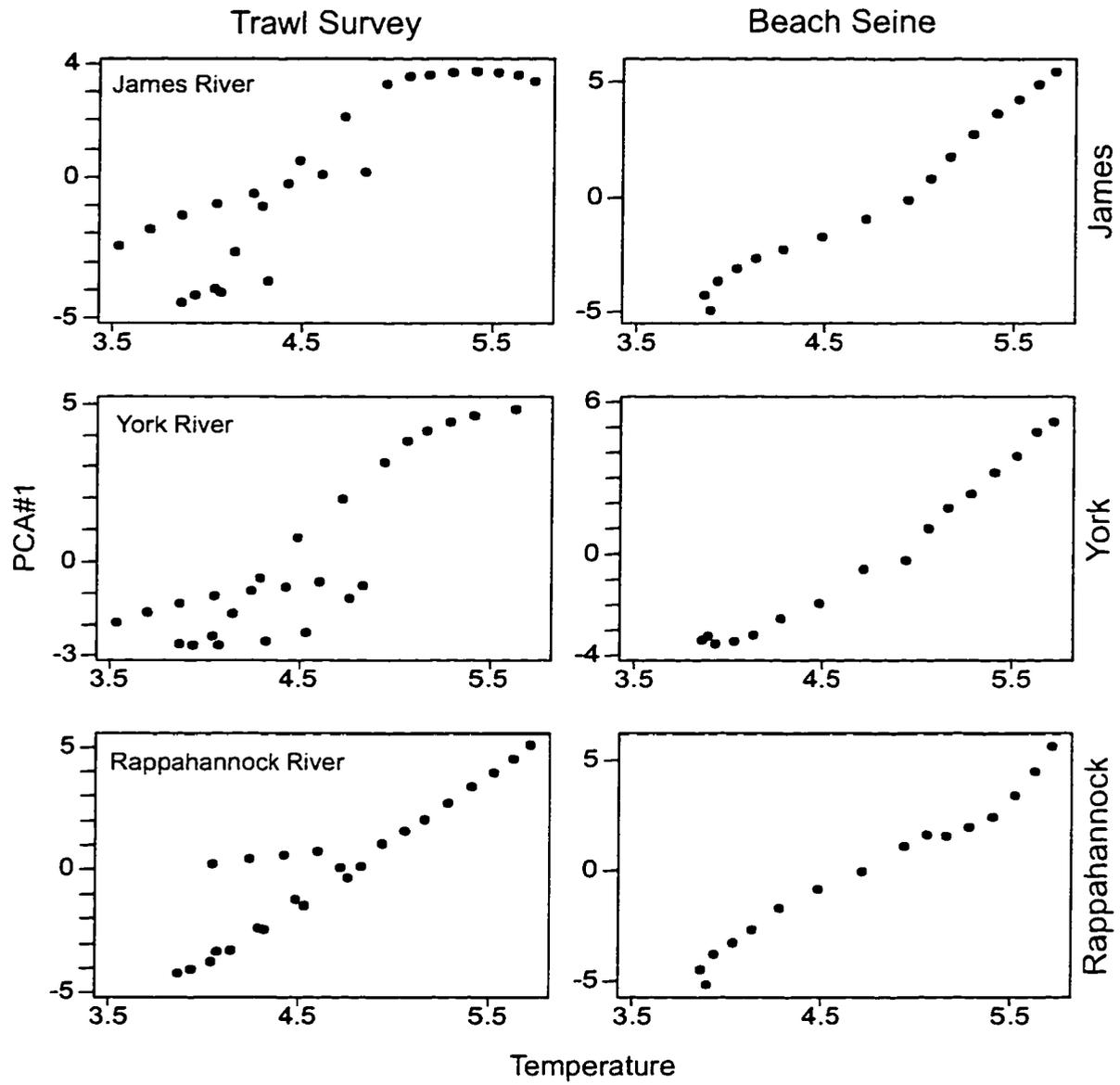


Figure 3.39. Cross correlations on the loess smoothed trawl survey PC's#1 vs. loess smoothed winter water temperature.

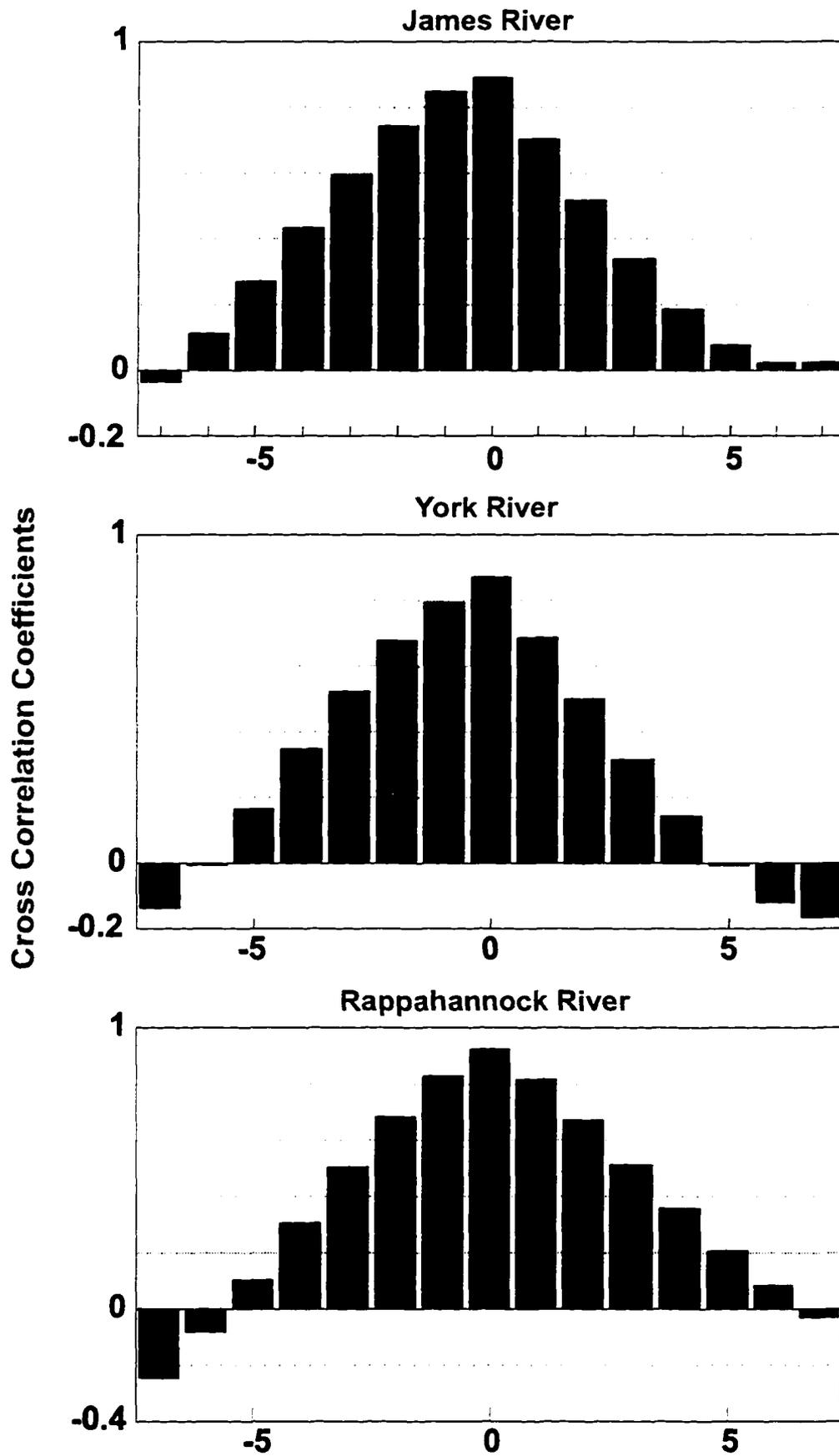
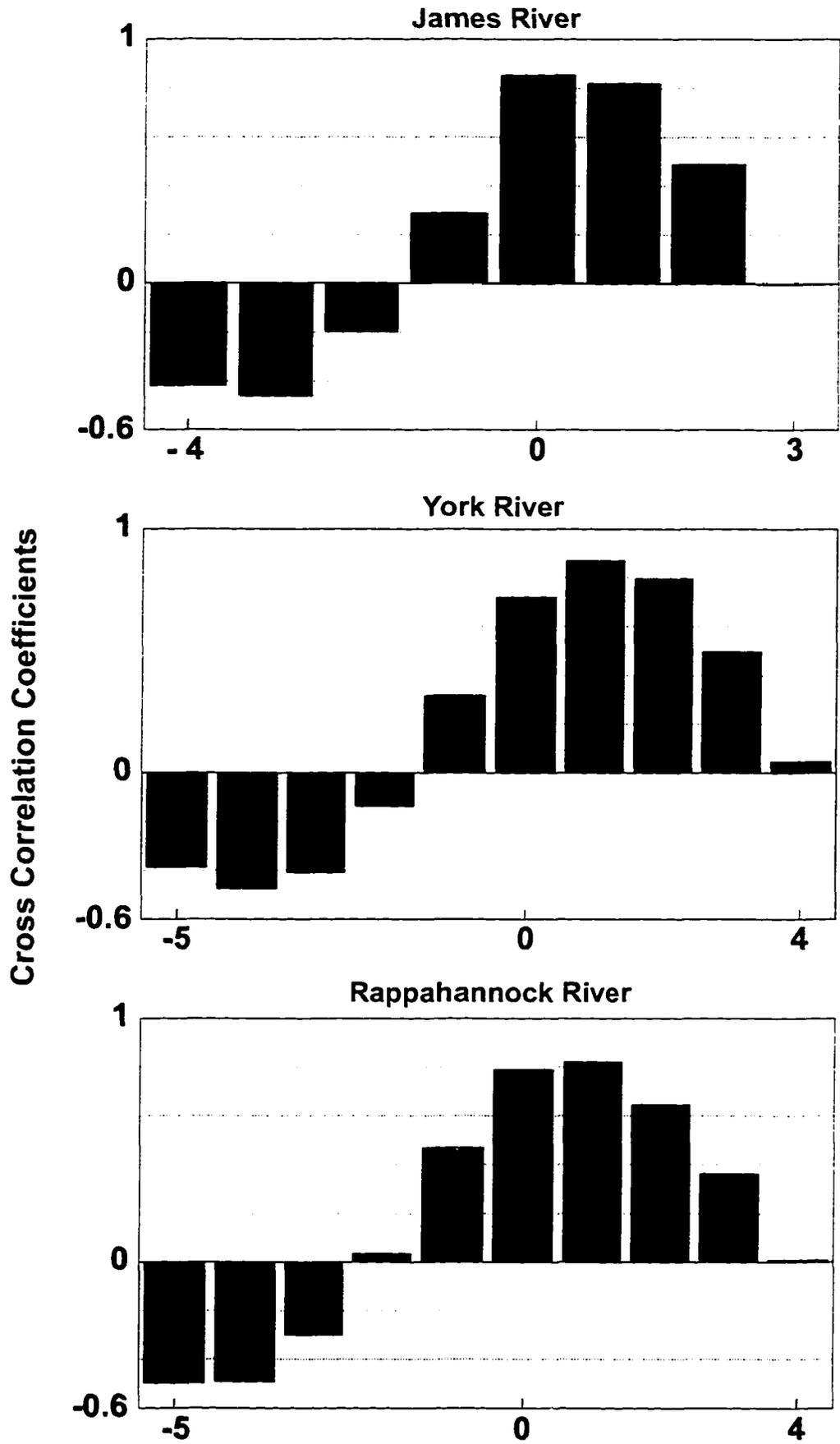


Figure 3.40. Cross correlations on a subset of the data in Figure 3.39, the years of anomalous temperatures. The period 1969 - 1982 was chosen to span the anomalous years.



Discussion

The relation of reproductive success of fish populations to environmental variability is a longstanding, difficult, and generally unresolved problem (Bakun 1986). The major conclusions drawn from this work are that Principal Components Analysis (PCA) of indices of juvenile abundance indicates a geographically broad coherence in the fluctuations of widely disparate populations, and winter water temperature is the environmental factor in control.

Temperature and dissolved oxygen are considered identifying characteristics of suitable habitat for juvenile striped bass in fresh and low-salinity waters (Coutant and Benson 1990). It has been very difficult to separate climate effects on population fluctuations and trends from intrinsic, density dependent factors and those of anthropogenic origin (Austin 1992, Manson and Patrick 1992). Some of the implicated factors are climatic in scale (Austin 1992), including a recent warming trend in winter temperatures implicated in the spread of the oyster disease caused by *Perkinsus marinus* (Ford 1996), and temperature has been found to be among the most important factors affecting disease progression (Chu 1994). The decline in oyster is thought to have a significant deleterious effect on water quality and estuarine health (Gottlieb and Schweighofer 1996, Ulanowicz 1992) and modeling exercises have suggested that recovery of the once huge oyster populations in Chesapeake Bay could lead to recovery of benthic primary production, and fish stocks (Ulanowicz 1992). Temperatures in the nonsummer months have been shown to regulate heterotrophic bacterioplankton abundance, production, and specific growth rates in Chesapeake Bay (Shaih 1994), and plankton abundance (not necessarily bacterioplankton) has been correlated with settlement of bluecrab megalopae (Lipcius *et al.* 1990). In turn, predation by bluecrab and spot partly regulates Chesapeake Bay benthic infaunal populations (Virnstein 1977). Springtime temperature in conjunction with freshwater discharge seems to regulate sea nettle infestations (Cargo 1990). Seagrass meadows had declined as of the 1980's in the Virginia half of Chesapeake Bay (Orth and Moore 1983), and are considered important nursery grounds for decapod crustaceans in lower Chesapeake Bay, leading to speculation that further decreases seagrass

beds will result in reduction of bluecrab populations (Heck and Thoman 1984). The seagrass *Zostera marina* is a northern species near its southern geographical extreme in Chesapeake Bay, but rising winter water temperatures could result in an extension of the growing season (Kenneth Moore, VIMS, pers. comm.). Winter water temperature is considered an important controlling influence on juvenile croaker populations, with lower temperatures leading to increased winter mortality (Norcross 1983, Cook 1981). Periodicities have been observed in the population dynamics of some species, including striped bass (Van-Winkle and Kirk 1979) and bluecrab (Hurt *et al.* 1979), and are probably related to density-independent factors such as temperature.

PCA is becoming more widely used as a multivariate analysis tool. Although the mathematical concept of PCA has been long known to statisticians, it was not until the proliferation of computers that the tool became truly useful to ecologists. The roles of chemical characteristics of habitat and anthropogenic influences in the distribution of diatoms have been identified using PCA (Sabater and Sabater 1988). Chemical pollutants have been linked to assemblages of benthic fauna (Vogt 1990). PCA on field data for 316 species and life stages of animals in Delaware Bay and Chesapeake Bay has identified five salinity zones in which these animals are likely to occur (Bulger *et al.* 1993). Similarly, habitat gradients for freshwater streams are also identified by PCA (Meffe 1988). Assemblages of birds on small Finnish islands have also been characterized by geographical location and ecological gradients (Von Numers 1995).

Pacific upwelling, sea level height, and surface temperature were analysed by PCA, and the PC#1 was found to reflect the effect of an ENSO the previous winter. This PC was found to significantly correlate with chinook salmon abundance their final year before leaving the ocean to spawn, and indicated a negative influence of ENSO on survival (Kope and Botsford 1990). The usefulness of PCA in partitioning and identifying components of ecological systems is well established.

The technique is used here to quantify the degree to which population fluctuations in juvenile finfish, bluecrab, and oyster are coherent, much in the manner by which Koslow (1984) identified

cohesive fluctuations in North Atlantic fish stocks. The strength of PCA is the ability to determine the number of significant signals within a set of variates. Using annual population indices for the variates allows us to ask, are population abundances varying according to intrinsic characteristics of the individual species, or are they fluctuating in response to extrinsic influences? Two groups of indices are used, the longer (1965 - 1995) being constructed from data collected by the VIMS trawl survey and the VIMS fall oyster dredge survey, while the shorter (1980 - 1995) data set was collected by the VIMS beach seine survey.

PCA of the indices reveals a relatively weak but nevertheless remarkable relationship between the indices (Tables 3.1, 3.2). The cohesiveness of this analysis, with only six or seven significant PC's out of 16 or 17 (trawl and beach seine, respectively), each repeated across three rivers, is a clear indication that something extrinsic is at work. Given the disparity of life histories within this collection of species, we could conclude otherwise only if most of the PC's were significant.

On the other hand, the analysis on the unsmoothed indices is not strong enough to be used to identify a controlling influence. The relative amount of variance in the first PC's of the six analyses is an indicator of how clearly we can "see" the most influential signal. Based on this observation, the indices were partitioned by the loess (locally weighted scatterplot smoother) method into long-term trend and interannual variation. Loess has been used with considerable success for analyses as varied as identifying growth curves for giant squid (Gauldie 1994), and the smoothing of rainfall data for identification of rainfall and moisture stresses on white clover (Hutchinson 1996). In Chesapeake Bay long term indices of juvenile oyster abundance have been successfully smoothed by loess for the purpose of comparing population fluctuations with environmental variables (Austin *et al.* 1995).

While it appears to the eye (Figures 3.1 - 3.33) that the interannual variation (loess residuals) of the juvenile indices used here may be mostly noise, PCA on these features of the indices reveals coherence of magnitude comparable to the whole indices (Tables 3.2, 3.4). The similarity of analysis on the residuals to the unpartitioned indices suggests that we are really seeing the same things. At the

same time, the weakness of the analyses indicates that interannual variation is masking a more important signal. That signal turns out to be the long-term behavior of the systems, as revealed by the smoothed indices.

The most remarkable set of analyses are the PCA on the smoothed indices (Tables 3.5. 3.6). By smoothing we filter out interannual variation, leaving behind the long term trend in behavior of the populations. This partitioning of the data provides a very clear view of underlying signal. PCA on the smoothed indices shows a degree of coherence in the long term trends that can only be the result of a long-term trend in the physical environment. It is beyond reason to suppose that coherence this strong could be a result of similarities in the life histories of species this diverse, so a physical forcing function is implicated.

Further, by correlation of the first PC (PC#1), within and between surveys, across the three Virginia rivers, we see that this forcing function is geographically large, not some feature of the individual rivers (Table 3.7). If an environmental factor that was unique to each of the rivers was in control, such as freshwater discharge which is a function of the respective watersheds, then these correlations would have been weak. The fact that some of these species reproduce offshore, and a single population splits up and migrates into the three rivers, accounts for some of the very strong correlation between the rivers. However, most of the species in this study have separate juvenile populations; for example, white perch spawned in York River are collected as juveniles in York River. The very strong correlations between rivers can only be explained by a single signal that is reflected in all three sets of indices.

By considering the PCA coefficients used to construct the first PC (Figures 3.34 and 3.35), we can gain some insight into how the various species contributed to this signal. However, it must be remembered that the direction (+/-) of the coefficients is arbitrary. The PC curves could just as easily be inverted; direction has no meaning in PCA. That is, the correlations might as easily be negative, and remain just as significant. This is not to say than any one coefficient might be changed, but that

if all of them are changed at once, the PCA is equally valid. We can compare the direction of individual coefficients to others within an analysis. To compare between analyses, we must consider the group to which a coefficient belongs, and ask if that affiliation persists. For example, consider the trawl survey coefficients (Figures 3.34) for bay anchovy, hogchoker, tonguefish, silver perch, bluecrab (species code 103, 151, 152, 213, 614, respectively) and oyster. In James River all but oyster are positive, while in the York all but oyster are negative. This is consistent behavior; the analyses assigned different signs but the grouping remains the same. The environmental forcing function that is at work here has the opposite effect on oyster and this group of finfish. Now consider the same group of animals in Rappahannock, compared to the other rivers. Again the relationship holds, except that hogchoker has changed. It might be that some geographical feature of the Rappahannock is sufficiently different from the other rivers to explain this change, or it may be uncertainty in the data.

Examination of James and York rivers smoothed PCA coefficients for PC#1 (Figure 3.34) reveals that the grouping of the species by sign makes identical groups of species; not a single species migrates to the other group when comparing the two rivers. The effect of the single most influential environmental forcing on croaker, weakfish, striped bass, white catfish, hogchoker, tonguefish, silver perch, and bluecrab is opposite the effect on summer flounder, alewife, blueback herring, white perch, spot, channel catfish, and oyster. Comparing these groups to Rappahannock River, we find several changes. Besides hogchoker noted above, weakfish and striped bass have migrated out, and channel catfish has migrated into the first group.

The contribution to PC#1 made by oyster (indicated by bar height in Figure 3.34) is small, and the correlations between smoothed oyster abundance and smoothed winter water temperature (Table 3.9) are insignificant, suggesting that oyster may not be responding to water temperature.

In the beach seine survey analyses the results persist. Croaker, striped bass, channel catfish, gizzard shad, spottail shiner, mummichog, and hogchoker are in one group for all three rivers, and likewise spot and menhaden are in the other group. The other eight species (white perch, tessellated

darther, bay anchovy, eastern silvery minnow, satinfofin shiner, banded killifish, inland silverside, and Atlantic silverside change positions (Figure 3.35). The species that persistently group together are responding to environmental forcing consistently.

Because it is the simplest explanation, and given that only three species changed relative sign within the trawl survey analyses, we shall assume sampling uncertainty as the cause. Loess is used here to partition interannual variation from long-term trends, but random error persists. This is remarkably consistent behavior, given the broad spectrum of species under consideration. However, although an in-depth investigation into single-species relationships is beyond the scope of this work, given the similarities of York and James Rivers, there may be a fundamental difference between them and the Rappahannock that causes some species to be affected differently. This should be the subject of a future work.

The relative magnitudes of the respective coefficients determines the contribution each species makes to the PC. Within the trawl survey analyses we find that the relative contributions of croaker, weakfish, alewife, white catfish, hogchoker and oyster change between rivers. In the beach seine analyses, spot, bay anchovy, menhaden, and the two silversides change magnitudes. Most of the species make relatively large or small contributions consistently, indicating that the common environmental signal is unfailing in its effect.

Temperature

PCA on the two sets of juvenile indices agree and indicate that there is a coherent signal in Chesapeake Bay juvenile recruitment. After smoothing by loess, PCA on the residuals continues to support the conclusion, while PCA on the loess smooths themselves very strongly indicates there is a long term signal that is driving at least a significant part of the recruitment of a wide spectrum of animals within each of the three Virginia tributaries to the Bay. Further, this signal is the same in each of the three rivers, demonstrating that the underlying signal is geographically broad. Not only

did the forcing function span the three rivers, but it spanned a distance from the river mouths to about 40 miles upstream. Only an environmental factor such as regional temperature could so uniformly affect such a spatially large system. Given the broad support in the literature for temperature as a forcing function, water temperature is a natural choice. Temperatures for the four seasons were considered. Many authors point to winter temperatures as causal factors in recruitment (*e.g.* Norcross 1983, Cook 1981, Massman and Pacheco 1060), and it was winter water temperatures that surfaced in this analysis.

It was because of the springtime correlation on the beach seine index PC#1's that the additional smooths were calculated at the $k = 0.4$ level. The more flexible smooth is less likely to correlate well with this number of data, making a more difficult test. At the $k = 0.4$ level the springtime water temperature correlations on the beach seine indices faded away. However, the correlations of all six PC's#1 on winter temperature remained strong at the $k = 0.4$ level, indicating that the relationship is robust, and more likely to be real. Based on the correlations, no further consideration was given the spring, summer and fall temperature indices.

As used here, PCA is based on the correlation matrix (the alternative is the covariance matrix) of each species with every other species. In order to clarify the relationship between individual species and temperature identified by PCA, correlations were performed between each individual smoothed index and smoothed winter water temperature (Table 3.9). Of 33 (x 3) cases, 19 (58%) have two or three significant correlations and agree in sign across all three rivers. In six additional cases there is one significant correlation with none conflicting. Four cases are nonsignificant, and in only four cases is there a conflict of signs (in trawl survey dataset croaker/York, weakfish/York and Rappahannock, channel catfish/all three rivers, and in the beach seine dataset spot/York River), indicating that for those for species (white perch, tessellated darter, eastern silvery minnow, and banded killifish) the analyses are inconclusive. If we group the species by sign (+/-), we find that these groups agree almost perfectly with the groups formed from the PCA coefficients. It is important to point out here that the

PCA coefficients are based on correlations between species with themselves, and the correlations here are between each species and temperature. These correlations between species and water temperature group individual species by sign into the same groups as PCA does, within each river. The corresponding groups are very strongly delineated.

In one set of biological indices, the trawl survey data, an anomaly of temperature is captured. The effects of the extremely warm winters of 1974-5 ($\bar{T} = 7.6, 7.8^{\circ}\text{C}$, respectively) followed by the coldest winter in the record in 1977 ($\bar{T} = 1.2^{\circ}\text{C}$) are seen in the scatterplots (Figures 3.38). Long term mean temperature is 4.6°C . The indications are that warm winter temperatures perturbed the system, causing it to oscillate, and the following cold winter was a further push to the system. The long term trend in the biological system seems to have returned to its undisturbed state sometime around 1980, when the gradual warming trend took over. It is truly unfortunate that the VIMS beach seine survey was terminated during this period of temperature anomaly. However, the data from all three rivers in the trawl survey support the perturbation hypothesis, giving strong corroboration.

Winter water temperatures bottomed out in 1977, and have been higher ever since. Loess smoothed temperature turns upward in 1981, and continues monotonically upward through 1995 (Figure 3.37), for a rise of 1.8°C from $3.9 - 5.7^{\circ}\text{C}$ over the period. This trend in winter water temperature is strongly reflected in the scatterplots for all six PC's#1 (Figure 3.38). The scatterplots of winter water temperature loess vs. the PC's#1 revealed an interesting behavior in the trawl survey data. In 1974 and 1975 the highest mean winter temperatures were recorded, followed by the lowest temperature of the record in 1977. This shows up as a loop in the scatterplot, and is best seen in York River (Figure 3.38). Behavior such as this indicates that a lag has been introduced into the system. The system was responding to a controlling influence and the behavior of the influence abruptly changed. The biological system was then out of sync with the forcing signal. It was not possible for recruitment to adjust to such large input changes in such a short period of time.

Cross correlations did not indicate any lag in the relationship, but the correlations on either

side of lag 0 were so large that they do not provide evidence disproving the lag either (Figure 3.39). Cross correlations on the years 1969 - 1982 revealed a lag of one year, with biological indices following temperature in York and Rappahannock rivers. James River was so close, that given the behavior demonstrated in the other rivers, and the fact that there were several years of missing data in this period for James River, we can safely conclude that the lag is present for James too (Figures 3.40).

Thus we have two indications that back to back severe anomalies in an environmental forcing function caused a lagged response in overall juvenile recruitment. The loop seen in the scatterplots indicate a perturbation in the physical system caused a lagged response in the biological system. Cross correlations on the "perturbation years" quantitatively confirm this conclusion. This is an important observation in general. Random but observable events such as wild temperature swings have predictable influence on recruitment in future years.

After the years of strong temperature anomaly, the PC's#1 strongly follow the winter temperature loess curve, which is itself monotonically increasing. From 1980 onward in the trawl survey data, and in all the beach seine data (which begin in 1980), the correlation between the long term trends is almost perfect.

The strength of the correlations between smoothed temperature and PC's#1 is unusual in biology, where significant but weaker correlations are more common. The reason biological correlation analyses do not typically demonstrate this level of association is because random fluctuations are a prominent feature in the data. The correlations presented here are between smoothed data sets; the random "jitter" has been removed. Given the smooth nature of the correlates, we should expect either strong associations or very weak ones; significant but moderate correlations would be unexpected in this situation.

Given the lag that appeared during years of extreme conditions (1975-75, 1977), we must conclude that temperature is exerting influence through the parent stock/recruitment relationship. The

indices of abundance used here are based on age 0 animals, which did not exist at the time of the preceding winter.

The relationship between parent stock and juvenile recruitment is not discounted by this analysis, because although the mechanics of recruitment control are not tested or explored, there can be no explanation that omits parent stock. The reason for this is that the water temperatures correlated with abundance temporally precede the birth of the animals. Whatever mechanism, be it enhanced or decreased mortality, effects on fecundity, or whatever, it probably operated directly on some parent stocks, and is revealed indirectly in this analysis of juvenile abundance. This is not always the case though. As an example, larval striped bass are known to benefit from a cold wet winter. Ice in the marshes grinds up detritus, and high discharge flushes it into the nursery areas, where it serves as food for copepods. The copepods in turn serve as food for the stripers.

Conclusions

This study highlights the importance of considering long term trends, or behavior, in the study of populations. There is certainly a long term trend in overall juvenile recruitment in Chesapeake Bay. There is also a strong trend in winter water temperature, particularly from 1980 onward. Correlations by themselves do not prove a causal relationship. However, we have several lines of evidence that point to temperature as a regulating physical factor without contradiction. PCA strongly suggests that juvenile population fluctuations within all three rivers are coherent. This indicates that a physical forcing function is in control. The first PC's of all six sets of smoothed indices are strongly correlated, which tells us that three river systems are under the control of a single, geographically broad factor, as opposed to more localized factors such as freshwater discharge, or anoxia. Correlations between temperature and PC's#1 are very strong. Scatterplots of temperature and trawl survey PC's#1 reveal a perturbation in the biological system that coincides with severe, back to back, opposite anomalies in temperature. Cross correlations on the period of the anomalies confirms that the biological system lags temperature during this period of perturbation, while cross correlations on the entire period of record show that the systems are in sync (0 lag) in general. Winter water temperature is an important factor controlling juvenile population fluctuations and abundance in Chesapeake Bay.

Appendix

Species profiles

The species used in this study represent several groups with substantial differences in life histories and locations within the Chesapeake Bay. Some are harvested commercially and by recreational fishermen; others are not. Some are found only in upper, low salinity regions, some are found in upper regions as well as lower, higher salinity areas and some migrate between the two zones as adults while others migrate as juveniles.

The harvested species with an offshore component in the juvenile life history:

All of these species are important to this study in that they have similarities in life history that may cause them to behave alike. The dependence on shelf wind is a common thread that may result in common behavior in recruitment dynamics.

Atlantic menhaden

The menhaden (*Brevoortia tyrannus*) is one of the most intensely harvested species in the Chesapeake Bay system, and together with the conspecific Gulf menhaden (*B. patronus*) accounts for up to 40% of U.S. commercial landings (Smith 1991). Menhaden are used directly as food for humans (outside of the U.S.), terrestrial animals, and aquacultured fish, as well as in the production of agricultural crops. The fish is used for uncountable industrial applications, and in particular the oil extracted from this species has widespread uses.

Menhaden spawn offshore, south of Cape Hatteras, NC. After transportation to estuarine nursery grounds, larvae metamorphose into the juvenile stage. Movement is a result of wind-driven currents, and like spot and croaker, the number of larvae reaching the nursery grounds is directly related to the prevalence of favorable winds (Govoni and Pietrafesa 1994). However, there is evidence that menhaden respond to changes in salinity by moving upward in the water column, with sufficient

vigor to facilitate cross continental shelf transport by moving into currents with favorable direction (De Vries *et al.* 1995). Growth of menhaden may be regulated by storm activity, which mixes the water column and reduces concentrations of plankton available to this obligate filter feeder (Maillet and Checkley 1991). Growth of the conspecific Gulf menhaden is inversely related to freshwater discharge, and directly related to temperature, while mortality is directly related to discharge and inversely related to temperature (Deegan 1990). Relations between commercial landings of menhaden and sea level anomalies (Morris *et al.* 1990) and the 18.6 year nodal cycle of the tides (Cabilio *et al.* 1987) have been demonstrated. Sea level affects the nursery grounds available in tidal marshes, and also affects production of *Spartina alterniflora*, which in turn may have an effect on primary production. The tidal nodal cycle modulates by a few percent the strength of tidal currents, and may have a significant effect on surface temperatures in shallow seas (Loder and Garret 1978). Adults migrate along the coast, and fishing takes place both in the Bay and outside. Although landings declined in the 1960's, under ASMFC management the fishery recovered during the 1970's and 1980's (Houde and Rutherford 1993, Smith 1991, Lewis *et al.* 1987), despite continued harvest pressure.

Croaker

Croaker (*Micropongonias undulatus*) spawn offshore in the late fall and winter months, and recruitment into the estuary depends upon the timing, duration and velocity of wind driven currents (Norcross 1983, Govoni and Pietrafesa 1994). While outside of the mouth of the Chesapeake Bay as pelagic plankton, larvae apparently exert some control over transport through vertical migration, as they are found near the mouth of Chesapeake Bay in greater concentrations in inward flowing water (Norcross 1991, Cook 1981). However, some spawning also may occur in the estuary (Barbieri *et al.* 1994).

Winds also play a role in the locations chosen for spawning, as onshore winds retain cool water near the mouth of the Bay. When this happens, croaker migrate farther south to locate sufficiently warm water (Norcross and Austin 1988).

Population abundance of Atlantic croaker was in decline, due in part to overfishing (McHugh and Conover 1986). As with weakfish, bycatch of the shrimp fishery was implicated (Branstetter 1995, Hendrickson and Griffin 1993, Murray *et al.* 1992). However, the croaker population has recovered.

Spot

Spot (*Leiostomus xanthurus*) spawn in the Atlantic Ocean in the late fall and winter months, and depend upon the timing, duration and velocity of wind driven currents to transport larvae to the Chesapeake Bay nursery grounds (Bodolus 1994, Govoni and Pietrafesa 1994). Spawning is probably restricted to areas south of Cape Hatteras by availability of suitably warm bottom water (Bodolus 1994), and it is in these waters that larvae are most often found (Govoni and Pietrafesa 1994).

Summer flounder

Summer flounder (*Paralichthys dentatus*) spawn offshore on the continental shelf in the early fall. Spawning generally begins in September (Able *et al.* 1990, Grimes *et al.* 1989), and may continue through January, although the peak is in the fall (Able *et al.* 1990). Juvenile (age 0) fish enter nursery areas, including the Bay, as transforming larvae in the fall, as early as October and as late as April (Norcross and Wyanski 1994, Keefe and Able 1993).

Nursery ground water temperatures play important roles in the population dynamics. Rapidity of metamorphosis and growth are directly related to temperature (Keefe and Able 1993, Malloy and Targett 1991), and metamorphosis can take several months from the time larval fish enter the nursery (Szedlmayer *et al.* 1992). Greatly reduced winter water temperature is fatal to age 0 summer flounder (< 4° C - Keefe and Able 1993, <2° C - Szedlmayer *et al.* 1992, < 3° C - Malloy and Targett 1991).

Bluecrabs

The bluecrab (*Callinectes sapidus*) is another species for which an important commercial fishery exists, one that probably over harvests. Most crabs are taken in pots (Erik Barth, VMRC, Newport News, Va. pers. comm.), and the number of crab pot permits shows a very strong positive

linear trend over time if one outlier (1982) is removed (Mosca, work in progress). The number of pots per fisherman has probably also increased (Erik Barth, VMRC, Va. pers. comm.). In addition to pots, commercial harvest methods include winter dredging, scrapes (a type of dredge used in grass beds to capture crabs due to molt), traps (pealer pounds), and trot lines (infrequently used in Virginia but important in Maryland). The species also supports a large recreational fishery. Increasing harvest pressure may be due in part to decreasing harvestable stocks of other species.

Although reproduction of the blue crab is not contained entirely in the Bay, and year class strength is also not entirely determined within the Bay, many important components of the determination of year class strength do exist within the Bay. Early larvae are transported offshore in the surface layers to the Continental Shelf where larvae mature, and postlarvae are returned to the Bay (Goodrich *et al.* 1990) in the lower estuarine circulation layers. Because freshwater discharge is a component of estuarine circulation, discharge also may influence blue crab recruitment. The postlarvae then metamorphose through numerous megalopal stages within the Bay, principally within the major rivers. The return of postlarvae is probably most heavily influenced by meteorological conditions (McConaugha 1990), notably wind driven currents (Johnson and Hester 1989, Goodrich *et al.* 1990). The postlarvae play an active role in transport by migrating vertically to place themselves in currents of favorable direction (Maris 1990). Juvenile blue crabs probably overwinter in grassbeds the first year (Oesterling 1985), as well as deep-water portions of the rivers where they are collected by the trawl survey.

Predation on blue crabs may play an important role in population dynamics, but it is not clear that predation controls population. The shrimp *Crangon septemspinose* and *Palaemonetes pugio* are voracious predators of megalopae, with the former consuming almost 100% of prey presented in laboratory trials (Olmi 1988). Predation on juvenile crabs by striped bass is documented, but this source of mortality has not been shown to be a controlling influence (Mosca *et al.* 1995). Adult crabs are prey to the oyster toadfish, *Opsanus tau* (Gibbons and Castagna 1985, Bisker and Castagna 1989),

and in molt stages are preyed upon by many finfish. Cannibalism also has been identified as a potentially important controlling influence on blue crab populations (Lipcius and van Engle 1990).

Blue crabs are themselves important predators, particularly of shellfish such as oysters (Krantz and Chamberlin 1978, Bisker and Castagna 1987, Eggleston 1988) and various species of clams, including the hard clam *Mercenaria mercenaria* (Gibbons and Castagna 1985). Crab predation is thought to be a controlling influence on populations of the soft-shelled clams *Mya arenaria* and *Macoma balthica* (Lipcius and Hines 1986, Hines and Lipcius 1990, Eggleston *et al.* 1992).

Harvested species with inshore juvenile life stages:

The catfish, striped bass, white perch and oysters share the common characteristic of being dependent upon upstream physical processes. These species are most likely to show similar dependence upon freshwater discharge and temperature.

The weakfish is in this group because it is a commercially harvested species that spawns within the Bay, but it favors deeper water for nursery grounds, and is therefore somewhat different from the others.

Catfish

Two species of catfish will be considered in this study, the channel catfish (*Ictalurus punctatus*) and the white catfish (*I. catus*). Channel catfish are extensively farmed for human consumption, and much of the literature describes feeding and preparation for market. There is an active fishery for wild fish in the Virginia portion of Chesapeake Bay, particularly on the James and Rappahannock Rivers. Catfish are found in abundance in low salinity waters, which serve as nursery grounds for many fish species. Juveniles of both species of catfish are known to prey upon yolk sac larvae of striped bass and white perch under laboratory conditions, and have been found to consume eggs of white perch (McGovern and Olney 1988).

Striped bass

The striped bass (*Morone saxatilis*) is among the most studied of fishes on the east coast, due in large part to the importance of the commercial and recreational fisheries for this species. Striped bass are an anadromous species with a well known migratory pattern. In Chesapeake Bay and Hudson River, striped bass less than two years old (< 300 mm) do not migrate extensively from their natal rivers (Vladykov and Wallace 1938, Raney 1952, Massman and Pacheco 1961, Mansueti 1961, Setzler *et al.* 1980). Approximately 10% of two year old striped bass usually leave the Bay (Raney 1952), although more two year-old striped bass leave the Bay when their cohort is strong (Austin and Hickey 1978). Extensive migration out of the Chesapeake Bay and northward along the Atlantic Coast normally begins at 3+ years of age (Mansueti and Hollis 1963). Maryland female bass typically make their first oceanic migration at an early age (3+), whereas males may not leave the Bay for the first time until they are 5 or 6 years old (Setzler *et al.* 1980). Most of the striped bass on the east coast originate in Chesapeake Bay, with minor contributions from the Hudson and Roanoke Rivers (Berggren and Lieberman 1978). During the winter, adult striped bass remain relatively inactive, reduce food consumption, and congregate in deep water portions (10-50 m) of river mouths and the Bay (Raney 1952). As waters warm in early spring, mature fish move upstream to freshwater spawning grounds. After spawning in April and May, migratory bass rapidly leave the Bay and move northward along the Atlantic Coast (Raney 1952). This migratory stock moves southward in the autumn, returning to the Bay in November and December to overwinter with younger bass that remained during the summer.

Striped bass are opportunistic feeders (Scofield 1931, Merriman 1941, Hollis 1952, Boynton *et al.* 1981), usually preying on most abundant food items (Raney 1952, Calhoun 1953, Thomas 1967). The most important foods of striped bass are schooling fishes such as anchovies, silversides, menhaden, spot, and killifishes (Scofield 1928, Hollis 1952). Invertebrates also constitute a portion of the diet of striped bass (Hildebrand and Schroeder 1928, Curran and Ries 1937, Townes 1937, Merriman 1941, Hollis 1952, Stevens 1966, Thomas 1967). The frequency of occurrence and percent volume of

invertebrates in the diet of striped bass are small (Hollis 1952, Manooch 1973) and decrease with bass size (Stevens 1966, Schaefer 1970). In Chesapeake Bay, striped bass stomachs contained negligible quantities of blue crabs (Hollis 1952), though striped bass are known to consume blue crabs in quantity when the opportunity presents itself (Mosca *et al.*, 1995). In Albemarle Sound, NC crustaceans were less than 3% of the volume of striped bass food items, though small blue crabs (18-30 mm) were the most frequently occurring crustaceans and were found in greater than 5% of striped bass stomachs (Manooch 1973).

Predicting future stock size is an important concern for striped bass managers, so it is not surprising that this receives much attention. However, it is difficult to estimate adult stock size directly, so surrogates are used. The presence or absence of striped bass eggs in springtime plankton tows is an indicator of spawning stock size (Uphoff 1993), as is the number of eggs per tow (Olney *et al.* 1991). However, the most commonly accepted predictor is the relative abundance of juvenile striped bass in the summer, and though calculated in more than one way, the measure is usually called the juvenile index. Juvenile indices are believed to predict as much as 83% of the variation in commercial landings (Goodyear 1985). Modeling exercises indicate that temperature and toxic chemicals may affect survival of eggs and striped bass larvae (Rose *et al.* 1992). On the other hand, sewage has been found to have a beneficial effect in the Potomac River, with high sewage discharge correlating positively with striped bass indices (Tsai *et al.* 1991). River discharge has been demonstrated to have a measurable effect on juvenile indices in the Roanoke River; flow correlates inversely with juvenile index (Rulifson and Manooch 1990). Simulations using temperature, size distribution of female parent stock, prey availability, and competition pressure from the congeneric white perch have demonstrated a possible 150-fold variability in juvenile recruitment in the Potomac River (Cowan *et al.* 1993). This study further supports the contention that determination of the size of striped bass year classes precedes metamorphosis. In addition to competition, juvenile white perch are known to prey on larval

striped bass (Monteleone and Houde 1989), as does the copepod *Acanthocyclops vernalis* (McGovern and Olney 1988).

Weakfish

Weakfish (*Cynoscion regalis*) along the east coast of North America share a common gene pool and are thought to form a single stock (Graves 1992, Crawford 1989). Weakfish (also known as grey trout) mature at age 1, and spawn in coastal waters and estuaries from March through September, and the deeper portions of estuaries, including the Bay, serve as nursery grounds (Mercer 1989). Chesapeake Bay serves as a nursery for weakfish, with upstream, lower salinity locations favored during summer (Mercer 1989). Weakfish tend to move farther upstream as they grow (Szedlmayer *et al.* 1990). Feeding and growth rates are directly related to water temperature (Lankford and Targett 1994). Larval weakfish are known to feed upon copepods, as well as larvae and eggs found in the water column (Goshorn and Epifanio 1991), while juveniles feed largely upon mysid shrimp and anchovies (Mercer 1989).

Stock size of weakfish has been declining, and reduced catches are attributed to overharvesting (McHugh and Conover 1986, VIMS and VMRC 1995), at least part of which is bycatch of the shrimp industry (Branstetter 1995, Murray *et al.* 1992).

White perch

White perch (*Morone americana*) are important in the river ecosystems both as predator and prey. As predator, juvenile white perch have been identified as potential contributors to mortality of striped bass larvae (McGovern and Olney 1988, Monteleone and Houde 1992) and the larvae of the two species have been identified as resource competitors (Cowan *et al.* 1993). Prey of adult white perch include killifishes (Morgan and Godin 1985), other small fish, and a variety of invertebrates (pers. obs.). Several species of fish are known to consume the eggs of white perch (McGovern and Olney 1988), the larvae are eaten by bluegill (*Lepomis macrochira*) (Margulies 1990), and the copepod (*Cyclops bicuspidatus thomasi*) (Smith and Kernehan 1981), and adults are food for bluefish

(*Pomatomus saltatrix*) (Juanes *et al.* 1993).

Growth of white perch larvae is positively correlated with temperature (Houde and Morin 1990), while hatching and duration of the yolk sac stage are inversely correlated (Margulies 1989). Other physical environmental factors that affect white perch are suspended sediment, which reduces hatching success (Auld and Schubel 1978), and river flow, which affects growth rate (Weisberg and Burton 1993).

White perch overwinter in deep holes in the rivers, where they may comprise 85% of the fish found (Kasul *et al.* 1992). Since white perch and striped bass occupy some of the same territory in the winter, and spawning and nursery grounds overlap extensively, it is not surprising to find occasional hybrids (Harrell *et al.* 1993) and similar patterns of YOY between these congeners. The early life history is strongly dependent upon juvenile recruitment. Indices of abundance of age 0 white perch collected in the nursery grounds predict the index of abundance of age 1+ fish collected by otter trawl a year later, in downriver locations (Mosca *et al.* 1994).

Oysters

One of the most studied species in Chesapeake Bay is the American oyster, *Crassostrea virginica*. Overfishing has substantially reduced stocks and is considered a more important cause of the observed decline in oyster population than disease or water quality (Hargis and Haven 1995, Rothschild *et al.* 1994). While disease, which is uncontrollable, reduces stocks in all but the least saline areas, overharvesting continues everywhere the oyster persists in Virginia. However, other influences also affect oyster life history.

Oyster setting in the James River is related to circulation patterns and fortnightly stratification (Haven and Fritz 1985). Viability of eggs, fecundity (Mann 1993), spatfall (Newell *et al.* 1989), and condition index (Austin *et al.* 1993) are related to salinity or riverflow. River discharge has been related to adult oyster population size in Apalachicola Bay, Florida (Wilber 1992).

Temperature controls several aspects of oyster biology. Oysters begin feeding when water temperatures rise above 10°C (Galtsoff 1964), and condition index generally increases until temperatures surpass 22°C, at which point spawning begins (Austin *et al.* 1993). Condition index has two peaks, one preceding spawning and another preceding overwintering (Haven 1960, Austin *et al.* 1993).

Freshwater discharge is influential in the life history of oyster. High flow in winter and spring can greatly reduce spat population, as happened when overwintering 1957 yearclass spat were killed by freshets in the spring of 1958 (Andrews *et al.* 1959), and again when mortality of the 1979 yearclass James River spat was induced by prolonged periods of low salinity (Haven 1982).

Extreme summer drought also will result in reduced spat populations. The 1960 drought in Tidewater, Virginia as reflected in the Palmer Drought Index is significantly reflected in reduced spat counts in the James and Rappahannock Rivers (Austin *et al.* 1995). The oyster diseases MSX and Dermo are important sources of oyster mortality, and are under the influence of salinity. In the period 1986-87 drought caused increased salinity in the Virginia rivers, and with the salinity increase both diseases proliferated up-river and up-Bay, causing extensive mortality (Hargis and Haven 1988). MSX has long been linked to oyster mortality in parts of the Bay where salinity averages 15+ ppt (Hargis and Haven 1988).

Oyster spat settlement, survival and growth are very dependent upon the dissolved oxygen (DO) content of the water column. Spat have been found to settle and grow little, and mortality is high under hypoxic conditions, and settlement and growth are nearly nonexistent, again with very high mortality during anoxia, compared to normoxic conditions (Baker and Mann 1992).

Predation plays an important part in oyster population dynamics. Blue crabs are known to consume juvenile oysters, with smaller animals being preferred prey (Krantz and Chamberlin 1978, Bisker and Castagna 1987, Eggleston 1988). Another important predator is the oyster drill. Drill predation is dependent upon water temperature and salinity, with refuges existing below temperatures

of about 12.5°C and salinities of about 7.5 ‰ (Garton and Stickle 1980). Further, prolonged exposure to salinities of less than 9‰ is fatal to oyster drills, while oysters can withstand considerably lower salinity (Gunter 1979). Low river discharges (and therefore increased salinities) probably result in increased predation pressure on oysters (Wilber 1992). Oyster drills locate prey by following chemical trails in the water (Rittschof *et al.* 1982). Oyster drills, especially small drills, feed most efficiently on small oysters (Garton 1986). Another important oyster predator is the flatworm *Stylochus ellipticus* (e.g. Landers and Rhodes 1970, Christensen 1973, Morales-Alamo *et al.* 1988). The sea anemone *Diadumene leucolena* is considered a controlling predator of oysters in the Maryland portion of the Bay (MacKenzie 1977). While not a predator, the relationship with the pea crab *Pinnotheres ostreum* is somewhat less than symbiotic, with crabs being associated with a lower oyster condition index (Haven 1959).

Species for which there is no fishery:

Because there is no fishery for these species, and the group to follow, they are important to this study precisely because the population dynamics lack harvest pressure as a source of mortality. This study will concentrate on forcing attributable to the physical environment, and comparisons between these species and harvested species with similar juvenile habitats will be important.

The minnows, gizzard shad, shiners and darters share nursery grounds with the catfishes, striped bass and white perch. Juveniles of these species exist in regions where freshwater discharge and temperature are likely to be important factors.

Eastern silvery minnow

The eastern silvery minnow (*Hybognathus nuchalis*), a freshwater species found in the nursery grounds of many estuarine species, is a phytophagous herbivore that crops algae (Harnois 1992, Cavender and Coburn 1988). There is also evidence that all members of the genus filter diatoms and other small food objects with an arrangement of pharyngeal taste buds (Coburn and Cavender 1989).

Gizzard shad

Gizzard shad (*Dorosoma cepedianum*) is an important forage fish, the recruitment dynamics of which are not well known (Allen and DeVries 1993). In experimental settings, growth of larval gizzard shad has been shown to be directly related to food availability and inversely related to population density, although growth did not correlate with density in the field (Welker *et al.* 1994). In closed systems, such as lakes, gizzard shad are known to have a controlling influence on the population dynamics of zooplankton, which are the forage of this open water planktivore (Beaver *et al.* 1994, Welker *et al.* 1994, Dettmers and Stein 1992, DeVries and Stein 1992, Lazzaro *et al.* 1992).

Shiners

The spottail shiner (*Notropis hudsonius*) and satinfın shiner (*Cyprinella analostanus*) inhabit freshwater portions of the major Virginia tributaries, and are collected in the VIMS beach seine survey. Both species are known to consume yolksac larvae of striped bass and white perch (McGovern and Olney 1988). They are among the host species used by freshwater mussels (Hove and Neves 1994, Weaver *et al.* 1991), many of which are endangered. Shiners are important bioindicator species in the study of water-quality and pollution (*e.g.* Suns *et al.* 1991, Heming *et al.* 1989).

Tessellated darter

The tessellated darter (*Etheostoma olmstedi*) is a small fish found in the upstream portions of the major Virginia tributaries, areas used as nursery grounds for many fish species. Under laboratory conditions the darter is known to prey upon larvae of striped bass, and will also probably consume white perch larvae (McGovern and Olney 1988). Tessellated darter is a host for the glochidia stage of some freshwater mussels (Michaelson and Neves 1995). The darter is tolerant of a wide range of environmental conditions and is widespread in distribution (Goodchild 1993), and unlike many congeneric species is neither endangered nor threatened.

Blackcheek tonguefish

The blackcheek tonguefish (*Symphurus plagiusa*) is an inhabitant of the lower Chesapeake Bay (Olney and Grant 1976) and the river mouths. This flatfish is not commercially harvested. Representatives of the genus are found off both coasts of North America, in deep oceanic (Yevseyenko 1990, Munroe and Mahadeva 1989) and shallow coastal water (Hendrix Kramer 1991, Brown *et al.* 1987). The blackcheek tonguefish is found at least as far south as Puerto Rico (Van Der Veer *et al.* 1994).

Bay Anchovy

The bay anchovy (*Anchoa mitchilli*) has tremendous reproductive potential. The species reproduces for up to a third of the year (Olney 1983, Luo and Musick 1991), with individuals spawning from once every one and a half to four days (Luo and Musick 1991). The abundance of food suitable for anchovy larvae determines the duration of the peak spawning season (Castro and Cowen 1991). A single female may produce over 45 thousand eggs in a season (Luo and Musick 1991). Bay anchovy larvae and eggs are among the most abundant of species in the ichthyoplankton, often dominating collections (Olney 1983, Setzler-Hamilton 1987).

Bay anchovy is a vital element of the Chesapeake Bay food chain (Tucker 1989). Predators include striped bass (Scofield 1928, Hollis 1952), bluefish (Friedland 1988, Juanes *et al.* 1993), ctenophores (Monteleone and Duguay 1988, Cowan and Houde 1990, Cowan and Houde 1991), and jellyfish (*Chrysaora quinquecirrha*) (Dorsey and Houde 1992). It has been estimated that bay anchovy could provide over 30 thousand kg of biomass per km² per year (Luo and Brandt 1993). Anchovies school during daylight, but not at night, perhaps in avoidance of predators (Luo 1993).

Other interspecies interactions involving bay anchovy are known, such as competition with or displacement by Atlantic silversides, and a positive relationship (perhaps enhancing of habitat by one species, or a benefit of mixed schooling) with the Atlantic brief squid (Ogburn-Matthews and Allen 1993).

Hogchoker

The hogchoker (*Trinectes maculatus*) is a species of considerable abundance in the Virginia rivers, and is well represented in the VIMS trawl survey data. Hogchoker eggs were among the three most abundant fish egg species in an eight year collection on the upper Chesapeake Bay (Setzler-Hamilton 1987). Spawning occurs in June in Elizabeth River (Smith 1986), and while spawning occurs in midsummer in the Hudson River, it may occur over a longer period of time in Chesapeake Bay (Koski 1978).

Geographic range and abundance are important considerations in choosing animals as indicators of water quality (Eisler 1986), and these characteristics may have been influential in choosing the species for a PAH study on Elizabeth River where hogchoker were found to exhibit skin lesions, fin erosion and hyperanemia in response to PAH exposure (Hargis and Zwerner 1984).

Hogchoker may be important controlling predators of soft-shelled clams (*Mya arenaria* and *Macoma balthica*). The influence is indirect, for the whole clam is not eaten, nor is it killed; siphons are "nipped" (Haddon *et al.* 1990, Hines and Lipcius 1990), causing clams to move closer to the surface where they are more vulnerable to predation by other species, in particular blue crabs, a whole-clam consumer (Hines and Lipcius 1990). Predation by hogchokers alone does not reduce infaunal densities (Virnstein 1977).

Meteorological and hydrological influences are known to affect hogchokers, particularly the survival of larvae (Mihursky *et al.* 1981). Adults are known to be driven out of deep water by hypoxic events, but usually return with the resumption of normoxia (Pihl *et al.* 1991). Fish of greater size and maturity are associated with greater salinity, and gradients of reduced salinity may restrict the geographical range and movements of hogchoker (Smith 1986). Although Smith (1986) was unconvinced of the importance of temperature as a signal to begin or end spawning, and though spawning site selection was found to be based on salinity, he found that upriver migration was initiated by a temperature decline to 12°C, and was completed by the time temperature fell to 10°C. The close

interaction of this species with temperature and salinity makes it a natural choice for this study.

Killifishes

Two species of killifishes are common in beach seine collections in the Virginia Chesapeake Bay tributaries, the striped killifish (*Fundulus majalis*) and the mummichog (*F. heteroclitus*). Killifishes are fairly well studied in scientific literature, but much of this attention is focused upon the role of the mummichog as an environmental indicator species (e.g. Eisler 1986). As a common salt marsh inhabitant, mummichogs, as prey, are an important link in the trophic structure of the marsh, as well as providing a controlling influence on infaunal community structure through predation on smaller predators (Kneib 1986).

The most important principles of theoretical ecology are demonstrated in the genus, for in addition to being predator and prey, and demonstrating a predation avoidance/foraging balance (Godin 1986), the four-species guild of *Fundulus* also exhibits interspecific competition within the Chesapeake Bay. While *F. heteroclitus* co-occurs with all members of the clan, *F. magalis*, *F. diaphanus* and *F. luciae* exclude each other from habitats delimited by tidal height and salinity (Weilberg 1986).

While killifishes are tolerant of a wide range of environmental conditions (Weisberg 1986), water temperature appears to have a controlling influence on reproductive timing (Hirshfield and Morin 1984). However, once water temperature is sufficiently elevated, killifish reproduce frequently (Lipcius and Subrahmanyam 1986). Eggs are deposited in the high marsh on spring tides, in ribbed mussel shells, and this may be the primary source of interannual variation for these species (Austin, pers. comm.). Like bay anchovy (Luo 1991), killifishes rarely attain an age of two years (Lipcius and Subrahmanyam 1986).

Although it is known that young killifishes avoid predation by inhabiting depressions and burrows in the intertidal zone during low tide (Kneib 1987), the role of these species in the salt marsh is considered to be poorly understood and in need of further study (Kneib 1986).

Silver perch

The silver perch (*Bairdiella chrysoura*) inhabits the higher-salinity (downriver) portions of the Virginia tributaries, and spawn concurrently with other sciaenids, such as weakfish and black drum (Daniel and Graves 1994). However, silver perch is also found in low-salinity waters (Rogers *et al.* 1984), and usually inhabits and spawns in relatively shallow areas (Ross and Epperly 1985, Sogard 1989, Rogers *et al.* 1984).

Silversides

The silversides (*Menidia sp.*) are an environmentally sensitive group, and the Atlantic silverside (*M. menidia*) has been selected as a bioassay organism by the Environmental Protection Agency because it is particularly sensitive to pollution (Poole 1978). Members of the genus have been used in bioassay studies of pH (Dunson *et al.* 1993), bromochlorinated estuarine water (Roberts and Gleeson 1978), and cadmium toxicity (Voyer *et al.* 1979). *Menidia sp.* are widespread (Conover and Present 1990) and abundant (Cadigan and Fell 1985), important characteristics of bioassay organisms.

The various species of *Menidia* are important to the trophic dynamics of salt marsh/estuarine systems, moving considerable energy outward from the marshes (Conover and Ross 1982, Cadigan and Fell 1985). They are important in the diets of predatory fish, such as the bluefish (*Pomatomus saltatrix*), for which a fish diet has been found to result in a higher condition factor than a diet of invertebrates (Friedland *et al.* 1988). *Menidia* are also important in the diets of birds, such as snowy egrets (*Egretta thula*), great egrets (*Casmerodius albus*) (Takita *et al.* 1984), and black skimmers (*Rhynchops niger*) (King 1989). The inclusion of *Menidia* in the diets of these birds may be related to the habitat preference of silversides in salt marshes. Silversides are found in great abundance in salt marsh creeks, as opposed to under cover of vegetation such as eelgrass (*Zostera marina*) and sea lettuce (*Ulva lactuca*) (Sogard and Able 1991).

Silversides are probably opportunistic feeders, and have been shown to take copepods (Poole 1978, Lucas 1982, Grover 1983, Cadigan and Fell 1985), plant material (Lucas 1982, Cadigan and Fell

1985), small fish (Cadigan and Fell 1985) including larval silversides (Lucas 1982), cypris (barnacle larvae) and amphipods (Lucas 1982), shrimp (Cadigan and Fell 1985), rotifers (Poole 1978), and crab larvae (Morgan 1990). It is interesting to note that silversides may be an important contributor to the population control of some crabs, at least in North Carolina (Morgan 1990). Feeding is thought to occur on ebb tides, perhaps because feeding is interrupted by turbidity on flood tides (Gilmurray and Daborn 1981). Many aspects of the life histories of *Menidia sp.* are related to temperature. Growth rate correlates positively with temperature; fish reared at temperatures typical of shallow salt marshes grow faster than fish reared at temperatures more typical of open bay waters (Narangansett Bay : 26–29 °C, 18–21 °C, respectively) (Bengtson and Barkman 1981). However, along the East Coast, Atlantic silversides grow faster at higher latitudes in shorter growing seasons, attaining the same size at the end of the growing season regardless of latitude, due to genetic differences among populations (Conover and Present 1990). Growth rate is also positively correlated with food availability (Letcher and Bengtson 1993). Batch fecundity (no. advanced ripeness eggs / g ovary-free body weight) increases from the beginning to the middle of the spawning season, then declines to the end of the season (Conover 1985), and at least the “turn off” mechanism seems to be temperature related (Hubbs and Bailey 1977). Temperature also controls the sex of silversides; young reared at cooler times of year predominantly become female, and those reared during warm months become male (Conover 1984, Conover and Fleisher 1986, Middaugh and Hemmer 1987). *Menidia* are also known to migrate to deeper water in winter (Conover and Ross 1982, Jessop 1983, Warkentine and Rachtin 1989), presumably based on temperature. In spite of this adaptive strategy, winter mortality can be as high as 99% (Conover and Ross 1982).

While the onset and termination of spawning season may be related to temperature, patterns of reproductive behavior within the season are tied to other environmental signals. Although spawning has been observed on the surface in somewhat deeper water (Moore 1980), it usually takes place in the intertidal zone during high tide (Middaugh *et al.* 1981, Middaugh and Takita 1983, Conover and

Kynard 1984, Middaugh *et al.* 1984, Middaugh and Hemmer 1984). Spawning occurs in daylight (Moore 1980, Middaugh and Takita 1983, Middaugh *et al.* 1984, Middaugh and Hemmer 1984) and is triggered by current velocity (Middaugh and Takita 1983, Middaugh and Memmer 1984). However, spawning coincides fortnightly with new and full moon, while frequency and intensity correlate with tidal height (Conover and Kynard 1984). Even more complicating is the observation that peaks of females with hydrated eggs occur when high tide occurs within one hour of sunrise (Middaugh *et al.* 1984). Eggs are deposited on plant stems or roots, and mats of detritus (Middaugh *et al.* 1981), and use of high intertidal regions seems to be related to predator avoidance rather than physical or chemical factors (Tewksbury and Conover 1987).

Although commercial fisheries exist for silversides at northern latitudes, notably Prince Edward Island and Annapolis River, Nova Scotia (Jessop and Morantz 1982, Jessop 1983), there are none in Chesapeake Bay. This, and the considerable and convoluted interactions with the physical environment, make silversides an attractive choice for this study.

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