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Synoptic scale climatic forcing of multispecies fish recruitment patterns in Chesapeake Bay

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SYNOPTIC SCALE CLIMATIC FORCING OF MULTISPECIES FISH RECRUITMENT PATTERNS IN CHESAPEAKE BAY

A Dissertation Presented to
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In Partial Fulfillment
of the Degree Requirements for the Degree of
Doctor of Philosophy

By
Robert J. Wood
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This dissertation is submitted in partial fulfillment of
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Abstract

Five fishery independent data sets were used to investigate multispecies fish recruitment patterns in Chesapeake Bay. Despite differences in sampling gear, sampled habitat, collection methods, and sampling sites, the strongest multispecies recruitment patterns within each data set (revealed by separate principal components analyses) depict a negative relationship between recruitment of spring spawning anadromous fishes and fall-winter continental shelf spawning species. This pattern was the evident within both low and high frequency components of the multispecies data set.

Because these two species groups utilize freshwater and oligohaline reaches of the Bay and its tributaries as springtime nursery areas, this Chesapeake Bay Anadromous-Shelf Spawner (CBASS) recruitment pattern was compared to spring climatic variability in the Mid Atlantic region. Using principal components analysis, cluster analysis, and a gridded sea level pressure (SLP) data set, an objective circulation classification technique identified ten synoptic-scale SLP patterns responsible for spring (Mar-May) weather conditions and interannual seasonal climate variability (1955-1998).

Classification and regression tree modeling, ordinary least squares, and least trimmed squares regression were used to compare covariability between the CBASS recruitment pattern and the thirty (3 months X 10 patterns) monthly frequency pressure pattern time series. March frequencies of two regional pressure patterns, the Azores-Bermuda and Ohio Valley high pressure systems, were found to account for a large portion of the CBASS pattern's variability.

Spring conditions in March, brought on by an early appearance of the Azores-Bermuda High, favor recruitment of shelf spawners while prolonged winter conditions, brought on by a relative dominance of the Ohio Valley high, favor anadromous spawning success. These observations are supported by an analysis of March temperature and precipitation anomaly patterns for the continental U.S.

Analyses of hydro-climatic, species specific zooplankton density, and juvenile fish abundance variables for three Bay tributaries clearly suggest that the timing of the winter-spring transition differentially influences nursery area habitat suitability in a pattern that is consistent with the climate-CBASS recruitment relationships described in this study. The climate-recruitment relationships described in this study represent a multivariate variant of Cushing's Match-Mismatch hypothesis.

SYNOPTIC SCALE CLIMATIC FORCING OF MULTISPECIES FISH RECRUITMENT PATTERNS IN CHESAPEAKE BAY

Chapter One

Multispecies recruitment patterns within the Chesapeake Bay

INTRODUCTION

Despite a century of fisheries research, few general statements can be made regarding the causes of the strong recruitment variability that occurs in many economically and ecologically important fish species. This lack of progress continues to hinder both effective fishery management and general progress in the field of fisheries science.

Mechanisms driving recruitment variability operate on a wide range of scales. For example, micro-scale turbulence, which governs prey encounter rates for larval fishes (Rothschild and Osborn, 1988), may affect growth and therefore, size-sensitive survival rates (Ware, 1975; Shepherd and Cushing, 1980). Synoptic scale (100's-1000's of kilometers) climatic variability may also influence recruitment levels through its affects on egg and larval transport/advection (Sinclair, 1988; Sinclair and Iles, 1989), spring bloom dynamics (Cushing, 1969, 1982), and physiological condition (Heath, 1992). Processes operating on these spatial scale extremes are difficult, if not impossible to address experimentally. For this reason, and despite critics (Walters and Collie, 1988), historical data analysis has been, and continues to be, an important method of investigating the role of environmental forcing in determining fish recruitment rates (Sharp, 1995; Francis and Hare, 1994; Myers, 1998).

Traditionally, historical analyses have focused on single species recruitment time series and utilized a correlative model building approach in trying to understand or forecast recruitment variability (Hollowed et al., 1987). To date, these types of studies have yielded little insight into the processes which determine recruitment levels and provided few, if any useful predictive models (Myers, 1998; Shepherd et al., 1984).

One problem correlative models may suffer from is the lack of accurate recruitment data. Many previous studies have relied upon recruitment time series hindcast from commercial catch, or catch-per-unit-effort (CPUE) data. Such time series can be strongly influenced by fishery-related factors unrelated to recruitment success, such as trends in discards (Myers et al., 1997a) and shifting management regimes.

An alternative approach to traditionally practiced correlative studies involves identifying repeating patterns in recruitment that occur across space (Koslow, 1984; Shepherd et al., 1984; Myers et al., 1997b), across species (Hollowed and Wooster, 1992; Zheng, 1996), or across both space and species (Luch-Belda, et al., 1989; Hollowed et al., 1987, Hollowed and Wooster, 1995; Spencer and Collie, 1997). One advantage of this approach is that patterns repeated across multiple data sources are likely to provide more reliable response variables in investigations of recruitment variability, compared to single stock, single species time series (Hollowed et al., 1987; Bakun, 1996; Myers, 1998).

Perhaps more importantly, the existence, scale, and interspecies relationships of repeated patterns may yield valuable insight into the nature of the processes driving recruitment variability (Koslow, 1984; Koslow, 1987; Cohen et al., 1991; Myers et al., 1997). Further, multispecies patterns may provide basic information required to devise effective multispecies and ecosystem fishery management strategies (Ludwig et al., 1993; Christensen, 1996).

This investigation employs a suite of fishery independent young-of-the-year (YOY) abundance surveys in the Chesapeake Bay (38° N & 76° W) to study the multispecies recruitment patterns within the estuary and its tributaries. Throughout this work, the term recruitment will refer to the number of fish surviving to the juvenile life stage. This choice is based upon previous findings that, at least for the most well researched Chesapeake fish within this study, the striped bass (*Morone saxatilis*), annual cohort strength appears to be set by this life stage (Goodyear, 1985).

Because of the wide range of collection methods employed by the surveys in this study (gear type, sampled habitat, geographical location, and species sampled), repeating patterns identified here should reliably characterize the temporal and spatial scales of recruitment variability over the last three decades within one of the world's largest and most productive estuaries. This information, coupled with the multispecies nature of identified recruitment patterns may prove valuable in the search for mechanisms which drive recruitment variability within this ecosystem.

METHODS

Data set descriptions

The primary data set

Five data sets are used in this study (Figure 1.1). Of these, the Maryland Department of Natural Resources' (MDNR) juvenile striped bass (*Morone saxatilis*) monitoring survey possesses the longest period of record, employing consistent sites and methods since 1966. This annual survey monitors fixed sites on a monthly basis from July through September using a 6.4mm bar mesh bagless beach seine 30.5m long and 1.24m high (Maryland Fisheries Service, 2000).

While designed to monitor the striped bass, this survey effectively monitors YOY relative abundance of other estuarine species as well. The fourteen most numerically abundant species over the survey's period of record (1966-1998) were used for this analysis. Due to the statistical advantages of longer time series, this data set is considered the 'primary' data set for this study. Five other (ancillary) data sets are similarly analyzed in order to corroborate the MDNR seine data results and investigate the spatial and temporal persistence of any identified patterns.

VIMS seine survey

The MDNR striped bass seine survey has a Virginia compliment. Using similar gear and methods, the Virginia Institute of Marine Science (VIMS) also effectively monitors YOY abundance for many estuarine species while targeting striped bass. Five rounds of sampling are carried out for eighteen fixed sites over the months of July-September since 1980. These sites are located between river miles 21 and 56 (upstream distance from the river mouths) on the three largest Bay tributaries in Virginia, the Rappahannock, York and James Rivers.

As with each ancillary data set in this study, species from this survey were included in the analysis only if they matched those fourteen chosen from the MDNR survey and had no zero annual catches. This latter criterion was designed to ensure that all species included were adequately monitored by their respective surveys. Each species excluded due to this zero annual catch criterion featured at least five 'no-catch' years during a survey's sampling period.

VIMS trawl survey

Annual recruitment in these same three Virginia tributaries is also monitored by the VIMS Juvenile Fish and Blue Crab Trawl Survey on a monthly basis. This survey's sample sites are fixed river channel sites at approximately five mile intervals, also within the three primary Virginian Bay tributaries. Initiated in 1955, methods and gear and sites have been consistent on all three river systems since 1979. Due to sampling gear and sampled habitat differences, only four of the fourteen MDNR seine survey species chosen are effectively monitored by the VIMS river trawl survey. For reasons described later in this paper, a fifth species, not included in the MDNR survey, summer flounder (*Paralichthys dentatus*) was also included.

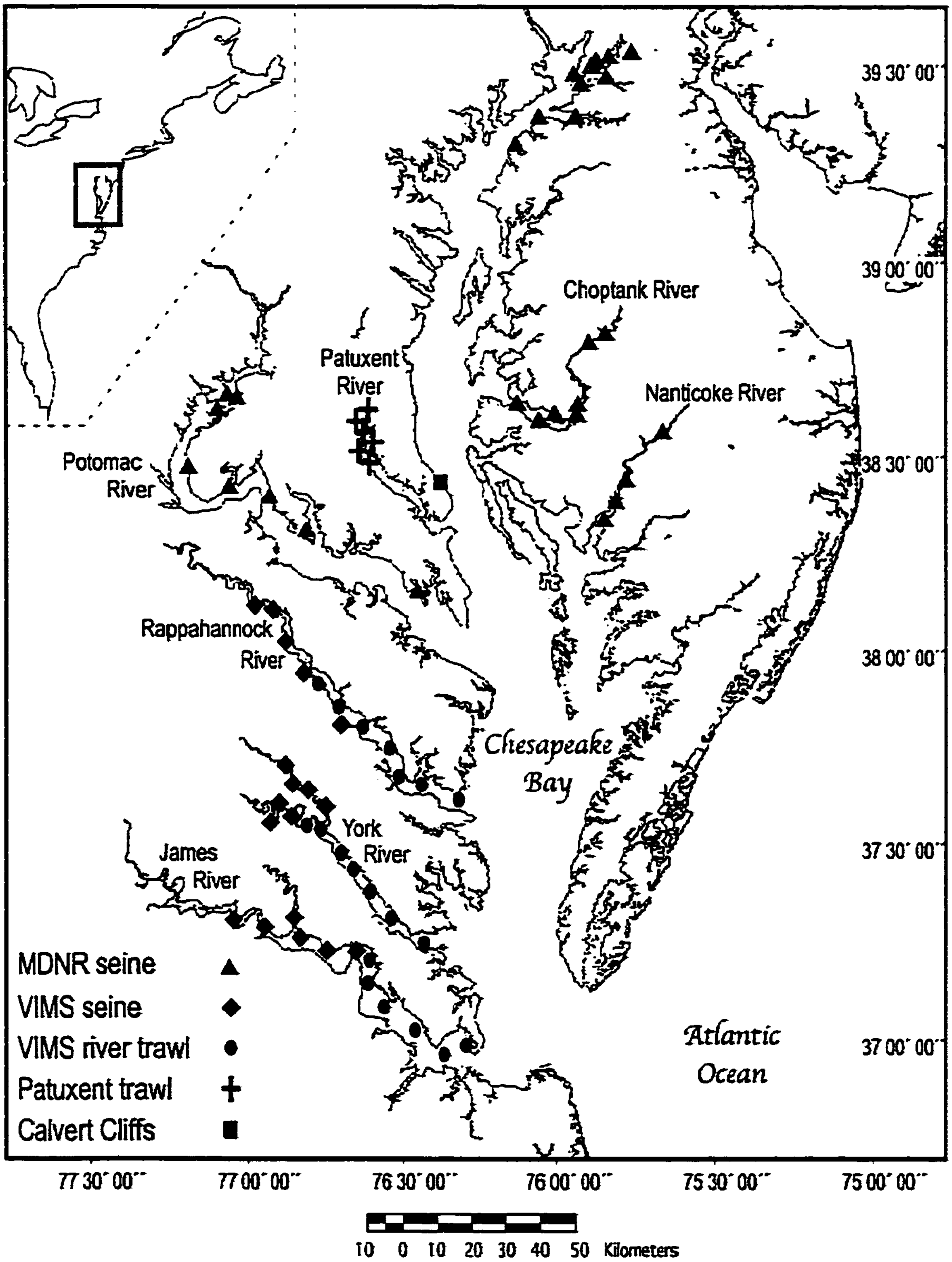

FIGURE 1.1. Sample location map for all study sites.

Patuxent river trawl survey

Another source of data was the Potomac Electric Power Company's (PEPCO) Patuxent River trawl survey. Also designed to monitor the abundance of YOY striped bass, this survey is similar to the VIMS trawl survey except that it uses a smaller (dimensions) bottom trawl, a smaller boat, and samples fewer locations (Jules Loos, personal communication). Again, because of methodological and habitat differences, only six of the fourteen MDNR seine survey species are effectively monitored by this survey.

Calvert Cliffs Nuclear Power Plant (CCNPP) impingement data

To further ensure that identified patterns were not gear- or site-derived artifacts and to increase the spatial coverage of this investigation, data from the Calvert Cliffs Nuclear Power Plant (CCNPP) impingement study was also acquired. While not designed to monitor YOY abundance, impingement of fishes and blue crabs (*Callinectes sapidus*) on 1 cm^2 mesh rotating screens protecting flow-through (0.3 m/sec) cooling water intake structures was sampled by the Academy of Natural Science's Estuarine Research Center (ANSERC) for the years 1975-1994 (Hixson and Breitburg, 1993). This unique data set provided an additional opportunity to examine the affects of gear and geographical location on the observed patterns of multispecies recruitment in the Bay. Eight of the fourteen MDNR species were effectively monitored by this 'survey'. Again, for reasons described below, summer flounder was included in the CCNPP analysis as a ninth species.

Data processing

The primary data set (MDNR seine survey) includes catches for over one hundred different species. A subjective decision was made to include only the fourteen most abundant species over the data set's period of record. Limiting the species to fourteen ensured a relatively high case to variable ratio (approximately 2:1) required for robust statistical results. In all other (ancillary) data sets, a subset of available species was used (Table 1). As previously indicated, species' inclusion is based upon occurrence in the primary (MDNR seine) data set and also sampling adequacy (no zero annual catches).

TABLE 1.1. Characteristics of surveys used in this analysis.

Survey	Sampling frequency	Sampling design	YOY distinction	Number of species	Period of record
MDNR beach seine	Monthly July-October	MD Bay and tributary fixed sites	Length-frequeny analysis	14	1966-present
VIMS beach seine	Bi-monthly July-September	Tidal VA tributary fixed sites	Length-frequency analysis	14	1980-present
VIMS river bottom trawl	Monthly Year-round	Rappahannock, York & James rivers, fixed channel sites	Length-frequency analysis	5	1979-present
Patuxent bottom trawl	Bi-monthly May-October	Patuxent River fixed river sites surrounding Chalk Point, MD	Length-frequency analysis	5	1988-present
Calvert Cliffs Nuclear Power Plant impingement study	Three six-day sampling periods per month. Two daily samples taken 3 hours apart.	Western shore central Bay site. Artificial lagoon walled from surface to six meters.	0.3 m/sec intake flow assumed YOY-selective	9	1975-1994

An exception to these criteria was made after analyses of the MDNR and VIMS data sets. These results demonstrated that spot (*Leiostomus xanthurus*) and Atlantic menhaden (*Brevoortia tyrannus*) annual recruitment is synchronous. Since these species share common life history characteristics, care was taken to ensure this possible 'life history group' was adequately represented in each data set's analysis. Because the VIMS river trawl does not adequately sample Atlantic menhaden, summer flounder was added to this data set's species assemblage. Summer flounder was chosen because it is well monitored by this trawl survey and, like spot and menhaden, summer flounder is a Mid-Atlantic fall-wintertime coastal spawning estuarine dependant fish relying upon favorable spring conditions to transport its larval and postlarval stages into the Chesapeake Bay.

Summer flounder was also included in the CCNPP data set. Since this data set adequately samples all three species, this allowed for a direct comparison of their annual recruitment patterns and therefore provided a check of the assumption that summer flounder was appropriately included as a coastal spawning proxy species for menhaden in the VIMS river trawl analysis.

YOY cohort distinction

Raw data for each data set was processed in order to arrive at the best survey-specific estimate of relative annual YOY abundance. Except for the CCNPP impingement data set, either all fish are measured, or all fish are counted and only a representative subsample is measured. Distinction between YOY and +1 year fishes was accomplished through historical length-frequency analysis (for an example, see Figure 1.2). For each species and data set, length frequency data over the entire time period was plotted for each calendar month. 'Cutoff' lengths and months were established using these plots in order to include only YOY fishes. These plots clearly display 'bell-shaped' Gaussian (or partial curve before full recruitment to the gear) fork length distributions for YOY fish which are distinct (smaller mean size) from the size distributions of older fishes also caught in the gear.

Unfortunately, no fish measurements are associated with the CCNPP impingement data. Because flow velocity at the impingement screens is relatively low (0.3 m/sec) however, most fishes were caught as YOY (Breitburg, personal communication). The exception to this rule may occur during the few years when hypoxic or anoxic conditions occurred in the intake lagoon. During these events, mass mortality occurred and older fish also became impinged. These events were documented in original data reports and were immediately apparent upon inspection of the data. Years featuring such events were excluded from the analysis.

Juvenile fish abundance observations during winter months (January-March) were not included for any data set. This step was taken in order to exclude variability unassociated with YOY population abundance. Such variability may result from interannual differences in winter conditions. For example, under colder conditions fish can concentrate near the bottom of the channel where temperatures are moderated. This would lead to unrepresentatively high catches in bottom trawl samples. It is also possible that prolonged or extreme cold could affect catchability through reduced gear avoidance responses of fishes.

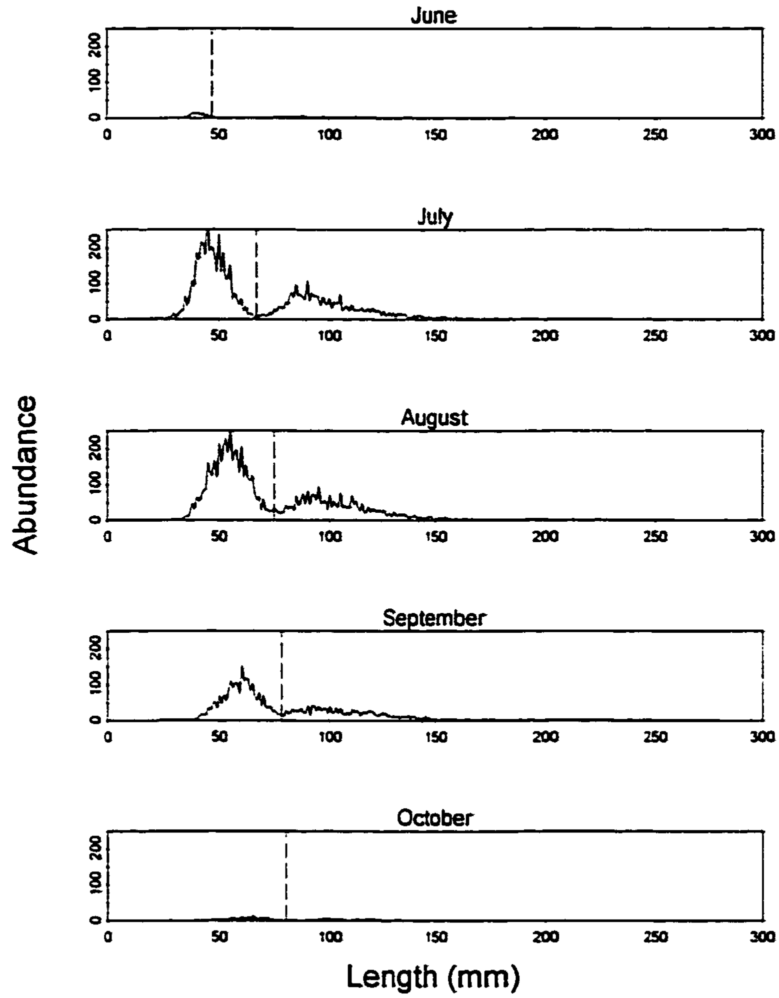

FIGURE 1.2. Monthly size frequency plot for white perch (*Morone Americana*) sampled by the VIMS seine survey 1980-1997 used for establishing the appropriate size range of young-of-the-year fishes.

Data Analysis

Principal component analysis (PCA) was used to identify and describe multivariate patterns in each data set because it has proven to be an effective, conceptually simple method of isolating important linear multivariate patterns among a set of intercorrelated variables (Pielou, 1984). Because it can simultaneously accomplish both signal isolation and data reduction, PCA has been, and continues to be, widely used in the marine sciences (examples include Koslow, 1984; Thompson and Hilden, 1987; Bianchi, 1992; Kope and Botsford, 1990; Mahon et al., 1998, Davidson et al., 1998; Tolimieri et al., 1998; Hare and Mantua, in press).

Principal components analysis was used to identify multispecies recruitment patterns present in each data set. In each of the five analyses, species' annual summed (over sampling sites) YOY catches served as variables. Following log transformation (base 10) of the recruitment time series, their distributions were approximately normal. Correlation matrices of the log transformed data were used as input for each survey data set's PCA. In using the correlation matrix as opposed to the variance-covariance matrix, each variable was standardized to feature a mean of zero and standard deviation of one prior to analysis. Because the catchability of each species is unknown for each gear, and is likely to differ among species, use of the correlation matrix was most appropriate. For this reason, this paper identifies multispecies patterns in relative (as opposed to absolute) abundance.

To account for all variance within a data set, a PCA always results in the same number of principal components (PCs or components) as original variables. Principal components are simply new variables formed from linear combinations of the original variables. These components are extracted sequentially from strongest to weakest, in terms of original data set variance captured. Variance accounted for by each PC, is in effect, 'extracted' after identification so that each PC is assured to be independent and uncorrelated with all others. Because the first few PC's often collectively account for a large proportion of the data set's total variance, fewer PC's than original variables are typically retained for further analysis. Remaining PC's are typically judged as unimportant and ignored.

Because little is known about multispecies recruitment patterns in the Chesapeake Bay, the concern here is to identify and define the 'strong' patterns evident in the data sets at hand. In this study, PC importance is evaluated by using two criteria. First, using Kaiser's (1960) 'eigenvalue greater than 1' rule and secondly, using Overland and Preisendorfer's (1982) N-rule.

Kaiser's rule simply judges any PC with an eigenvalue greater than one as likely to contain useful information. This is because, for any correlation-based PCA, the sum of all PC eigenvalues equals the number of original variables analyzed. In the context of PCA, eigenvalues are proportional to the variance of a PC's observational scores and therefore are indicative of a PC's signal strength. Theoretically, a data set with no important multivariate patterns (where all variables are uncorrelated) would feature a spheroidal data cloud without a major axis. In this case, all PC's would be equally (un)important and feature eigenvalues of one. Therefore, eigenvalues greater than one theoretically occur only for PC's containing meaningful signals.

In reality, even randomly generated data will not be perfectly spheroidal. Therefore eigenvalues will always range from greater than 1 to less than 1, even when no real information is present. Overland and Preisendorfer's N-rule acknowledges this, by using monte-carlo simulation to set variance or eigenvalue based standards for each PC. To do this, a large number (1000 in this case) of randomly generated data sets are created with the same dimensions as the study data set (n observations by p variables). These (1000) random data sets are analyzed resulting in p eigenvalues in each case. Typically, the 95th percentile eigenvalue (based on an alpha of 0.05), for each of these p PC eigenvalue distributions, is used as a threshold in judging the importance (signal to noise ratio) for each of the respective study data set PCs. Any study data set's PC featuring an eigenvalue greater than its corresponding monte-carlo derived threshold, is considered to represent an important multivariate signal.

Perhaps the simplest method of interpreting a PC is through the correlation between its observational scores and the time series of the original variables. When correlation between a PC and variable (species in this case) is high. that variable is an integral part of the multivariate signal the PC represents.

Because autocorrelation and time series stationarity have been an issues in previous multispecies recruitment studies (Koslow, 1984; Cohen, 1986; Koslow et al., 1987; Thompson and Page, 1989; Cohen et al., 1991), recruitment time series and PC scores will be evaluated for these characteristics. Lowess smoothing (Cleveland, W. S., 1979; Chambers, et al., 1983) and first differencing (Cohen et al., 1986; Thompson and Page, 1989; Pyper and Peterman, 1998) are used to remove autocorrelation and attenuate high frequency variability in the original recruitment time series. Resulting processed or 'prewhitened' data sets (both first differenced and lowess fit residual series) will be analyzed in the same manner as the original recruitment data.

RESULTS

PC species loadings

The number of PC's meeting both the N-rule and the eigenvalue greater than one rule (EV>1) criteria are listed in Table 1.2 (see also Figures 1.3 and 1.4). As expected, the N-rule was the more severe criteria and yielded between zero and three important PC's depending upon the data set. Two to five PC's were deemed important by the EV>1 rule. Because the objective of this study is to isolate and compare the strongest signals within the data sets, only the first two PC's from each analysis were retained. These two PC's together accounted for between 51% and 72% of their respective data set's total variance (Table 1.3).

TABLE 1.2. Number of important PC's using N-rule and Eigenvalue > 1 criteria (alpha = 0.5).

	MDNR	VIMS seine	VIMS trawl	Patuxent trawl	CCNPI
N-rule	3	1	1	0	2
Eigenvalue > 1	4	5	2	2	3

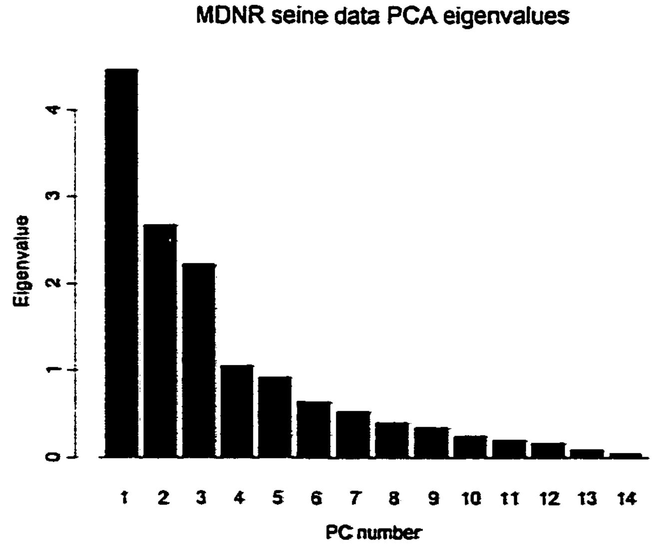

FIGURE 1.3. Scree plot of MDNR seine data analysis PC eigenvalues.

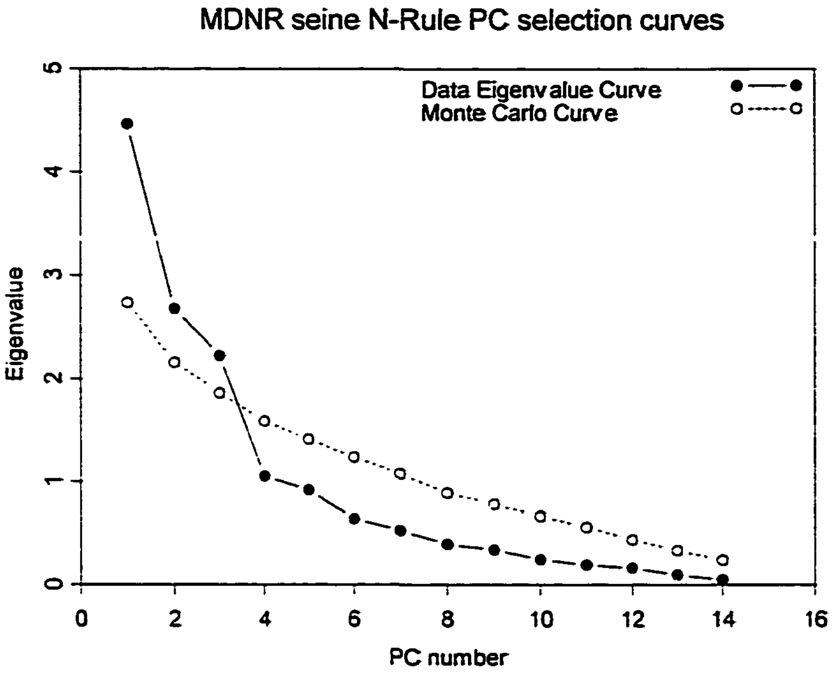

FIGURE 1.4. Results of the N-rule test of PC importance for the MDNR seine survey analysis (alpha=0.05)

TABLE 1.3. Proportion of total data set variance accounted for by PC1 of log transformed multispecies annual abundance across all data sets.

	MDNR seine	VIMS seine	VIMS trawl	Patuxent trawl	CCNPI
PC1	0.32	0.36	0.45	0.42	0.42
PC2	0.19	0.17	0.22	0.30	0.24
Sum	0.51	0.53	0.67	0.72	0.66

Since two PC's were retained for all data sets, PC biplots are the most efficient way to display the analyses' results. Biplots simultaneously ordinate scores and loadings for any two PC's. Since a PC is merely a linear composite variable formed from the original data set variables, they can be defined by the importance (a.k.a. weight or loading) of each variable for each PC. Component variable weights or PC loadings are correlations between a PC and the original variables, scaled to (divided by) the PC's standard deviation. Annual component scores indicate the magnitude and direction of a PC's signal for each observation. Biplots of all five analyses are displayed in Figures 1.5-1.9.

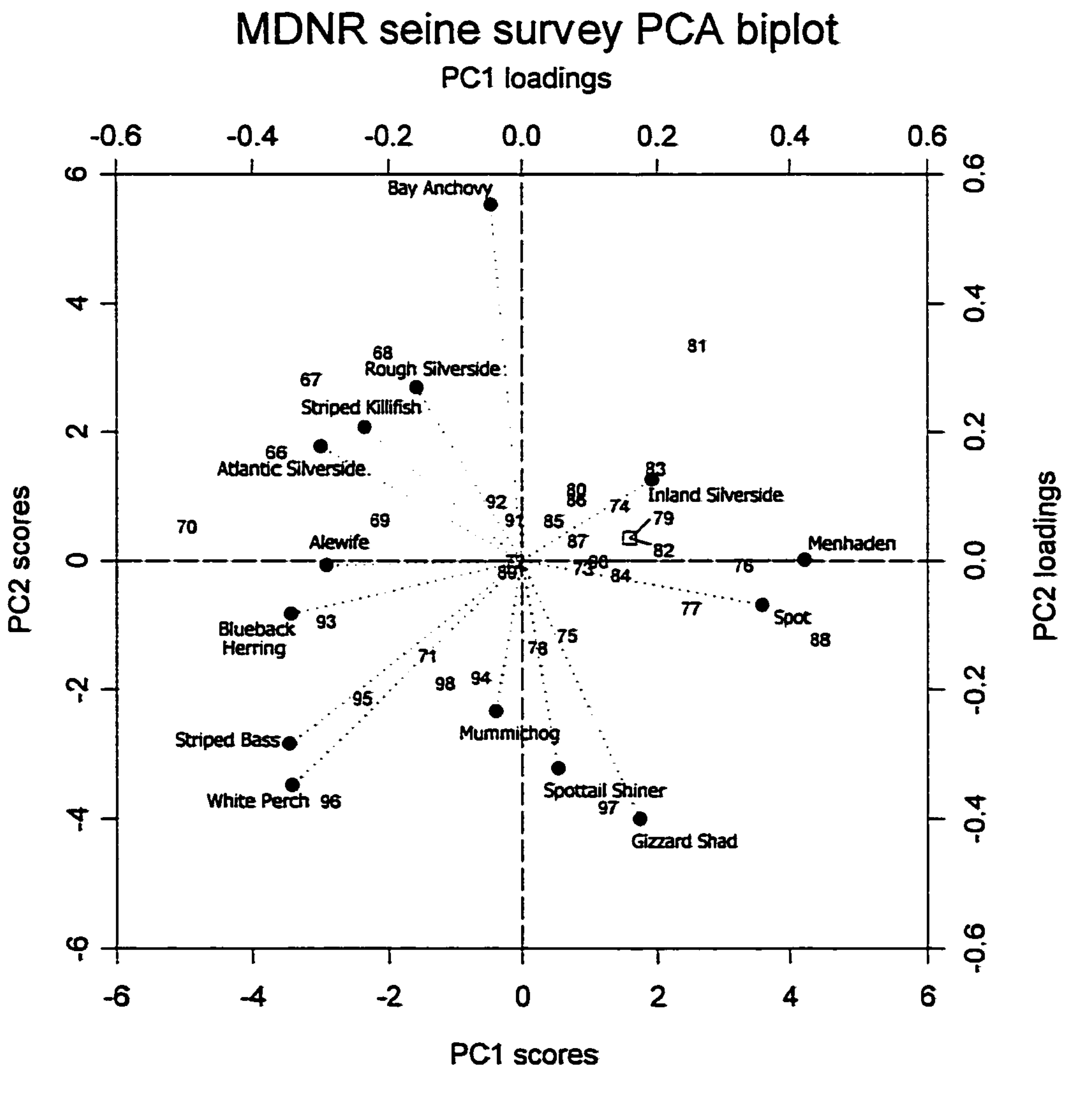

FIGURE 1.5. Biplot of MDNR seine survey PC's 1 and 2.

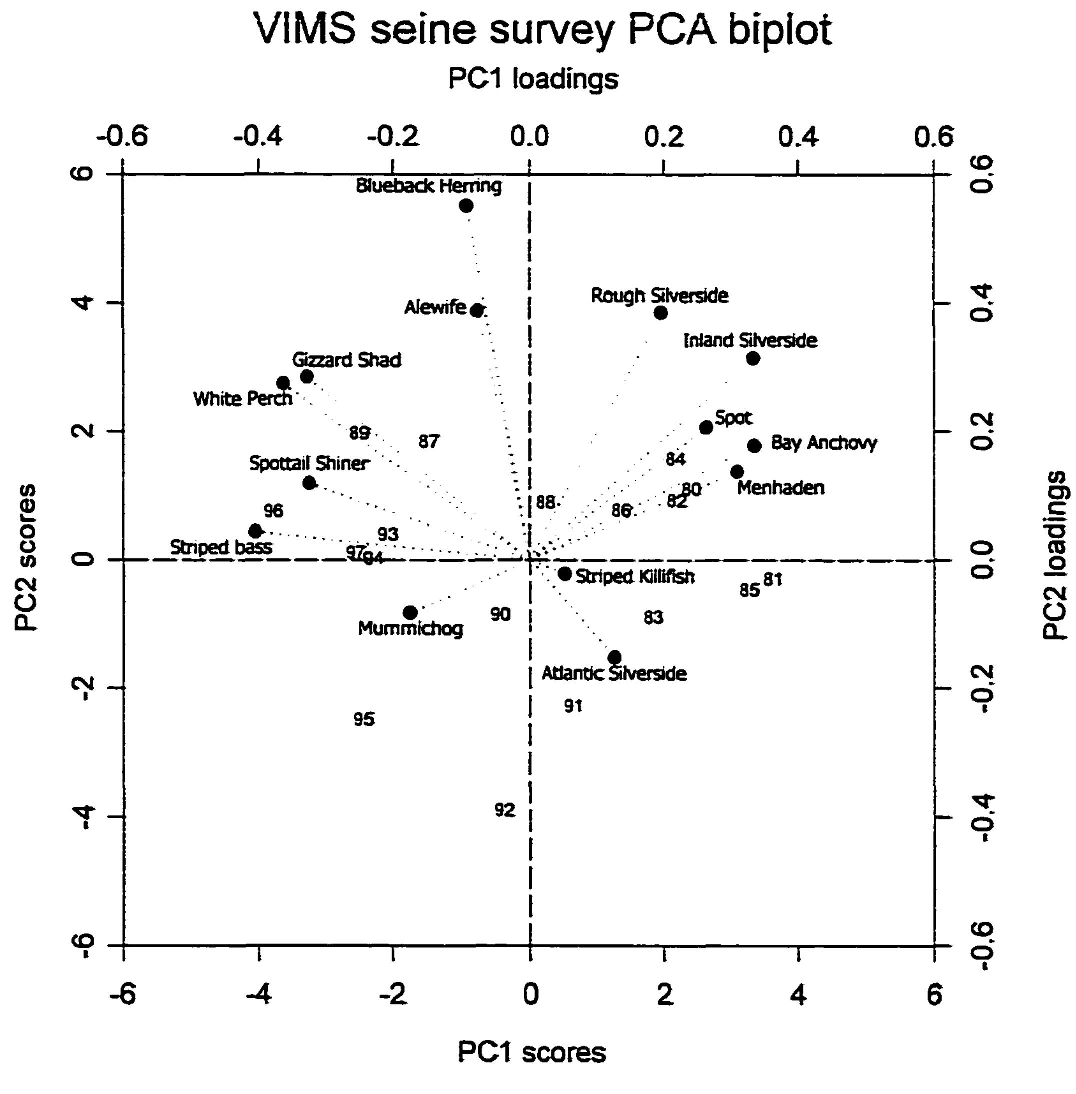

FIGURE 1.6. Biplot of VIMS seine survey PC's 1 & 2

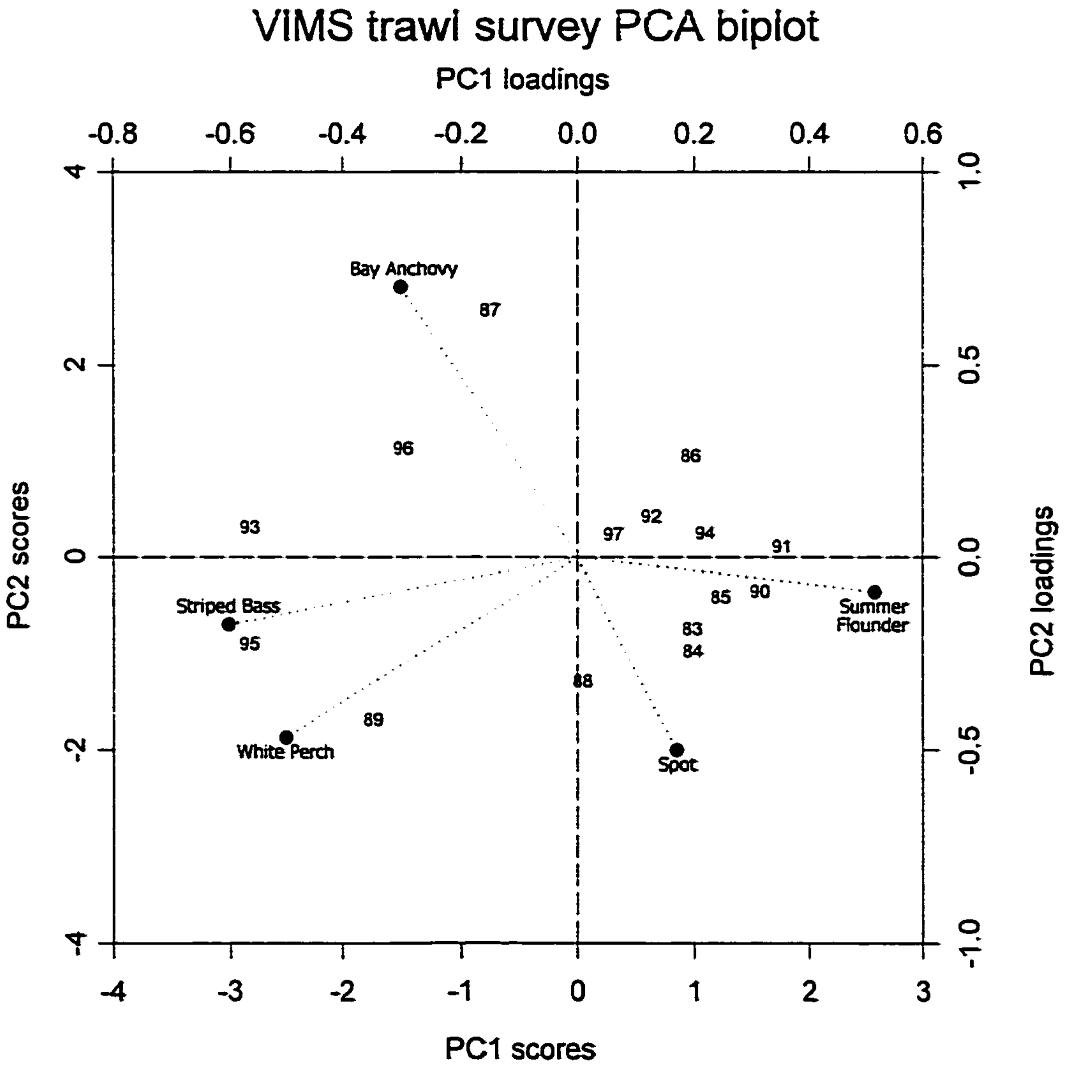

FIGURE 1.7. Biplot of VIMS seine survey PC's 1 & 2

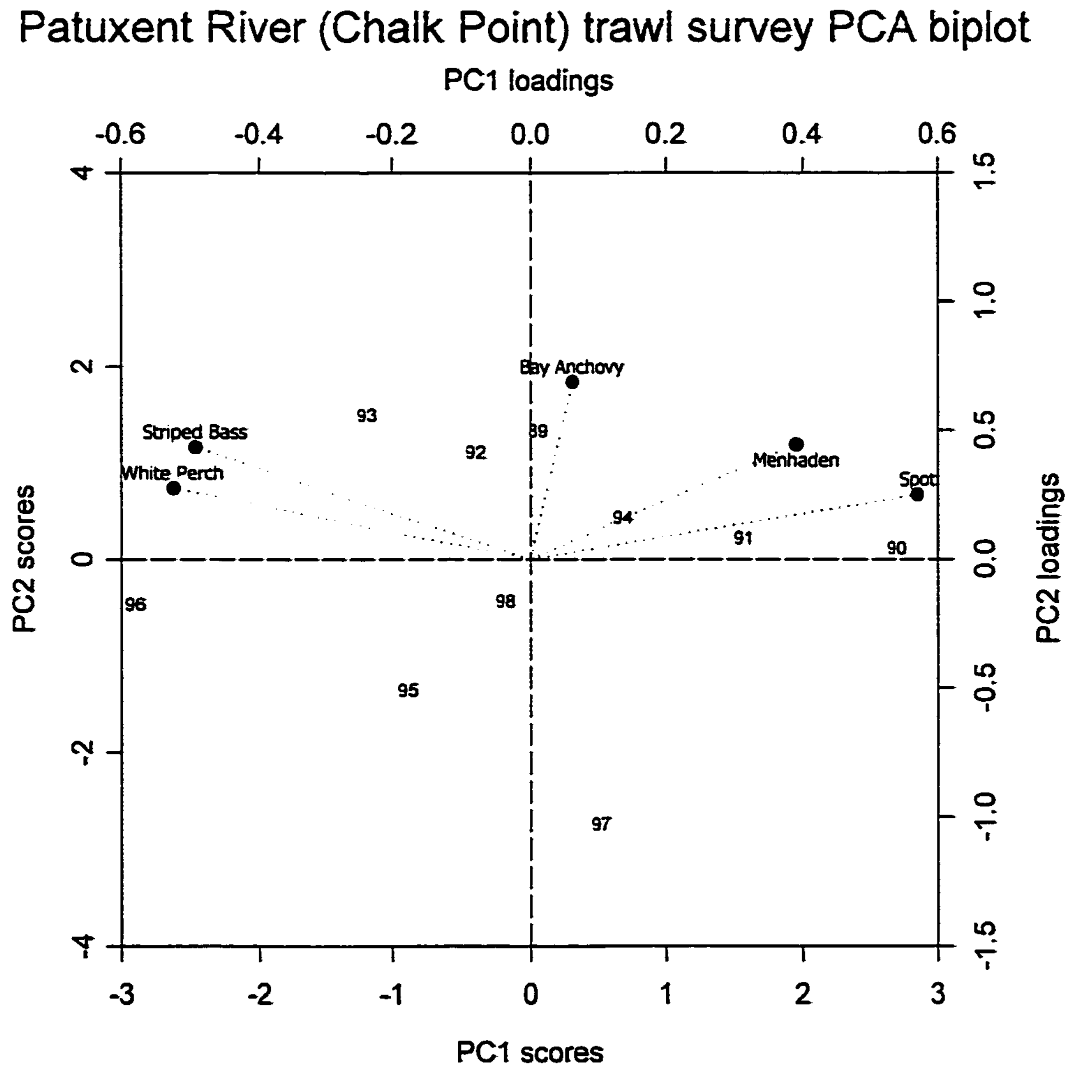

FIGURE 1.8. Biplot of Patuxent River trawl survey PC's 1 & 2

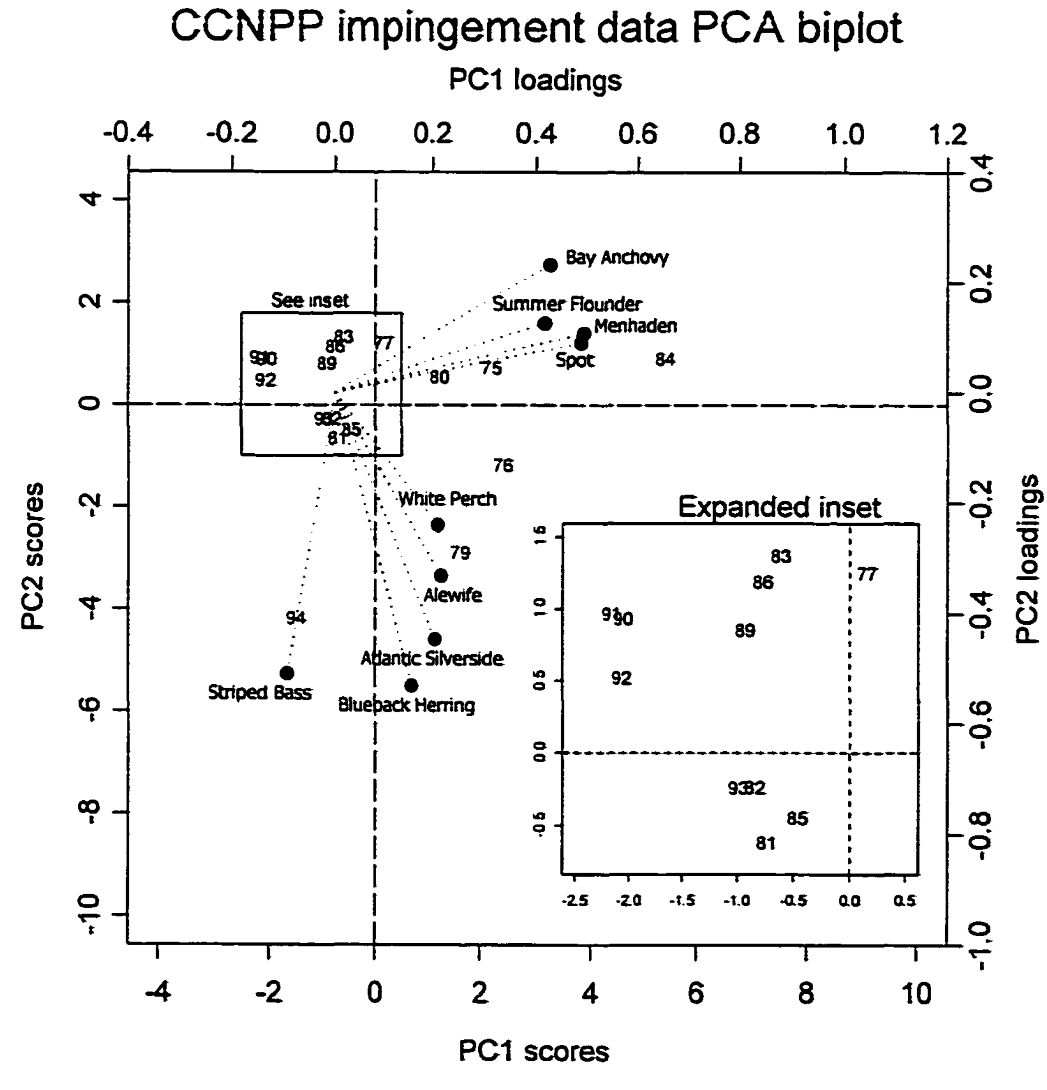

FIGURE 1.9. Biplot of Calvert Cliffs Nuclear Power Plant (NPP) impingement PC's 1 & 2

Despite the wide variation in collection methods and locations among the data sets, obvious consistencies exist among the biplots. With the exception of the CCNPP data set, anadromous fishes including striped bass, blueback herring (*Alosa aestivalis*), alewife (*Alosa pseudoharengus*), and white perch (*Morone americanus*) are strongly and negatively weighted on PC1. Conversely, coastal spawning, estuarine dependant species (spot, menhaden, and summer flounder) are strongly positively weighted on PC1. Because the first PC accounts for a sizable proportion of total data set variance, correlations among these strongly weighted species should be evident when their annual recruitment series are plotted against one another. As Figure 1.10 demonstrates, this is the case.

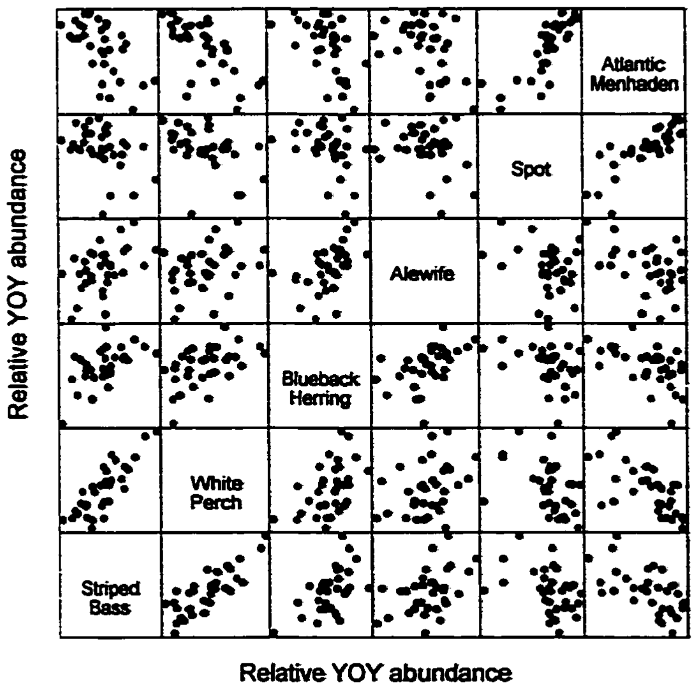

FIGURE 1.10. Scatterplot matrix comparing annual relative abundance of MDNR anadromous and coastal spawning estuarine dependant species strongly weighted in PC1.

While these two fish groups are negatively related in all other data sets, they are individually represented by PC's 1 and 2 of the CCNP analysis. Because PC's are orthogonally defined, this implies that the interannual variability of these two species groups is unrelated. The unique results of the CCNP data analysis may be due to its unique characteristics. While substantial differences exist between the collection methods and locations of each data set in this analysis, the CCNP data set is the only 'survey' utilizing a single sampling site. Further, fishes were not sampled using traditional means, instead they were collected from a screened intake apparatus where water velocities were approximately 0.3 meters per second.

Species groupings defined by PC1 are consistent among all data sets, however the same cannot be said of the second PC. This is in part due to the lack of equal species representation across data sets. Some of the species strongly weighted on PC2 are absent in all but the VIMS and MDNR seine surveys. Even in these two cases, where all species are represented, a number of these 'missing' species are oppositely weighted. Correlation values between each species and PC1 (annual score) time series are listed in table 1.4. Both PC1 and PC2 values are presented for the CCNPP analysis since coastal spawning and anadromous fish groups are represented separately by these two components respectively.

TABLE 1.4. Correlation between each species variable and each data set's PC1. Both PC1 and PC2 of the CCNPP data analysis are presented since, in this data set only, anadromous and shelf spawning fishes (in bold) are seperately accounted for by the first two PC's.

Species Variable	MDNR seine PC1	VIMS seine PC1	VIMS trawl PC1	Patuxent trawl PC1	CCNPP impingement PC1	CCNPP impingement PC2
Striped Bass	**-0.74**	**-0.91**	**-0.90**	**-0.72**	**-0.22**	**-0.76**
White Perch	**-0.73**	**-0.81**	**-0.75**	**-0.77**	**0.54**	**-0.35**
Blueback Herring	**-0.73**	**-0.21**			**0.33**	**-0.75**
Alewife	**-0.62**	**-0.17**				
Striped Killifish	-0.50	-0.11				
Gizzard Shad	0.37	-0.73				
Spottailed Shiner	0.11	-0.72				
Inland Silverside	0.41	0.75				
Rough Silverside	-0.33	0.44				
Mummichog	-0.08	0.39				
Atlantic Silverside	-0.64	0.28			0.12	-0.80
Bay Anchovy	-0.10	0.75	-0.45	0.09	0.74	0.37
Summer Flounder			**0.77**		**0.67**	**0.17**
Spot	**0.76**	**0.59**	**0.25**	**0.83**	**0.92**	**0.09**
Atlantic Menhaden	**0.89**	**0.69**		**0.57**	**0.94**	**0.13**

TABLE 1.5. Correlation values among overlapping time periods of all data sets' PC1 scores. PC2 also included for the CCNP analysis (see text for explanation).

	MDNR seine	VIMS seine	VIMS trawl	Patuxent trawl	CCNPP PC1	CCNPP PC2
MDNR seine	1	0.62	0.60	0.83	0.51	0.11
VIMS seine		1	0.66	0.71	0.51	0.28
VIMS trawl			1	0.74	0.02	0.01
Patuxent trawl				1	0.47	0.15
CCNPP PC1					1	0.00
CCNPP PC2						1

Annual PC1 variability

The species groups represented by MDNR PC1 have been shown to be prominently featured in the strongest multispecies signals within all data sets analyzed. Correlations among the PC1 observational scores are also relatively high considering the diversity among the survey locations and methods (Table 1.5).

The time series plot of PC1 annual scores (Figure 1.11) clearly reveals that correlation among the data sets is due to shared low and high frequency variability. It is important to evaluate the relative importance of these two components of variability, since this information may prove useful in research designed to identify the process(es) causing this multispecies recruitment pattern.

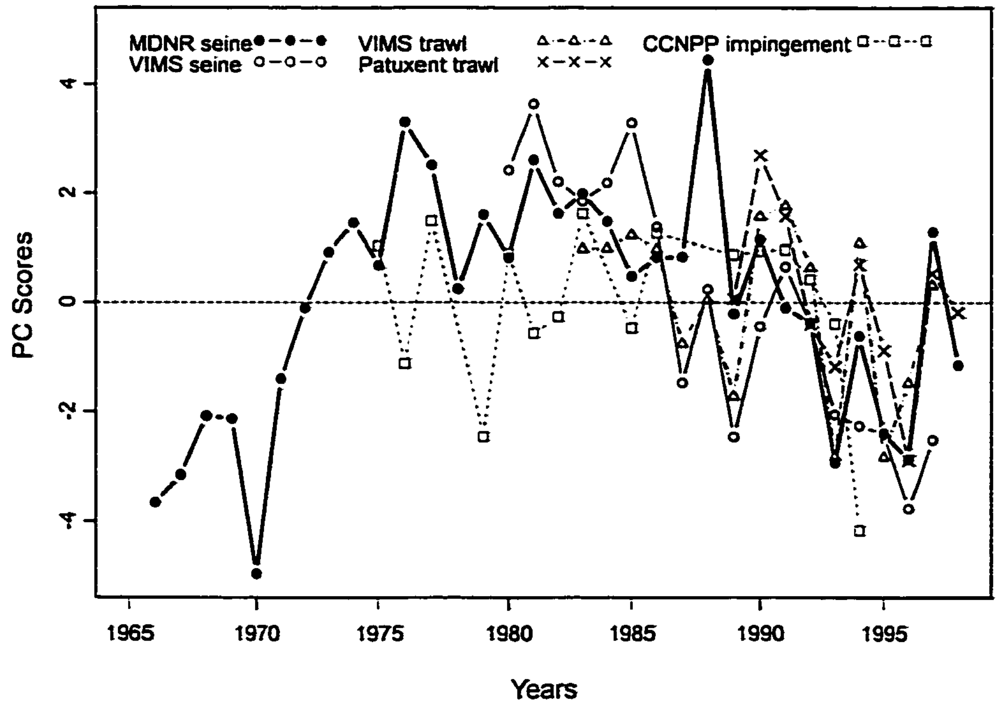

FIGURE 1.11. Time series plot of each data set's PC1 (annual) scores. Positive values correspond to strong Atlantic menhaden and Spot recruitment and weak recruitment of anadromous fishes. Negative scores correspond to the opposite scenario.

The relative contribution of low and high frequency variability in the MDNR PC1 time series was determined by using lowess smoothing and linear regression in combination. The low frequency component was isolated from the PC1 time series using a lowess fit featuring a smoothing span of 0.40. As seen in figure 1.12, lowess smoothing with this span accurately represents long period variability in the PC1 score time series. Residuals from this smoothed curve represent the high frequency variability component.

These two time series components (lowess fit values and residuals) were used as independent variables in a linear model of the (parent) PC1 time series. Since these variables are additive components of PC1's time series, this model was perfectly fit. The proportion of variance accounted for by each variable could then be calculated from the regression beta weights (Bx_1 & Bx_2), the standard deviations of all variables (Sy, Sx_1, & Sx_2), and the correlation values between each independent variable and the PC1 time series (Ry,x_1 & Ry,x_2), according to the following equation:

$$R^2_{model} = \{ [Bx_1 * (Sx_1/Sy) * Ry,x_1] + [Bx_1 * (Sx_2 / Sy) * Ry,x_2] \}^{0.5} \text{ (Hays, 1988).}$$

These calculations reveal that 56% and 44% of the MDNR PC1 time series variance is accounted for by its low frequency (lowess fit) and high (fit residuals) components respectively (Figure 1.12).

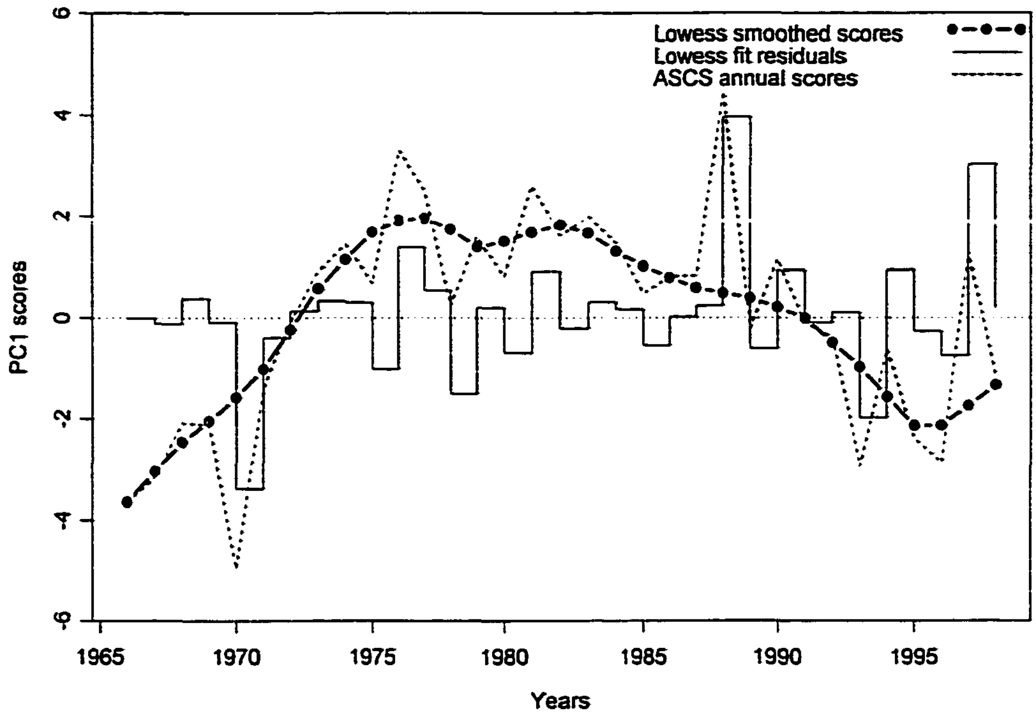

FIGURE 1.12. Time series plot of MDNR seine survey PC1 scores (dashed), lowess fit (bold points and lines), and lowess residuals (stairsteps). A span of 0.4 was used for lowess smoothing.

Analysis of 'prewhitened' data sets

These results indicate that a majority of the variance within the PC1 time series can be accounted for by low frequency variability. Unfortunately, recruitment time series are often autocorrelated (Walters and Collie, 1988; Thompson and Page, 1989). The presence of autocorrelation within recruitment time series is problematic, since it can suggest important relationships where none exist (Cohen et al., 1991), while its removal can eradicate true and important relationships (Pyper and Peterman, 1998). One method of dealing with this problem is to suppress autocorrelation within the recruitment time series and reanalyze them. If the first PC resulting from this 'prewhitened' data set analysis features similar variable loadings as the unfiltered PC1, concerns over 'inflated' multispecies correlations can be laid to rest.

To evaluate the potential bias inflated correlations may present in this study, lowess smoothing and first differencing were used independently to remove autocorrelation from MDNR recruitment time series prior to reanalysis. Spans were chosen to minimize overall autocorrelation within each recruitment series. For striped killifish (*Fundulus majalis*) and Atlantic silverside (*Menidia menidia*) lowess smoothing did not reduce their relatively low (non-significant) autocorrelation, therefore their unsmoothed series were used in place of lowess residuals.

In this study, lowess residual series featured lower autocorrelation than their first differenced counterparts. In fact, nine first differenced series featured significant autocorrelation. Typical results obtained by both methods of prewhitening are shown for Spot in Figure 1.13.

Both first differenced and lowess smooth fit residuals of the MDNR log transformed (as in the original analysis) recruitment series were analyzed with PCA. Biplots and correlation analysis of these detrended and the original MDNR data sets are shown in figures 1.14 and 1.15 and table 1.6.

Unfiltered, lowess residual, and first differenced data set PC1 species loadings are very similar. First differenced PC1 loadings for blueback herring and spot have been reduced however. Because nine of fourteen first differenced series featured significant autocorrelation, more weight should be given to the lowess residual analysis. These results demonstrate that the basic pattern isolated in PC1 is found in both low and high frequency components of multispecies recruitment variability in the Chesapeake Bay.

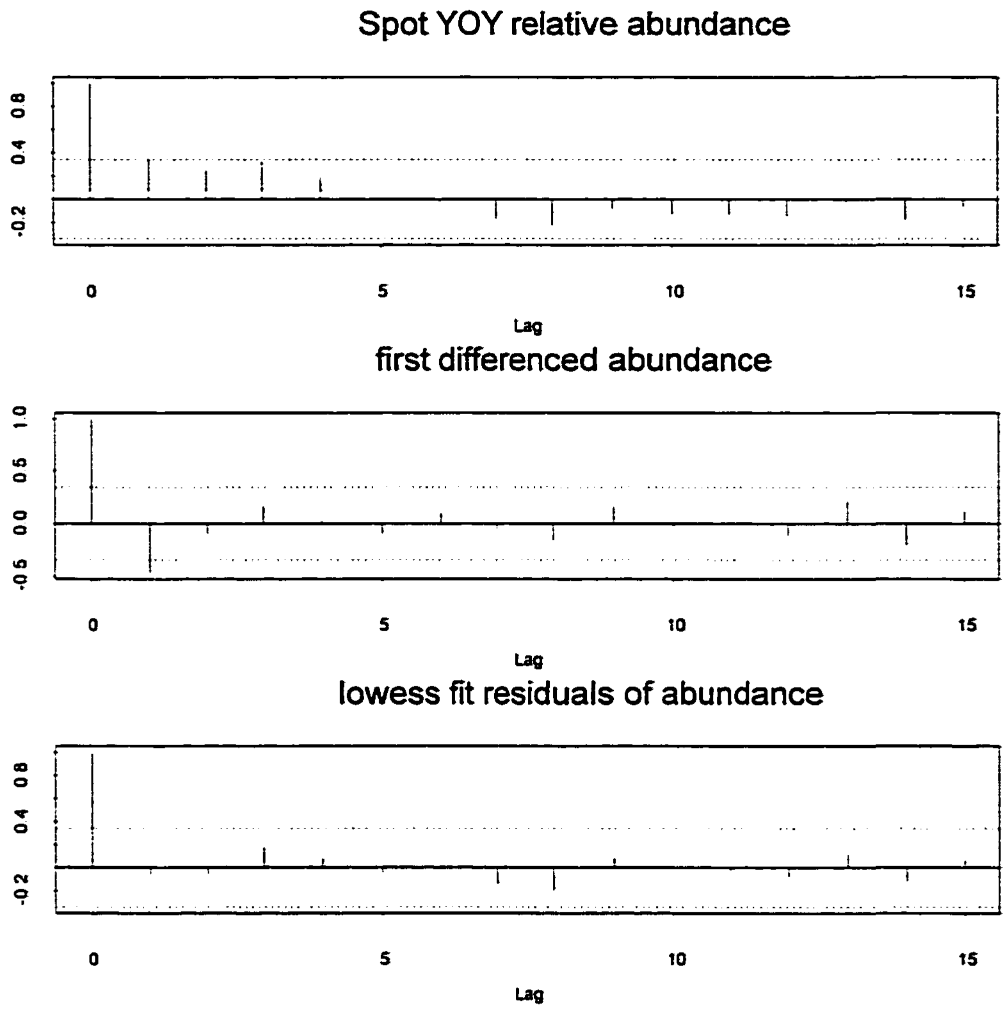

FIGURE 1.13. Autocorrelation plots for juvenile spot relative abundance in the MDNR seine survey data set, first differenced abundance, and the lowess fit residuals of the abundance.

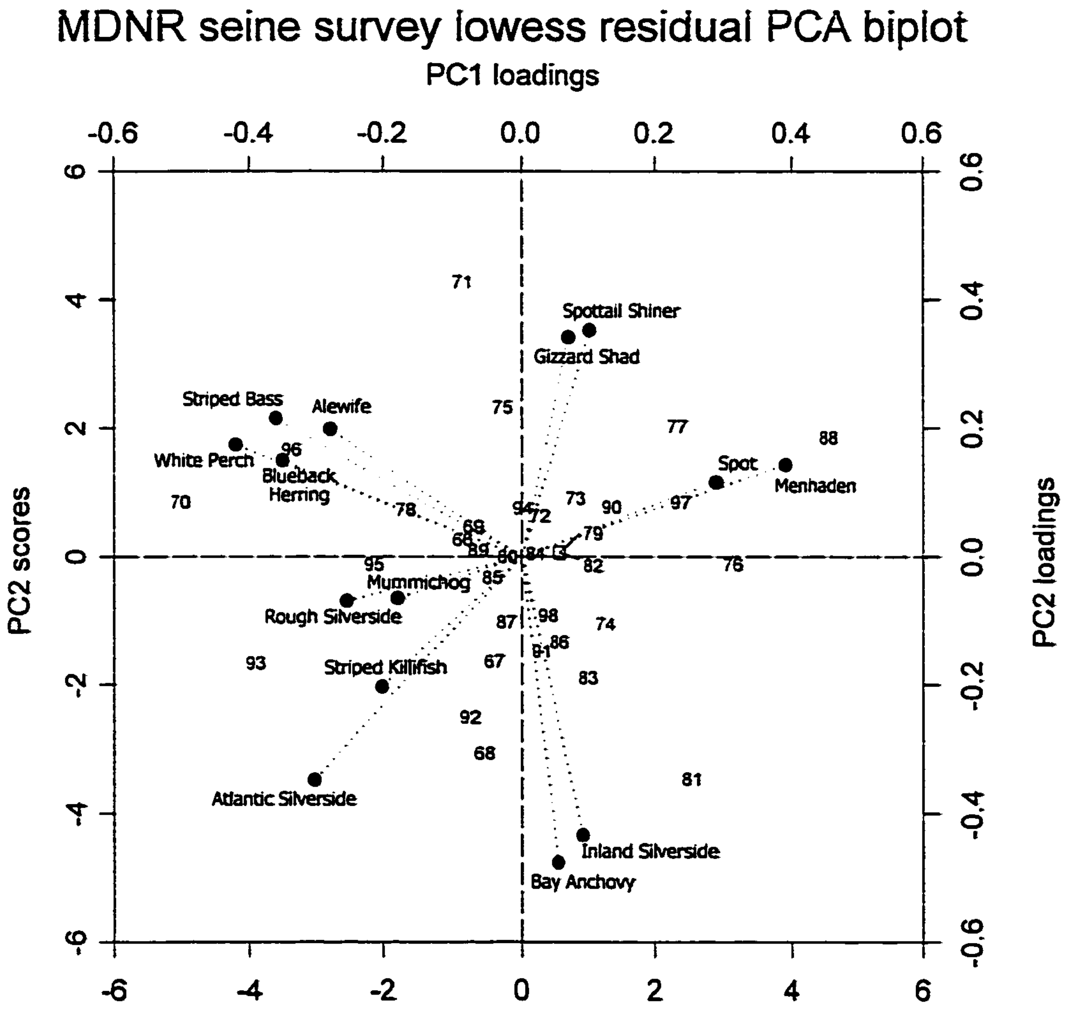

FIGURE 1.14. Biplot of MDNR seine survey lowess residual PC's 1 & 2.

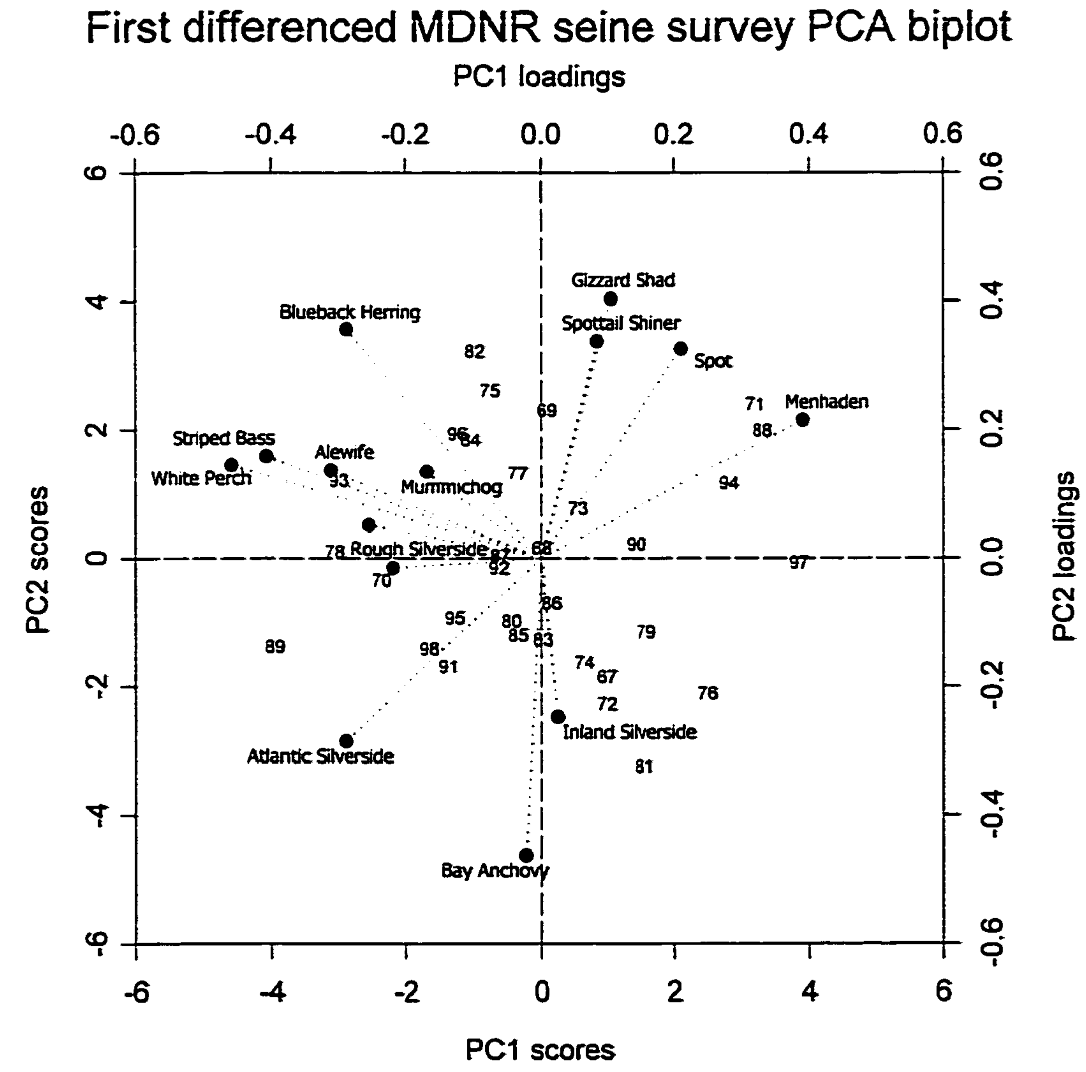

FIGURE 1.15. Biplot of first differenced MDNR seine survey PC's 1 and 2.

TABLE 1.6. Correlation between MDNR species annual relative abundance and PC1 scores resulting from analysis of log transformed species abundance, their lowess residuals, and first differenced time series. For reference, bold values indicate significance for an alpha of 0.01. Total data set variance accounted for by each PC is listed in column headings.

MDNR seine species variables	Annual abundance PC1 (31%)	Lowess residual PC1 (26%)	First differenced PC1 (25%)
Striped Bass	**-0.74**	**-0.69**	**-0.65**
White Perch	**-0.73**	**-0.80**	**-0.80**
Blueback Herring	**-0.73**	**-0.67**	-0.13
Alewife	**-0.62**	**-0.53**	**-0.47**
Striped Killifish	**-0.50**	-0.39	-0.44
Gizzard Shad	0.37	0.13	0.15
Spottailed Shiner	0.11	0.19	0.27
Inland Silverside	0.41	0.18	- 0.16
Rough Silverside	-0.33	**-0.49**	-0.23
Mummichog	-0.08	-0.34	-0.35
Atlantic Silverside	**-0.64**	**-0.58**	-0.30
Bay Anchovy	-0.10	0.10	0.12
Spot	**0.76**	**0.55**	0.26
Atlantic Menhaden	**0.89**	**0.74**	**0.59**

DISCUSSION

Overall, these results have demonstrated that annual abundance of young-of-the-year (YOY) anadromous fishes is negatively related to coastal spawning, estuarine dependant fishes in Chesapeake Bay. Because it features two species groups, each of which is comprised of species with similar spawning strategies, this contrasting Chesapeake Bay anadromous-shelf spawning estuarine dependant (CBASS, pronounced *sea-bass*) recruitment pattern is consistent with previous multispecies studies that have found positive correlations among species or stocks that share similar early life history characteristics and similar geographic distributions (Hollowed et al., 1987; Garrod and Colebrook, 1978; Koslow, 1984; Shepherd et al., 1984; Cohen et al., 1991; Hare et al., 1999; Hare and Mantua, in press).

CBASS species groups' spawning strategies

Recruitment of coastal spawners (spot, menhaden, and summer flounder) to the Chesapeake Bay begins with adult spawning November through February in shelf waters of the Atlantic, from Massachusetts to North Carolina (Pacheco, 1962; Kendall and Reintjes, 1975; Bodolus, 1994; Ahrenholz, 1991; Able and Kaiser, 1994; Quinlan et al., 1999). Larvae are transported towards and into the Bay arriving from late winter to early spring (Massmann et al, 1961, Norcross and Wyanski, 1994; Ahrenholz, 1991, Bodolus, 1994). Postlarvae and juveniles of spot and menhaden utilize the shallows of upper tributaries to the turbidity maximum as nursery areas from March through the summer (Massmann et al., 1954; Merriner et al, 1979).

While most studies have identified coastal shallows or fringing marshes of river mouths, embayments, and the Chesapeake Bay mainstem (Able and Kaiser,

1994) as summer flounder settlement and nursery areas, analyses of Maryland Department of Natural Resources and Virginia Institute of Marine Science seine surveys reveal the presence of 46 to 100mm flounder in the upper Bay and its Virginia tributaries more than thirty-five miles upstream of river mouths, approaching the turbidity maximum. A recent April 2000 survey targeting summer flounder YOY in the York River (Virginia) also found flounder sizes (34-90mm) more than 30 miles upstream of the river mouth (W. Reay, Virginia Institute of Marine Science, personal communication).

In contrast to the coastal spawners, anadromous and semi-anadromous species spawn in upper Bay and tidal freshwater zones of its tributaries usually within the April to June time frame, though spawning has occurred as early as March in association with unusually warm conditions (Mansueti, 1961; Mansueti, 1964; Setzler-Hamilton, et al., 1981; Seccor and Houde, 1995; Jenkins and Burkhead, 1994; Kline, 1990). Alewife generally spawn earlier, from March to April (Jenkins and Burkhead, 1993). While larvae of these species may be displaced downstream immediately after hatching, they remain most abundant above the salt front (Ritchie, 1968; Lippson et al., 1979, Setzler-Hamilton, et al., 1981; Grant and Olney, 1991; Secor and Houde, 1995).

It is generally believed that year class strength is most likely to be established in the pre-recruit (egg to postlarval or early juvenile) life stages (Heath, 1992). Considering the early life history characteristics of the CBASS species groups and the lack of clear spawner-recruit relationships of species within both groups (Goodyear, 1985; Vaughan and Smith, 1999), it is likely that the CBASS pattern is ultimately the result of abiotic factors during the late winter to early spring months. Because the two species groups utilize river and upper Bay reaches adjacent to and on both sides of the freshwater interface respectively as nursery areas for their early life stages (anadromous upstream and shelf spawners predominantly downstream), and the spatial-temporal coherence of the CBASS recruitment pattern throughout the Bay, it is most likely that large scale climatic forces are differentially affecting recruitment success of these two groups.

This conclusion is supported by previously identified relationships between winter-spring climatic variables and recruitment for the most studied species comprising the CBASS pattern, including the coastal spawning Atlantic menhaden (Quinlan and Crowder, 1999; Quinlan et al., 1999; Checkley et al., 1988; Reish et al, 1985; Nelson et al, 1977) and spot (Bodolus, 1994), and the anadromous striped bass (Ulanowicz and Polgar, 1980; Goodyear and Christensen, 1984; Polgar et al., 1985; Uphoff, 1989; Olney et al., 1991; Rutherford and Houde, 1995; Secor and Houde, 1995).

Climatic forcing of the CBASS recruitment pattern defined in this study would also be consistent with many previous findings that climatic variability can have profound affects on marine ecosystems and recruitment of fish stocks (Russell, 1973; Heinle et al., 1976; Lasker, 1981; Chelton et al., 1982; Cushing, 1982; McGowan, 1985; Koslow et al., 1987; Norcross and Austin 1988; Peterman and Bradford, 1987; Dickson, et al., 1988; Sharp and McLain, 1993; Myers et al., 1992; Fromentin and Planque, 1996; Francis et al., 1998; Hare, 1999; and others). If found to be true in this case, it could be shown that climatic variability is capable not only of affecting recruitment success in fishes, but also of dramatically altering the relative composition of ecologically and economically important fish species in the Chesapeake Bay, as occurred from the late 1980's through the 1990's when annual abundance of menhaden YOY steadily declined, in contrast to that of the anadromous fishes included in this study. Obviously, such a finding would have to taken into account when formulating multispecies fishery management strategies for Chesapeake Bay.

Variability in spawning stock biomass (SSB), potentially caused by fishing and management activities in commercially important stocks, is another factor capable of influencing recruitment over large geographical areas. For this to be important in driving the CBASS pattern, a relatively strong SSB-recruitment (density-dependent) relationship must exist for the stock(s) of interest. Available data for the two most commercially important species comprising the CBASS pattern (striped bass and Atlantic menhaden) suggest their SSB-recruitment relationships are weak, at best.

Since 1982, the MDNR has both monitored annual YOY striped bass abundance and conducted a fishery independent survey of SSB (Hornick et al., 2000). Analysis of annual recruitment/SSB ratios derived from these data show these ratios to be highly variable (Richards and Rago, 1999). This indicates that environmental variability plays a dominant role in determining annual recruitment of striped bass. This conclusion is supported by previous studies (Martin et al., 1985; Olney et al.,1991) which have found annual juvenile abundance not to correspond well with annual densities of eggs and larvae.

Harvest data from the National Marine Fisheries Service (NMFS) is a longer time series with which to investigate the relationship between adult striped bass abundance and annual recruitment. The time series covered the years 1966-1997 excluding 1985-1994 when strong limits were placed on commercial harvests (Rago and Richards, 1999). Both series were log transformed to ameliorate the effects of (relatively few) dominant year classes.

Analysis by these authors reveal that correlation between log transformed annual Atlantic states' striped bass harvest and (log transformed) recruitment is relatively low or negative. This is in sharp contrast to correlation values between annual harvest and recruitment 2-10 years prior (Table 1.7). While harvest data are an imperfect measure of spawning stock abundance, a stronger (positive) relationship between recruitment and future harvests than between harvests and concurrent or future recruitment suggests that density-independent environmental variability is more important than spawning stock biomass in determining annual recruitment for the striped bass.

TABLE 1.7. Lag correlation analysis of striped bass annual MDNR juvenile abundance and NMFS harvests for Atlantic waters. Data for both series limited to the years 1966-1997 excluding 1985-1994 when catch restrictions severely limited commercial harvests.

Years listed lagged (start delayed)	NMFS harvest data for Atlantic waters (log transformed MT)	MDNR seine survey juvenile abundance (log transformed)
0	0.19	0.19
1	0.33	0.06
2	0.59	-0.09
3	0.61	-0.24
4	0.69	-0.22
5	0.70	-0.41
6	0.64	-0.54
7	0.44	-0.44
8	0.35	-0.64
9	0.27	-0.64

The spawner-recruit relationship in another intensively fished species strongly weighted in the CBASS pattern, Atlantic menhaden, also appears to be strongly influenced by environmental variability. Vaughan and Smith (1999) found that recruitment in recent years has been low despite rising SSB, and since 1955 SSB-recruitment ratios have been highly variable.

CONCLUSION

In this paper, we have identified a bipolar recruitment pattern among fish featuring anadromous and coastal spawning, estuarine dependant spawning strategies in the Chesapeake Bay (CBASS). Principal components analysis revealed that the CBASS recruitment pattern exists within a number of Chesapeake Bay fishery independent data sets despite differences in survey methods and collection sites. Further, the strength and sign of this recruitment pattern were shown to be synchronous among these data sets and throughout the Bay.

Because the two negatively correlated CBASS species groups utilize areas adjacent to the tidal freshwater interface in the upper Bay and its tributaries during spring months, it is likely that the processes driving the CBASS pattern operate on larval and postlarval stage fishes during their transport to, or within that estuarine zone. Since the annual sign and magnitude of this pattern is similar in each of these areas, its driving mechanism must be capable of acting over a large geographical area.

For these reasons, covariability between large-scale atmospheric processes and the CBASS pattern is examined in Chapter Two. Progress in this area would narrow the search for the specific mechanism(s) which drive the variability inherent in a number of ecologically and economically important fishes of the Chesapeake Bay. Regardless of its causes, it is hoped that the species composition, geographic extent, and temporal dynamics of the CBASS recruitment pattern will prove useful in the future development of multispecies and ecosystems fisheries management for the Chesapeake Bay.

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Chapter Two

Climatic forcing of a multispecies recruitment pattern in Chesapeake Bay

INTRODUCTION

Interannual recruitment variability is perhaps the most important and complex problem facing fishery managers (Kendall et al., 1998). Often referred to as 'the recruitment problem', the search for factors responsible for highly variable recruitment in many marine fisheries has focused upon processes affecting survival in the early life stages of fishes. This focus can be attributed to Hjort's (1914) conclusions that fluctuations in Northern Europe's great fisheries were primarily due, not to changes in population migration patterns, but the 'highly irregular nature' of their 'renewal'.

The importance of Hjort's landmark work is evident in the persistence of the ideas he put forth regarding the potential mechanisms forcing interannual recruitment variability. The conceptual beginnings of the most often cited theories addressing processes governing recruitment variability, the match-mismatch (Cushing, 1974; Cushing, 1990) and member-vagrant (Iles and Sinclair, 1982; Sinclair and Tremblay, 1984; Sinclair, 1988), can be traced to ideas originally proposed by Hjort.

These and other theories, such as Cury and Roy's (1989) "optimal environmental window" and Lasker's "stable ocean hypothesis" (Lasker, 1981), describe processes which are ultimately influenced by interannual variability in climatic-hydrographic conditions (Anderson, 1988; Heath, 1992). This emphasis on extrinsic, abiotic (density independent) factors rather than intrinsic factors, such as spawning stock biomass, can be attributed to work by Hjort and others who have presented evidence suggesting cohort recruitment strength in many populations is not strongly influenced by parental stock biomass or egg abundance (Walters and Korman, 1999).

This is not to imply that spawner-recruitment relationships should be ignored. In fact, Myers and Barrowman (1996) recently used non-parametric methods to demonstrate that most of the 364 stocks they studied exhibited some degree of spawner-recruit dependence. Still, in many cases these relationships are subordinate to, or at least less pronounced than the stochastic variance often attributed to abiotic factors.

Because of difficulties associated with direct observations of the early life stages of fishes, correlative analysis of historical data has been the most common approach used to investigate recruitment variability and its causes. Despite the large number of such studies, few have yielded information which is directly applied by fisheries managers (Myers, 1998). This has lead some to question the usefulness of this approach (Rose, 1997; Walters, 1989; Walters and Collie, 1988; Myers, 1998). Other researchers, while supporting the use of historical recruitment data in these types of analyses, have called for the use of new and more carefully applied conceptual and statistical approaches (Tyler, 1992; Bakun, 1996; Sharp, 1995; Myers, 1998).

Given the importance of understanding the forces influencing recruitment variability, difficulties of direct observation in the field, problems associated with reproducing realistic conditions in an experimental setting, and a lack of strong spawner-recruit relationships in many fisheries, it seems foolish to ignore continually accumulating environmental and recruitment data sets.

This paper examines the role of synoptic-scale (100's to 1000's of kilometers) climatic variability in influencing the abundance of young-of-the-year fishes in Chesapeake Bay, while avoiding many of the pitfalls associated with traditional correlative environmental-recruitment investigations. Let it be stated at the outset, as Myers (1998) has urged, that this investigation is exploratory in nature and therefore not designed to confirm a specific mechanistic theory describing how year class strength is determined. Instead, the goal of Chapter Two is to evaluate the hypothesis that climatic variability is ultimately responsible for the multispecies recruitment patterns described in Chapter One.

METHODS

Data sources

There are a number of methodological, statistical, and data related factors that can contribute to the high failure rate of correlation-based historical analyses. Perhaps the most basic problem is the lack of accurate recruitment data. Because of the difficulties and expense in collecting recruitment data, many studies rely upon 'reconstructed' time series. Most often, reconstructed recruitment time series are derived from virtual population analyses (VPA) of commercial catch-at-age data, where recruitment is hindcast using catch-at-age data. Unfortunately, VPA requires accurate natural mortality values, which are extremely difficult to obtain (Quinn and Deriso, 1999). As Lapointe and Peterman (1991) have pointed out, incorrectly specified natural mortality estimates can lead to incorrect specification of environmental-recruitment relationships due to problems associated with spurious correlations.

Regardless of data source, recruitment time series are often short and autocorrelated. These characteristics increase the likelihood of identifying spurious correlations in historical analyses (Thompson and Page, 1989; Walters and Collie, 1988; Cohen et al., 1991; Pyper and Peterman, 1998). Pyper and Peterman (1988) have demonstrated methods capable of successfully dealing with the autocorrelation problem. Pyper and Peterman also point out that caution must be exercised in the exorcism of autocorrelation since evidence continues to emerge suggesting that climatic patterns featuring low frequency variability (trends or oscillations) may be important in determining year class strength (Koslow et al., 1987; Francis and Hare, 1994; Mantua et al., 1997; Francis et al., 1998). With this in mind, Pyper and Peterman (1998) point out that removing autocorrelation from recruitment series may mask true climate-recruitment relationships (leading to type II errors).

The problem of short recruitment time series is more difficult. In some cases, the only solution is to wait until more data can be collected. One strategy which might be employed as a partial remedy to this problem is the examination of multiple species from one locality, or multiple stocks of the same species throughout a larger region, when searching or testing for environmental-recruitment relationships (Tyler, 1992; Myers, 1998).

Recruitment data

These data related problems are minimized in this work by using the Chesapeake Bay anadromous-shelf spawner (CBASS) multispecies recruitment pattern, defined in Chapter One, as a response variable. This pattern is ideal for an environmental-recruitment investigation for a number of reasons. First, it was shown to be the most important multispecies pattern within five fishery independent pre-recruit (juvenile) fish abundance data sources, featuring as many as fourteen species. This group of data sources was methodologically diverse, featuring a wide variety of sampling protocols, sample sites, and sampling gears. Considering these facts, this multispecies pattern is likely to feature a strong signal to noise ratio, something which is not often possible to establish in many single species recruitment time series (Tyler, 1992; Myers, 1998).

The CBASS pattern is so named because it describes the negative relationship between recruitment success (as depicted by the abundance of YOY juvenile fishes) of spring spawning anadromous and coastal shelf spawning species. Synoptic-scale (hundreds to thousands of kilometers) climatic forcing of this pattern is suggested by its the Bay-wide spatial scale of operation (Koslow, 1984), and is consistent with the differential affect upon species groups employing different spawning strategies and dependant upon similar reaches of the estuary above and adjacent to the freshwater interface (Lippson et al., 1979).

While the CBASS recruitment pattern was identified as the strongest recruitment pattern to exist in each of the five multispecies data sets available, the Maryland Department of Natural Resources' (MDNR) striped bass (*Morone saxatilis*) seine survey is the data source with the longest period of record. Due to the statistical advantages of long time series, this data set will be used as the subject of this investigation.

The MDNR beach seine survey has maintained consistent sampling protocols and sites since 1966. Using a large number of fixed sites in the upper and middle portion of the Chesapeake Bay and its tributaries (Figure 2.1) this survey is specifically designed to monitor the annual abundance of YOY striped bass, however it effectively monitors the abundance of at least fourteen other fish species. Principal components analysis revealed that the CBASS recruitment pattern is the dominant multivariate pattern in this fourteen species annual abundance data set. For more details regarding this data set and analysis see Chapter One.

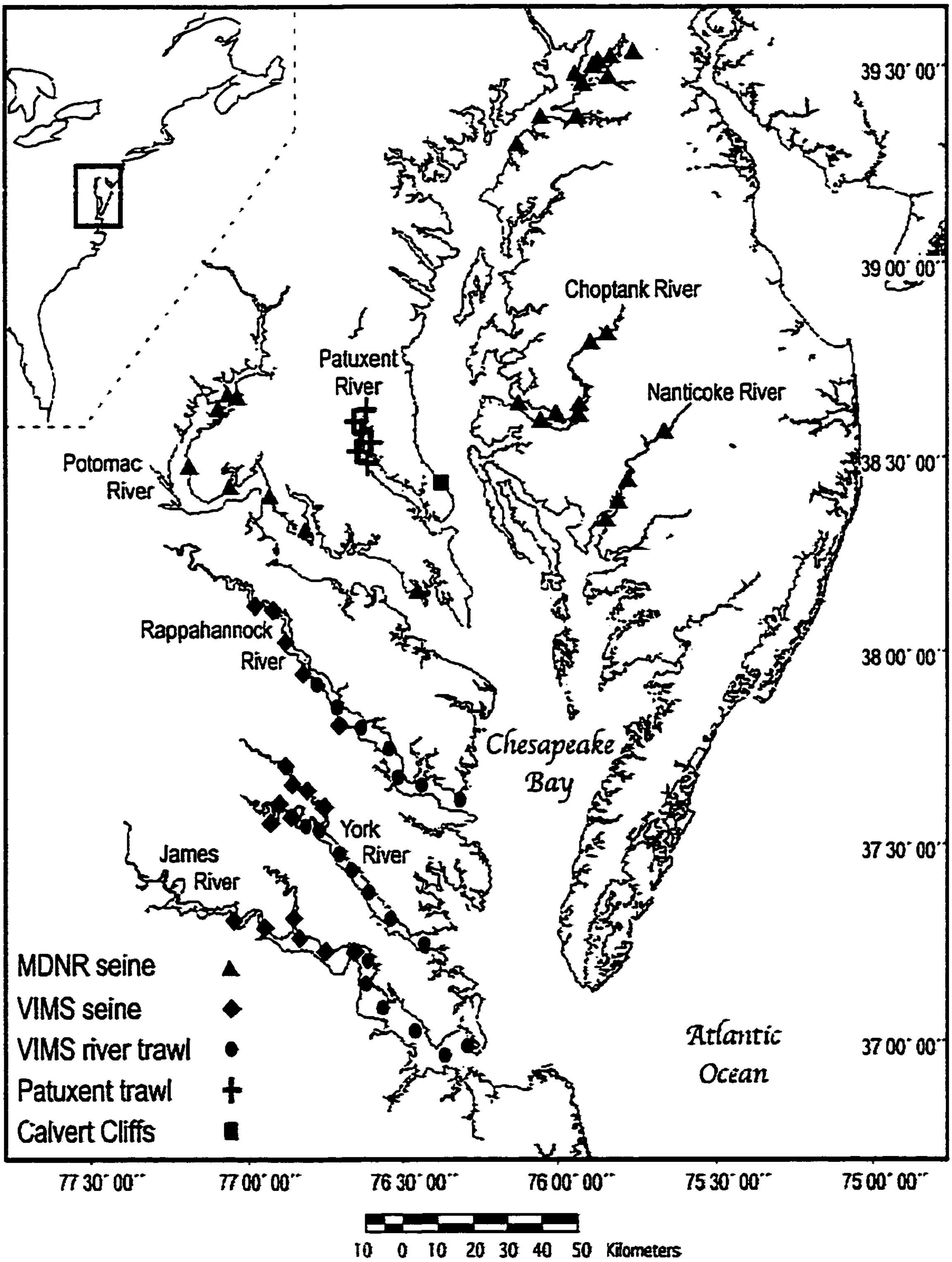


FIGURE 2.1. Study site map.

Climate Data

Synoptic-scale climate variability affecting the Chesapeake Bay estuarine system was characterized using a subset of the National Center for Environmental Prediction's (NCEP, formerly the National Meteorological Center, NMC) Northern Hemisphere gridded sea level pressure (SLP) data set. This data set, obtained from the National Center for Atmospheric Research (NCAR), is archived and distributed by the NCAR Data Support Section (DSS), and contains twice daily (00:00 and 12:00 UTC) data for a 1977-point octagonal grid. For this study the octagonal grid system was converted to a 5° latitude by 5° longitude grid. Once daily (12:00 UTC) SLP observations over the region bounded by 25°N to 50°N latitude and 55°W to 90°W longitude (48 grid-nodes) were extracted for the months March, April, and May for the years 1957-1998 (3757 total observations).

Statistical operations

Other potential problems with correlation studies are statistical in nature. Walters and Collie (1988) discuss many of these problems in detail and suggested three 'basic precautions' which should be taken to reduce the risk of describing relationships based upon spuriously correlations. These were: report all data sets scanned when searching for potential predictor variables; do not promote mechanistic relationships based on correlation studies without support from a variety of independent measurements; and report all evidence, especially negative, which supports or refutes the existence the defined relationship(s) for different populations or different species. Care was taken in the planning stages of this investigation to address and follow each of these recommendations.

A more complex, often unaddressed issue related to spurious correlation is that of confounding variables. Freeman (1999) defines confounding variables as those which are "associated with the putative cause and with its effect" and "may explain part or all of an observed association." As Freedman demonstrates, even when care is taken to avoid all other potential pitfalls possible in correlative studies, confounding variables can still lead to erroneous theories regarding mechanistic relationships (Freeman, 1999). If correlation between the confounding and causal variables should wane, the model eventually fails. Since hydrographic, climatological, and weather variables are often strongly intercorrelated, strong potential exists for misidentification of environmental-recruitment relationships.

In this study, both intercorrelated climate variables, and avoiding *a priori* scanning of potentially influencing abiotic time series are dealt with by treating weather and climate in a more realistic sense. As Davis and Kalkstein (1990) point out, climatic conditions are, "determined entirely by the cumulative effect of the weather systems that have passed through that region. Therefore, a complete representation of climate is not merely the long-term record of temperature and precipitation, but is determined by the entire ensemble of weather elements interacting over time and space." These authors provide a case example where, "the environmental parameter being studied is not merely related to changes in an individual weather element, but to the totality of weather or the synoptic situation." Since fish simultaneously experience changes in a variety of meteorological-hydrographic parameters with climatic variability, one might expect that, as Davis and Kalkstein found "the application of raw weather elements within a regression analysis is often misleading, as the integrative nature of the various elements is ignored."

Consider a hypothetical example. Assume recruitment on a given species and location is affected by the oceanic turbulence and low temperatures accompanied by coastal storm passage. A researcher might find precipitation is significantly correlated with a recruitment time series. If, in the coming years the climate changes such that different weather systems bring much of the precipitation to the area, ones which do not influence oceanic turbulence or bring cold weather, a forecast model based upon the previously established precipitation-recruitment relationship would fail. In this way, confounding variables may partially explain the failure of correlative-based recruitment forecast models soon after their construction (Sharp, 1995).

In this paper, we examine the possibility that synoptic-scale climatic variability may influence recruitment in Chesapeake Bay using a spatially explicit climatological classification technique similar to that outlined by Davis and Kalkstein (1990). Typically, this temporal synoptic classification scheme is used to describe long term climatic variability for a particular region by identifying a finite series of weather maps that typify seasonal weather patterns. Since each date is categorized as one of these weather pattern types, annual frequencies for each are generally analyzed. This investigation will use sea level pressure (SLP) to describe daily weather patterns in the Mid-Atlantic region. While investigations of the links between SLP patterns and fish populations are not unique in the literature (see Koslow et al., 1987, for example), this type of synoptic classification scheme has never been used in the field of fisheries recruitment.

The pool of predictors used to explore the role of climatic variability in driving multispecies recruitment patterns in Chesapeake Bay will include only the month-specific (March-May) SLP map pattern annual frequencies. Since synoptic scale SLP patterns are expected to produce characteristic weather conditions (temperature, precipitation, wind speed, wind direction, etc.) over the Mid-Atlantic, their annual frequencies can be compared to recruitment time series. This approach is superior to typical climate-recruitment investigations which use individual weather variable time series since these SLP patterns realistically describe weather conditions that might affect the estuarine system.

Traditional approaches such as stepwise multiple regression and correlative-base linear modelling, as well as non-traditional methods such as Classification and Regression Tree modelling (Breiman et al., 1984) are used to identify and describe the relationships between spring weather and climate variability and the multispecies recruitment patterns in Chesapeake Bay.

1. Synoptic SLP Classification procedure

Principal components analysis

Unrotated Principal components analysis (PCA) has been and continues to be widely used to investigate multivariate problems in ecological studies. Here PCA is used primarily as a data reduction technique at the first stage of this synoptic SLP classification procedure. Principal components analysis recharacterizes the variance within a multivariate data set by creating new 'composite' variables (called principal components or PC's) formed from linear combinations of the original variables such that the first PC describes the longest axis (most variability) within the data cloud. Subsequent PC's are similarly isolated with the restriction of mutual orthogonality, assuring all PCs are independent and uncorrelated.

This results in the same number of PC's as original variables, with the data set variance accounted for by each PC declining in order (first to last). In an ideal case, most of a data set's variance is accounted for by far fewer PC's than original variables. These characteristics facilitate data reduction since only a few PC's (ideally far fewer than original variables) can often account for most of the variance within a data set. Generally only these 'few' PCs are retained for further analysis. To determine the number principal components to retain in this study, results of Catell's (1966) scree test, Jollife's (1972) averaged root test, the eigenvalue separation test (North et al., 1982), and Overland and Priesenforfer's (1982) 'Rule N' were all considered.

Because the original variables are gridded SLP coordinates, their variable weights or loadings for each PC can be plotted on a latitude-longitude coordinate system to construct SLP pressure pattern maps (again, one for each PC). While this step reveals the primary modes of SLP variability over the study period, each daily observation typically has non-zero scores for more than one PC. The goal here is to describe each daily observation using one of a relatively small number of SLP pattern map 'types' which are characteristic of spring climate conditions in the Mid-Atlantic region. To accomplish this, daily observations are grouped according to the similarity in their (retained) PC scores. Once group membership is determined, the generalized SLP pattern, characteristic of each group, can be mapped. A single map representing the observations within each group or cluster is formed from a linear combination of each PC map. Mean scores for each PC, within each group, are used as linear weights in this process when deriving these composite maps.

Cluster analysis

Daily observations were grouped according to the similarity in their retained PC scores using a two-step clustering process. Two stages of clustering are required because, while the k-means, non-hierarchical, clustering technique is superior to other methods in synoptic climatological classification (Davis and Kalkstein, 1990), this method requires initial 'seed' values. Average-linkage cluster analysis is a hierarchical clustering technique found to be best for this purpose (Cunningham and Ogilvie, 1972; Hawkins et al., 1982; Kalkstein et al., 1987; Jones, 1998). Group means from the final solution of the average-linkage analysis were used for this purpose.

With cluster analysis, as with PCA, a decision must be made as to how many clusters the final solution should contain. After Davis and Kalkstein (1990), the pseudo-F and pseudo-T^2 (SAS, 1988) were examined in conjunction with the standardized change in the R^2 value (Davis, 1988) in determining which step of the clustering process should be accepted as the final solution.

2. Climate-recruitment comparison

CART and linear regression modeling

This classification procedure yielded a series of ten maps (see Results section), each representing a characteristic SLP pattern typically occurring during the March to May timer period. Since all days were classified as one of these ten patterns, annual time series for each of the three months could be constructed for each of the ten SLP patterns. This resulted in thirty annual SLP map pattern time series, which could then be compared to recruitment using correlative techniques, linear modelling methods, and classification and regression tree (CART) models (Breiman et al., 1984).

Correlation and linear modelling techniques are the standard fare of recruitment studies, however the use of CART models for fisheries applications is relatively new. Recent examples of their use include Norcross et al. (1997), Magnuson et al. (1998), and Norcross et al. (1999). An advantage of CART models is that they are able to account for complex data set structures traditional linear techniques cannot. For example, CART models are capable of incorporating complex predictor variable interactions and nonadditive structures, without having to specify their multiplicative form as must be done with linear regression (Breiman et al., 1998; Clark and Pregibon, 1997). These models are also specifically designed to accept discontinuous or categorical variables as those used in this study (weather pattern frequencies).

Since these models predict observational group means rather than the value of each observation, it is relatively robust with respect to outliers and observational errors. This is advantageous when modeling biological survey data, since the response variable(s) can be expected to feature some level of error or 'noise'.

Where linear regression techniques model a response variable using linear combinations of the independent (predictor) variables, the CART algorithm is a binary recursive partitioning method that splits observations into homogeneous groupings. Threshold values derived from any one of some number of potential predictor variables, are used to split the data into relatively homogeneous groups (Clark and Pregibon, 1997). Results are typically displayed as a dendrogram or 'tree', usually oriented so that the 'root' is at the top and the 'leaves' are at the bottom.

Using this tree analogy, an alternate explanation of CART modeling is that the response variable's observations are successively split, at branch 'nodes', in the way which maximally distinguishes the response variables' observations (splitting high from low values, for example) into new and diverging (left and right) branches. At each splitting stage the stepwise CART algorithm seeks to minimize misclassified observations or total deviance of the model. Misclassified observations are those placed into a group which deviate from the general group profile. Deviance is defined as the sum of the squared differences between each observation in a group, and the group mean. Therefore, not only does each group have a deviance value, but the sum of deviance values over all groups is the model's deviance. When all variables are numeric, as opposed to categorical, deviance is the more convenient measure of model 'fitness', both will be discussed in this case.

Provided with many potential predictors, the CART algorithm will often overfit the model. Theoretically, the number of final groups (or 'leaves') in the tree can equal the number of observations. In this case, model deviance will be zero since deviance is a function of the difference between the group mean and each observation value, and each group has only one observation. However, an overfit model is so specific to the particular observations provided, it is of little use in describing ecological relationships and will not prove useful in predicting future values (Breiman et al., 1984). In this study, the optimal number of modeled groups or tree leaves is determined using cross-validation procedures.

In an effort to avoid overfitting, the CART function (available in the S-PLUS4 exploratory data analysis software package used in this study) uses minimum group membership and minimum group deviance rules to halt splitting. The function does not split leaves containing ten or fewer observations or featuring deviance values that are less than one percent of the root node (all observations) (Venables and Ripley, 1997). Despite these precautions, overfit models may still result.

To evaluate the best tree size the S-PLUS (version 4) cross-validation routine is implemented. This procedure randomly splits the data into ten equal partitions. Nine of these are used as a test data set to construct a model that will be used to fit the tenth, unused partition. With ten partitions, this can be done in ten different ways. The model deviance at each split is averaged for these ten iterations. Because results are dependent upon the initial random partitioning, it is advisable to run the cross-validation procedure more than once (Venables and Ripley, 1997). This avoids the possibility that the results are not unduly influenced by an unrepresentative random partitioning. Mean deviance for each split was determined in this study from the (averaged) results of twenty cross-validations.

In this study, CART is used to estimate the threshold values of climatic variables which appear to influence multispecies recruitment in Chesapeake Bay. CART model 'goodness of fit' is judged by examining the distribution of the tree's leaves or end points. Specifically, a good fit is judged as one which minimizes observational misclassification.

Linear regression models will also be used to compare SLP pattern frequencies to the CBASS recruitment pattern. Standard least squares regression will be used along with the more robust least trimmed squares regression (Rousseeuw, 1984; Mathsoft, 1997). Least trimmed squares regression is a linear method much like least squares regression except that it is robust with respect to outliers and outlier 'clusters'. While least squares regression fits the model that minimizes the sum of the squares of all residuals, least trimmed squares fits the model that minimizes the sums of square for a subset or 'trimmed' portion of the residuals. This trimmed portion is often represented as q described in the equation: $q = (n/2) + ((p+1)/2)$, where p is the number of predictor variables and n is the number of observations (Venables and Ripley, 1997). Least trimmed squares regression is helpful in identifying outliers and fits models which are relatively unaffected by them. The fit of both regression models will be evaluated by the proportion of response variable variance they account for, as indicated by their r-squared values.

RESULTS

Synoptic-Scale Climate-Recruitment Relationships

Temporal synoptic SLP pattern classification

The first five of the forty-eight daily SLP principal components account for 82% of the total SLP data set variance and were retained (Figure 2.2). Scores from these five PC's were submitted to average-linkage cluster analysis. Cluster solution criteria (see Methods) indicated that the 77-cluster solution was most appropriate. Of these 77 clusters, ten accounted for greater than three percent of total data set daily observations. These ten clusters are used to seed the k-means cluster analysis. Therefore, the final k-means solution also yielded ten clusters. Mean PC scores for each of these cluster were used as linear weights to construct the ten composite SLP pattern cluster maps (Figures 2.3-2.11).

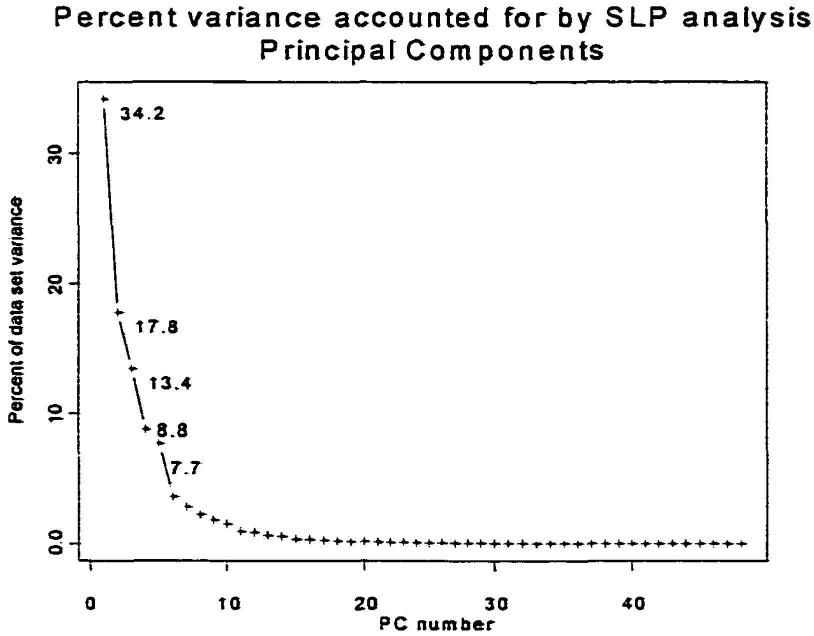


FIGURE 2.2. Scree plot of SLP principal components analysis. Three PC's were retained based upon this information.

Cluster one (Figure 2.3) describes a frontal pattern and occurs on 392 (13.5%) spring days during the study period. The front occurs between a cold high pressure air mass over the Great Lakes region and a warmer high pressure system in the Atlantic. A low pressure system southeast of the Atlantic Canadian maritime provinces and another in the southeastern U.S. is associated with the trough extending along the eastern U.S. seaboard. Temperatures over the Chesapeake Bay region would vary depending on the juxtaposition of these air masses. If the front is to the north of the region conditions are likely to be relatively warm due primarily to southerly flow. If located to the south, opposite conditions would prevail.

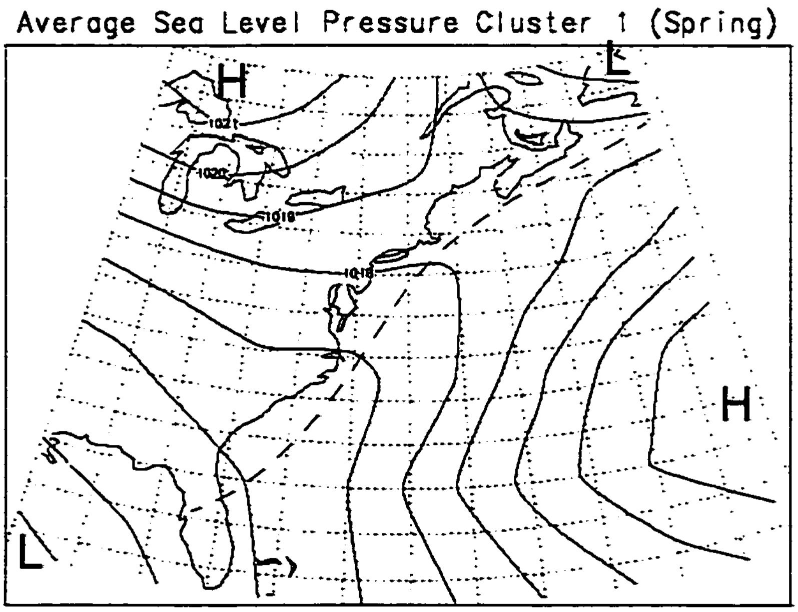


FIGURE 2.3. Spring (March-May) Sea level pressure (SLP) pattern 1. Sea level pressure contours (one milibar interval) are drawn (solid lines. Fronts (dasshed lines), high (H), and low (L) pressure systems are also indicated.

Cluster two (Figure 2.4) occurs on 216 days (7.4%) and represents a strong and large low pressure system with a center over Nova Scotia, Canada. Relatively strong flow from the Great Lakes region would bring cold air into the

Bay area due to the strong northwest-southeast orientation of the pressure gradient.

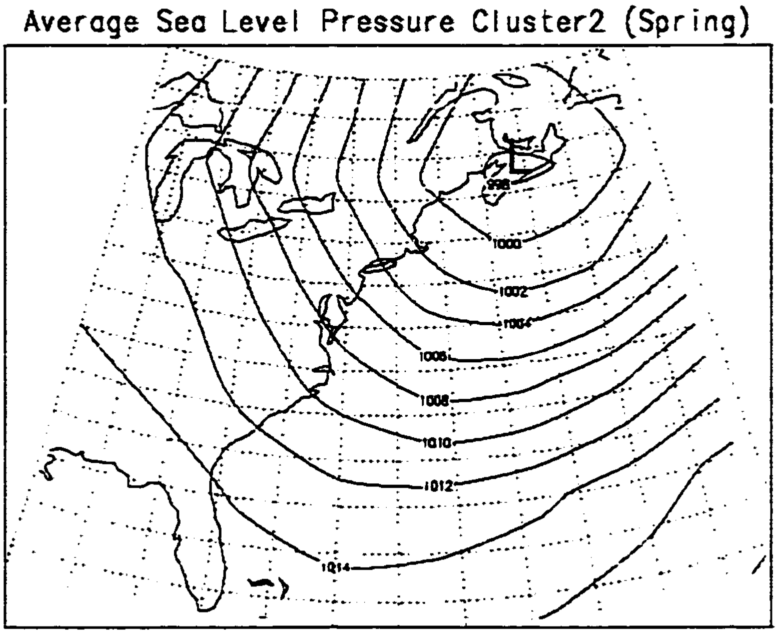


FIGURE 2.4. Spring SLP pattern 2. Markings explained in figure 2.3.

Cluster three (Figure 2.5), which often preceeds cluster two, depicts a classic 'Hatteras Low'. Occurring for 312 days of the study period (10.7%), this low pressure system is not as strong as that of cluster two. This is consistent with observations that low pressure systems formed at Hatteras often intensify as they track northeasterly (hence the name 'northeaster') along the Atlantic coast. Cluster three can bring rain or snow to regions of the Chesapeake Bay watershed depending upon the storm's size and track (Davis et al., 1993; Knappenberger and Michaels, 1993; Jones and Davis, 1995). Generally, warm conditions prevail in the north and eastern sectors while low temperatures occur in its western and southwestern quadrants.

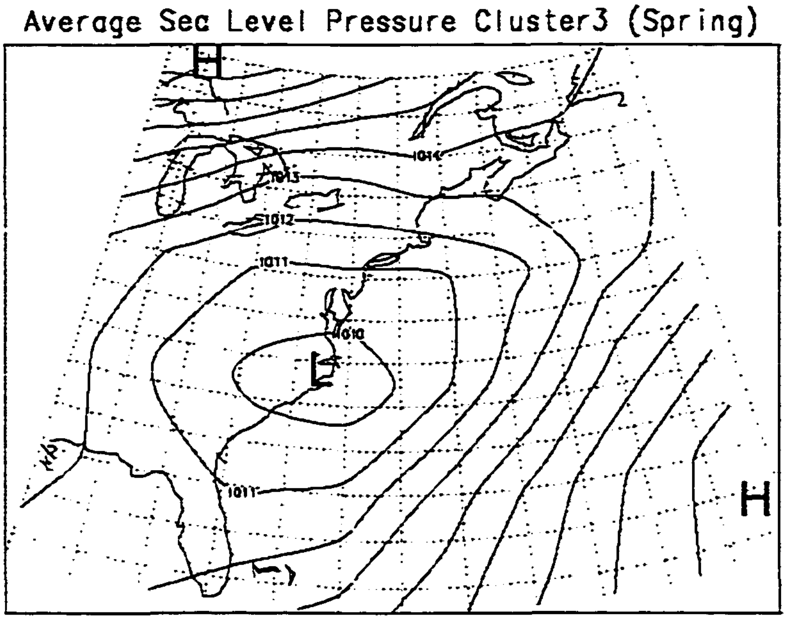


FIGURE 2.5. Spring SLP pattern 3. Markings explained in figure 2.3.

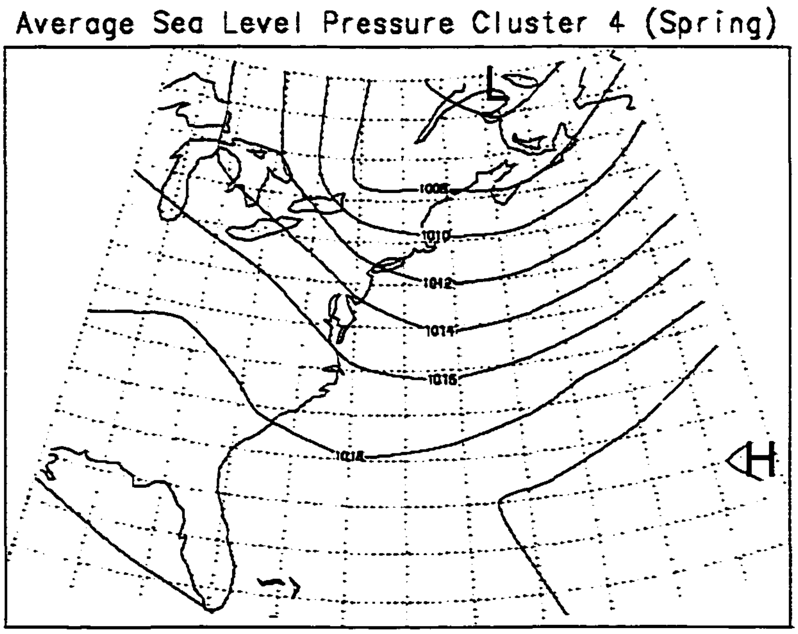


FIGURE 2.6. Spring SLP pattern 4. Markings explained in figure 2.3.

Cluster three also often preceedes cluster four (Figure 2.6). The dominant feature of cluster four is also a low pressure system near the Canadian maritime provinces. This system is much weaker and further inland than that of cluster two. The west-northwesterly flow would again bring cool to cold air into the region. Cluster four occurs on 316 days, equating to 12.6% of the study period's observations.

Cluster five (Figure 2.7) occurs for 215 days (7.4%) and features a very strong east-west pressure gradient. This gradient is formed at the intersection between a large strong high pressure system centered over the Great lakes that extends to the Gulf of Mexico and a similarly large low pressure system centered to the northeast of the Canadian Maritimes. The resulting strong northerly flow undoubtedly results in cold and perhaps windy conditions over the Bay region.

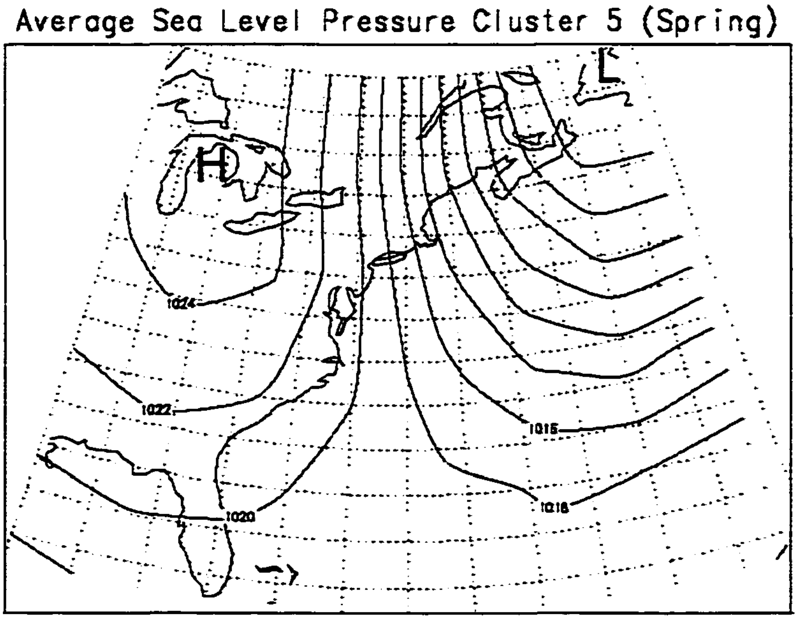


FIGURE 2.7. Spring SLP pattern 5. Markings explained in figure 2.3.

Cluster six (315 days or 10.5% of observations) features relatively warm conditions as a result of southwesterly flow (Figure 2.8). This flow is the result of a large low pressure system, again centered over the Great Lakes region, and the seasonal encroachment of the Mid-Atlantic subtropical anticyclone often referred to as the 'Bermuda High'. It is not unusual for cluster six to precede cluster seven.

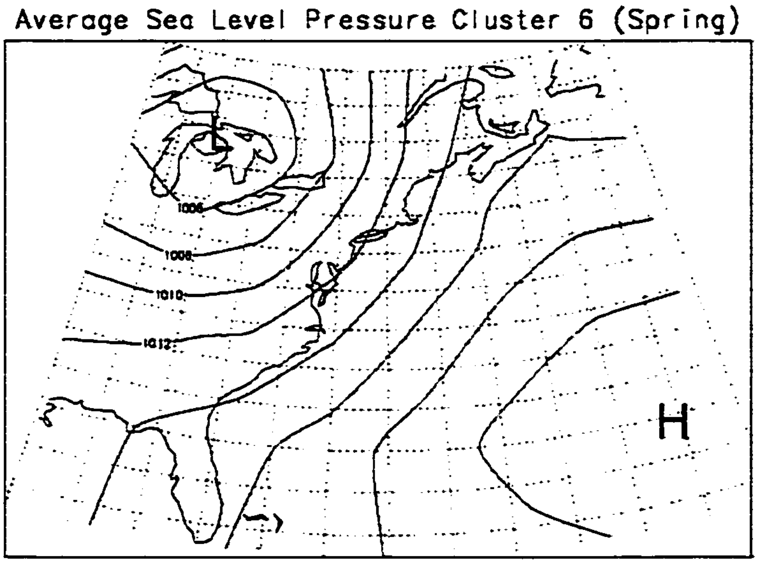


FIGURE 2.8. Spring SLP pattern 6. Markings explained in figure 2.3.

Cluster map seven (330 days or 11.4%) features even stronger south-southwesterly flow than six (Figure 2.9). This cluster (Figure 2.8) features an intensified and more westerly positioned high pressure system influencing much of the western Mid-Atlantic Ocean and the eastern half of North America. Due to the subsidence and atmospheric circulation associated with this pattern, warm conditions and low precipitation prevail under its influence.

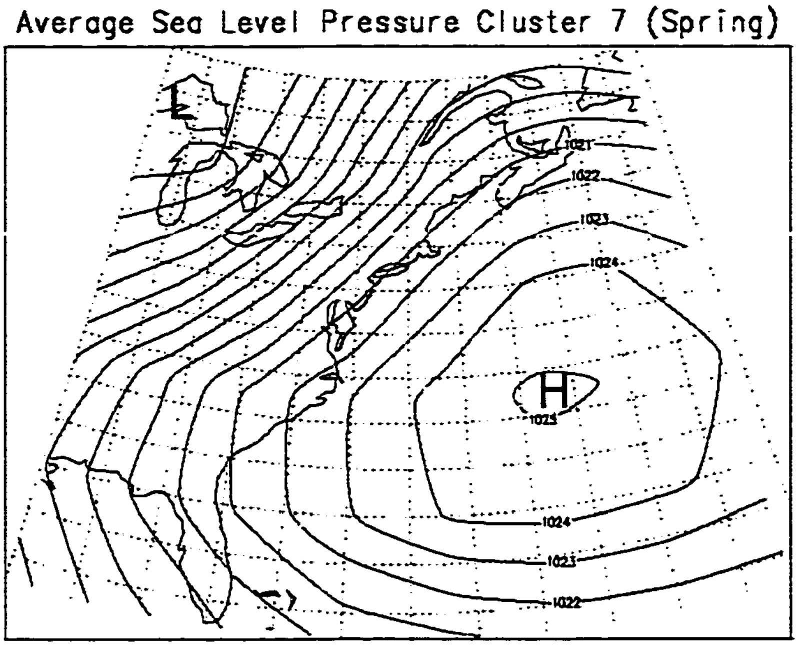


FIGURE 2.9. Spring SLP pattern 7. Markings explained in figure 2.3.

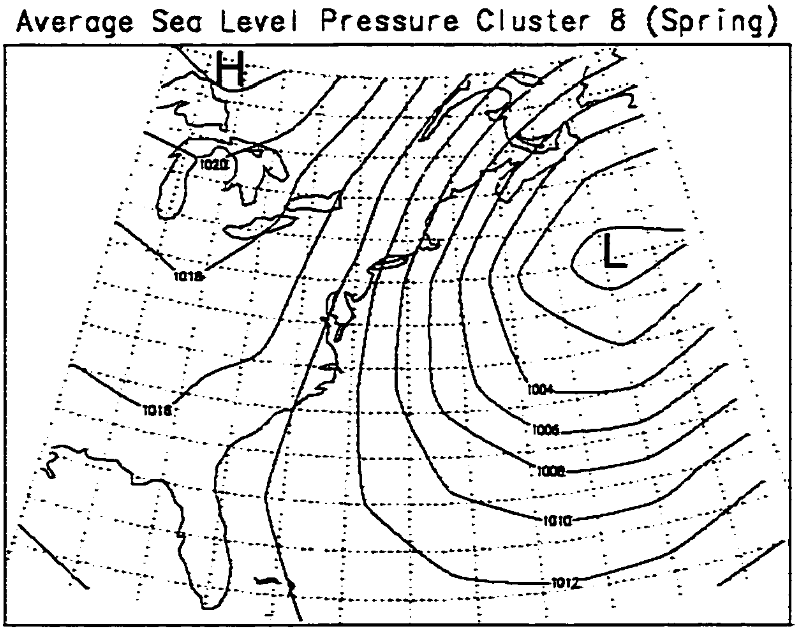


FIGURE 2.10. Spring SLP pattern 8. Markings explained in figure 2.3.

Cluster eight (Figure 2.10) occurs only 5.85% of the time or on 167 days during the study period and is similar to cluster five. Cluster eight, like five, features a large low pressure system in the Atlantic, a large high pressure system on the continent and a resulting strong northerly flow. Important differences lie primarily in the more northerly position of the high pressure system of cluster eight relative to five and the more southerly position of the low pressure in cluster eight. As a result the flow is north-northeasterly in eight as opposed to the northward flow in five. Cursory examination of the daily data indicated that cluster eight often precedes cluster five and the eight to five sequence sometimes precedes cluster nine.

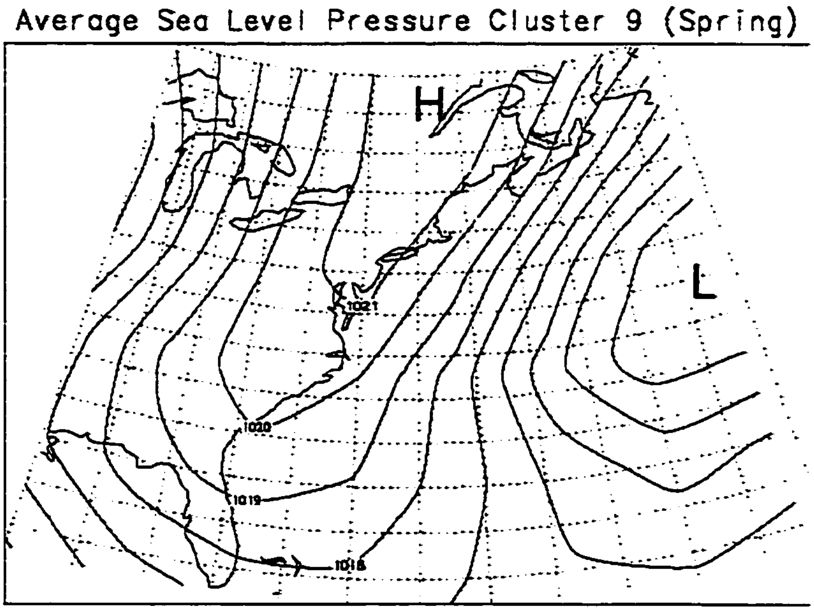


FIGURE 2.11. Spring SLP pattern 9. Markings explained in figure 2.3.

This ninth cluster (Figure 2.11) appears in 311 days of the study period (10.7%). The arctic high pressure system seen in cluster eight moves eastward, and perhaps a bit southward in cluster five until, in cluster nine its movement appears to be impeded by the Appalachian mountain chain. This scenario is often referred to as 'cold air damming' since the anticyclonic circulation of cold air is laterally compressed as it encounters these mountains. It appears from cluster nine that this lateral compression extends the central pressure region much further south. This 1021mb isobar reaches the upper Chesapeake Bay region. Low temperatures would be expected over the entire eastern seaboard under these conditions.

Warming as it moves, the cold high pressure system seen in cluster ten (Figure 2.12) may precede cluster seven. While climatologically related in sequence, these two clusters can bring very different weather to the Mid-Atlantic U.S. This is because cluster ten high pressure systems arrive from the northwest. When they arrive these continental polar systems feature low temperatures which can become more moderate the longer they reside over the southeastern states. Cluster ten occurs in 290 or 10% of the daily observations.

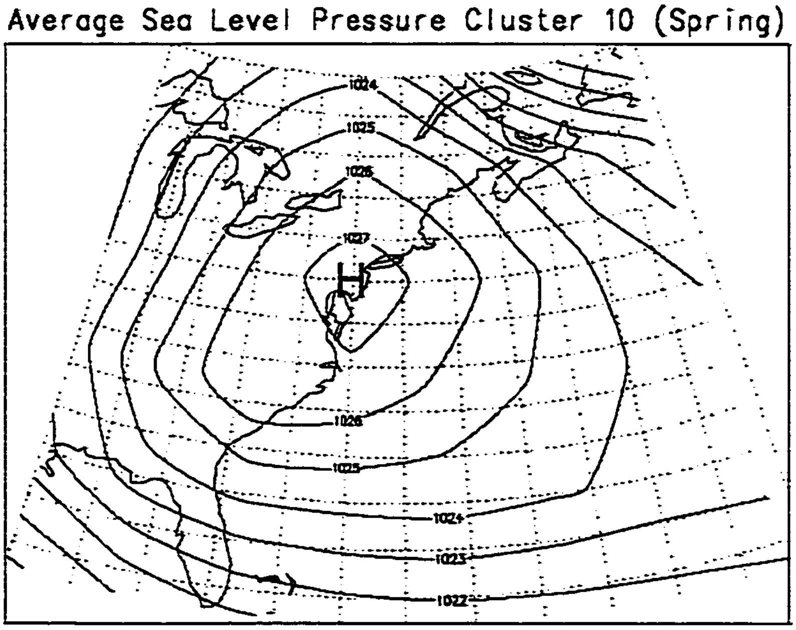


FIGURE 2.12. Spring SLP pattern 10. Markings explained in figure 2.3.

CART

Monthly annual frequencies for each SLP pattern cluster were calculated for each year of the study period (1966-1997). These thirty time series were used as input variables to the CART procedure used to explore climate-recruitment relationships. Annual CBASS recruitment scores for the MDNR seine survey served as the response variable. The initial model resulting from this analysis featured six tree 'leaves' or observational groupings, each described by a different combination of SLP pattern frequency threshold values (Figure 2.13).

Initial CART model of SLP patterns-CBASS relationships

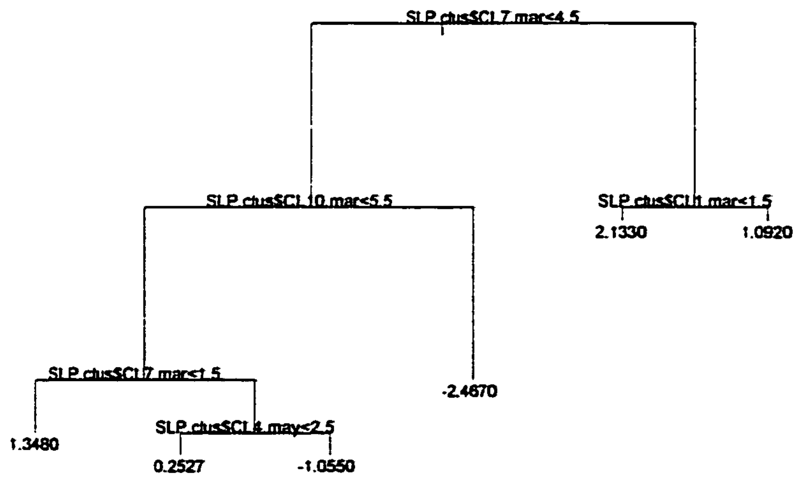


FIGURE 2.13. Initial regression tree resulting from CART analysis of annual MDNR CBASS recruitment pattern scores. Annual frequency of each SLP pattern (1-10) for each month (March-May) were used as potential predictors. Predictors used were March SLP patterns seven, ten, and one, and May SLP pattern 4. Observational classification rules are labled at each node. Observations described by each rule follow the right branch of each node while those do not follow that rule follow the left branch. Mean CBASS pattern scores for the observations within each terminal node are also provided.

This model features March cluster seven (twice), March cluster ten, March cluster one, and May cluster four. Deviance for this model is a decreasing exponential function of tree size (Figure 2.14). Evaluation of the results from twenty cross-validation procedures revealed that the most robust tree size was that which featured four leaves. The initial model was pruned accordingly (Figure 2.15).

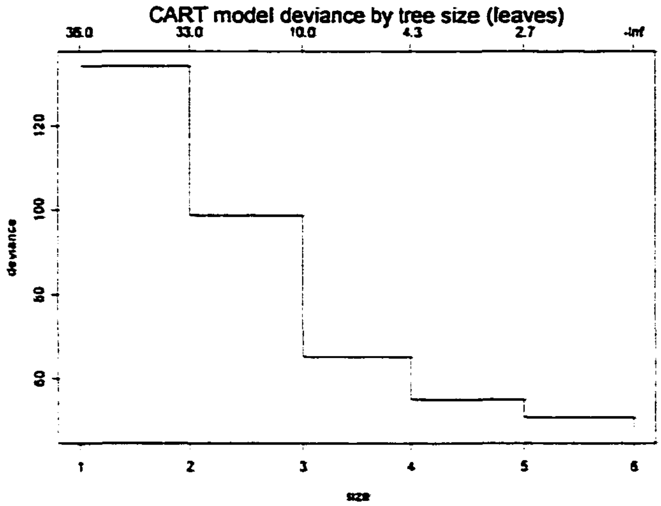


FIGURE 2.14. Step plot of the initial CART model's deviance by tree size (number of 'leaves' or observational groupings).

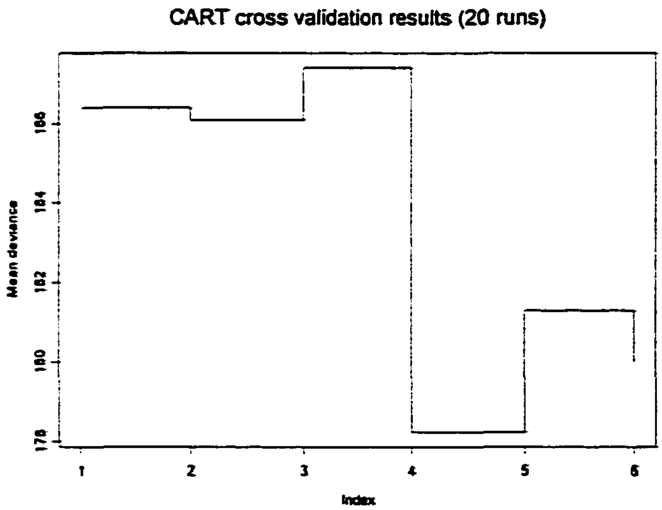


FIGURE 2.15. Cross-validation results of the CART model. The four leaf tree was chosen as the best model based upon these results. See text for further explanation.

Surprisingly, of the thirty monthly SLP pattern time series available, the final model features only two, both for the month of March. These results indicate that, while the 'extra' variables included in the initial model slightly reduced the model's overall deviance, they proved to be unreliable predictors. The frequency plots of Figure 2.16 reveal the distribution of CBASS index values included in each group while the barplots indicate the individual scores for each annual observation included in each group.

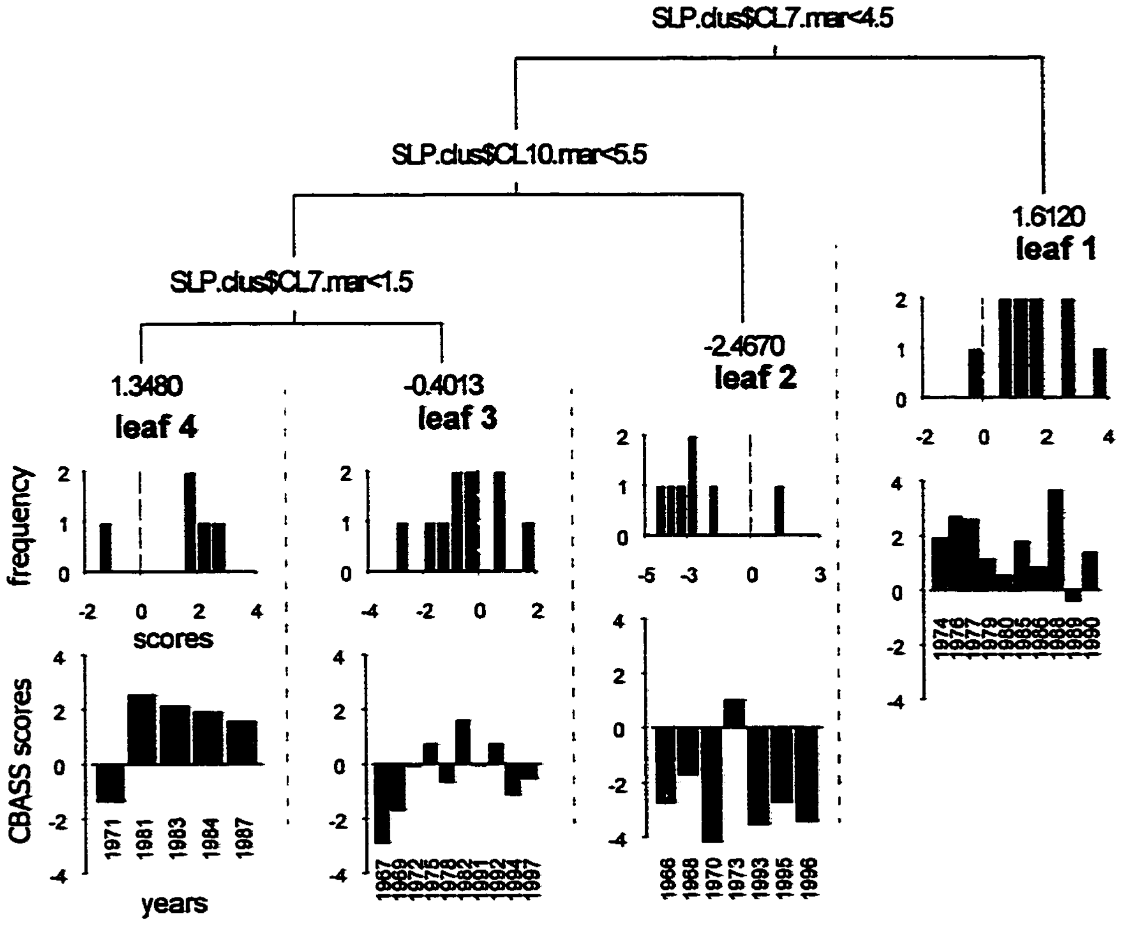


FIGURE 2.16. Final CART model of MDRN CBASS recruitment scores (1966-1996). The tree diagram is descibes in figure 2.13. Frequency histograms of observation values and individual (annual) scores plots are also provided for each tree leaf.

The clearest result of this model is that the years featuring greater than four cluster seven days during March consistently yield positive CBASS recruitment pattern scores. These years, featuring strong shelf spawner and poor anadromous fish recruitment are contained in leaf 1 of the model. Leaf two contains mostly strong negative CBASS pattern scores. The observations grouped in this leaf occur in years featuring fewer than four cluster seven days and greater than five cluster ten days, again in March.

Years not falling under the conditions describing leaves one and two fall into leaves three or four depending once again on the number of cluster seven days in March. Leaf three days occur when March features between 4.5 and 1.5 cluster seven days and less than 5 cluster ten days and are nearly normally distributed around the leaf mean value of -0.4013. The final leaf, leaf four, contains mostly strong positive scores occurring in the early and mid 1980's and one negative score for 1971. It is interesting to note that leaves three and four occur during years which are not strongly affected by cluster ten or seven SLP patterns during March. While cluster four appears to group primarily strong positive values, these all occur during the early to mid 1980's when striped bass spawning stock and egg production were severely depressed (Richards and Rago, 1999; Maryland Fisheries Service, 2000).

Consideration must be given to the possibility that, while splitting the data to create leaves three and four decreases overall model deviance, this split is of no ecological importance. Since both leaves three and four occur when neither cluster seven nor cluster ten occur often in March, it is important to note that if not split, the subset of data not included in either leaves one or two would feature a nearly Gaussian distribution with a mean value near zero. In other words with neither climate feature dominant, the CBASS index values are randomly distributed around zero.

Graphical representation of the final CART model's goodness-of-fit are presented in Figures 2.17 and 2.18 in the scatterplot and time series comparisons of model fit values versus actual CBASS recruitment index scores. Because the CART model featured four leaves, fit values can take on only four (leaf mean) values.

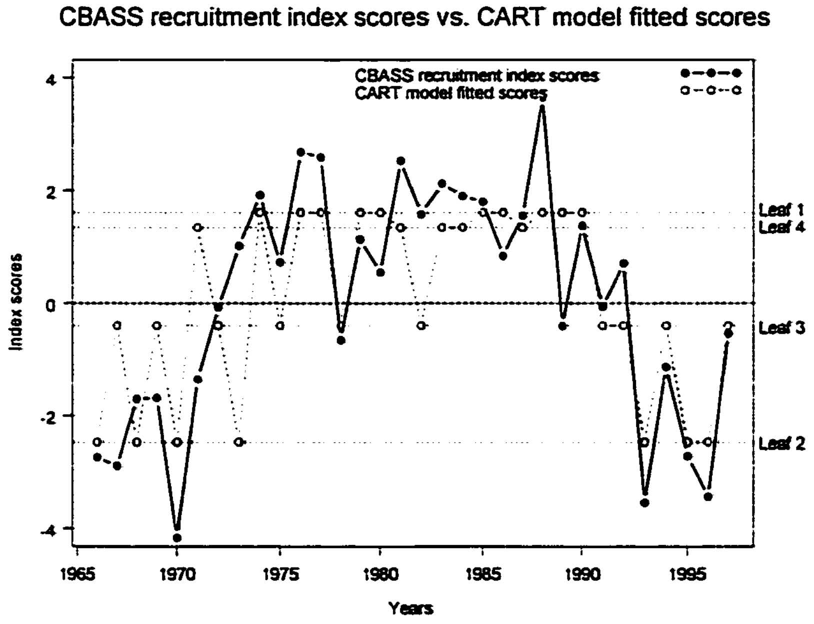


FIGURE 2.17. Time series plot of annual CBASS index scores and the CART model's fitted scores.

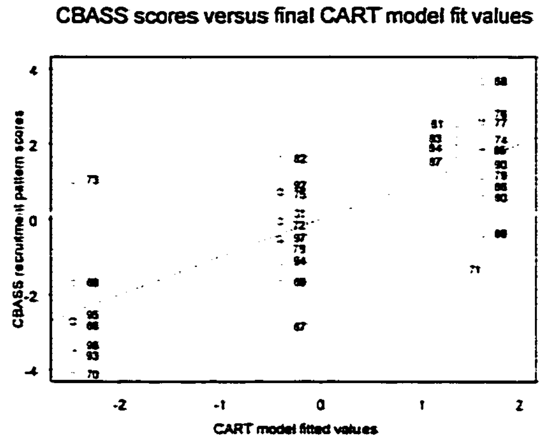


FIGURE 2.18. Scatterplot of annual CBASS index scores and fitted scores provided by the CART model.

Linear models

For comparison, a least squares linear model of CBASS scores was constructed using the two predictor variables indicated by the CART model (March clusters seven and ten). Thirty-seven percent of the CBASS score variance (r-square of 0.37) is accounted for by the resulting least squares model. Each of the predictors, as well as the model itself, were significant using an alpha of 0.05. Figures 2.19 and 2.20 compare the least squares model fitted values to the actual CBASS index scores. This model also appears to model most years well. The exception are the years 1981,1983,1984,and 1987.

The more robust least trimmed squares (LTS) regression also produced a well fit model using the predictive variables identified in the CART model (cluster seven and ten annual March frequencies). Scatterplots and time series of annual CBASS index scores and the LTS model fitted values show that, as in the CART and least squares models, both low frequency decadal scale trends and high frequency interannual variability are well modeled (Figures 2.21-2.22).

As expected, the years 1981,1983,1984, and 1987, which were not well described by the least squares model were treated as outliers by the more robust LTS model. Ignoring these years improves the r-squared value from 0.38 (ordinary least squares fit) to 0.52.

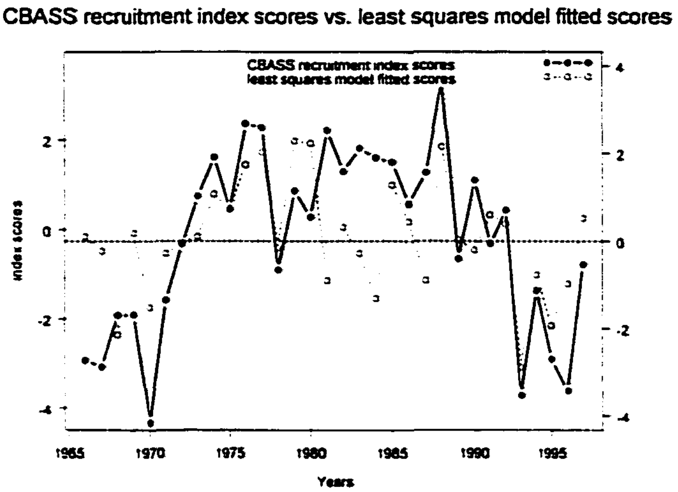


FIGURE 2.19. Time series plot of annual CBASS index scores and the least squares linear model's fitted scores.

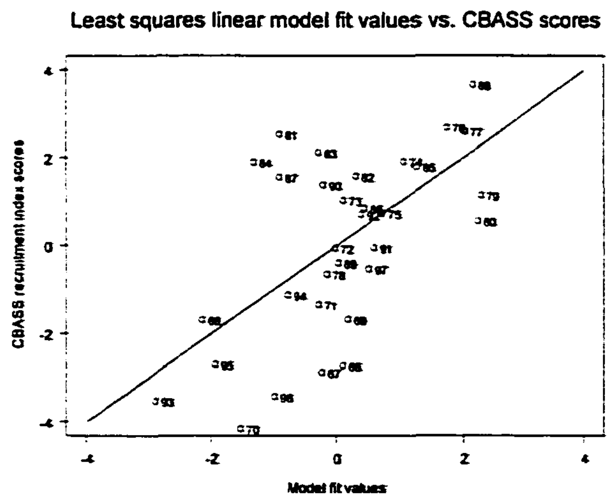


FIGURE 2.20. Scatterplot of annual CBASS index scores and fitted scores provided by the least squares linear model

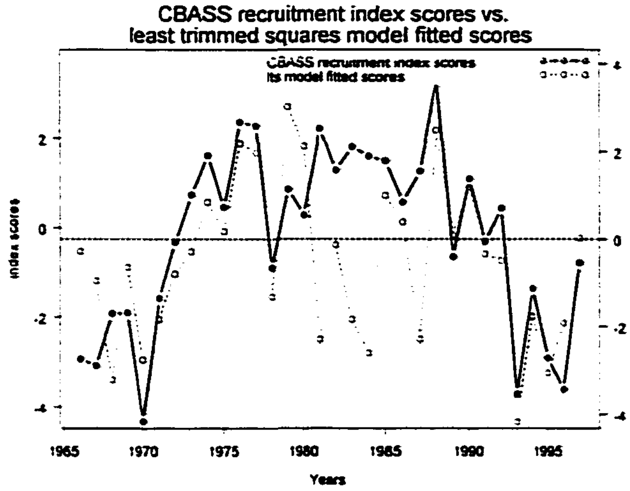


FIGURE 2.21. Time series plot of annual CBASS index scores and the least trimmed squares linear model's fitted scores

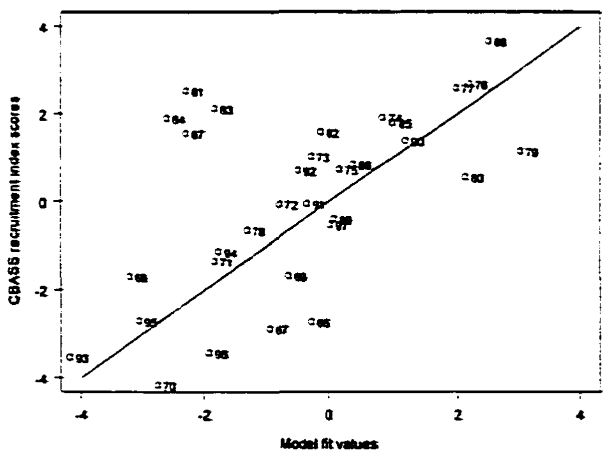


FIGURE 2.22. Time series plot of annual CBASS index scores and fitted scores provided by the least trimmed squares linear model.

DISCUSSION

Influential climate patterns

Results of the synoptic climate classification analysis used in this paper proved effective in describing the temporal and spatial variability in spring climate over the Chesapeake Bay region. A wide variety of synoptic conditions were identified, many of which are capable of influencing physical variables important to the biotic components of the Bay ecosystem. Examples of potentially influential systems identified by this classification include those related to cyclogenesis and precipitation such as cluster map patterns one, two and three, as well as those capable of strongly influencing springtime temperatures such as clusters two, five, seven and ten.

A surprising result of this investigation is that while thirty weather pattern time series (ten clusters for each of the three spring months, March-May) were available to the CART algorithm, the only two included in the CBASS pattern-climate model were clusters seven and ten for March. Both the CART model and linear regression models using these same predictors were able to fit both the low frequency decadal scale trends and high frequency interannual variability within the CBASS recruitment index time series quite well. Least trimmed squares clearly demonstrated that the years 1981,1983,1984, and 1987 were not well using a linear combination of clusters seven and ten. It is likely that these years may have registered near zero, or perhaps had negative CBASS index scores (favoring anadromous fishes) if striped bass spawning stock had not been severely depressed during this period. Least trimmed squares de-emphasized these years when fitting the model and its explained variance increased to 52%.

These results indicate that the negative relationship between spring shelf spawning and anadromous species (the CBASS recruitment pattern) is influenced by the number of March days characterized as SLP clusters ten and seven. Specifically, a large number of cluster seven days in March (more than 5) has been indicative of poor anadromous and strong shelf spawning recruitment (positive CBASS scores) since 1966. The reverse recruitment situation (negative index values) prevails when both few cluster seven, but a relatively large number (more than 5) of cluster ten days occur in March.

A recent investigation of the seasonal and interannual dynamics of the North Atlantic Subtropical Anticyclone by Davis et al. (1997) revealed that this migratory semi-permanent circulation feature has two primary modes. The winter mode is dominated by persistent continental high pressure systems over the eastern U.S. (a.k.a. the semi-permanent Ohio Valley High) and western Europe. During the summer, a single western Atlantic high pressure center exists, generally migrating from the eastern to western Atlantic from January to June and back again from August to January. This summer feature is often referred to as the Azores-Bermuda High. This migratory behavior is not a smooth progression, but can feature rather erratic behavior featuring distant relocations of the central high pressure. For example, Davis et al. found that the Azores-Bermuda high, "moves as far west over a two-month period from early January to early March as it moves east over the six months from July to January."

Davis et al.'s (1997) North Atlantic Subtropical Anticyclone climatology provides some insight into both SLP cluster patterns seven and ten and their contrasting effects upon Chesapeake Bay recruitment. Cluster ten represents the wintertime Ohio Valley High pattern which, in the absence of cluster seven or the spring-summer Azores-Bermuda high pattern during March, positively influences anadromous recruitment while inhibiting recruitment of the shelf spawners. January is the peak month of influence for the Ohio Valley High while July is its summertime counterpart, the Azores-Bermuda. According to Davis et al. (1997), "March marks a winter minimum of anticyclonic activity" and is situated between the demise of the Ohio Valley High, occurring in early February, and the transition to the summer Bermuda High pattern, which occurs in April and May.

Interestingly, Davis et al., also performed PCA on their anticyclone data set, which is derived from the sea level pressure data set used in this study. Semi-monthly frequencies of sea level pressure greater than 1020mb, at 5 by 5 degree latitude-longitude grid nodes were used as variables in their analysis. The study area included the area within and surrounding the northern hemisphere Atlantic Ocean basin and spanned the years 1899-1989.

The fourth principal component of their analysis features two blocking high pressures, one over western Europe and the other over the western Atlantic. The western Atlantic anticyclone depicted in this PC represents the Azores-Bermuda High pattern represented in cluster seven of our study, and peaks from March to June. An area of low pressure is located on the continental U.S. to the east of this blocking pattern. The PC score annual time series of this pattern shows a strong and significant declining trend since 1899. More importantly, the period from 1966 to 1989 mimics the annual March time series of the seventh cluster pattern map of this study during the overlapping years 1966-1989. Annual scores are negative from 1966 (indicating Ohio Valley High dominance) and rise to strong positive (dominant Azores-Bermuda High) values in the mid-70's. They fall again and are negative through the early 80's only to rise sharply and feature strong positive values in both 1985 and 1989.

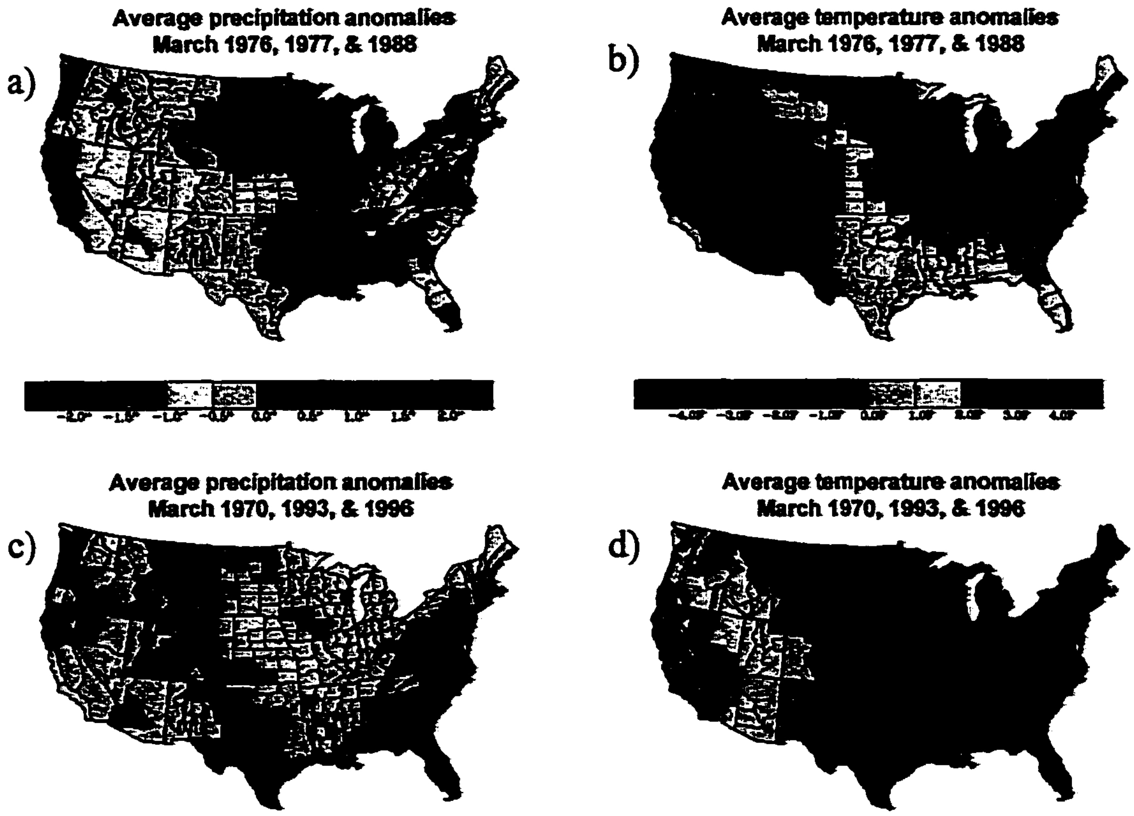
Knappenberger and Michaels' (1993) investigation of the relationship between cyclone tracks and winter climate in the Mid-Atlantic U.S are also relevant to this study. These authors used canonical correlation analysis to define the primary patterns of variability among late winter (January-February) precipitation, snowfall, temperature, and cyclone frequency data sets for the Mid-

Atlantic. Their primary pattern depicts two primary cyclone tracks. The first begins over the north central Gulf of Mexico and tracks through the Ohio Valley. Storms following this path generally pass to the northwest of the Mid-Atlantic region. Storms following the second track originate in the northeastern Gulf of Mexico, crossing Florida, and travel north-northeastward, along the coastal U.S.

Knappenberger and michaels (1993) reported, "a strong correlation between an abundance of cyclones in the Ohio Valley, and below normal precipitation and snowfall amounts, and above normal temperatures across most of the mid-Atlantic region" while, "an abundance of storms along the southeastern Atlantic coast is associated with above normal precipitation and snowfall amounts, and lower than normal temperatures over the region." As described, these cyclone track modes should be inversely related to the Ohio Valley and Azores-Bermuda Highs respectively. The coastal storm track, and its associated cold and wet Mid-Atlantic weather would occur with a jet stream trough and high pressure over the Ohio Valley. Conversely, a relatively strong Azores-Bermuda High pattern would result in a westward displacement of the storm track Mid-Atlantic weather under these conditions would be relatively warm and dry. This climate pattern is associated with a ridge in the jet stream over the eastern U.S.

The results of Davis et al. (1991) Knappenberger and michaels (1993), and those of this study all suggest that variability in the relative dominance of the Azores-Bermuda and Ohio Valley high pressure systems should be directly related to CBASS recruitment index scores. To confirm this, precipitation and temperature anomaly maps were produced for the continental U.S. using the National Climatic Data Center's climate division dataset web page (http:// www.cdc.noaa.gov/USclimate/USclimdivs.html, 2000). These maps were generated by plotting the difference between actual precipitation and temperature and the long term (1950-1995) mean conditions for each U.S. climate division.

Annual anomalies were averaged and plotted for two different year groups. The first included the years 1976, 1977, 1988, and the second, the years 1970, 1993, and 1996. The groups were chosen to represent the three years featuring the strongest positive (favoring shelf spawners) and negative (favoring anadromous fishes) CBASS index scores respectively. Since the CBASS recruitment index is correlated with the Azores-Bermuda and Ohio Valley High pressure patterns, these precipitation and temperature anomaly maps (Figure 2.24) convey the March weather conditions defined when clusters seven and ten are dominant, respectively.



Source: NOAA-CIRES/Climate Diagnostics Center

FIGURE 2.23. Composite precipitation and temperature maps for the three strongest positive (a and b) and negative (c and d) CBASS recruitment pattern years. Anomalies are relative to 1950–1995 long term means within each U.S. climate division.

These maps clearly show that the climatic patterns presented by the dominance of clusters seven and ten have been correctly interpreted from the work of Davis et al. (1991) and Knappenberger and michaels (1993). Years in which anadromous fishes recruited strongly, shelf spawners weakly, and the Ohio Valley High predominated (1970. 1993. 1996), are those featuring lower than average temperatures over the eastern two-thirds of the U.S. Further, the precipitation anomaly pattern for these negative CBASS recruitment index years are above normal along the U.S. east coast from Florida to New England. Conversely, the positive CBASS index and dominant Azores-Bermuda High year group (1976, 1977, 1988) depicts dry conditions over much of the Chesapeake Bay watershed. The precipitation maps clearly show that this is due, as Knappenberger and michaels (1993) suggested, to the westward displacement of the dominant winter time storm track. During these years, temperatures were also well above normal over the eastern two-thirds U.S.

Climate-fish connections

This exploration of the link between climate and the CBASS recruitment pattern indicates that extension of cold stormy winter conditions into the month of March result in negative CBASS index scores or enhanced anadromous and poor wintertime shelf spawning fish recruitment to the Chesapeake Bay. These weather conditions occur with a jet stream trough over the eastern U.S. and the associated accentuation of the Ohio Valley High. Conversely, positive CBASS scores (strong shelf spawning and weak anadromous species spawning) occur when March is warmer and drier than normal. This scenario is associated with ridging of the jet over the eastern U.S., earlier than normal presence of the spring-summertime Azores-Bermuda High climatic pattern, and the associated westward displacement of the storm track from the Atlantic coast to the Ohio Valley and northern New England.

Coastal spawning/climate relationships

Research regarding the climate-recruitment relationship(s) for winter spawning coastal shelf spawners indicate that dominance of the Azores-Bermuda high would likely lead to enhanced recruitment for these species while dominance by the Ohio Valley High would inhibit their recruitment to Chesapeake Bay. The prime winter spawning grounds for these species is thought to be off the coast of southern North Carolina primarily during December and January (Pacheco, 1962; Kendall and Reintjes, 1975; Warlen, 1994). Larvae and postlarvae are thought to depend upon wind driven coastal currents to be transported to the mouths of coastal embayments including the Chesapeake Bay. Planktonic surveys have revealed that these winter-spawned fishes begin to recruit to these embayments in late winter and begin to reach their oligohaline-mesohaline riverine nursery habitats beginning in March (Massmann et al., 1954; Massmann et al, 1961; Pacheco, 1962; Kendall and Reintjes, 1975; Merriner et al., 1979; Olney and Boehlert, 1988; Ahrenholz, 1991; Warlen, 1992; Bodolus, 1994; Norcross and Wyanski, 1994; Warlen, 1994).

Pressure gradient orientation during years of dominant Azores-Bermuda High (cluster seven) days in March dictate that prevailing winds over the southern Mid-Atlantic and South Atlantic Bights should be southerly. This has been confirmed by studies of both wind and coastal sea level (Bryson and Hare; 1974; Blanton et al., 1985; Schwing et al., 1988). These same studies indicate that winter-spring climate transition features mixed wind patterns and domination of the Ohio Valley

High (cluster ten) leads to north-northeasterly winds that would likely advect larvae away from the Chesapeake Bay.

These observations suggest that the positive correlation between CBASS index scores March Azores-Bermuda High days, and the negative correlation between CBASS scores and persistence of the Ohio Valley High into March, are the result of either favorable or unfavorable wind regimes over coastal Mid-Atlantic Waters. This is borne out in the modeling efforts of Nelson et al. (1977), Reish et al. (1985), and Bodolus (1994) which suggest that recruitment of these species is enhanced by southerly or southwesterly winds. Based upon size and age distributions of shelf species larvae, Warlen (1992) concluded that their cross shelf transport decreases by April. Therefore, if the Azores-Bermuda High spring circulation patterns set up earlier, cross shelf transport would likely be enhanced along with recruitment to Chesapeake Bay. Likewise, if late winter circulation patterns extend into March, recruitment would likely be inhibited.

Wind is not the only weather characteristic which is consistent with the climate-recruitment patterns observed in this study. Otolith hindcast birth dates, daily incremental growth, and meteorological conditions during the January-March period led Maillet and Checkley (1991) to conclude that coastal storms passage, and the accompanying increased wind speed and oceanic heat loss, reduced growth in larval Atlantic Menhaden off the North Carolina coast. Since growth rate appears to be inversely related to mortality (Ware, 1975; Miller et al., 1988; Bailey and Houde; 1989; Pepin, 1993), Maillet and Checkley concluded that winter coastal storms may reduce annual recruitment. This would be consistent with the climate-recruitment patterns described in this paper given the contrasting dominant winter-spring storm track patterns associated with the Azores-Bermuda and Ohio Valley Highs, as explained above and seen in figure 2.23.

This climate-recruitment relationship also leads to dry and warm conditions during the upriver migration and first weeks of tidal oligohaline nursery habitat utilization by shelf spawners. It is reasonable to assume precipitation and cold weather in March could reduce the ability of these early life stage fishes to migrate upstream and reduce survival, though no direct supporting evidence is currently available.

Cold weather and precipitation may also affect the riverine nursery habitat suitability and extent for these species through their effects on physical parameters likely to impact the prey of larval fishes. Massman et al. (1962) found larvae from 18-28mm (fork length) within the mouth of the Chesapeake from December to March. Transformation to the juvenile form occurs in the fishes' riverine nursery area habitats at 38mm (Kendall and Reintjes, 1975). Analysis of 738 larval and postlarval fish (19mm-55mm) digestive tracts by Jane and Carlson (1971) demonstrated that fishes depend upon adult copepods until they reach about 40mm (size of transformation) when phytoplankton began to comprise a majority of their diet by volume. This developmental-dietary schedule suggests that an earlier spring phytoplankton bloom would provide for enhanced zooplankton appropriately timed for the needs of these critical life stages of Atlantic menhaden. Since spot and summer flounder also recruit to the Bay in March as larvae and postlarvae, an early spring bloom may also increase growth and survival during their critical early life stages.

Anadromous fish/climate relationships

The recruitment dynamics of the striped bass has been the focus of a large number of studies. This can largely be attributed to the recreational and commercial importance of the fishery and the dramatic decline in the Atlantic coast population during the 1970's. This study indicates that recruitment is strongly influenced by forces other than spawning stock biomass and egg abundance (for example, Ulanowicz and Polgar, 1980; Mihursky et al., 1981; Polgar et al., 1985; Uphoff, 1998; Richards and Rago, 1999). There is also strong observational evidence (Boynton et al., 1981; Goodyear, 1985; Uphoff, 1998; Olney et al, 1991), confirmed by individual-based modeling (Cowan and Rose, 1993), suggesting that annual striped bass recruitment strength is set between the early larval and early juvenile life stages.

During the last several decades, a number of variables have been proposed to explain recruitment variability in the Atlantic striped bass population. A non-inclusive list includes toxin and pH related mortality of eggs and larvae (Palawski et al., 1985; Mehrle et al., 1987; Hall, 1988; Setzler-Hamilton et al., 1988; Hall, 1987), nutrient loadings (Price et al.,1985; Lindstrom, 1993; Tsia et al., 1991), temperature (Heinle et al., 1976; Merriman, 1941; Ulanowicz et al., 1982; Secor and Houde, 1995; Rutherford and Houde, 1995), riverflow-salinity effects (Rulifson and Manooch, 1990; Van Den Avyle and Maynard, 1994), and the combined effects of both temperature and riverflow (Mihursky et al., 1981; Polgar et al., 1985: Uphoff 1992).

Some of the proposed theories appear contradictory. For example, Price et al. (1991) suggested that increased phytoplankton biomass, related to eutrophication, was behind the decline of the striped bass stocks. According to this theory, increased nutrients leads to increased phytoplankton biomass which, in turn, reduced both adult and young-of-the-year habitat through decreased deep water oxygen levels and shading of submerged aquatic vegetation, respectively. In contrast to this theory, Tsia et al. (1991) proposed that more advanced sewage treatment in the Potomac River has reduced spring nutrient levels and led to decreased phytoplankton and the zooplankton prey of striped bass larvae.

One reason existing evidence supports a wide variety theories is that many of the forcing variables identified by various researchers are correlated. For example, this study has shown that temperature, precipitation, and therefore riverflow are often correlated during the late winter-early spring months. Uphoff (1992), in his study of factors affecting egg and larval survival in the Choptank River, a tributary of Chesapeake Bay, also found that he could not differentiate between the effects of April riverflow, temperature, pH, and conductivity on striped bass survival rates.

Temperature is another variable credited with having both positive and negative effects upon striped bass cohort strength. The contrasting effect of this variable however seems to be directly related to seasonal timing. Cold winter conditions are associated with positive recruitment anomalies (Heinle et al., 1976; while abrupt cold periods in mid to late spring appear to increase mortality rates (Polgar et al., 1976; Rogers and Westin, 1981; Secor and Houde, 1995; Rutherford and Houde, 1995).

The majority of observed temperature and riverflow effects found in the literature regarding recruitment variability of the Atlantic striped bass population(s) appear to be consistent with the findings of this study. One of the most comprehensive studies available is Mihursky et al. (1981). These authors observed that:

a). striped bass young-of-the-year abundance was strongest in years featuring anomalously cold winters, strong spring riverflow, and higher than average April temperatures,

b). egg density increased in an upriver direction within the spawning area,

c). larval gut fullness increased upstream as well, in accordance with ambient zooplankton densities, d). larvae fed upon the largest available zooplankton prey they could capture,

e). larvae selected for prey species in accordance with their (prey) spatial distributions.

Based on this evidence, Mihursky et al. concluded that cold, high flow late winter-early spring conditions result in further upstream migration of the spawning run and therefore a general upstream displacement of the egg distribution. This scenario places developing larvae in a location of peak larval fish prey (zooplankton) abundance. Following Heinle's theory, normally high zooplankton densities should be enhanced by the larger supply of detrital material provided by cold high flow late winter and early spring conditions. They further suggest that areas in which ideal larval prey conditions exist are larger and extended further downstream under these hydro-climatic conditions.

While not specifically addressed by Mihursky et al., low temperature may also act to expand the nursery area in time by prolonging the dominance of the winter-early spring zooplankton assemblage striped bass have been shown to utilize as prey. This is indicated by seasonal and spatial distribution of winter-dominant zooplankton species important in the diet of larval striped bass, most notably *Eurytemora affinis*, *Bosmina longirostris*, and cyclopoid copepods (Merriman, 1941; Setzler-Hamilton et al., 1981; Martin et al., 1985; Limburg et al., 1997 Beaven and Mihursky, 1980; Robichaud-LeBlanc et al., 1997). Further, it has been shown that the growth rate and productivity of the summer dominant estuarine copepod *Acartia tonsa* are higher than those of *E. affinis* as temperatures rise from 10 to 15 degrees Celsius (Heinle, 1969).

CONCLUSION

The negative relationship between recruitment of winter shelf spawning species and spring spawning anadromous species in the Chesapeake Bay, appears to be dictated by weather-driven hydrographic and biological variability. The negative correlation or 'see-saw' pattern contrasting recruitment of shelf spawned with that of anadromous fishes may be related to the combined dependence of both species groups on similar river reaches within the estuary and the contrasting spawning strategies. These contrasts are most evident in the different ways in which the early life stages of these two species groups are 'carried' to these nursery grounds. Anadromous species are spawned in tidal freshwater river reaches while shelf spawned pre-metamorphosed (larval and postlarval) fishes, without the ability to sustain upstream movement, depend upon tidal currents and bilayer estuarine countercurrent circulation for their transport to these areas.

While most recruitment research pertaining to CBASS species to date has focused on winter (December - February) or spring (April - June) months, the statistical models used in this study demonstrated the importance of March climatic forcing. March can be thought of as the 'fulcrum' month upon which the bipolar 'see-saw' CBASS pattern 'teeters'. The importance of March over April and May makes sound ecological sense since it is during this time that shelf spawners are in the final leg of their up-estuary migration to their nursery grounds. Further, conditions in March largely determine the physical and chemical environment during the initial phases of the annual spring phytoplankton bloom. Since the early life stages of both species groups inhabit the upper tidal rivers and Bay during the early spring, March hydroclimatic variability within these areas likely influences the quality, timing, and extent of suitable nursery habitat.

For example, persistence of the winter Ohio Valley High synoptic scale climate pattern would extend cold and fresh conditions into March. This would, in turn, increase the spatial and temporal extent of suitable anadromous fish nursery areas, since anadromous fishes feed primarily on mesozooplankton species dominating the winter assemblage.

In contrast to this scenario, March dominance by the Azores-Bermuda High climatic pattern presents relatively warm and dry conditions within the Chesapeake Bay watershed. This early spring scenario likely leads to an early spring productivity bloom and an early transition from the winter to the spring zooplankton community. Since shelf spawned species arrive in their upper estuarine nursery areas as postlarvae as early as March, an early bloom may be to their benefit.

In summary, March appears to be the 'fulcrum' in the interannual 'see-saw' pattern favoring either the recruitment of anadromous or shelf spawned species in the Chesapeake Bay. Environmental conditions 'swing' to benefit anadromous fishes given prolonged cold and fresh conditions within the Mid-Atlantic region, through a spatial and temporal extension of suitable nursery area habitat. Recruitment 'swings' to benefit shelf spawned species when northwesterly winds, dry conditions, and high temperatures exist in March.

These findings are consistent with both leading theories proposed to explain the general causes of recruitment variability in marine fishes; Sinclair and Iles' (1989) Member-Vagrant and Cushing's (1990) Match-Mismatch. Plausibility of the climate→nursery area→recruitment relationships suggested in this Chapter will be investigated through a detailed simultaneous comparison of nursery area hydrography, zooplankton community structure, and annual juvenile fish abundance data sets in Chapter Three.

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Chapter Three

The effect of winter-spring seasonal transition dynamics on multispecies recruitment in Chesapeake Bay

INTRODUCTION

Chapters One and Two described the temporally and spatially pervasive CBASS multispecies fish recruitment pattern and attributed its interannual variability to the nature and timing of the seasonal climate transition from winter to spring. During the course of this study, the striped bass and Atlantic menhaden are often used as 'model' species for the anadromous and shelf spawning species groups respectively, due to the volume of detailed spawning and early life history information for these species.

Based upon the life history requirements and strategies of the two negatively correlated species groups and the statistical model results in Chapter Two, it was hypothesized that persistence of the seasonal Ohio Valley high pressure system leads to colder, and perhaps wetter, than normal winters as well as a late winter to spring transition. This scenario appears to benefit recruitment of anadromous fishes and inhibit recruitment of winter spawning continental shelf (coastal ocean) species that recruit to the Bay in early spring. Conversely, relative dominance of the Azores-Bermuda high pressure system during the late winter-early spring period (specifically March), brings relatively warm and dry conditions and leads to an early transition to spring.

Review of the available life history requirements and spawning strategies of key CBASS anadromous and shelf spawning species suggested that the mechanisms most likely responsible for the bipolar recruitment pattern affect the survival of the fishes from the egg to juvenile life stages. For the anadromous fishes, these processes must influence spawning conditions, or egg and larval survival within the tidal freshwater-oligohaline river reaches that they utilize as nursery areas from early April through the summer months. For shelf spawners, these processes could operate on their late winter to early spring larval and postlarval migration into these same nursery areas, as well as on the March to summer period that they too spend in the rivers.

Based on feeding, distribution, and survival research by Heinle et al, (1976), Polgar (1976), Ulanowicz and Polgar (1980), Beaven and Mihusky (1981), and Setzler-Hamilton et al. (1981), Mihursky et al. (1981) proposed three factors which might account for recruitment variability in the best researched species of the CBASS pattern, the striped bass. First, among these was that late winter-early spring high flow and cold conditions supply and transport more detritus and detrital derived nutrients to the striped bass nursery area. As Heinle first proposed, this should increase the production of the zooplankton prey of striped bass larvae and postlarvae.

The second proposal by Mihursky et al. extended the first, adding that high spring flow and higher zooplankton production likely increases the nursery areas of the striped bass. The last proposal by these authors was that cold fresh conditions in the early spring delay spawning of adult fish until they have migrated into the upper end of their spawning habitats. Since these areas were believed to be more productive areas than those further downstream, Mihursky et al. hypothesized that, 'emerging larvae have sufficient time to grow through the critical feeding stages prior to being transported out of the rich nursery area.'

To examine the likelihood that an upstream displacement of the striped bass spawning zone increases survival during the egg to juvenile developmental period, egg abundance data and juvenile abundance survey data were used to calculate egg-juvenile survival. These survival estimates were then compared to spatial distributional characteristics of the eggs. Further, these same data were used to determine whether either the Azores-Bermuda (warm and dry) or Ohio Valley (cold and wet) high pressure systems were correlated with striped bass survival.

To examine the likelihood that the increased late winter-early spring flow and the timing of the winter-spring transition influence the tidal fresh-oligohaline river reaches both CBASS species groups utilize as nursery areas, hydroclimatic and zooplankton data sets are examined with relative annual abundance of four key CBASS species, the striped bass (*Morone saxatilis*), white perch (*Morone americana*), spot (*Leiostomus xanthurus*), and the Atlantic Menhaden (*Brevoortia tyrannus*).

The prime focus of this chapter will be to determine whether interannual hydroclimatic variability, accordant with the synoptic scale climatological features defined in Chapter Two, influences the quality and quantity of the habitat in the tidal freshwater-oligohaline river zones in ways that are consistent with the CBASS recruitment pattern.

METHODS

The first step in the simultaneous analysis of river-specific nursery area conditions and key CBASS species' recruitment is to establish the existence of the CBASS pattern on local scales in the three largest Virginia tributaries of Chesapeake Bay. Relative annual juvenile fish abundance was calculated for the Rappahannock, York, and James river systems by summing annual catches from consistently sampled sites for the Virginia Institute of Marine Science's (VIMS) striped bass seine survey in each river.

Since principal components analysis was used to initially isolate the CBASS pattern, it was used here as well. The number of observations (cases) used in this analysis was limited to include years when consistently sampled stations were visited (1980 -1998). Since higher case to variable ratios help ensure robust PCA results, the annual relative abundance for only four species (variables) were used in the analysis. These species, spot (*Leiostomus xanthurus*), Atlantic menhaden (*Brevoortia tyrannus*), striped bass (*Morone saxatilis*), and white perch (*M. americana*) were chosen since they represented the four species most consistently and strongly weighted in the CBASS patterns previously isolated in Chapter One. Further, the former two species represent the shelf spawner group while the latter pair represents the anadromous group.

Striped Bass egg distribution and survival and climate

The first set of analyses focus on Mihursky et al.'s (1981) theories that fish spawned from eggs distributed further upstream have lower mortality rates. In addition to exploring the egg distribution-survival relationships, survival of striped bass eggs to the juvenile life stage was compared to the number of March days classified as Azores-Bermuda or Ohio Valley High pressure systems. These latter analyses were designed to test the relationship between synoptic scale climate features and the CBASS recruitment pattern defined in Chapter Two.

Unfortunately only six years of detailed annual egg distribution data were available. These data were found in a striped bass study of the Pamunkey river published by Olney et al. (1991). These researchers sampled striped bass eggs from single randomly chosen stations within each of ten 4.8 km long river segments or strata. Strata were sampled semiweekly to weekly with dual (bongo) 333 μm plankton nets in a stepped-oblique manner for 2-6 minutes. Egg densities were calculated using flow meter derived volume filtered values.

Juvenile striped bass annual abundance was calculated using five bi-weekly seine samples taken from stations at river miles 41, 45, and 50, in all years except 1980 and 1988. Year 1980 was dropped from the analysis since only one of these three stations was sampled in this year. Two of the three stations sampled in 1980-1988 were sampled in 1989, as station 41 was permanently moved one mile upstream. Data for mile 42 was used in place of 41 for this year. Relative survival estimates for five of these years were calculated by dividing the annual juvenile abundance in the Pamunkey River (see below), by the total Pamunkey River egg production estimated by Olney et al. (1991).

To test Mihursky et al.'s theories, annual survival estimates were compared to rivermile location of the downstream 50th percentile of eggs. Survival was compared to the distance between the lower and upper most Pamunkey river transects found to contain eggs, also provided in Olney et al. (1991). Finally, comparisons were made between annual survival estimates and the number of March days of both high pressure patterns of interest. A least squares linear model was also constructed to determine if the climate-CBASS relationships defined in Chapter Two could be related to survival striped bass during their early life stages in the Pamunkey River.

River specific climatic-hydrographic-zooplankton-fish recruitment analyses

The synoptic classification methods used in Chapter Two represent a 'top-down' approach in exploring the link between climate and interannual recruitment variability. The term, 'top-down' refers to the fact that climatic variability is described in its most general form. This is in contrast to studies employing methods such as stepwise regression, which choose the 'best' predictors from a pool of very specific (and intercorrelated) individual weather and climate variables.

The synoptic classification approach is a more appropriate first step in establishing a climate-recruitment link primarily because it treats climatic variability realistically. However, if synoptic-scale climatic variability influences recruitment on large scales, it must do so through biological or hydrographical processes operating on smaller, river basin scales. Therefore, these processes should be evident in major river systems throughout the Bay, as is the CBASS recruitment pattern.

Hydrological (salinity), meteorological (heating degree days), biological (zooplankton), and recruitment data, are used for the three largest Chesapeake Bay tributaries in Virginia. These rivers were used because they provide a degree of independence in the analysis since they were not used to establish the climate-recruitment relationships described in Chapter Two. These data are examined to explore the possibility that nursery area habitat suitability or areal extent for CBASS species are differentially affected by the weather and climate conditions which result from dominance of the Azores-Bermuda High over the Ohio Valley High, or vice versa during March.

The Virginia Institute of Marine Science (VIMS) conducts a seine survey using methods and gears similar to the MDNR survey (see Chapter One for details). Also targeting the striped bass this seine survey samples the three largest

Chesapeake tributaries in Virginia, the Rappahannock, York, and James river systems. By summing the number of fishes sampled at consistently sampled stations, river-specific indices were calculated.

While the CBASS recruitment pattern operates on large scales, it could not be assumed to be present and strong on the scale of individual river basins. Principal components analysis is used to examine the primary modes of variance among the recruitment time series of four species: striped bass (*Morone saxatilis*), white perch (*M. americana*), spot (*Leiostomus xanthurus*), and Atlantic menhaden (*Brevoortia tyrannus*). These four 'indicator' species were chosen because they were consistently strongly weighted either positively (shelf spawners-spot and menhanden) or negatively (anadromous fishes-striped bass and white perch) in the CBASS pattern.

The PCA results described above were used only to confirm the existence of the CBASS pattern within each of the Virginia river basins studied here. Annual relative pre-recruit abundance time series for each of the four indicator fish species are used to examine the possibility that climate-forced interannual variation in pre-recruit habitat extent and suitability may be responsible for the CBASS recruitment pattern.

Zooplankton

The U.S. Environmental Protection Agency's Chesapeake Bay Program (CBP) monitors monthly zooplankton densities throughout the Bay and its major tributaries. Since zooplankton are influenced by hydrographic conditions and serve as prey for larval fishes, these data will serve as indicators of nursery area habitat suitability for the fish species of interest. Zooplankton sampling consists of oblique five minute tows of 0.5m dual bongo nets. Net mesh is 202 microns. Each net is equipped with a flow meter to determine the sampled water volume.

Zooplankton are enumerated using a coefficient of variation stabilizing method (Alden et al., 1982).

Data for the three largest Virginia Bay tributaries, the Rappahannock, York, and James river systems, were used for this analysis. Available data for the spring months included the years 1986-1996, except for 1995 when June zooplankton samples were not taken for the York and Rappahannock Rivers. Stations used for this study are coded as RET3.1, RET4.3, and RET 5.2 by the CBP for the Rappahannock, York, and James rivers respectively by the CBP (Figure 3.1).

These stations were chosen because analysis of CBP hydrographic survey data revealed that they are in the general vicinity of the freshwater interface during the spring months and were the closest available sites to the nursery areas utilized by both CBASS species groups. Furthermore, due to their proximity to the freshwater interface, these stations are likely to be more responsive to climatologically induced hydrographic variability than those further up or down river.

Prior quality control screening of the zooplankton data for the rivers of interest indicated that species resolution was variable throughout the study period. For example, calenoid copepods are often, but not always, identified to species level as adults, but not as nauplii. Barnacle species are not identified to species level although a life stage identifier (indicating cypris or nauplius) is provided. These inconsistencies have been attributed to changes in the personnel responsible for taxonomic identification (Jacqueline Johnson, CBP Living Resources Data Manager, personal communication).

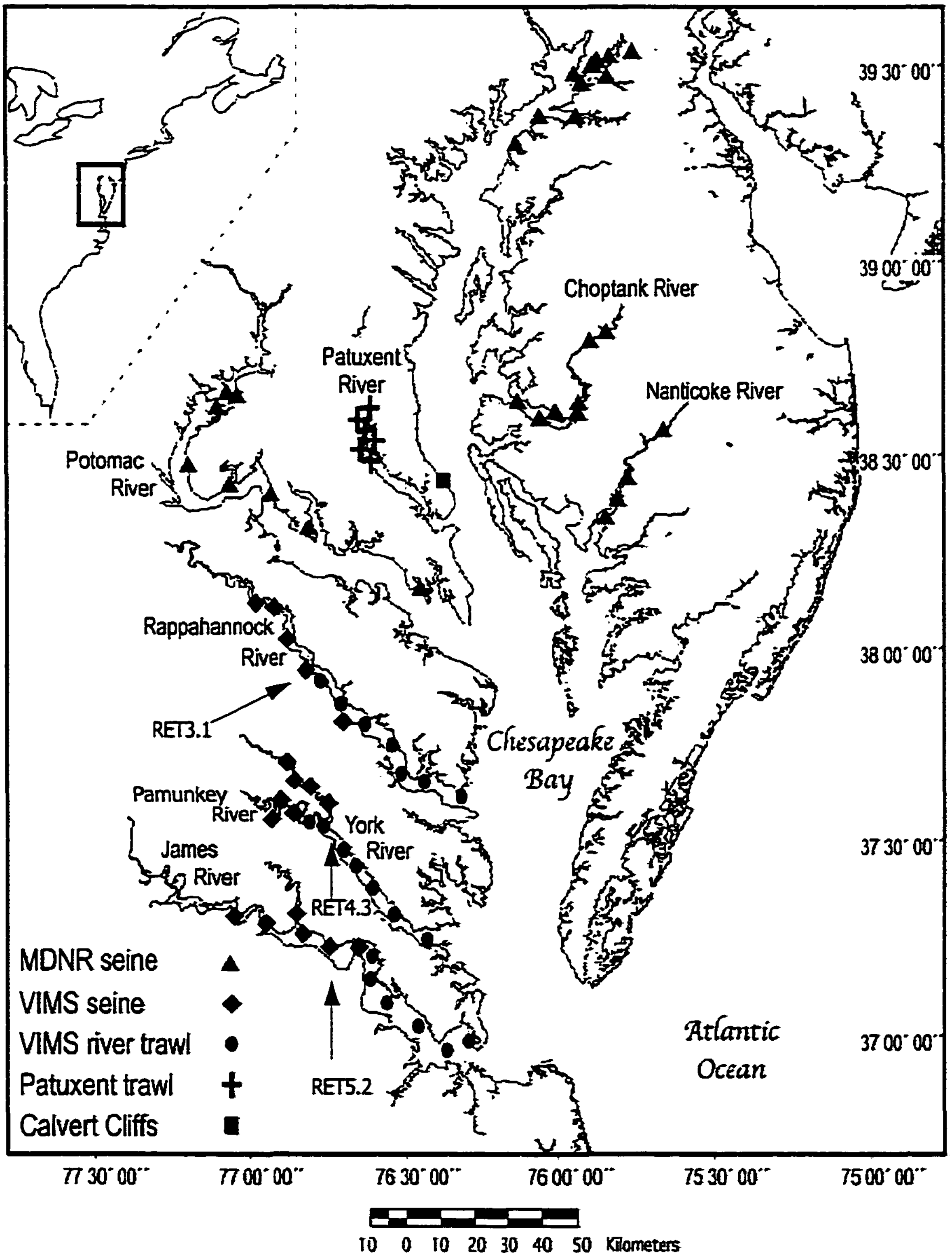

FIGURE 3.1. Zooplankton (RET) and fish (only the VIMS seine data were used here) sample sites.

To overcome this problem, the data were subsetted to include only those taxa likely to be important in the diet of larval fish prey for the primary species of interest (Lippson et al., 1979; Mihursky et al., 1981; Setzler-Hamilton et al., 1981; Martin et al., 1985; Rutherford and Houde, 1995; Limburg et al., 1997). Within this subset, abundance values were summed across related taxa featuring inconsistent levels of taxonomic identification. Rarely occurring species were not considered. Regardless of taxonomic level, taxa that appeared to be consistently identified were never grouped. As a result, taxonomic resolution of the processed data set is as high as species level in some cases, as with the mysid *Neomysis americana*, and as low as order level as with the cyclopoid copepods.

Local weather data

Heating degree day (HDD) data from the International Airport meteorological station in Richmond, Virginia (cooperative weather station 447201) were also included in this analysis. This variable, acquired from the National Climatic Data Center (NCDC), served as an integrative measure of springtime warming for the region of study. Heating degree days are caclulated by subtracting from 65 Fahrenheit degrees (18.33 C), the mean daily temperature for each day of the month. Monthly HDD are merely the summed postive daily HDD. The Richmond airport station was chosen after considering proximity to the tidal freshwater reaches of the tributaries of interest, period of record, and likelihood of contamination due to the urbanization (known to cause elevations in recorded temperature). Spatial variability of heating degree days in the region was also considered and it was found that this single station could be used to adequately describe conditions for each of the three rivers (Owenby et al.,1993).

Salinity data

The CBP also conducts hydrographic data cruises in the Bay and its tributaries on a semi-monthly basis. Surface salinity for the Virginia tributaries on the first cruise of every month was used at this stage. Bottom salinity was also available, however it was not used because it would mimic the variability in surface salinities except when counter-current, bi-layer estuarine circulation is important. In this case, bottom salinity would not be an appropriate proxy for river flow. Neither would it be indicative of pre-recruit (juvenile) fish habitat suitability since YOY fishes generally inhabit shallow areas of rivers and creeks during the spring and summer months.

A variable indicative of the location of the freshwater interface and turbidity maximum zone was derived from the salinity data for each river. Specifically, the variable identifies the longitude of the station featuring the smallest recorded salinity value greater than zero. Since west longitude values are recorded as negative, larger values occur when the freshwater interface and turbidity maximum zone displaced further downstream (eastward). Since this variable is indicative of the amount of freshwater habitat available in the rivers, it is abbreviated as 'FWextent' in figures.

Local scale data analysis methods

Covariance of zooplankton, salinity, and fish recruitment for each of the three river systems is explored using PCA. Principal components analysis is conducted on the combined, river specific HDD-surface salinity-zooplankton-CBASS data correlation matrices to describe the primary modes of variance in the nursery area habitats of the Rappahannock, York, and James river systems. The correlation matrix is used as the input for the PCA since this is appropriate when variables are measured in different units.

While inclusion of so many variables can provide a relatively complete picture of climatically forced hydrographic and ecological variability among this set of intercorrelated variables, it comes at a price. PCA of a data matrix featuring a low case to variable ratio allows for the possibility that the results are biased by extreme (and perhaps unrepresentative) data points. This problem is compounded in data sets that feature no strong patterns. In geometric terms, these data sets feature spherical data clouds. The degree of 'sphericity' can and will be assessed through a scree plot of the PC eigenvalues or percent (or proportion) variance accounted for. Non-spherical data sets will feature few PC's accounting for much of the total data set's variance. Here the problem is also mitigated by independently analyzing three regional river systems simultaneously. If the data sets are non-spheroidal and results are consistent among these river systems, the low case to variable ratio of these analyses will not be considered problematic.

RESULTS

River-specific CBASS patterns

The negative relationship between anadromous and shelf spawning species previously described as the CBASS recruitment pattern is evident in each of the three Virginia rivers analyzed. Figure 3.2 reveals that this pattern is the primary mode of annual multispecies recruitment variability for the Rappahannock and James Rivers accounting for 43% and 49% of the total data set variability.

For the York River, the CBASS pattern is represented by the second PC. For this river the CBASS pattern accounts for 25% of the variability within the four species annual abundance data set. The first PC of the York River and second PC's of the James and Rappahannock systems is a pattern of high or low abundance for all species together. Exceptions to these general descriptions occur in the James River PC's where spot, in PC1 and white perch, in PC2 feature near zero weights.

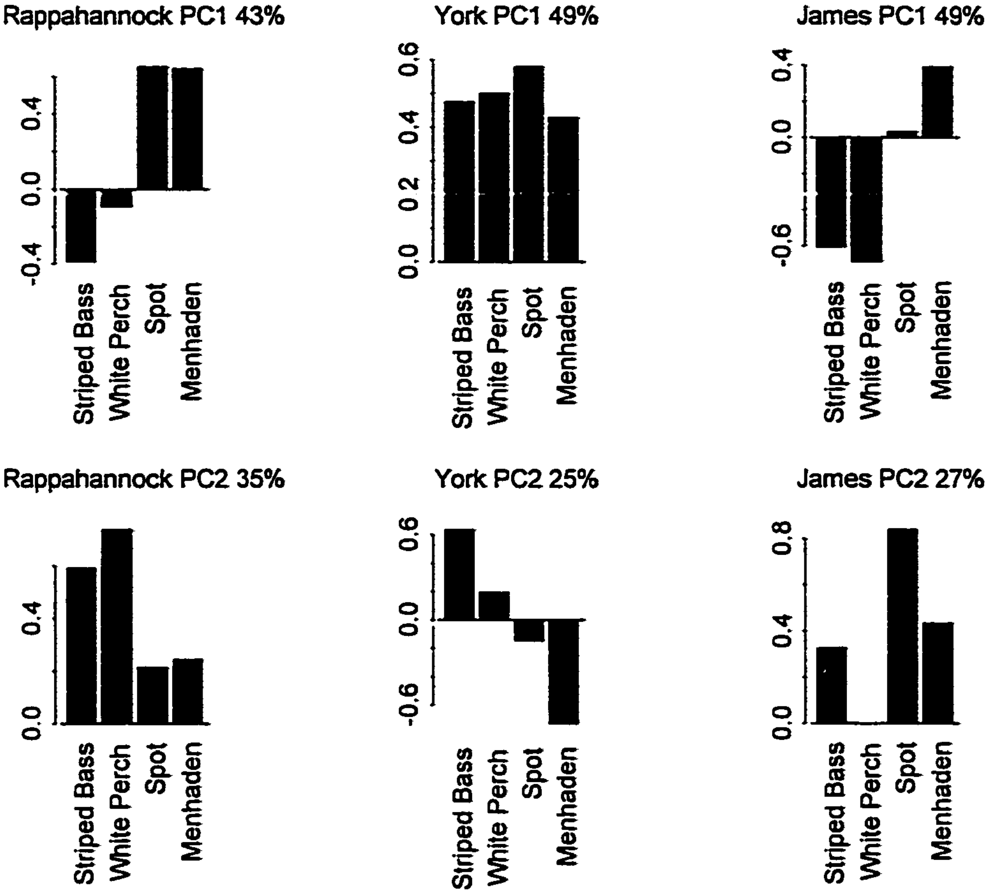

FIGURE 3.2. Component loadings for the first two PC's resulting from the principal component analyses of the relative annual abundance of four key CBASS species within the Rappahannock, York, and James Rivers. Also listed are percent of total data set variance accounted for by each PC.

Figure 3.2 clearly shows that the time series of the CBASS patterns for the rivers are very similar in trend and interannual variability. These results once again support the likelihood that large scale climatic factors drive these negative abundance relationships between anadromous and winter shelf spawning species defined in Chapter One as the CBASS pattern.

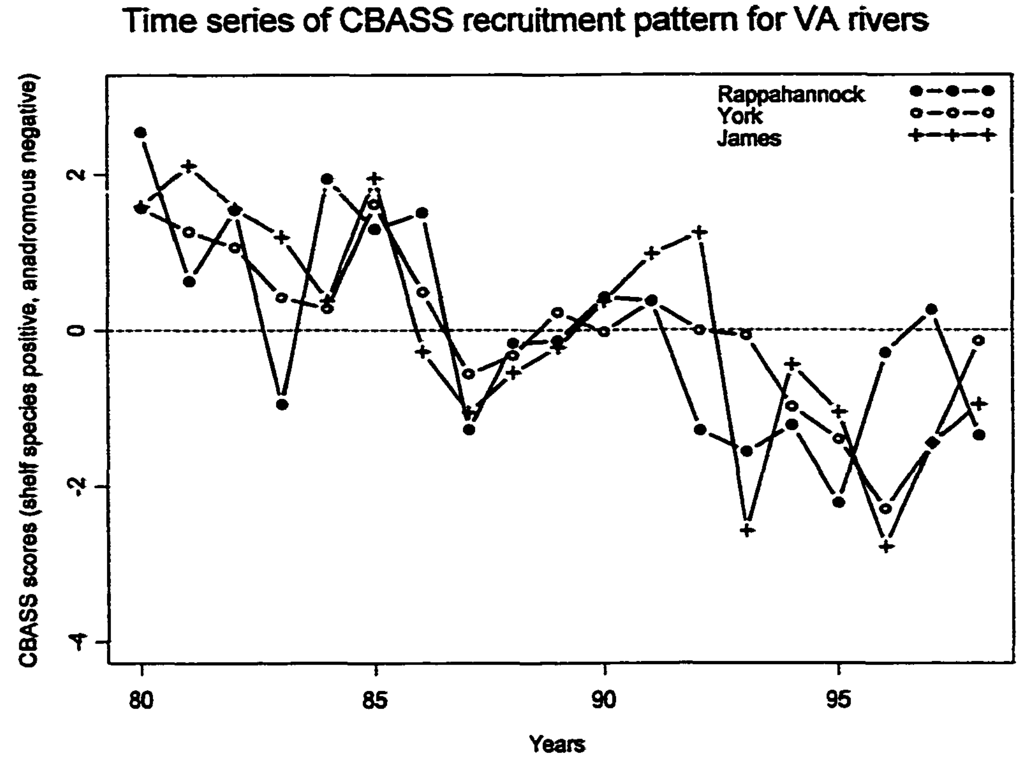

FIGURE 3.3. A comparison of annual PC scores accounting for the CBASS recruitment pattern for the Rappahannock (PC1), York (PC2), and James Rivers (PC1).

Striped bass egg distribution patterns

As described in Chapter Two, Mihursky et al., (1981) theorized that low temperatures in March, which were shown in this work to be related to the persistence of the Ohio Valley High, may lead to striped bass spawning further upstream and hence, an upstream displacement of egg distribution patterns. This, Mihursky et al. argued, may lead to enhanced survival from egg to juvenile life stages and therefore increased annual recruitment, since they believed zooplankton prey densities to be higher and overall mortality lower for larvae in the upper most regions of the spawning area.

Comparing survival estimates in the Pamunkey River to the distribution of eggs in that year directly conflict with this theory. Figure 3.4 suggests that survival is strongly related to a downstream displacement of the eggs. Figure 3.5 shows that the spread of eggs is also strongly related to survival. Comparing survival to the number of March Azores-Bermuda High and Ohio Valley High days revealed negative and positive relationships respectively (Figures 3.6 and 3.7). These results are consistent with the relationships described in Chapter Two. Most convincing is the nearly perfect agreement between survival estimates and survival predicted from a least squares linear fit of survival using the number of both High pressure systems in March seen in figure 3.8.

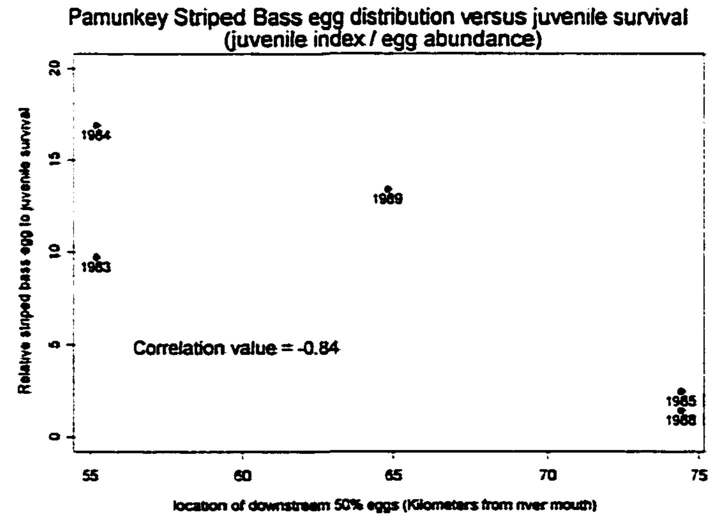

FIGURE 3.4. Scatterplot of relative striped bass survival from egg to the juvenile life stages versus location of the downstream 50th percentile of the egg distribution for the Pamunkey River.

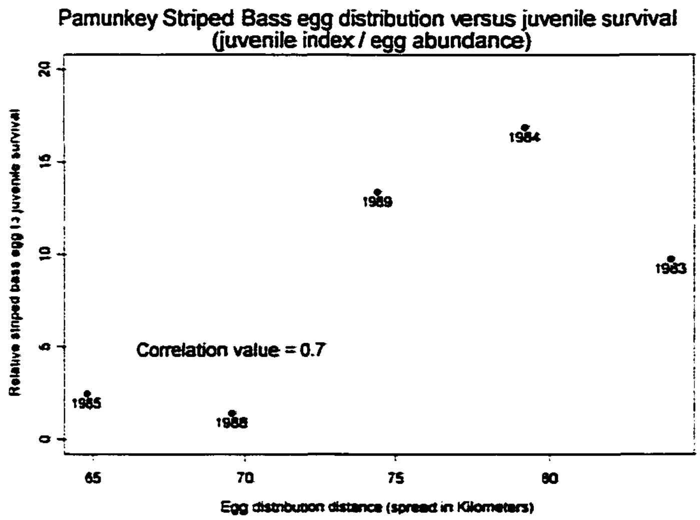

FIGURE 3.5. Scatterplot of relative striped bass survival from egg to the juvenile life stages versus distance over which eggs were distributed (from the river mouth).

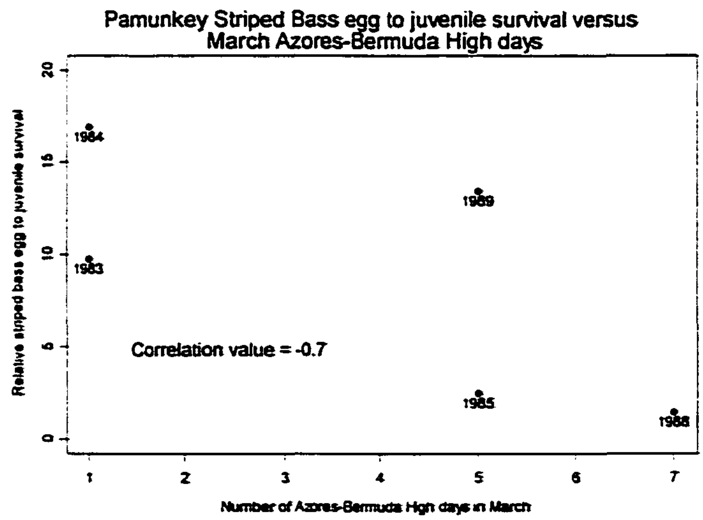

FIGURE 3.6. Scatterplot of relative striped bass survival from egg to the juvenile life stages and annual March Azores-Bermuda High frequency (as determined by the results of the synoptic classification scheme used in Chapter Two). Years of observation are plotted.

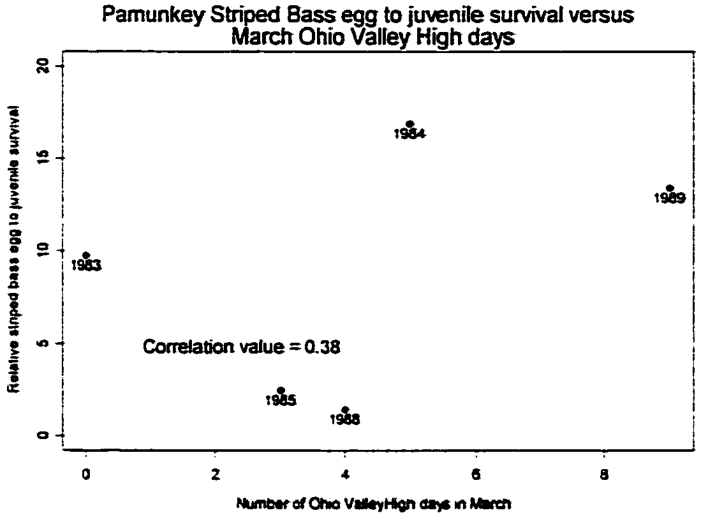

FIGURE 3.7. Scatterplot of relative striped bass survival from egg to the juvenile life stages and annual Ohio Valley High frequency. Years of observation are plotted.

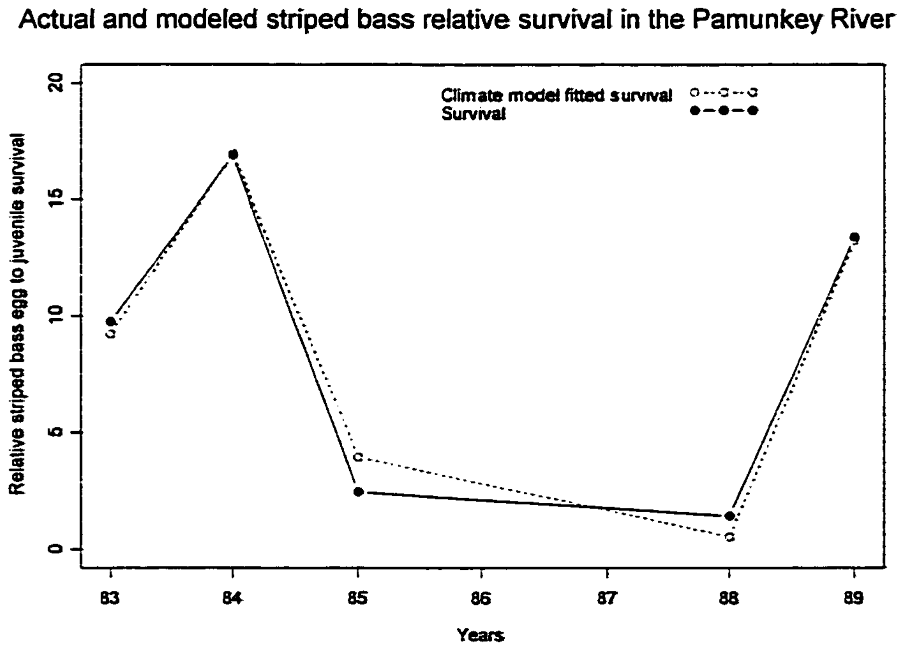

FIGURE 3.8. Comparison of the annual striped bass survival from egg to juvenile life stage for the Pamunkey River with model fitted survival estimates. Variables in the model are annual March frequencies for the Azores-Bermuda High and the Ohio Valley High.

These results indicate that cold wet conditions during March, brought on by the dominance of the Ohio Valley High over the Azores Bermuda High result in an expanded spawning area, a downstream displacement of eggs, and increased egg to juvenile stage survival for striped bass. These results are consistent with theories that striped bass recruitment is enhanced by extension of winter conditions into March. Further, it appears these conditions lead to an expanded nursery area zone and perhaps enhanced spring productivity with the supply of a larger than normal detrital pool. These theories can be put to the test by examining the physical and biological conditions within the CBASS species groups' nursery areas of the Rappahannock, York, and James rivers.

River nursery area conditions analysis

Since earlier analyses revealed that the CBASS pattern was described by either the first or second PC of key CBASS species juvenile abundance in the Rappahannock, York, and James river systems, results of the nursery area habitat conditions were presented as biplots of the loadings and scores of PC's one and two. These biplots (Figures 3.9-3.11) reveal that these two PC's account for between approximately 39% to 50% of the multivariate data sets describing CBASS species' nursery area conditions. Biplots will be described by river.

<u>Rappahannock River</u>

Figure 3.9 reveals that the primary mode of variance (PC1) within the Rappahannock River nursery area multivariate data set is defined by a downstream displacement of the freshwater interface (relative to its mean position for a given month). These conditions are undoubtedly brought on by higher than average flow. High FWextent years (1989, 1993, 1994, and 1996) also feature

higher than normal densities of zooplankton generally found in oligohaline and tidal freshwater, such as *Eurytemora affinis* and *Bosmina* spp. The more estuarine (downstream) zooplankton taxa, *Acartia* spp. and Barnacle nauplii occur during dry, negative PC1 score years.

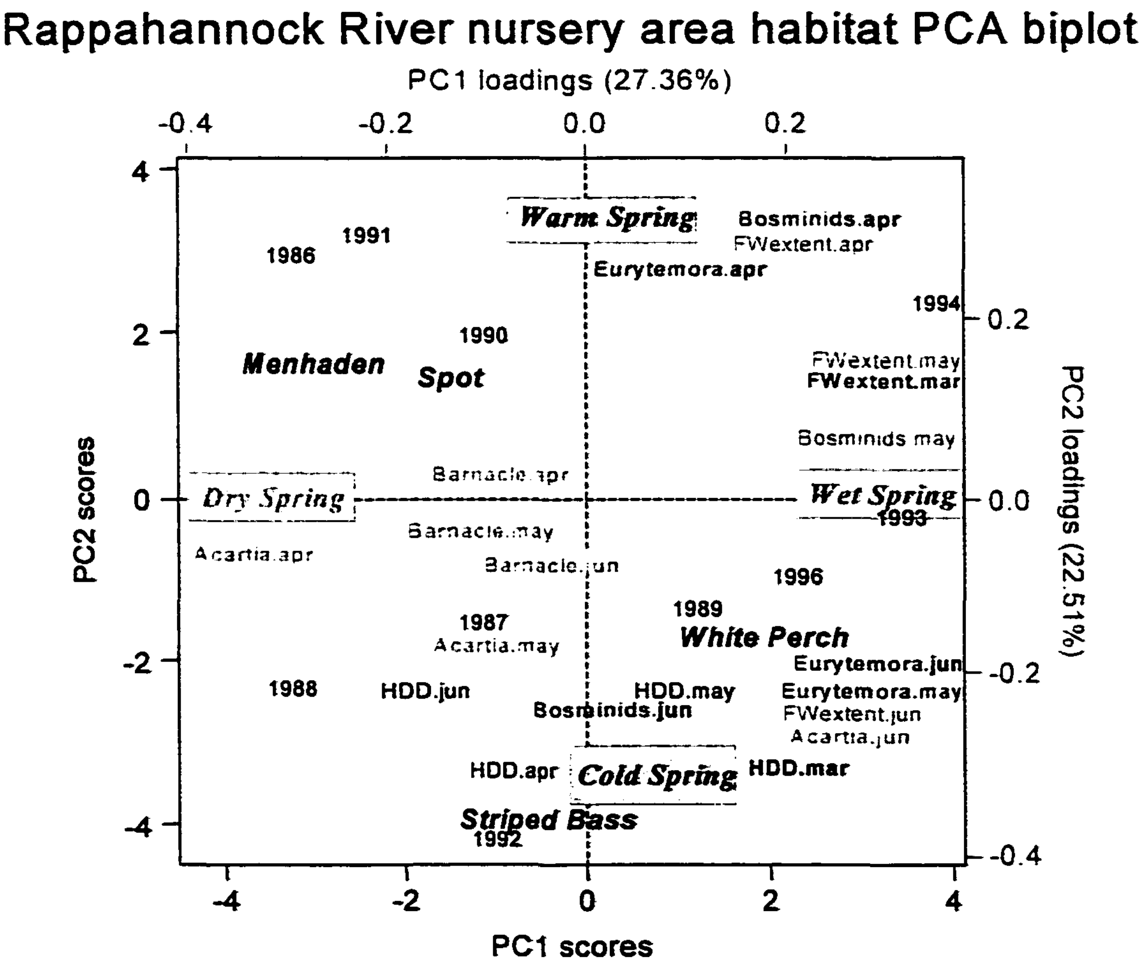

FIGURE 3.9. Biplot of the first two PC's resulting from the analysis of Rappahannock CBASS species nursery area conditions.

The second PC differentiates years with colder than average springs from warmer years. This component also contrasts years when zooplankton taxa peak earlier rather than later. When springs are warmer than normal taxa peak in April while in colder springs their peaks occur in June. This effect is most pronounced for Bosminids and *E. affinis* since they respond both to cold and warm conditions. The lack of strong positive loadings for Barnacles and *Acartia* spp. variables in any month indicate that while they tend to bloom later in cold years, warmer springs do not affect their timing any more than do springs featuring near normal temperatures.

Given these zooplankton and climate patterns, the four CBASS species variables ordinate in a manner that is surprisingly consistent with previously described observations and theories. Juvenile abundance of shelf spawning spot and Atlantic menhaden is higher than normal in the Rappahannock River when warm and dry conditions occur in the spring. Striped bass abundance is higher than normal during cold springs while white perch are associated with cold and wet conditions.

York River

Results for this river are similar to those of the Rappahannock (Figure 3.10), though some differences exist. The first PC describes years featuring cold conditions in March, slightly warmer than normal in June, and wetter than normal conditions March-May. Under these conditions, the oligohaline zooplankton species tend to prosper while *Acartia* spp. and barnacles appear to be benefitted most by a warm March, with the exception of the May barnacle variable which also ordinates with fresher spring conditions.

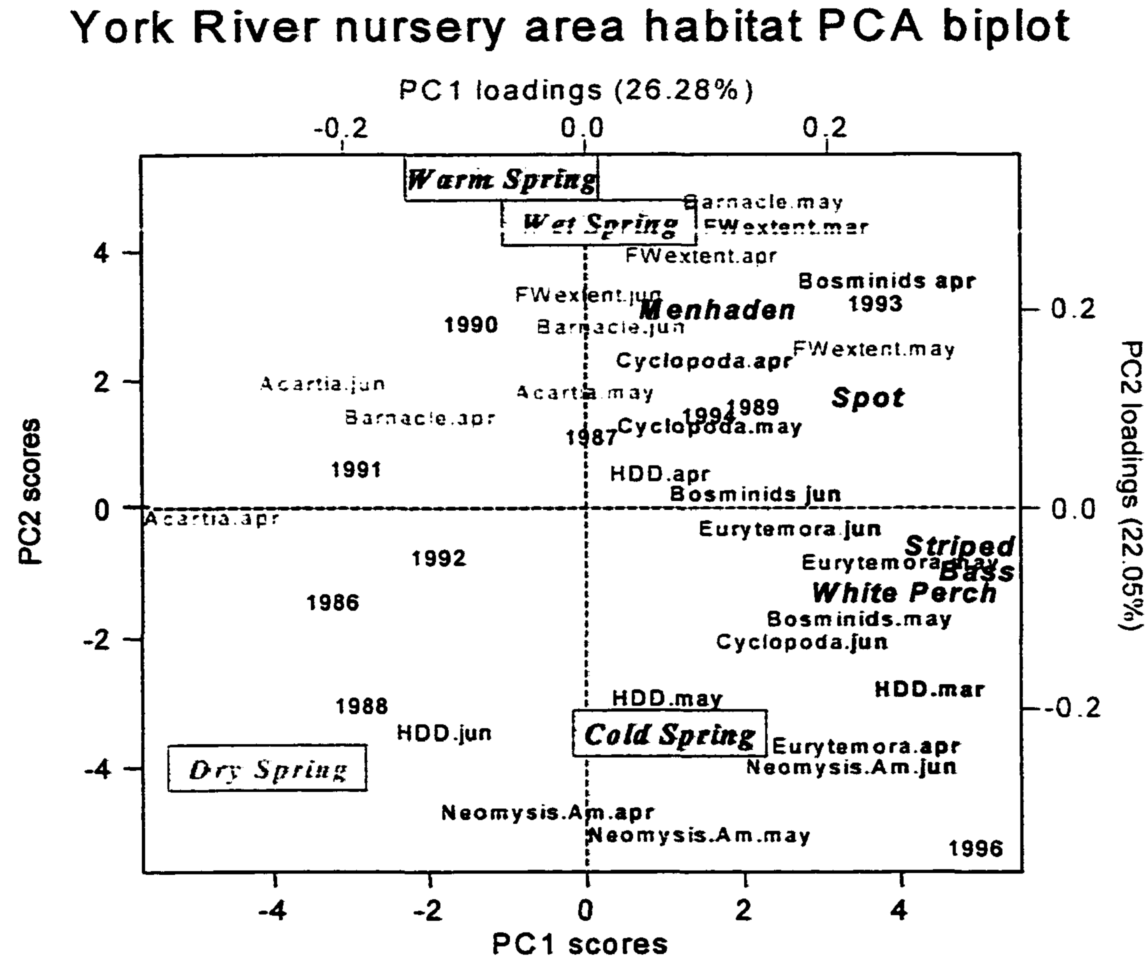

FIGURE 3.10. Biplot of the first two PC's resulting from the analysis of York CBASS species nursery area conditions.

Taking PC 2 into account, peaks of the oligohaline Bosminids, Cyclopoid copepods, *E. affinis*, and the mysid, *Neomysis americana* occur in June when Marches are cold. While Bosminids and Cyclopoids peak in April following a warmer than normal March, *E. affinis* peaks are always associated with a cold March.

All fish species appear to benefit, as do the majority of zooplankton taxa, from wetter than normal conditions. The CBASS recruitment pattern for the York River is primarily associated with the difference between cold and warm March conditions.

James River

The James River biplot (Figure 3.11) is similar to the York River results. The first PC generally describes cold March and April conditions and wet springs in general with negative scores and the reverse conditions with positive scores.

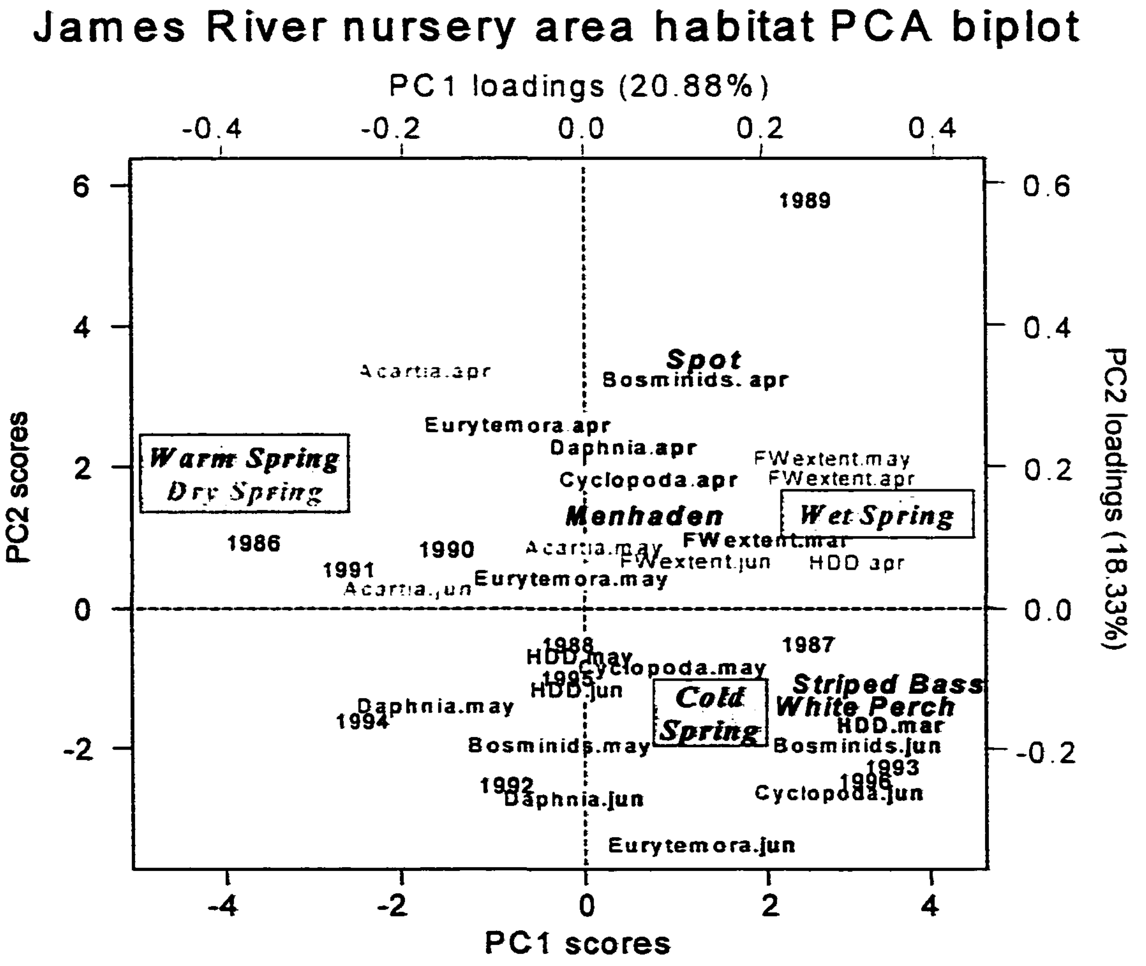

FIGURE 3.11. Biplot of the first two PC's resulting from the analysis of James CBASS species nursery area conditions.

While Barnacles were not identified consistently enough to be included in this data set, *Acartia* spp. tend to occur during moderately warm and dry springs. The oligohaline taxa are again favored in wetter springs featuring cold March temperatures. As described for the York River, the CBASS fish recruitment pattern is most closely associated with March temperature conditions while wetter conditions benefit all species, though perhaps benefitting anadromous species more than shelf spawners.

DISCUSSION

This chapter investigated the link between climatically influenced nursery habitat conditions and the CBASS recruitment pattern defined in Chapter One. The initial phases of this work confirmed that the negative relationship between anadromous and shelf spawning fishes, evident in the analysis of regional Chesapeake Bay multispecies juvenile fish survey data sets, also exists on local river basin scales.

The second phase of analyses examined the theoretical link, proposed by Mihursky et al. (1981), proposing that enhanced recruitment in the striped bass during colder than normal Marches is due to an upstream displacement of the spawning grounds. These analyses found evidence suggesting that striped bass survival is higher when eggs are distributed further downstream (figure 3.4). It should be noted that colder than normal conditions in the late winter-early spring period are often associated with higher than normal flows.

Further, Grant and Olney (1991) demonstrated that eggs are distributed further downstream during years of high flow. These results are consistent with theories, also proposed by Mihursky et al. (1981), that cold and high flow conditions promote successful striped bass recruitment due to expanded nursery habitat and enhanced production of their zooplankton prey through enhanced nutrient and detrital pools.

The linear model featuring positively weighted Ohio Valley High and negatively weighted Azores-Bermuda High March frequencies provides a nearly perfect fit of Pamunkey River striped bass egg to juvenile survival for the five years in the 1980s for which reliable data are available. These results strongly suggest that annual recruitment is influence by synoptic scale March circulation patterns as described in Chapter Two.

These results are also consistent with the hypothesis, also proposed in Chapter Two, that the negative relationship between anadromous and shelf spawning species seen in the CBASS recruitment pattern is the result of mutually exclusive ideal nursery area habitat requirements for these two CBASS species groups. Specifically, favorable migration conditions and prey species abundance for the shelf spawning species were hypothesized to be associated with the warm and dry conditions and prevailing southerly winds associated with the Azores-Bermuda High. In contrast, when cold and high flow conditions prevailed, associated with the a persistant Ohio Valley High, the anadromous fishes recruited strongly while shelf species did not. To further explore the feasibility that this constitutes a multispecies variant of Cushing's Match-Mismatch recruitment theory, spring nursery area conditions were analyzed for each of three major Virginian Bay tributaries.

Results of these analyses were remarkably similar among river systems. In each case, the negative relationship between anadromous and shelf spawning species juvenile abundance is related to contrasting March temperature conditions, where March temperatures were positively correlated with juvenile abundance of the shelf spawners, spot and Atlantic menhaden. The relationship between the extent of freshwater habitat (the FWextent variable) and the CBASS pattern is less clear. FWextent is negatively related to shelf spawning annual cohort strength and positively with anadromous juvenile abundance in the Rappahannock River. For the other rivers, all species appear to benefit from the flow related FWextent variable, though the relationship appears to benefit anadromous fishes more than shelf spawners.

The zooplankton-hydroclimatic relationships evident in these analyses are remarkably supportive of the multispecies Match-Mismatch hypothesis. First, timing of the peaks in freshwater-oligohaline zooplankton taxa, upon which striped bass and presumably other anadromous fish feed, best match the May-June feeding period for larval and postlarval anadromous fishes in years when March is colder than normal. When March is warmer than normal, these taxa peak in April and are less abundant than normal in May and June.

Normal or higher than normal abundances of the estuarine calanoid copepod genus *Acartia* (generally comprised primarily of *A. clausi* in the early season and *A. tonsa* later in the season), occur in years featuring warm and dry March periods. The relative dominance of the warm and dry Azores-Bermuda High and accompanying southerly winds present migration conditions, zooplankton assemblages, and zooplankton bloom timing that match the needs of winter shelf spawning species which utilize the upper tidal reaches of estuarine rivers as nursery areas.

The river basin specific hydroclimatic-fish recruitment patterns relationships described in this study are remarkably consistent. They clearly demonstrate that the nursery area conditions presented to larvae and postlarvae of key CBASS species are radically altered by winter-spring climatic variability.

CONCLUSION

Within this study it has been shown that the early life stages of anadromous and winter spawning estuarine dependant shelf species may be affected differentially by the nature and timing of the annual winter-spring seasonal transition. This seasonal transition was shown to be largely dependant upon the relative dominance of the Azores-Bermuda or Ohio Valley High synoptic scale circulation and weather patterns during March in Chapter Two.

Dominance of the Azores-Bermuda High leads to a warmer and drier March and a more rapid winter to spring transition. Analyses conducted in this Chapter demonstrate that these conditions promote an early spring (April) peak in the winter-spring dominant freshwater-oligohaline zooplankton taxa such as *Eurytemora affinis*, cyclopoid copepods, *Neomysis americana*, and both Bosminids and *Daphnia* spp. (cladocerans). Conversely, extended persistence of the winter dominant Ohio Valley High during March, leads to a June peak in these species.

These two climatic patterns were also shown to affect flow conditions during the late-winter and early spring period. The seasonal storm track associated with the Ohio Valley High occurs along the Mid-Atlantic coast. It is displaced westward when the Azores-Bermuda High is dominant, so that the Chesapeake Bay watershed becomes dryer than normal. The resulting wet versus dry regimes have been shown to differentially and dramatically affect the composition of the annual spring bloom. The high flow mode, evident in the downstream displacement of the freshwater interface, results in a dominance of freshwater-oligohaline zooplankton species over the estuarine taxa (*Acartia* and Barnacles) for the upper tidal river reaches studied in this work. Conversely, under drier conditions the freshwater interface recedes upriver and the spring zooplankton composition is dominated by the estuarine zooplankton species.

These findings are consistent with the theory that late winter-early spring synoptic scale climatic variability affects multispecies recruitment patterns throughout Chesapeake Bay. The importance of March temperature and precipitation conditions suggested by statistical models in Chapter Two were confirmed in the nursery area habitat analyses in this Chapter. It appears that climatic variability in March is key to determining the timing of the seasonal transition from winter to spring. March conditions apparently determine whether conditions in the upper tidal rivers within Bay are more conducive for successful anadromous or shelf spawning species recruitment success. While direct causal connections cannot be determined with the analysis of historical data sets, temperature, flow, wind, and zooplankton conditions within these critical nursery areas appear to favor shelf spawners with an early spring and anadromous fishes with a late spring.

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Summary

As the title of this dissertation indicates, the overall goal of this work was to define and describe the role of synoptic scale climatic variability in forcing multispecies fish recruitment patterns within Chesapeake Bay. In Chapter one, a single dominant multispecies recruitment pattern was identified. This multidecadal pattern, referred to as the CBASS recruitment pattern, depicts a negative relationship between the relative annual abundance of Chesapeake Bay anadromous and winter shelf spawning fishes utilizing the upper tidal reaches of the Bay and its tributaries.

The Bay-wide multidecadal persistence of the CBASS pattern strongly suggests a climatic forcing mechanism. This possibility was explored in Chapter Two. The investigation relied upon a synoptic scale climate classification procedure similar to that described by Davis and Kalkstein (1990). Using this procedure, each spring day (March-May) of every year in the study period (1966-1997) was classified as one of ten sea level pressure (SLP) patterns, each describing weather features typically occurring in the Mid-Atlantic region during this season. Monthly annual frequencies of each SLP pattern were compared to the CBASS recruitment index.

This synoptic classification approach, never before used in published fisheries recruitment investigations, has two primary advantages. First, since each typical spring SLP pattern can be described in terms of its characteristic weather profile, SLP pattern time series more realistically describe weather and climate variability eacting the ecosystem and its living resources compared to individual weather parameters such as temperature, rainfall, and wind speed. Not only is this a more realistic characterization of climatic variability, but it also acknowledges that weather variables are often strongly intercorrelated. These two features of the synoptic scale climate characterization approach provide both theoretical and statistical advantages over traditional correlation approaches which typically use a single, or a combination of individual weather variables to model recruitment variability.

This approach proved extremely effective in defining the relationships between two well known regional climatic features and the CBASS recruitment pattern. It was found that the sign and magnitude of the CBASS pattern was largely determined by the relative dominance of the Azores-Bermuda or Ohio Valley high pressure systems during the month of March. If the former dominated, spring arrived earlier and drier than normal. Winter is prolonged with the persistence of the latter feature since it extends cold and relatively fresh conditions. Years in which spring 'sprang early' benefited shelf spawners and resulted in depressed populations of juvenile anadromous fishes. Conversely, when winter conditions extend into March, the anadromous spawning strategy seems superior to that of the winter spawning shelf species which utilize the upper Bay and its tributaries as nursery areas.

Anadromous fishes are spawned in April and develop into the juvenile life stage within these areas. In contrast, shelf spawners arrive from their winter spawning grounds as postlarvae as early as March. The life history similarities and contrasts suggest that climate may be influencing the CBASS recruitment pattern through processes occurring within these nursery grounds. Based upon previous research and the climate relationships described in Chapter Two, it was hypothesized that differences in the seasonal transition from winter to spring might differentially effect these two species groups immediately prior to (i.e. during adult spawning or larval migrations), or during their nursery period. Using hydroclimatic and zooplankton data for sites located near the freshwater interface, Chapter three evaluated this theory evaluated using data from the Rappahannock, York, and James Rivers.

The results of the three multivariate analyses were similar and demonstrated that the timing and nature of the winter-spring transition strongly influences nursery area conditions. Early springs feature April blooms of the freshwater zooplankton upon which the anadromous fishes likely rely. However, this means that May and June, important months for the early life stages of these species, feature declining and lower than average densities of these zooplankton species. Conversely, the estuarine copepods of the genus *Acartia*, upon which the early life stages of shelf spawned fishes likely depend, are more abundant in years featuring a warm March.

When winter conditions extend into March, the nursery areas appear ideal for anadromous fishes. As Heinle et al. (1976) and Mihursky et al. (1981) theorized with respect to the striped bass, cold and wet late winter-early spring conditions appear to extend the suitable nursery area of the anadromous fish group in time and space, where suitability is indicated by abundance of preferred prey and hydrographical conditions. The preferred prey of this species (*Eurytemora affinis*, Daphnia, Bosminids, cyclopoid copepods, and *Neomysis americana)* persist throughout the spring, peaking in June when March is colder than normal. Further, these species remain the dominant mesozooplankton assemblage in all spring months (considered April-June for zooplankton) when fresher conditions prevail. The more estuarine *Acartia* copepods are depressed under these conditions.

Lastly, winds during the critical late winter-early spring cross-shelf advective transport period for shelf spawned species do not favor recruitment to Chesapeake Bay under the Ohio Valley High winter circulation pattern. Conversely, wind direction is favorable for their northwestward surface transport across the shelf and into the Bay when the spring-summer Azores-Bermuda High is dominant.

These findings suggest the interannual recruitment variability for many commercially and ecologically important Chesapeake Bay species can be accounted for by the seasonal dynamics of the winter-spring transition. While more detailed research will be needed to ascertain which specific factors and processes affect larval and postlarval survival for the CBASS species groups, the research presented here represents a generalized multispecies variant of Cushing's Match-Mismatch hypothesis (1970, 1975). As depicted in Figure S-1, Cushing focused on the match or mismatch between temperate water marine stocks, which he described as having fixed spawning seasons, and their larval prey (Cushing, 1969, 1982). Since the zooplankton prey of these larval fishes were shown to be dependant upon the highly variable timing of the spring production bloom (Colebrook, 1965; Colebrook and Robinson, 1965; Robinson, 1975; Colebrook 1979), annual spring conditions can match or be mismatched for larval fish survival.

Figure S-2a and S-2b describe the multispecies variant of the Match-Mismatch hypothesis that seems to apply to Chesapeake Bay. Figure S-2a represents spring climate and nursery area conditions that are matched for the shelf spawner species group and simultaneously mismatched for the anadromous fishes. Figure S-2b describes the opposite scenario. Further work will be necessary before it can be determined whether zooplankton assemblages and densities directly affect larval fish survival or whether the zooplankton are independently responding to the same climatic conditions which influence larval fish survival.

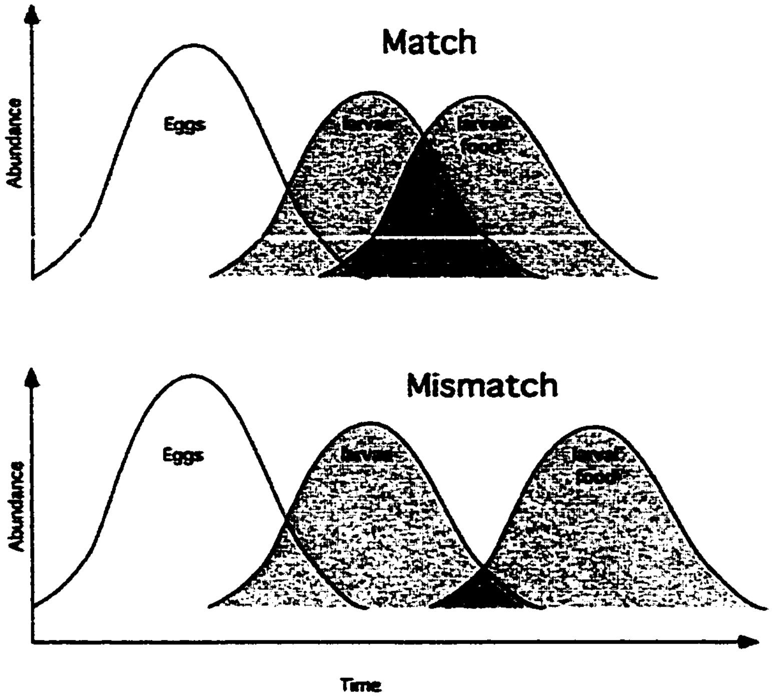

FIGURE S-1. Cushing's original Match-Mismatch hypothesis. Originally applied to North Sea stocks, Cushing proposed that good recruitment occurs when environmental conditions allow for a spring bloom timed such that larval fish abundance and their prey overlap (match). Mismatched conditions occur when lower temperatures delay the spring bloom until after the period of peak larval abundance.

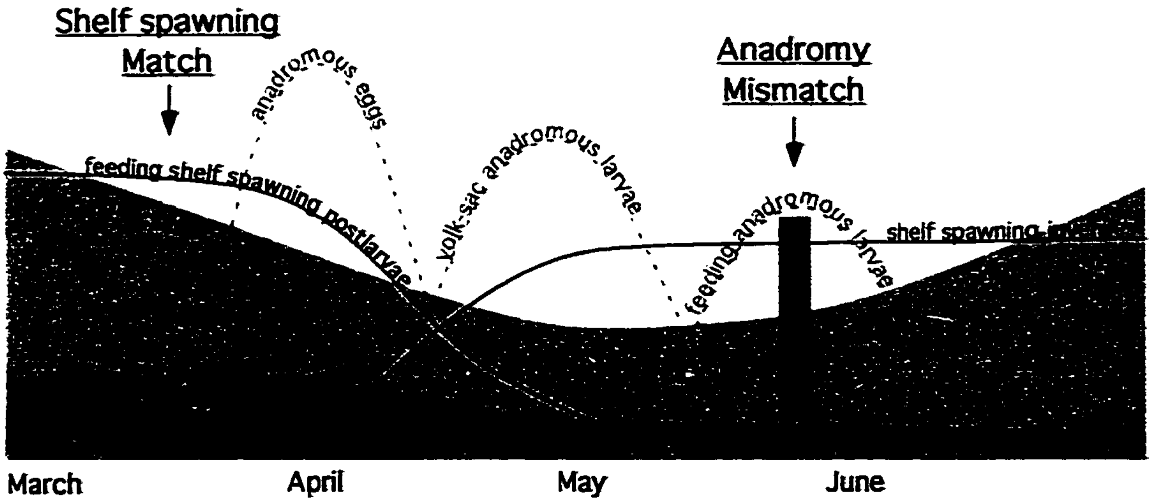

FIGURE S-2a. Hypothesized scenario for climate-forced nursery area conditions favoring winter shelf spawning species over anadromous. This is a match for positive CBASS index conditions.

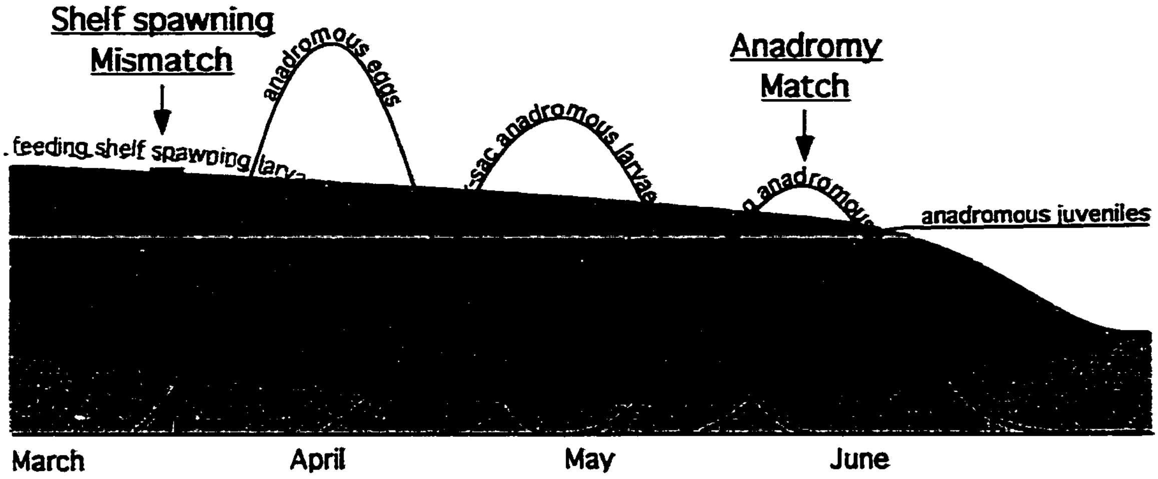

FIGURE S-2b. Hypothesized scenario for climate-forced nursery area conditions favoring anadromous species over winter shelf spawning. This is a match for negative CBASS index conditions.

More research will also be needed to determine what role, if any, wind direction, as influenced by the Azores-Bermuda and Ohio Valley high pressure systems, plays in influencing successful advective transport of shelf spawners to their tidal river nursery areas. If the a wind effect can be demonstrated recruitment of the shelf spawners would follow the Member-Vagrant hypothesis (Sinclair 1988; Sinclair and Iles; 1989). This hypothesis proposes that recruitment for many coastal spawning species has evolved to occur in the time and space where eggs and larvae would usually be contained and transported to a juvenile nursery area. In this case temperature only delays or speeds development and advective transport conditions determine recruitment strength.

As fisheries science begins enters its second century, fisheries management appears to be headed towards a multispecies approach. The goal is to begin setting realistic harvesting strategies that are no longer primarily based upon the 'maximum sustainable yield' of single species. Instead, managers will seek to formulate strategies which acknowledge that fisheries removals have cascading ramifications at the ecosystem level capable of providing negative feedback to the fish populations (NMFS, 1999). This dissertation provides basic information that should be considered when formulating future fishery management plans.

For example, if the climate-recruitment relationships influencing striped bass recruitment had been taken into account during the late 1970's and early 1980's, the drastic reduction in spawning stock biomass and subsequent population crash may have been avoided (Richards and Rago, 1999). While strong management actions helped to restore the spawning stock until favorable recruitment conditions returned for that species, these same climatic conditions seem to have reduced annual recruitment in spot and Atlantic menhaden over the last decade. Fishery plans for these species should incorporate the winter-spring climate patterns described in this study as 'trigger variables'. Under unfavorable climatic conditions, these 'triggers' could be used to dictate more conservative annual harvests so that adequate spawning stock biomass is preserved in the face of poor recruitment.

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