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A RETROSPECTIVE TIME SERIES ANALYSIS OF OYSTER, *CRASSOSTREA VIRGINICA*, RECRUITMENT (1946–1993)

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ABSTRACT Temporal patterns of eastern oyster, *Crassostrea virginica* (Gmelin 1791), spatfall in the Virginia tributary rivers to the Chesapeake Bay showed a decline in all rivers from 1946 through the early 1970s, with a subsequent leveling off. The decline was most severe in the James and less so moving north to the York and Rappahannock Rivers; it was least severe in the Potomac River. Yearling patterns generally mirrored the spat. Cluster analyses grouped the bars naturally by up- and downriver spatfall patterns. They also clustered this way when between-river comparisons were made. Spatfall showed a significant cross-correlation with yearlings a year later in all Virginia rivers, which suggests that the "yearling" designation was accurate and that spat counts may be used to predict yearling abundance. The relation of spat to later seed was significant for the James River at 2 and 3 y, but none was found between spat and market oyster. James River seed demonstrated a slightly significant relation to market oyster 4 y later. Regression analyses between spat counts and spring and summer water temperatures and river discharge produced little explanation of spat variation. There was, however, a significant relation between spat count and the Palmer Drought Index. The drought index is a combination of rainfall, soil type, and evapotranspiration. When the period of the greatest change in the drought index was correlated with spatfall, there was found to be a significant 2- to 4-y lag. We suggest that this reflects a response by the ecosystem to changing environmental conditions.

KEY WORDS: Oyster, *Crassostrea virginica*, recruitment, spat, yearling oyster

INTRODUCTION

The Chesapeake Bay estuarine system has, since colonial times, produced the highest harvest of oyster, *Crassostrea virginica* (Gmelin 1791), in the United States. These harvests reached a peak during the late 1880s, when Maryland and Virginia annually produced some 20,000,000 Bu (Hargis and Haven 1988). After the turn of the century, the landings declined; then, after the early 1960s, there was a dramatic decline, primarily on the private leased bottoms in Virginia's higher salinity waters of the lower bay. The cause(s) of the decline has been a major focus of many studies (reviewed by Richkus et al. 1992) and recommendations (Haven et al. 1978, Newell and Barber 1992).

The Virginia Institute of Marine Science (VIMS) has, since 1946, collected abundance data on both weekly and annual spatfall and annual yearling oyster abundance on the public rocks ("Baylor Survey"). This brackets the time when the oyster stock in the Chesapeake Bay declined dramatically. Although there have been numerous studies over the years examining the spatfall results of VIMS (Haven and Fritz 1985), none have examined them in their 45-y entirety. Further, most studies have not taken advantage of recent advances in time series analyses. Chai (1988) investigated the spat and market oyster relationship in Maryland's rivers using time series analysis (autoregressive integrated moving average, ARIMA), but no such analysis has been performed on Virginia's stock.

Virginia commits significant resources to the annual monitoring of the spatfall, yearling oyster, and market oyster abundance on the public rocks. Data on spatfall are collected during the summer on shellstrings and again in the fall as surviving spat-on-shell, but there has been no systematic examination of the spat relation to yearling or market oysters by use of time series analyses. Management agencies (ASMFC, MAFMC, PRFC, and VMRC) use juvenile indices as predictors of later life stages and/or adult brood stock as the "spawner" in spawner-recruit relationships (Richkus et al. 1992). Although this has been established and tested for many finfish species, there still remains the validation of spatfall as a predictor of later oyster abundance. The Chesapeake Bay Stock Assessment Committee (CBSAC) has outlined the need for an examination of the indices of oyster recruitment (CBSAC 1988). Further, the Chesapeake Bay–wide (Maryland and Virginia) bistate oyster management plan (CEC 1994) cites the need for an analysis of the relationship between the abundance of juvenile and subsequent life stage oysters. The objectives of this study are to (1) describe deterministic and stochastic fluctuations in spatfall and yearling oyster abundance on Virginia's public oyster rocks; (2) correlate spatfall with subsequent yearling, seed, and market counts; (3) run cluster analyses of spat between oyster rocks and rivers; and (4) examine possible physical environmental forces that may drive the fluctuations in spat abundance.

MATERIALS AND METHODS

The VIMS oyster program has collected data on spatfall since the summer of 1946. Counts are made weekly of spat on summer shellstrings and late fall spat-on-shells and live oyster dredged from the bottom. Shellstrings are hung cup side down in the water column at representative public oyster rock (Fig. 1) for a week at a time starting in June each summer. They are removed, and spat that have "struck" on the smooth lower surface are counted. Fall surveys incorporate counts of spat-on-shell from a Virginia bushel of shell collected by standard oyster dredge. Also counted during the fall survey are yearling, "small" oyster (<3", 7.62 mm), and market oyster. All data are stored in the VIMS Fisheries Data Management Unit and are available by request.

DATA TRANSFORMATION:

Biologic count data are frequently skewed. A logarithmic transformation produces data that are more nearly normally dis-

VIMS Contribution No. 2032.

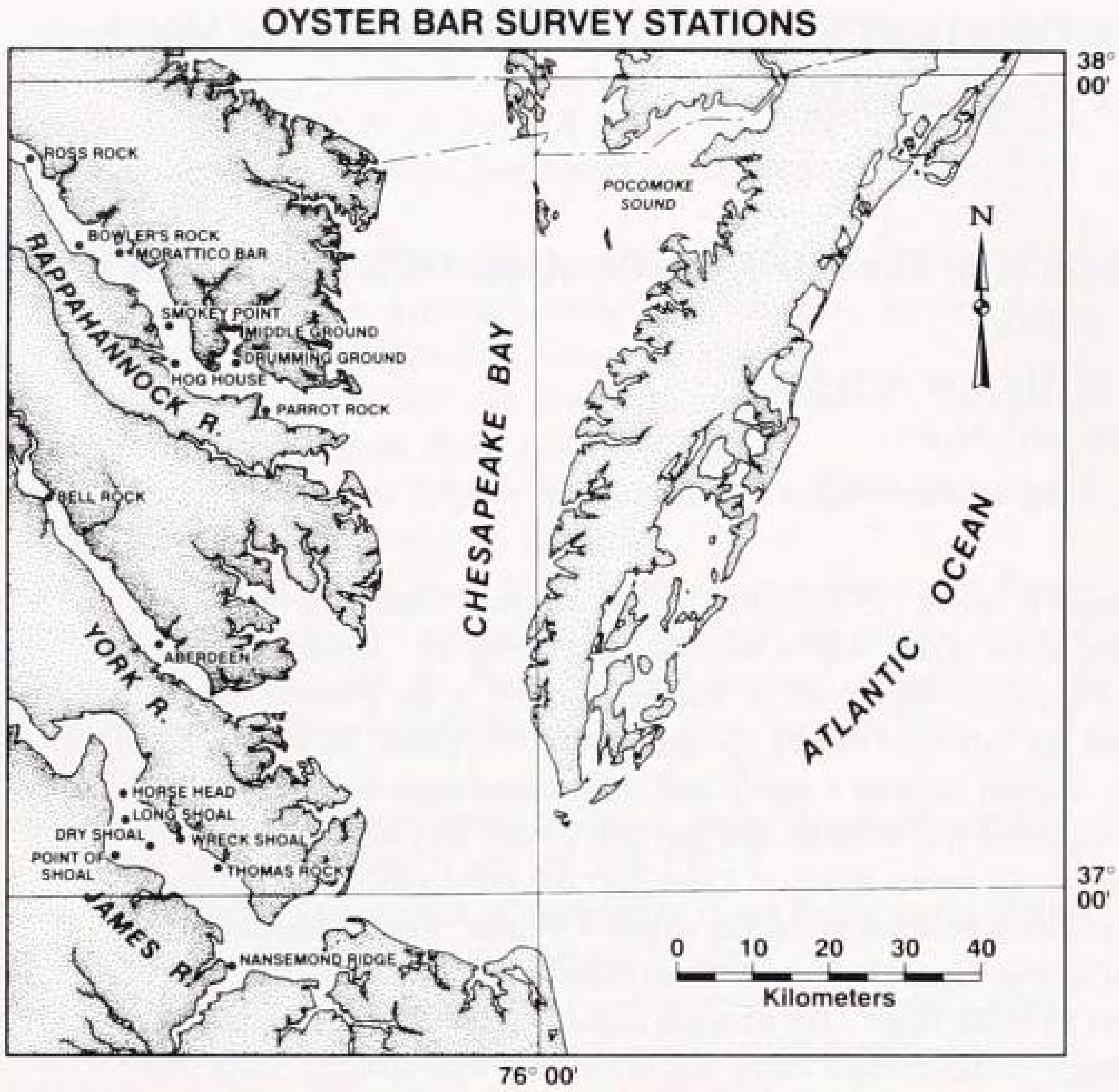


Figure 1. Locations of Virginia Chesapeake Bay Oyster Reefs.

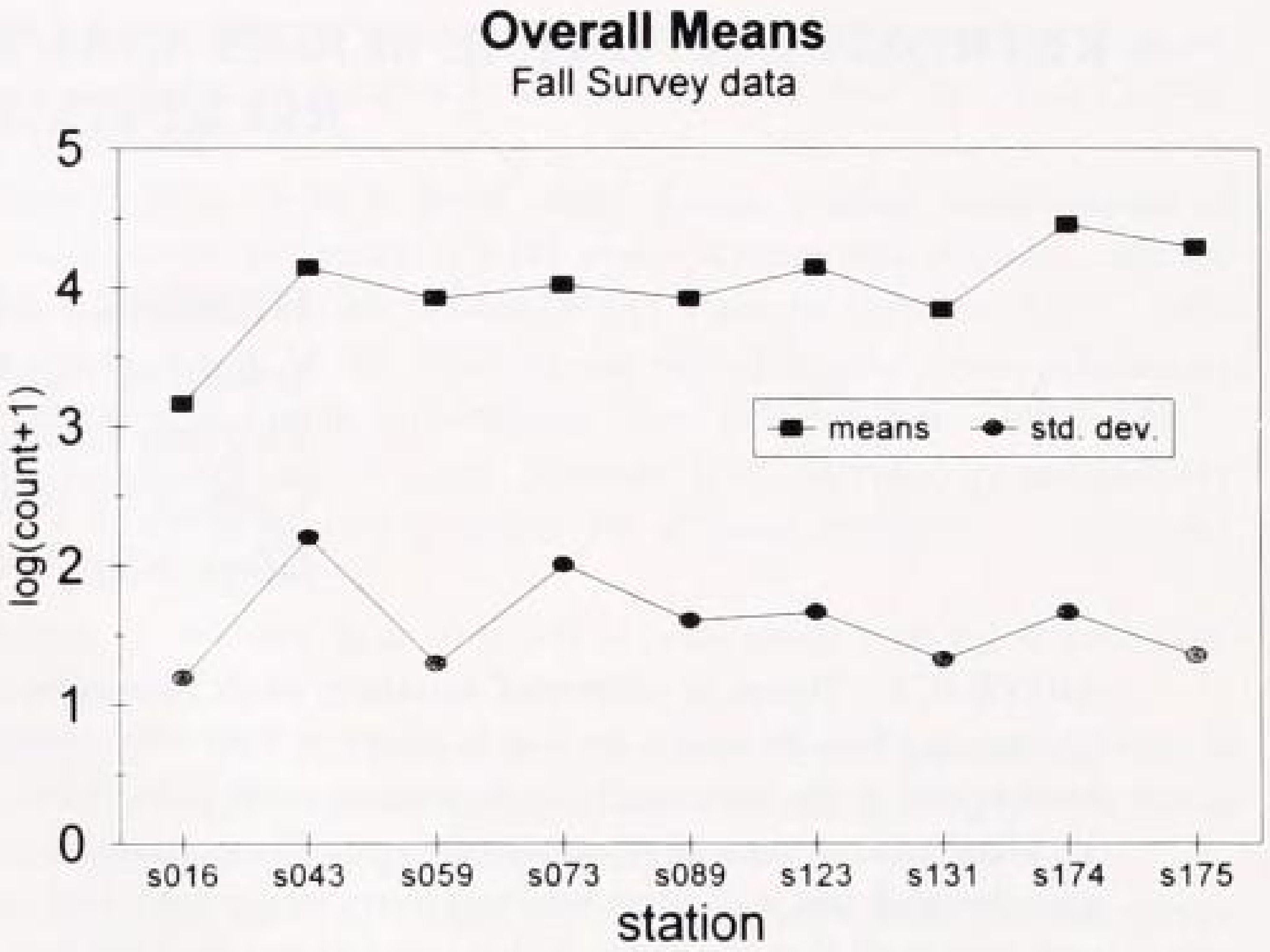


Figure 3. Overall means and standard deviations of fall survey data, 1946–1995.

tributed and allows the use of standard statistical procedures and inferences. The transformation used here is of the form log(X + 1). We plotted the means and standard deviations over time of the logarithmically transformed data. Figures 2 and 3 show the overall means and standard deviations for a group of stations and demonstrate the interstation variation for the shellstring data and the fall survey data, respectively (1946–1993). For both sets of data in the James River (shellstring and fall survey), the means are relatively constant from station to station, as is the standard deviation. This may be an indication that the time variation at stations in the James show a degree of synchronicity.

Shellstring data are sporadic during the period from 1947 to 1952, nonexistent for many bars through 1963, and fairly complete from that date through the present. Even so, however, only three or four bars have an unbroken record from 1963 to 1993. The fall survey continuity for spat-per-bushel and larger oysters is better, and the length of the series is longer (1946 to present). Following our examination of the length and completeness of the records, it was decided to focus on the fall surveys and not to consider the shellstring data. Fall yearling data were also available for all of the oyster rocks from which we had spat data.

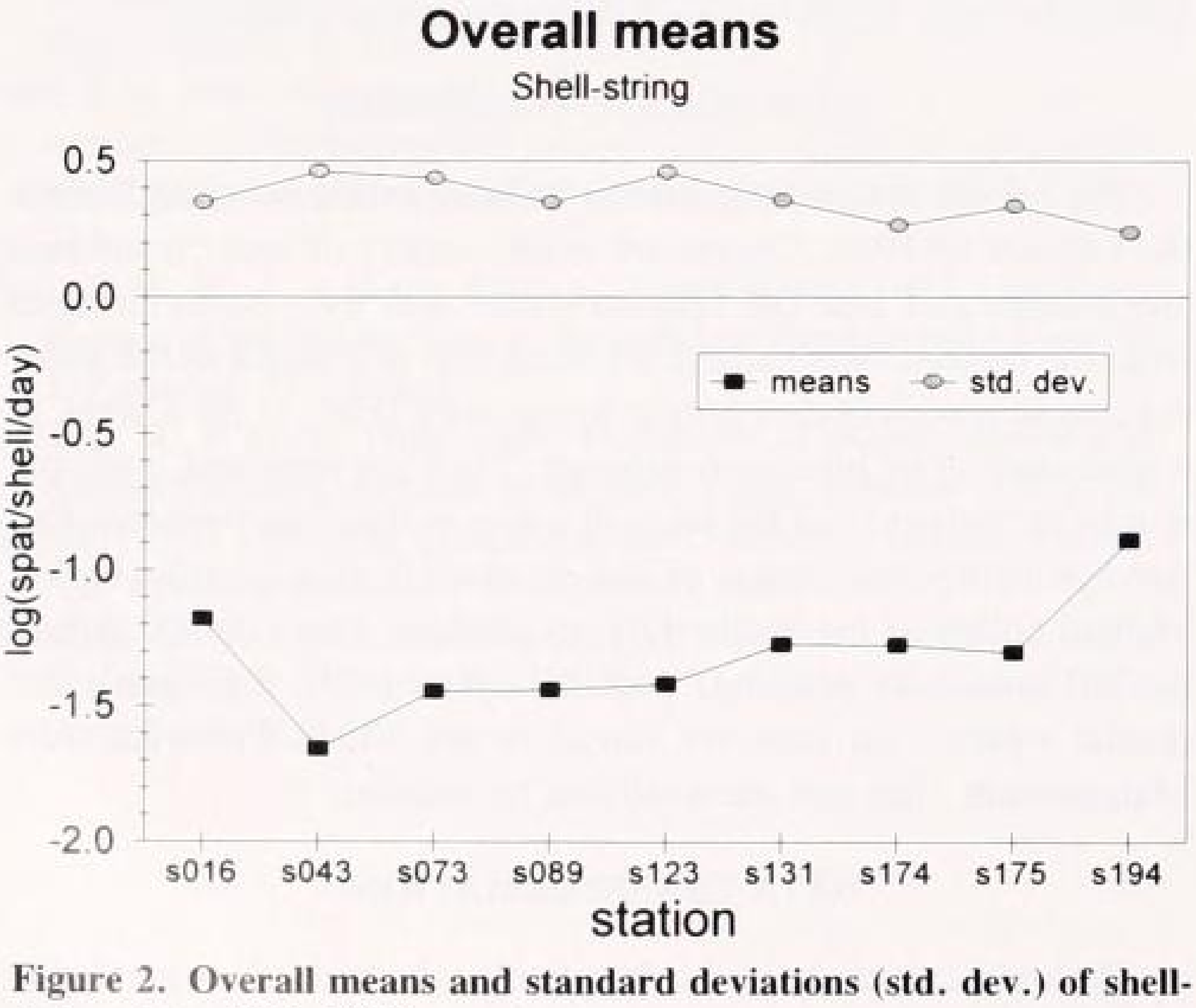


Figure 2. Overall means and standard deviations (std. dev.) of shellstring data, 1946–1995.

The length of the time series varied widely from station to station, ranging from almost continuous coverage since 1947 to measurements made in only a few years. It was decided to select a group of stations that contained the most usable information. The data were originally organized in computer files, with each file containing the total time series of observations for a single station. Each line in a file contained the following data items: year, the log transform of the spat count, the log transform of the yearling count. As noted above, the length of the time series varied considerably from station to station. Because the formats of all files were identical, the size of the file in bytes is a good measure of the quantity of information contained, i.e., the number of years for which data were collected at that station. Time series analyses require sequences that should be at least about 30 points in length and that are continuous, that is, have no gaps. The total size of all 67 data sets was 67,665 bytes. One-half of the information was contained in 14 data sets, with sizes ranging from 2,772 to 1,953 bytes. It was determined that these stations should be subjected to detailed analysis. Most of the selected stations are fall survey data. A further six files were over 1,500 bytes in size. Although Chai (1988) used an ARIMA to fill in missing data for Maryland spatfall, and Austin et al. (1993) used a linear extrapolation for Virginia oyster condition indices, the annual variability of our data is such that neither method is generally applicable, although in a few cases, a 1- or 2-y interpolation was appropriate. The quantity of data aggregated over all stations consists of 1,009 yearly measurements, although not all years have both spat and yearling data. Of this total amount of information, the stations selected for analysis comprise 518 yearly data values organized into 14 time series, all of which exceed 30 y in length.

Data for landings (seed and market) for the James River (1963 to present) were obtained from the Virginia Marine Resources Commission, as were the number of boat days (1983–1995). Spatfall data for the Potomac River were obtained from Chai (1988) for 1940–1985.

All station data and the yearly environmental data (temperature, river flow, and Palmer Drought Index [PDI]) were incorporated into a QUATTRO PRO FOR WINDOWS® spreadsheet. Most of the analyses were run with QUATTRO or MINITAB® for WINDOWS. Where appropriate, the following statistical analyses were used: Pearson correlation coefficient, linear regression (including multiple regression), cross-correlation, agglomerative cluster analyses, *loess* smoothing, differencing.

It is appropriate to make a comment here on the use of the *loess* procedure. Almost all of the time series in the data set show features with different timescales, short-term fluctuations from year to year that are superimposed on long-term trends that span decades. These features are separated by smoothing the data to produce the trend; the signal with a shorter term variation is produced by subtracting the trend from the original data. A common technique for smoothing is a moving weighted average filter. This procedure has the disadvantage that the smoothed series is necessarily shorter in duration than the original. The degree of smoothing necessary for the data in this study would require the order of the filter (the number of points averaged together) to be so high as to cause a severe loss of data at the extremities of the time series. Another common technique, recursive filtering, also has similar end effects, as well as imparting a phase shift to the data. The smoothing technique initially known as LOWESS (LOcally WEighted Scatterplot Smoother) (Cleveland 1979) does not suffer from these problems and in addition is robust (is not unduly affected by outliers). This smoothing procedure is sufficiently well accepted to have been incorporated into a number of well-known statistical packages, including SPSS and Minitab. The method does not lend itself to a simple formulaic statement, and neither can it be described in a single paragraph; consequently, a more detailed description is presented in an appendix. The originator of the method, W. S. Cleveland, has renamed the procedure "*loess*" (Cleveland 1993); this usage will be adhered to in all subsequent references to the method.

RESULTS AND DISCUSSION

General Temporal Patterns

Plots of the mean spatfall and yearling counts for each river were generated and inspected visually. In many cases, there were insufficient or incomplete data at any given bar or reef to maintain the time series. By combining them, however, and developing a mean annual index for each river, a robust data set was generated. Initially, we attempted to use a 5-point moving average to examine both long-term trends and periodic bay-wide cycles. The *loess* procedure, however, provided a better representation of a combination the 5-y moving average and the long-term trend. Consequently, we used *loess* as implemented in MINITAB. Although there were some area-wide coherent events, such as the droughts of the mid-1960s and early to mid-1980s, and a general post-1960s decline, spatfall in the four rivers exhibited a temporally independent pattern of set.

James River

The 0.2 degree of smoothing *loess* filter for spatfall in the James River showed a stable period before 1960 and then a period of decline (1960–1975). The later decade (1966–1975) of this decline was characterized by wide interannual variation. Although after 1975 there was a period of renewed set (Fig. 4a), it never returned to the pre-1960 levels. The long-term trend, revealed by the 0.7 smoothing filter, depicts a long-term decline from the mid-1940s through the early 1970s, followed by a leveling off of the decline. Spatfall ranged from five to eight spat per bushel during the pre-1960 decline, one to five during the 1960s–1970s, and three to six during the late 1970s and 1980s. Patterns of yearling abundance mirrored the spat (Fig. 4b), although the decline during 1950 to the early-1970s is more pronounced. Yearling dropped from a high of around 6 per bushel to a variable number of around 1.5–5/Bu after the decline.

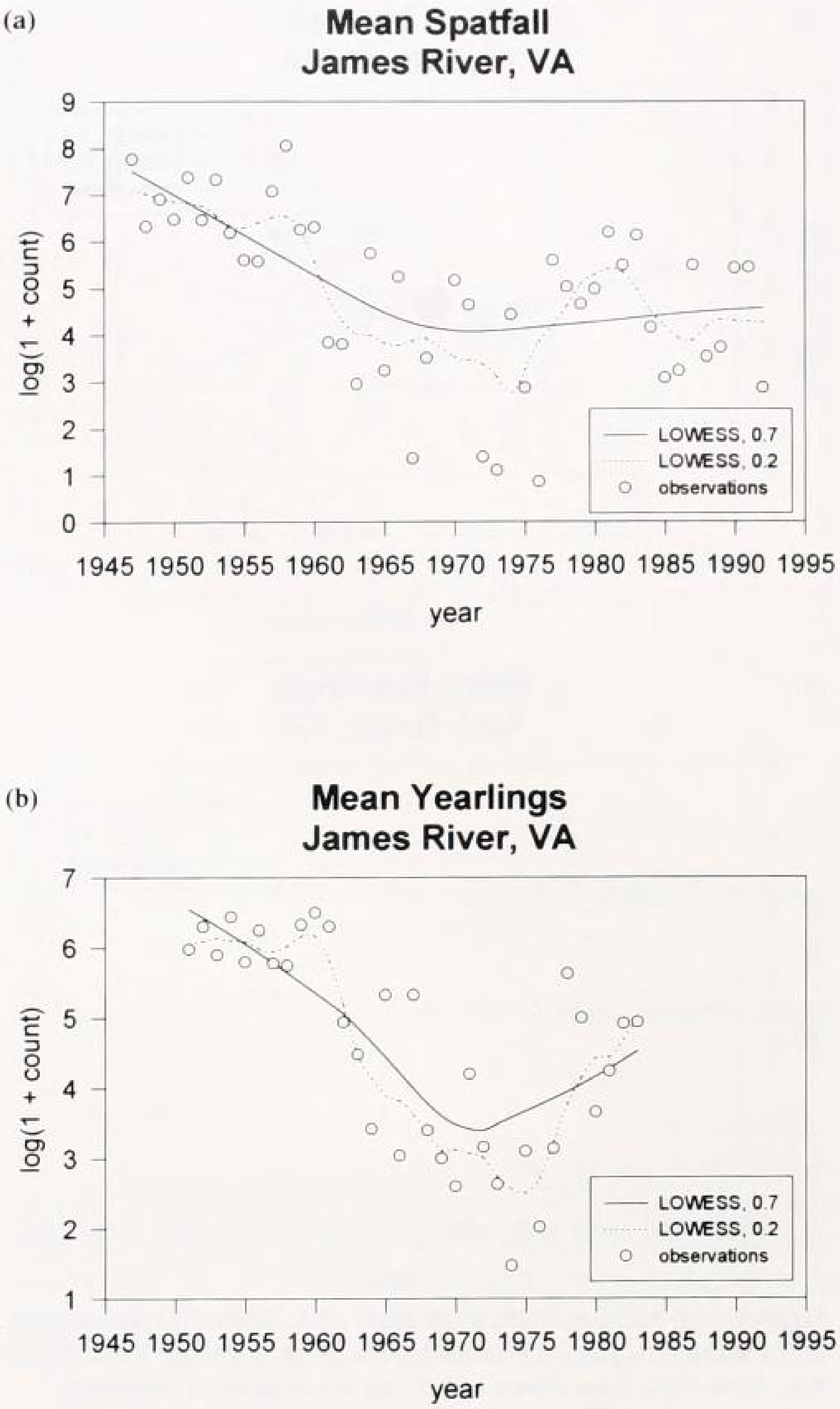


Figure 4. (a) Mean spatfall (number of spat-on-shell per bushel), James River, VA, 1946–1992; *loess* filters at the 0.2 and 0.7 degrees of smoothing. (b) Mean yearlings (number per bushel), James River, VA, 1948–1983; *loess* filters at the 0.2 and 0.7 degrees of smoothing.

York River

The empirical York River (Fig. 5a) spat-on-shell data exhibit no obvious pattern of set, although the *loess* 0.7 smoothing filter suggests a steady decline between 1950 and 1990, interrupted at 7- to 8-y intervals. Wide interannual fluctuations are apparent from 1946 through 1970. The 7- to 8-y periodic cycle is strikingly similar to the pattern in condition index described by Austin et al. (1993). The yearling oyster abundance (Fig. 5b) in the York River

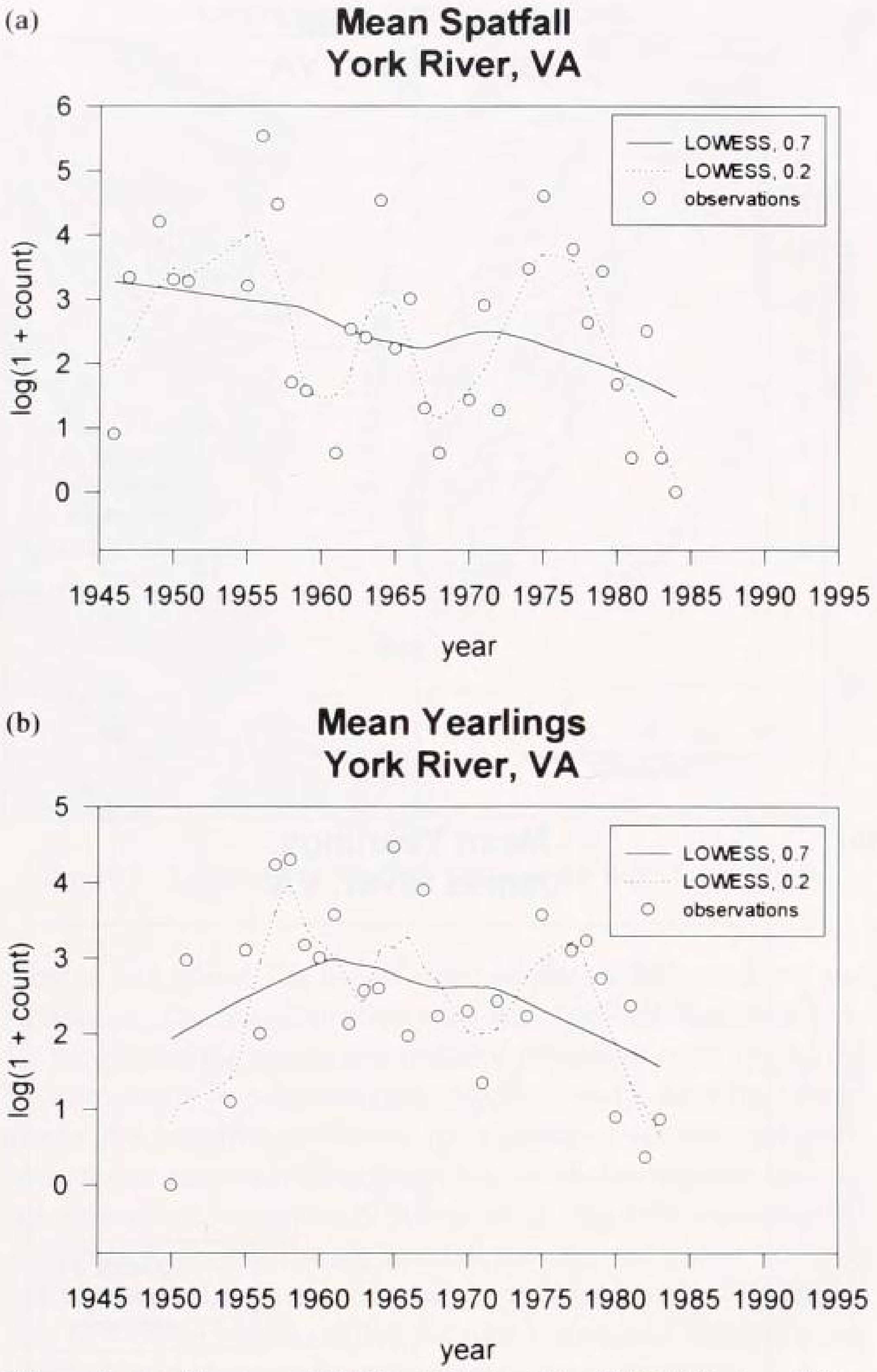


Figure 5. (a) Mean spatfall, York River, VA, 1946–1992, *loess* filters at 0.2 and 0.7 degrees of smoothing. (b) Mean yearlings, York River, VA, 1950–1982, *loess* filters at 0.2 and 0.7 degrees of smoothing.

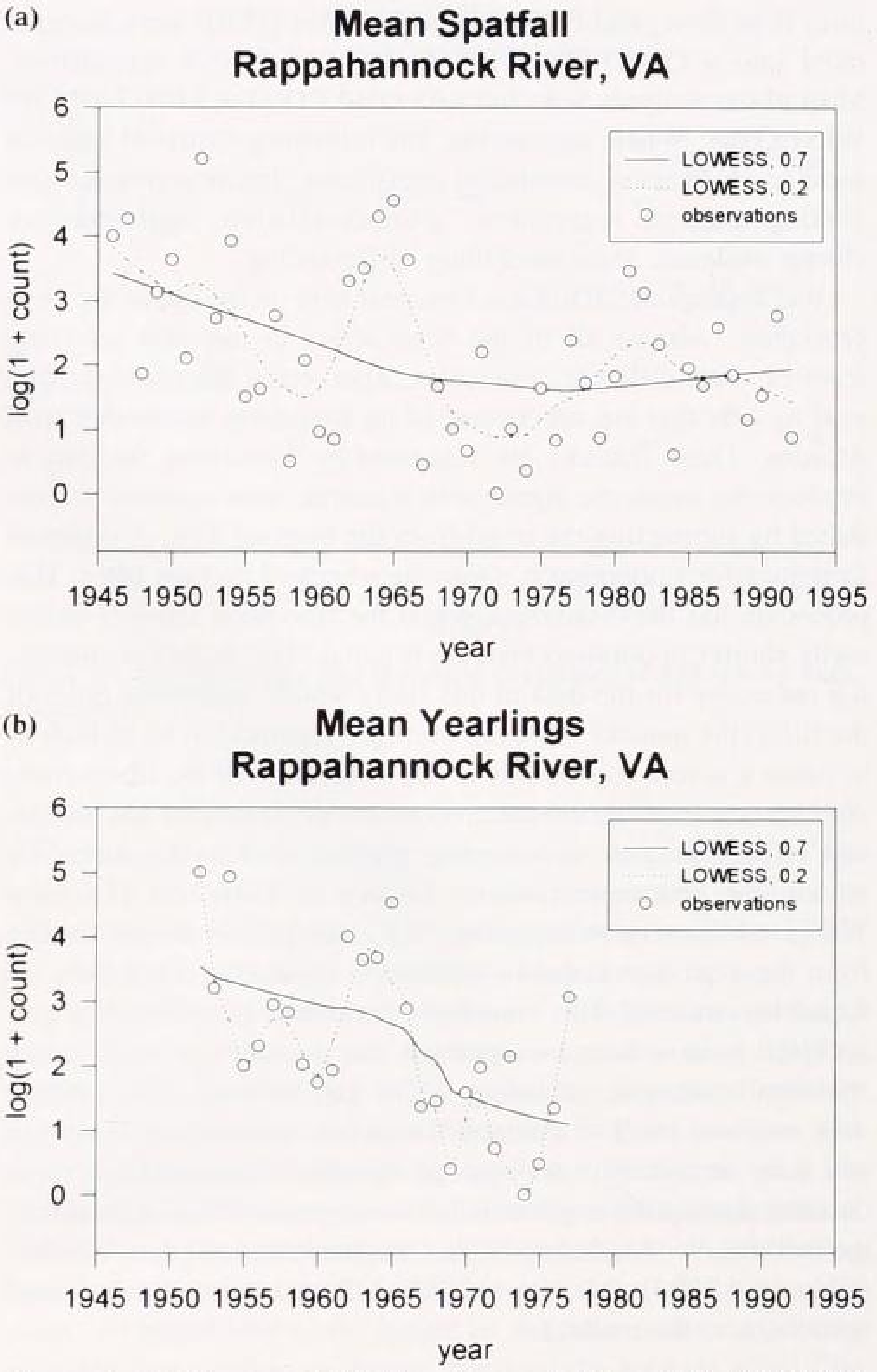


Figure 6. (a) Mean spatfall, Rappahannock River, VA, 1946–1992, *loess* filters at 0.2 and 0.7 degrees of smoothing. (b) Mean yearlings, Rappahannock River, VA, 1946–1977, *loess* filters at 0.2 and 0.7 degrees of smoothing.

exhibit peaks around 1957–1958, 1965 and 1975, and followed a general pattern similar to that of the spat.

Rappahannock River

The spat pattern in the Rappahannock (Fig. 6a) shows a degree of coherence with the James: high values (two to five) but quite variable before 1955, with a decline through 1961 (less than one), then a significant "recovery" (greater than three) during the mid-1960s drought, a return to poor set (one to two) by 1970, and finally, a slight increase through 1990. There is also a short response (1981–1983) to the drought during the early 1980s. The yearling abundance patterns parallel that of the spat, exhibiting a decline from 1950 through the early 1970s, followed by a slight recovery (Fig. 6b).

Potomac River

The Potomac spatfall (Fig. 7) has remained fairly constant since 1950, with short 1- to 3-y responses to the droughts in the 1960s and 1980s. The *loess* filters show no "1960s decline," only a moderate increase during the 1960s drought, and a subsequent decline through the early 1970s. It is possible that the decline from 1950 through 1972 was interrupted and partially masked during the drought. An apparent recovery is seen from the early 1970s through 1985.

Interreef and Intrareef Coherence

The coherence of the cumulative abundance of annual spatfall patterns was examined between oyster reefs within river and between rivers by use of the MINITAB Agglomerative cluster analyses and Pearson correlation. The analyses were run on James, Rappahannock, and Potomac River reefs. There was an insufficient number of either reefs or unbroken data strings of sufficient length in the York to allow comparisons in that river.

The degree to which two time series exhibit the same features of temporal variation can be measured with the simple Pearson correlation coefficient between the two sets of data. Correspondingly, a visual comparison can be made from a scatterplot where each year is represented by a point, the (x, y) coordinates of which are given by the respective observations at the two stations. If the series from the two stations are approximately synchronous, the scatterplot will show the pattern associated with two well-correlated variables.

These more complex relationships are conveniently explored

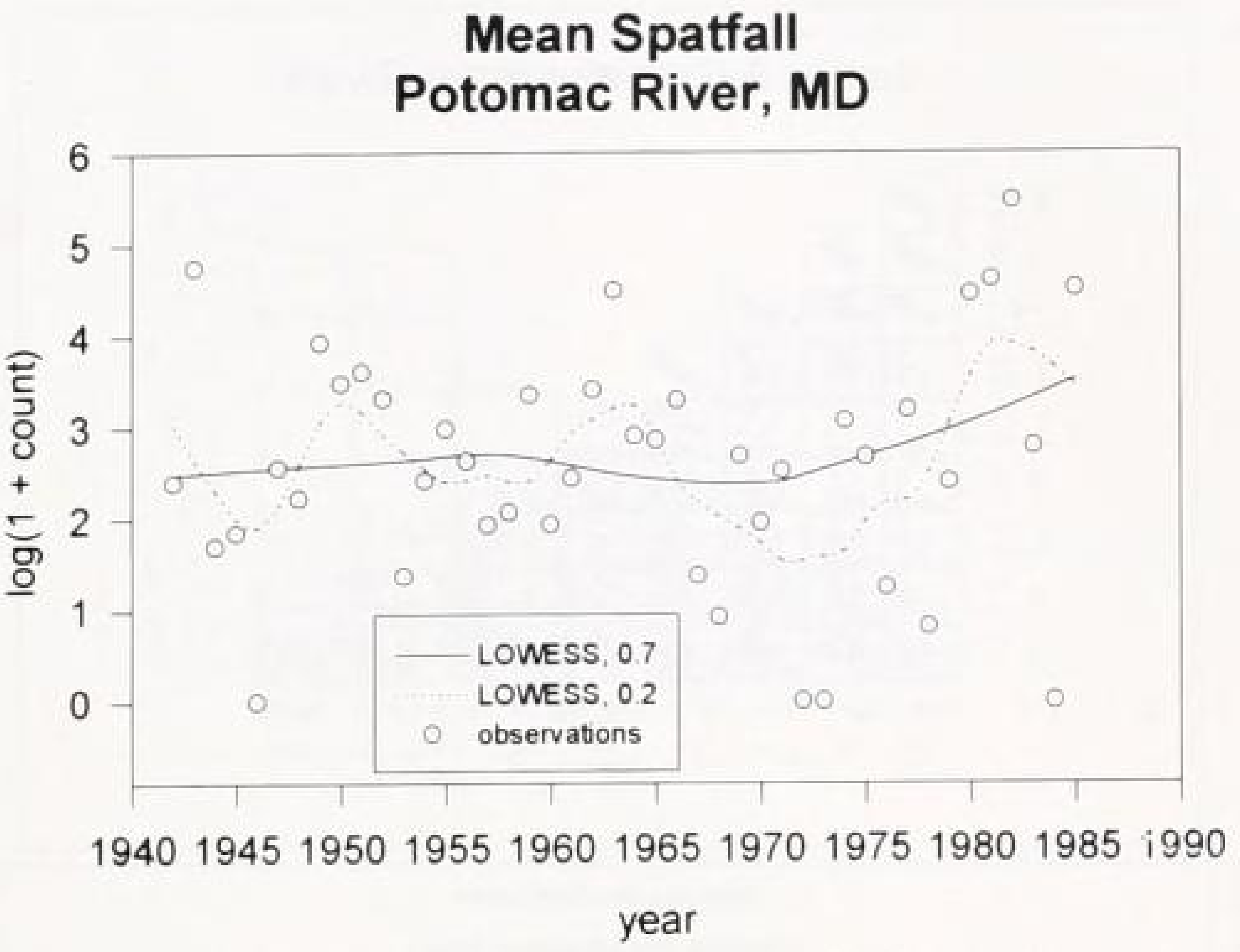


Figure 7. Mean spatfall, Potomac River, MD, 1942–1986, *loess* filters at 0.2 and 0.7 degrees of smoothing.

by use of the cluster analysis technique. The starting point is the calculation of a distance matrix, D, the elements of which, d_{ij}, are given by:

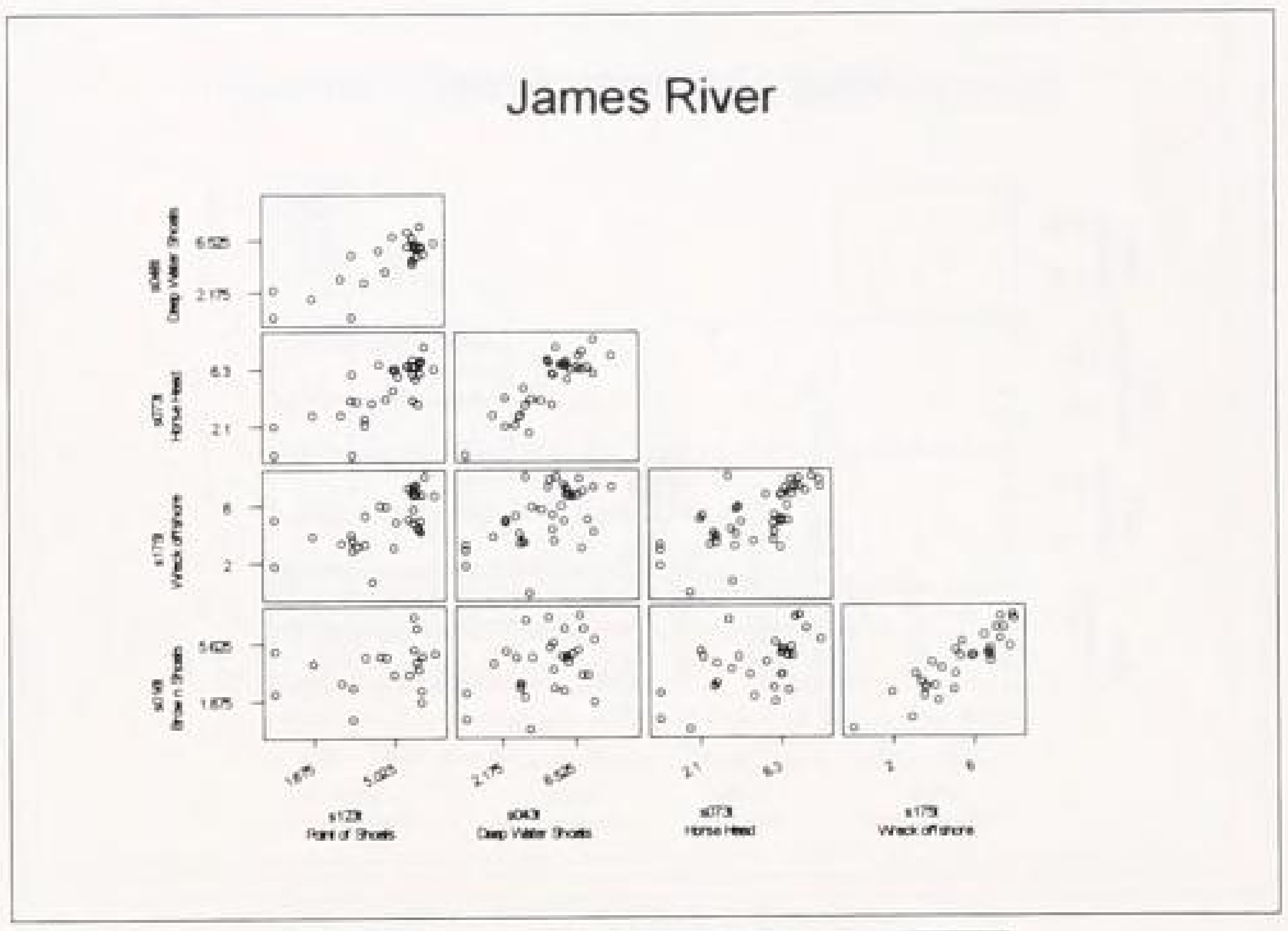
$$d_{ij} = 1 - r_{ij}$$

where r_{ij} is the correlation coefficient between stations *I* and *j*. The closest pair of stations, using this distance measure, is combined into a single cluster. The distance matrix is recalculated for the new set of stations (now one less in number), and the closest pair are combined into a cluster. The process can be repeated until a single cluster is produced. The results are best displayed in a dendogram, as shown, for example, in Figure 9, which clearly demonstrates the clustering hierarchy and the presence of two distinct groups of stations with regard to their temporal structure of spatfall counts.

James River

Figure 8 is a matrix of scatterplots for all 10 possible pairs of the five stations in the James River. The corresponding correlation coefficients are shown in a parallel matrix representation. It is seen that the highest correlation of 0.891 (d_{ij} = 0.109) occurs for the Horse Head–Deepwater Shoals pairing, with a slightly smaller value, 0.886, for the pair Wreck Shoals–Brown Shoals (d_{ij} = 0.114). A third station, Point of Shoals, also shows a high correlation of 0.802 (d_{ij} = 0.198) with one of the first pair, Deepwater Shoals, and a slightly less value, 0.767 (d_{ij} = 0.233) with the other station of the first pair, Horse Head.

The cluster analysis (Fig. 9) shows that James River stations fell into two groups. Stations along the southwest shore (Group I), Deepwater Shoals and Horse Head, demonstrated a high degree of similarity (95), as shown in the previous paragraph. These two were also similar to Point of Shoals (90). A second similarity grouping (Group II) was exhibited between Wreck Shoals and Brown Shoals, but at a lesser degree of similarity (88). This second group included the stations along the northeast shore. The same rankings and similarity were also independently described by the Pearson correlation coefficients (Fig. 8). Haven and Fritz (1985), looking at the synchrony of setting pulses in the James, found identical groupings of reefs for Groups I and II; Austin et al.



Correlation Coefficients

James River Stations

	s123t	s043t	s073t	s175t
s043t	0.802			
s073t	0.767	0.891		
s175t	0.588	0.546	0.692	
s016t	0.243	0.367	0.534	0.886

Figure 8. Cross-correlation matrix for spat on James River oyster reefs.

(1993), looking at oyster condition indices, found the same Group I and Group II classifications.

Rappahannock River

The results of a similar analysis on the stations in the Rappahannock River are shown in Figures 10 and 11. Downriver and midriver reefs, Smokey Deep and Hog House, were closest in resemblance (d_{if} = 0.253), followed by their grouping with Drumming Ground (0.386). Upriver reefs, Morattico and Bowlers Rock, were independent and showed no similarity to other reefs.

James Versus Rappahannock

When the stations from both rivers were analyzed together, the same groupings emerged (Figures 12 and 13). Southwest shore James (Group I) reefs, Deepwater Shoals and Horse Head, formed their own similarity cluster, including Point of Shoals in the James. A second, more diverse group was composed of mid- and

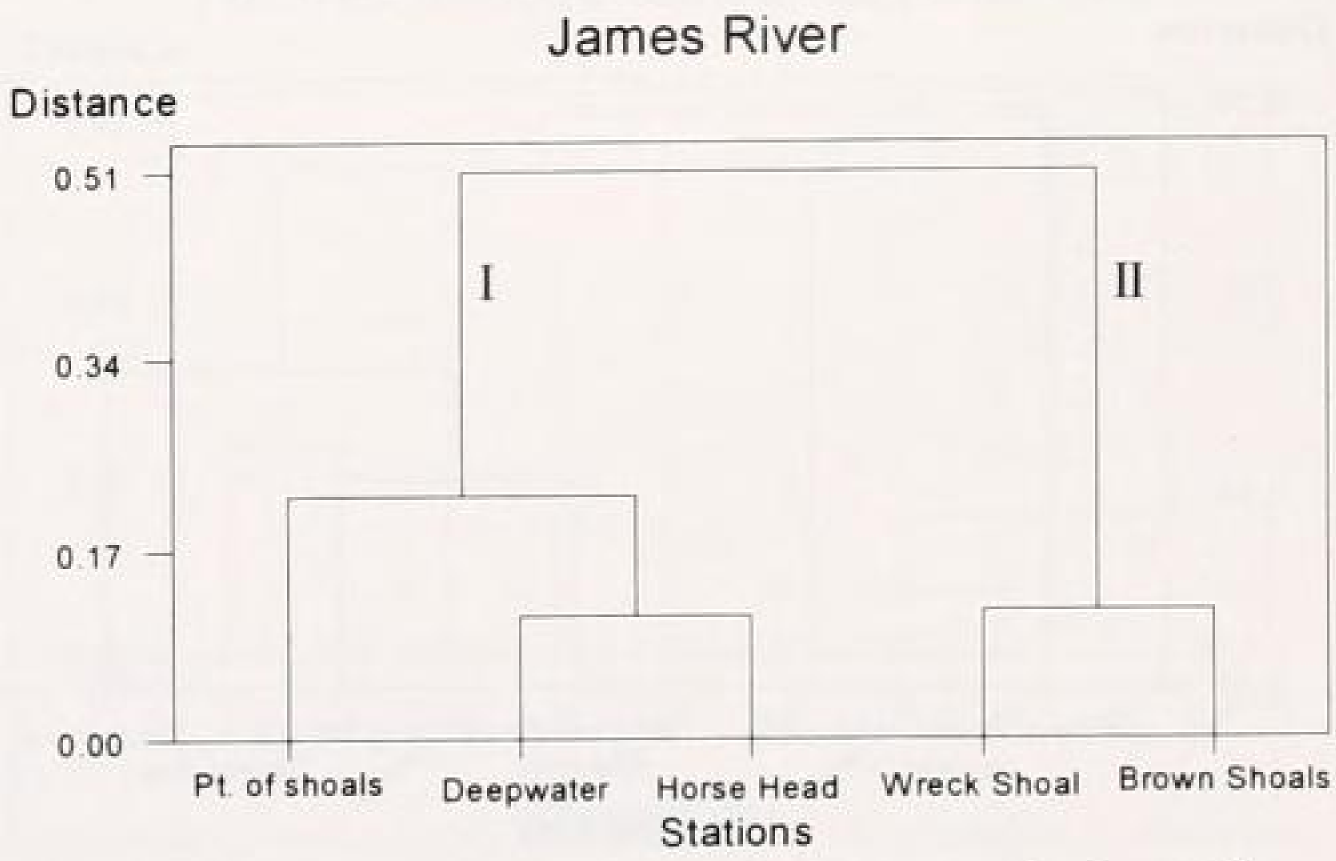
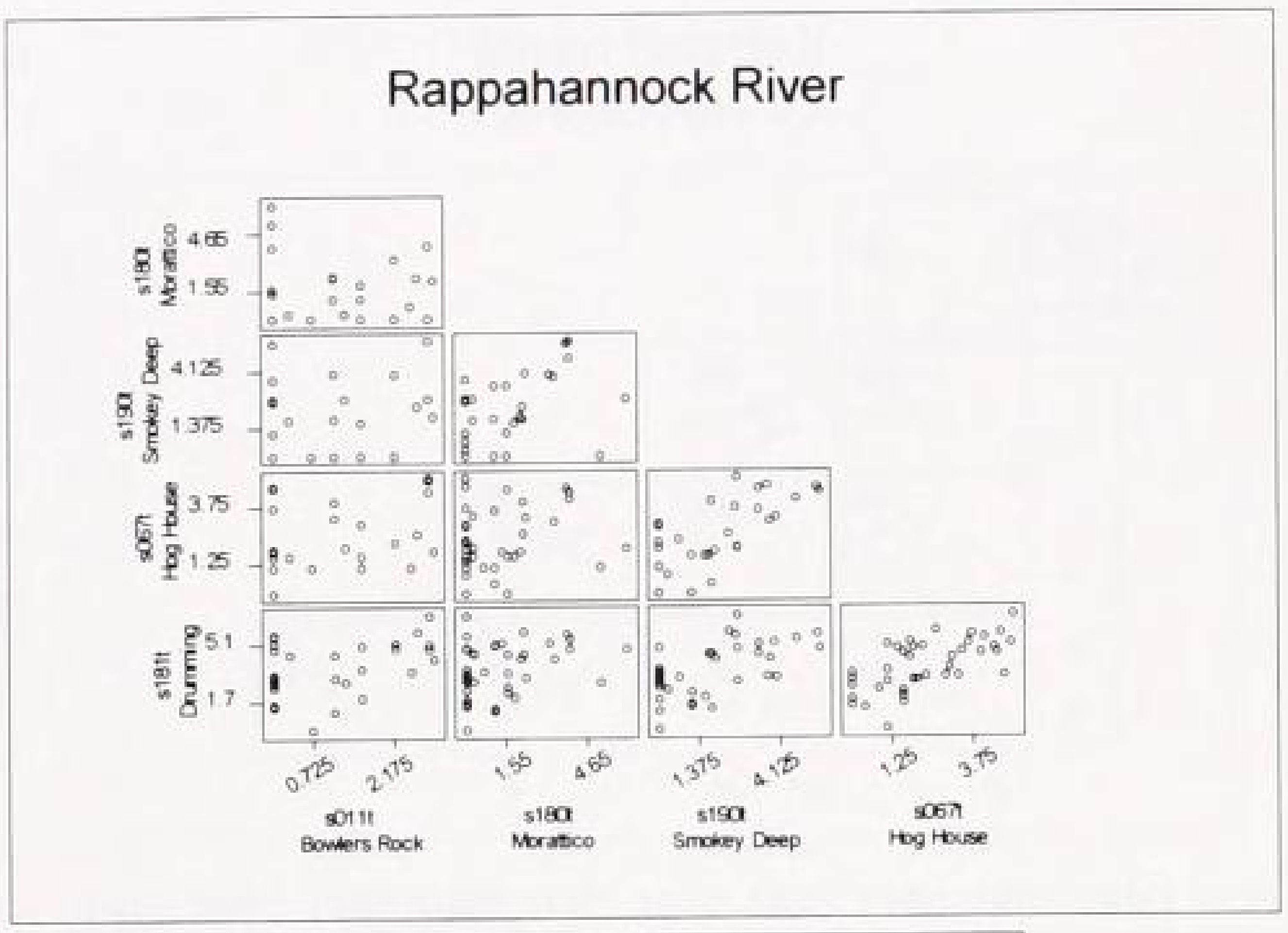


Figure 9. Agglomerative cluster analysis of oyster reefs, James River. Pt., Point.

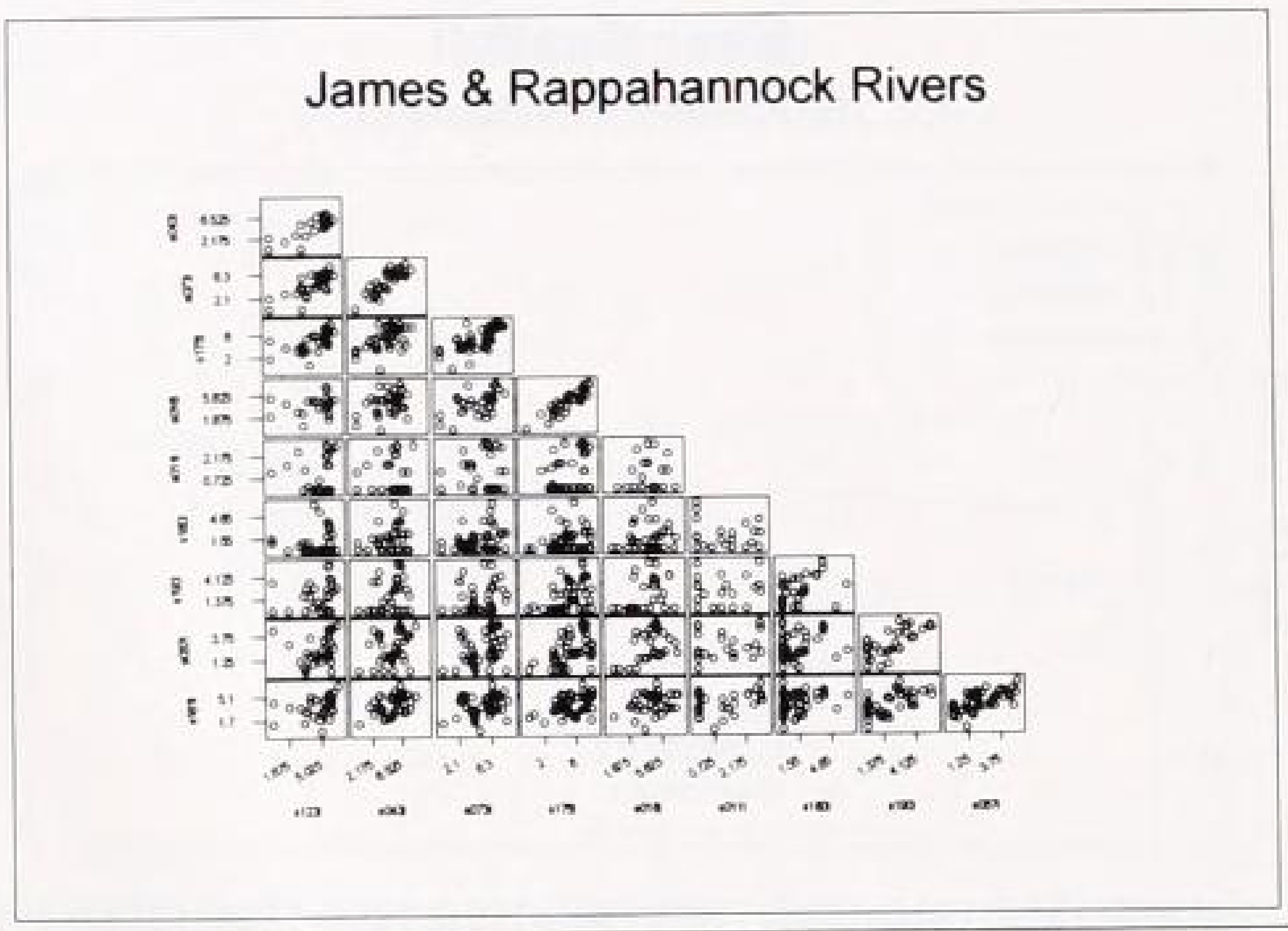


Correlation Coefficients

Rappahannock River Stations

	s011t	s180t	s190t	s067t
s180t	0.084			
s190t	0.307	0.533		
s067t	0.404	0.266	0.747	
s181t	0.382	0.297	0.589	0.638

Figure 10. Cross-correlation matrix for spat on Rappahannock River oyster reefs.



Correlation Coefficients

James & Rappahannock Rivers

	s123t	s043t	s073t	s175t	s016t	s011t	s180t	s190t
s043t	0.802							
s073t	0.767	0.891						
s175t	0.588	0.546	0.692					
s016t	0.243	0.367	0.534	0.886				
s011t	0.170	0.080	0.039	0.194	0.125			
s180t	0.175	0.261	0.220	0.149	0.129	0.084		
s190t	0.305	0.352	0.243	0.410	0.349	0.307	0.533	
s067t	0.161	0.307	0.247	0.474	0.471	0.404	0.266	0.747
s181t	0.383	0.425	0.318	0.450	0.333	0.382	0.297	0.589

Figure 12. Cross-correlation matrix for spat on James River and Rappahannock River oyster reefs.

lower-Rappahannock and lower-James (Group II) reefs. This included Smokey Point Deep (Rappahannock) and Wreck Shoals (James); Hog House (Rappahannock), Brown Shoals (James), and Drumming Ground (Rappahannock). The upper-Rappahannock reefs, Morattico and Bowlers Rock, again demonstrated no coherence with either other Rappahannock or James River oyster reefs.

Potomac River

The stations in the Potomac River grouped by distance from the mouth of the river. Not all stations had sufficient data and were rejected by the cluster analysis. Figures 14 and 15 show the composition of the similarity groups. Popes Creek, the only station north of the Route 301 bridge, grouped with the "midriver" stations (Cobb Island, Cedar Island, Heron Point, and Swan Island). The three downriver stations, Jones, Ragged Point, and Cornfield Harbor, were grouped, with Ragged and Cornfield being the most similar.

All Rivers

When the cluster analysis was run on the two James groups (I and II), mean Rappahannock, and six Potomac stations, several new groups aligned (Figs. 16 and 17). The two James groups clustered with Jones Shoal, Potomac River, and the mean of the Rappahannock stations clustered with the midriver Potomac. Cornfield Harbor, at the mouth of the Potomac River, did not group with any other station(s).

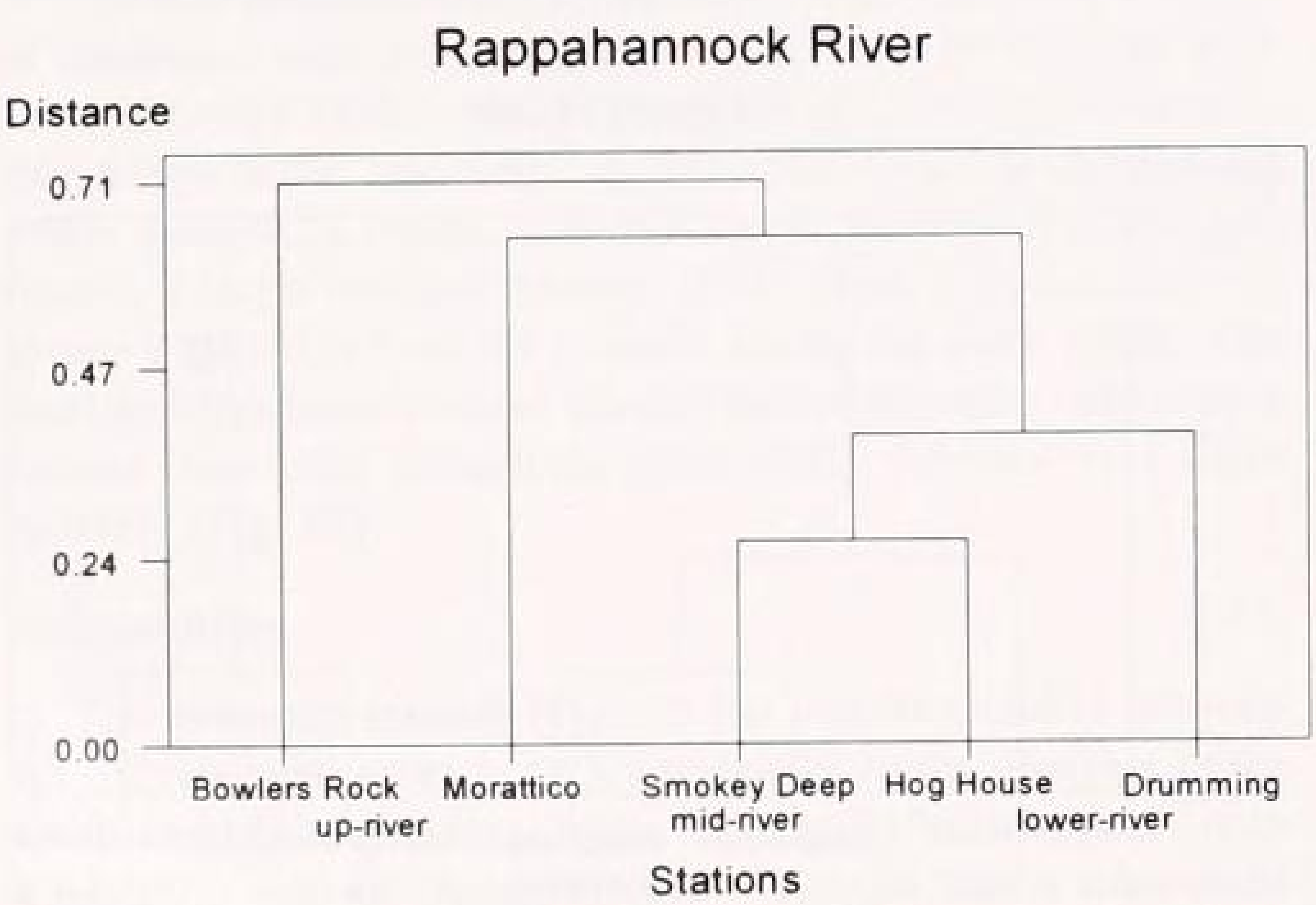


Figure 11. Agglomerative cluster analysis of oyster reefs, Rappahannock River.

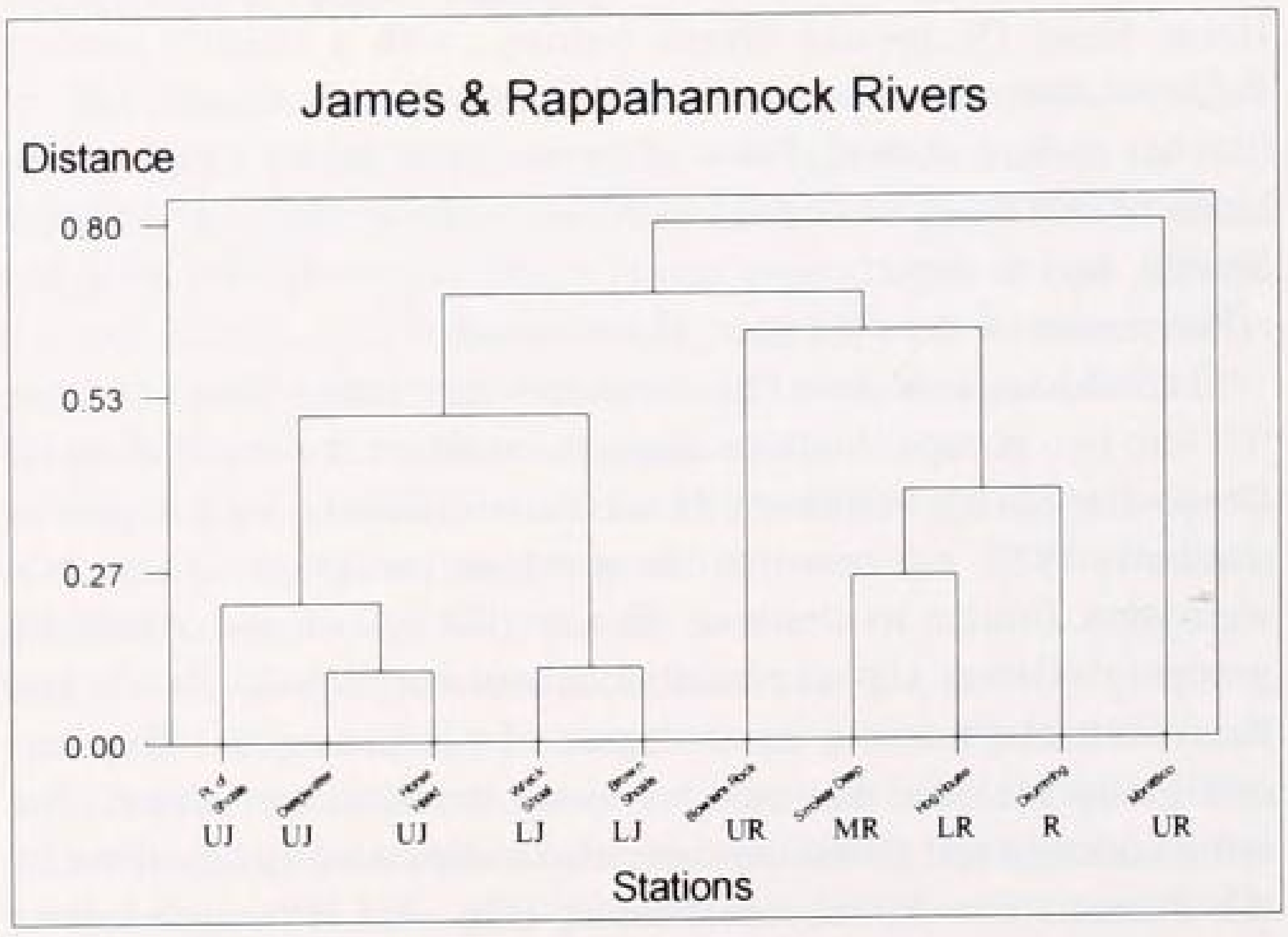
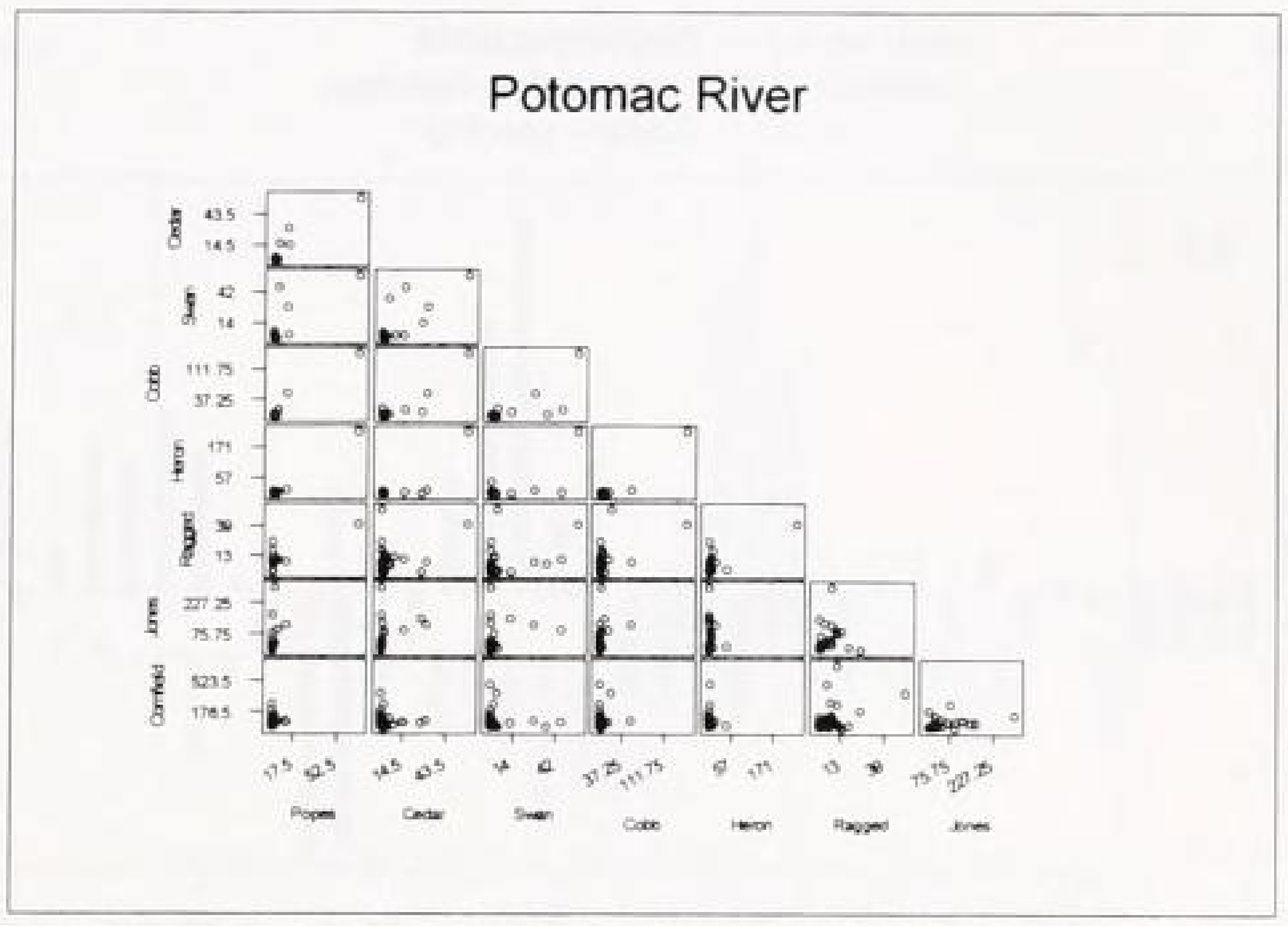


Figure 13. Agglomerative cluster analysis of oyster reefs, James and Rappahannock Rivers.

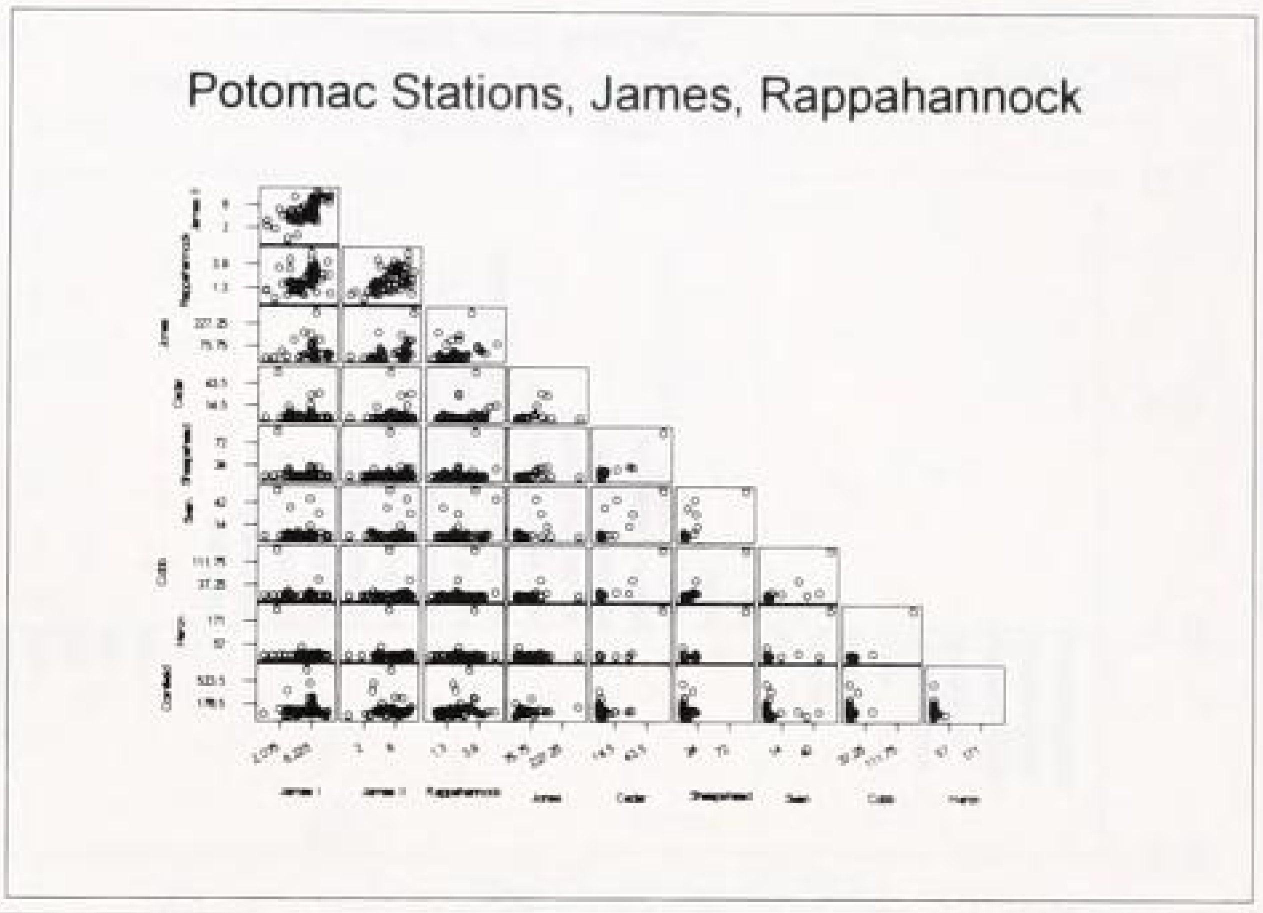


Correlation Coefficients

Potomac River

	Popes	Cobb	Cedar	Heron	Swan	Jones	Ragged
Cobb	0.979						
Cedar	0.930	0.913					
Heron	0.993	0.953	0.821				
Swan	0.759	0.747	0.787	0.693			
Jones	0.309	0.258	0.303	-0.125	0.210		
Ragged	0.764	0.550	0.348	0.737	0.337	-0.037	
Cornfield	-0.037	0.090	-0.078	-0.122	-0.125	0.253	0.400

Figure 14. Cross-correlation matrix for spat on Potomac River oyster reefs.



Potomac Stations, James, Rappahanock

Correlation Coefficients

	James I	James II	Rapp.	Jones	Cedar	Sheepshead	Swan	Cobb	Heron
meanII	0.621								
meanrapp	0.354	0.458							
Jones	0.151	0.436	0.201						
Cedar	-0.197	0.093	0.275	0.303					
Sheepshead	-0.284	0.067	0.266	0.333	0.920				
Swan	-0.203	0.148	0.245	0.210	0.787	0.776			
Cobb	-0.261	0.046	0.200	0.258	0.913	0.964	0.747		
Heron	-0.330	-0.043	0.192	-0.125	0.821	0.932	0.693	0.953	
Cornfield	0.053	0.072	0.136	0.253	0.078	0.079	-0.125	0.090	0.122

Figure 16. Cross-correlation matrix for spat on James, Rappahannock, and Potomac oyster reefs.

Relationship Between Spat and Subsequent Cohort Stages

Counts of spatfall have been maintained by Virginia and Maryland since 1946. The original purpose of the spatfall monitoring in Virginia was to provide the state's oyster growers with information on the location and timing of peaks in spatfall to allow them to broadcast shell to receive best the annual "strike." Over the years, and after the prolonged decline in market oyster landings that coincided with the decline in spat abundance, the annual spatfall report became a forecast for the status of the Virginia oyster harvest (e.g., Barber 1991). This relationship was never documented.

Spat Versus Yearling

The relationship between spat and subsequent cohort stages can be conveniently investigated by obtaining the cross-correlation function (ccf) for the spat and the yearling times series. Figure 18a shows the ccf for the James River data. The structure in the function is primarily due to the long-term trend in the data. It appears that, superimposed on this background, there is an enhancement at a lag of 1 y, indicative of the expected relationship between spat density and yearling density in the following year. This relationship is revealed more clearly by removing the long-term trend from both data sets and computing the ccf of the residuals (Fig. 18b).

The long-term trends are estimated by use of the *loess* smoothing technique. The ccf of the residual series is shown in Figure 18b. It is seen that there is a significant correlation between the series when lagged by 1 y (i.e., spat in year t are compared with yearling in year $t + 1$) and that the correlation does not extend

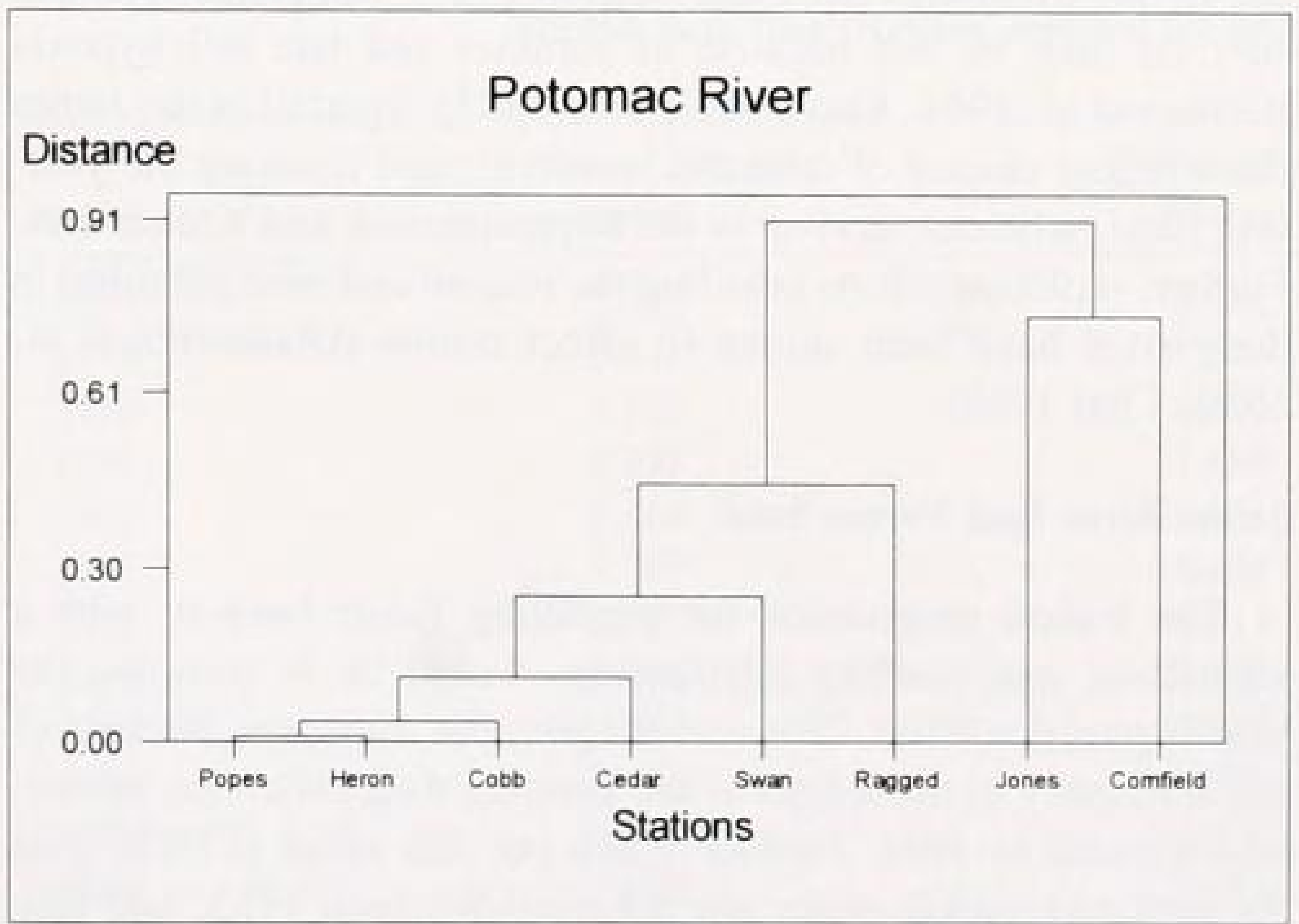


Figure 15. Agglomerative cluster analysis of oyster reefs, Potomac River.

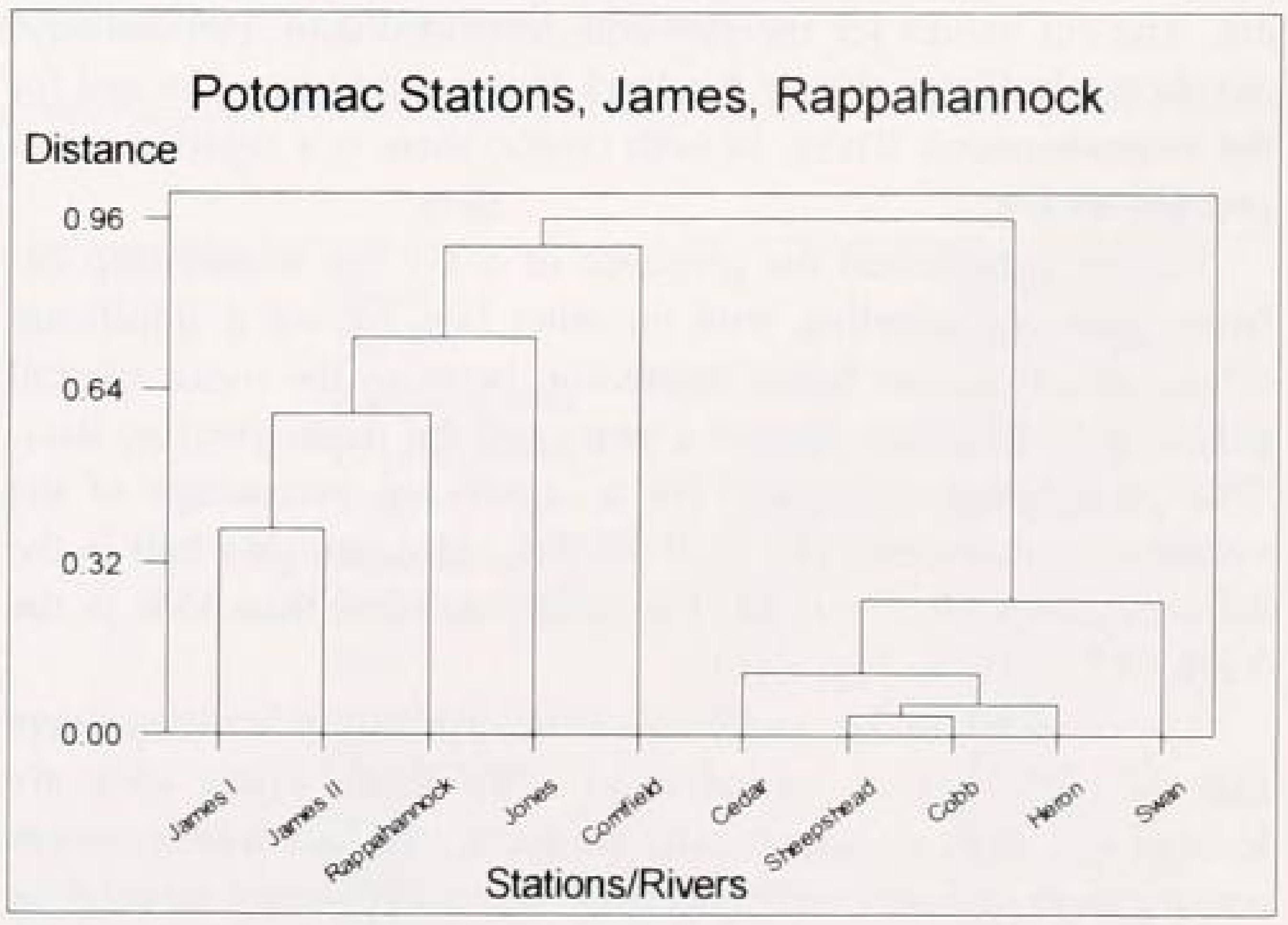


Figure 17. Agglomerative cluster analysis of oyster reefs, James, Rappahannock, and Potomac Rivers.

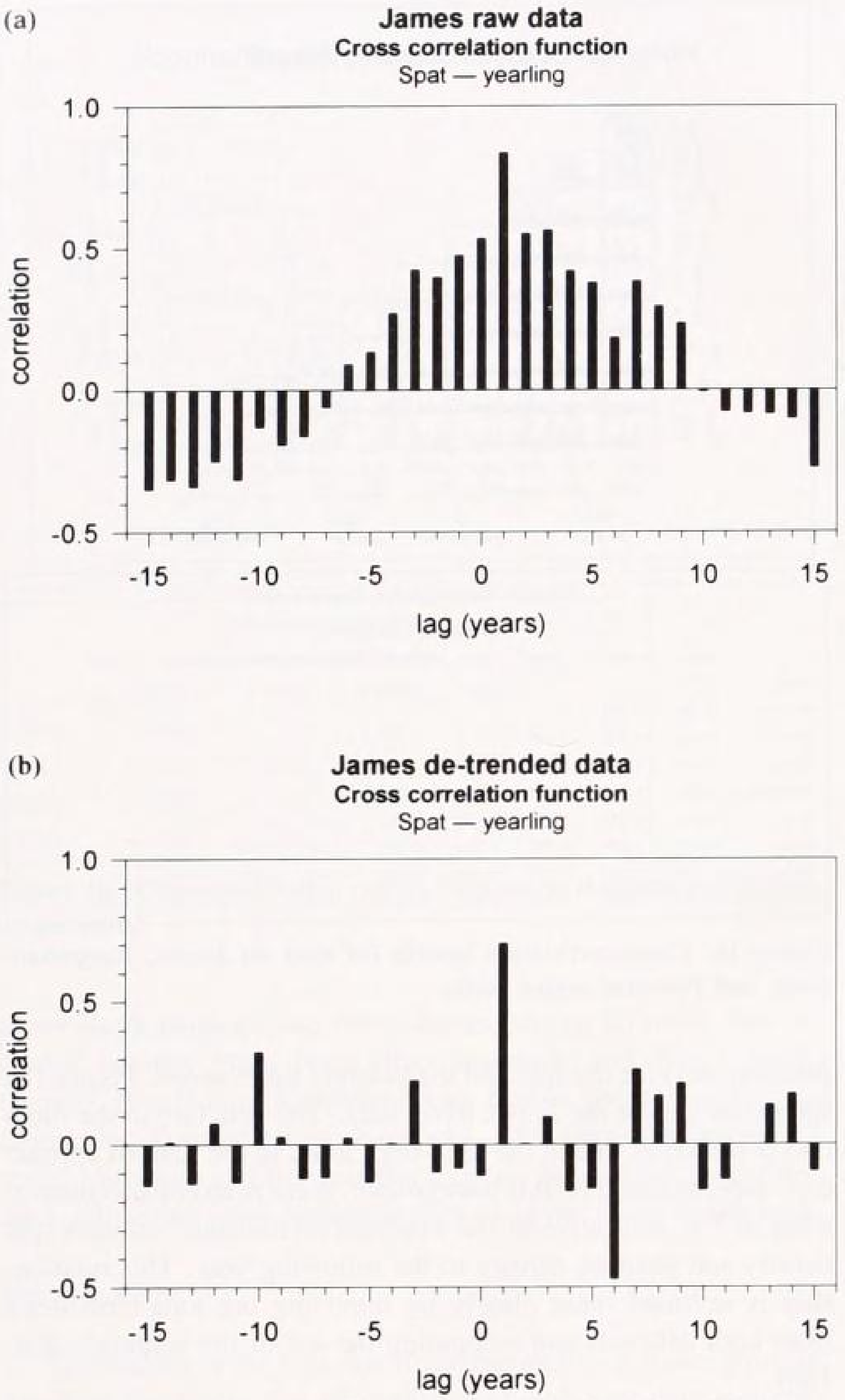


Figure 18. (a) ccf for James River spat and yearling. (b) ccf for James River spat and yearling (detrended).

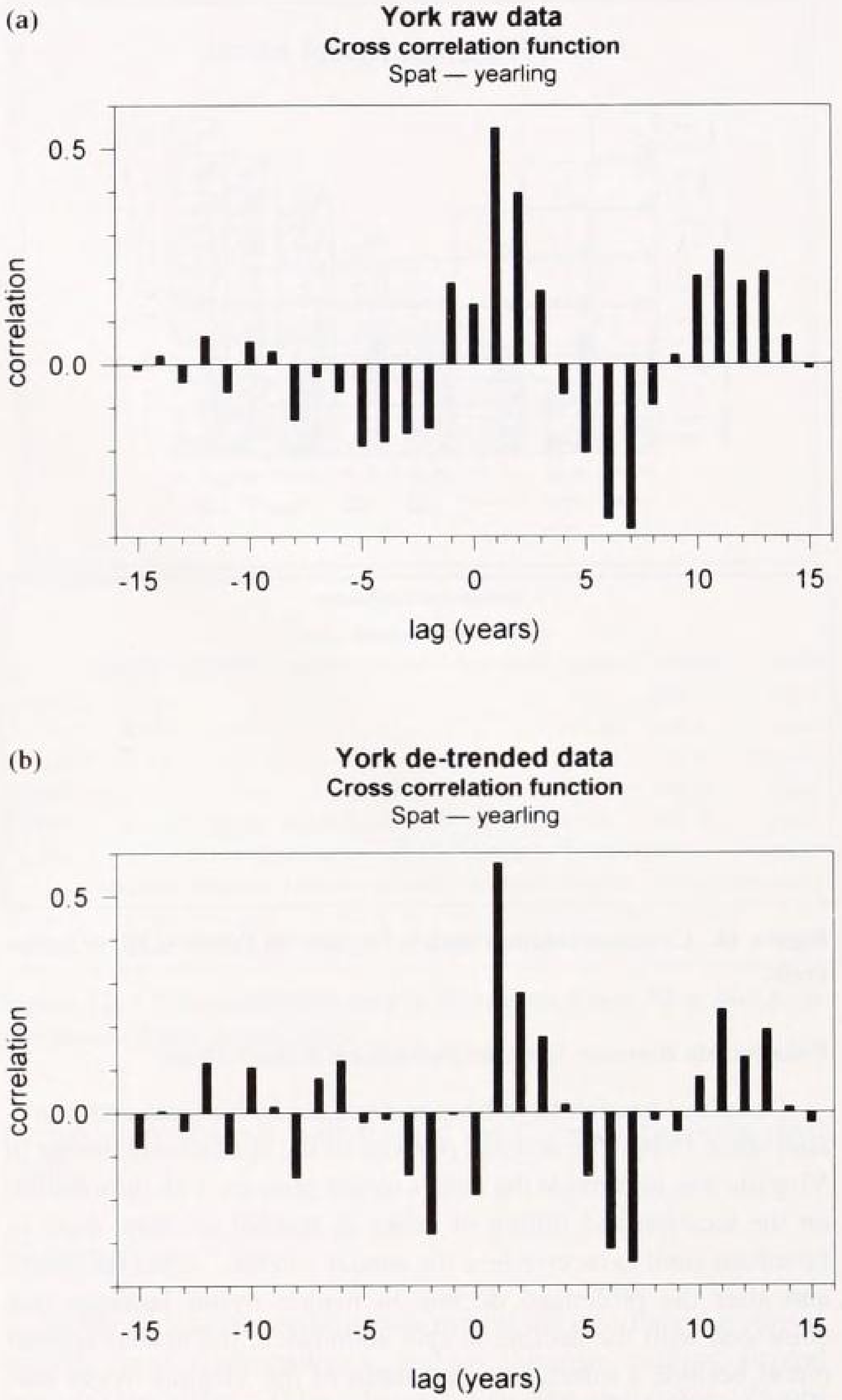


Figure 19. (a) ccf for York River spat and yearling. (b) ccf for York River spat and yearling (detrended).

beyond 1 y. This can be considered to be a confirmation of the accuracy of designating "yearlings."

Similar results are found in the York and Rappahannock Rivers. The ccf values for the raw and detrended data, respectively, are shown in Figure 19 for the York River and Figure 20a and for the Rappahannock River. In both rivers, there is a significant ccf at a lag of 1 y.

Having established the presence of a 1-y lag relationship between spat and yearling with no other lags having a significant effect, one may use linear regression between the mean spatfall values for each river, lagged a year, and the mean yearling data. This relationship accounted for a significant percentage of the variation in the James ($R^2 = 0.73$; Fig. 21a), roughly half in the Rappahannock ($R^2 = 0.48$, Fig. 21b), and less than 15% in the York ($R^2 = 0.14$, Fig. 21c).

The disparity in the coefficient of determination between rivers may be explained in several ways. The James oyster reefs are located in a more geographically compact area, but with a diverse environment strongly influenced by the gravitational circulation (salinity driven deeper "salt intrusion"; Pritchard 1952), which results in a retentive circulation pattern in the lower river (Kuo et al. 1990). It has also been suggested that the proximity of the lower James to the ocean provides a "healthier" environment than the up-bay tributaries (Kuo and Neilsen 1987). Rappahannock spat survival may be less because of summer and late fall hypoxia (Officer et al. 1984, Kuo and Neilsen 1987). Spatfall in the James has a higher chance of retention, survival, and reaching the yearling stage, whereas survival in the Rappahannock and York is less. Further, repletion efforts (shelling the bottom and seed planting) in these river have been shown to affect results (Ulanowicz et al. 1980, Chai 1988).

James River Spat Versus Seed

The logical progression for predicting future harvest, with a significant spat-yearling relationship, would be to examine the yearling-seed relation. This was not possible, however, because of the deficiency in the length of the yearling data collection period, which ended in 1984. Further, catch per unit effort (CPUE) data for seed and market oyster are not available until 1983, and then only for the James. This allows only a 1-y overlap, in only one river. Consequently, we examined the James River spat-seed/day

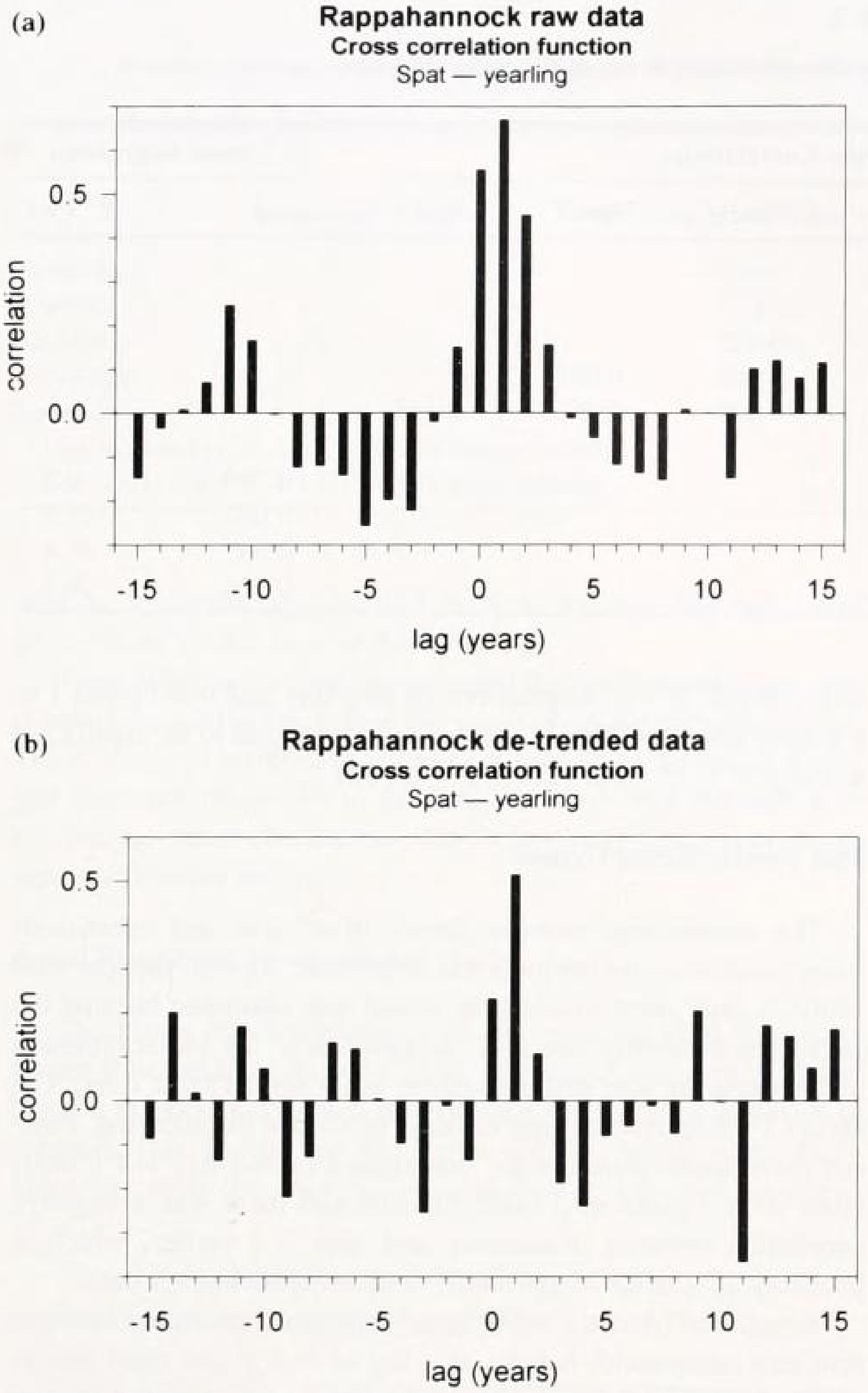


Figure 20. (a) ccf for Rappahannock River spat and yearling. (b) ccf for Rappahannock River spat and yearling (detrended).

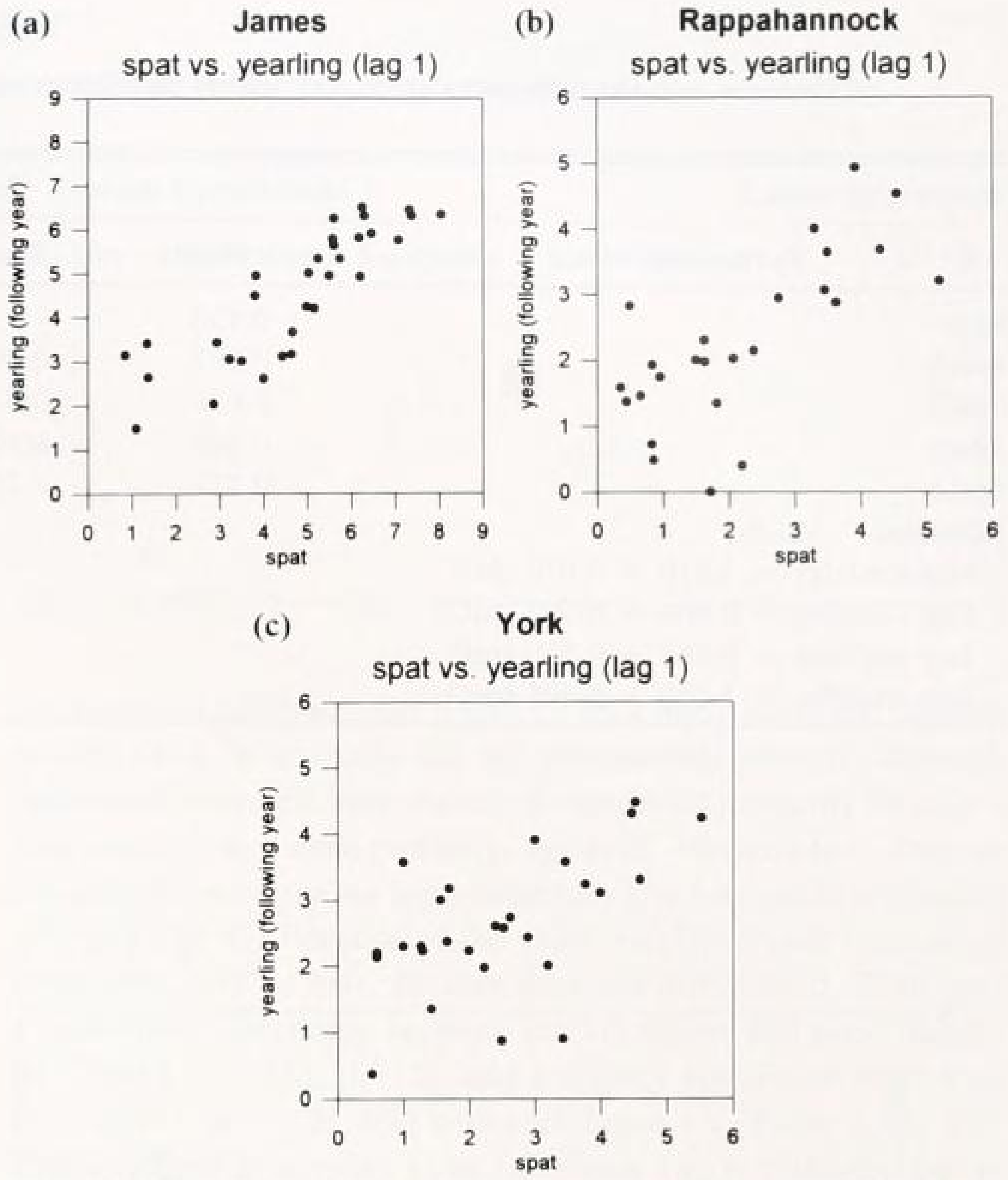


Figure 21. (a) Regression of James River spat versus yearling (lag 1 y). (b) Regression of Rappahannock River spat versus yearling (lag 1 y). (c) Regression for York River spat versus yearling (lag 1 y).

relationship. Unfortunately, the short time period of the CPUE data prevented reliable differencing, or detrending, so analyses were conducted with the trend present in the data. Spat and yearling data were collected by fishery-independent surveys, seed from fishery-dependent commercial harvest data reported to the VMRC by watermen.

Pearson correlations were run between log(seed/day) and the spat value lagged 1 through 4 y as a mean of narrowing the field of observations for subsequent regression analyses. Significant correlations were found at lags of 2 and 3 y (Table 2), and to a

TABLE 1.

Station data files (stations selected for analysis contain 50% of all available information).

Station	Size of File (bytes)	Cumulative (bytes)	River	Station Name
S073	2,772	2,772	James	Horse Head
S175	2,772	5,544	James	Wreck Offshore
S180	2,772	8,316	Rappahannock	Morattico Bar
S181	2,772	11,088	Rappahannock	Drumming Ground
S001	2,583	13,671	York	Aberdeen Rock
S067	2,583	16,254	Rappahannock	Hog House Bar
S190	2,457	18,711	Rappahannock	Smokey Point Deep
S043	2,268	20,979	James	Deepwater Shoals
S179	2,268	23,247	York	Bell Rock
S050	2,142	25,389	Piankatank	Ginney Point
S109	2,142	27,531	York	Pages Rock
S016	2,016	29,547	James	Brown Shoals
S123	2,016	31,563	James	Point of Shoals
S011	1,953	33,516	Rappahannock	Bowlers Rock

TABLE 2.

Pearson correlation coefficients and linear regression of James River spat versus seed/day.

Parameter	Pearson Correlations					Linear Regression	
	Log seed/day	Spat	Spat1	Spat2	Spat3	p	R^a (%)
Spat	−0.130						
Spat1	0.097	0.098					
Spat2	0.676	0.035	0.125				
Spat3	0.681	0.107	0.061	0.097			
Spat4	0.517	0.282	0.104	0.066	0.103		
Equations							
Log seed/day = 2.610 + 0.078 spat1						0.790	0.9
Log seed/day = 0.606 + 0.507 spat2						0.032	45.8
Log seed/day = 0.565 + 0.520 spat3						0.30	46.4
Log seed/day = 1.040 + 0.408 spat4						0.126	26.7

lesser degree at 4 y. Regressions of seed/day and spat lagged 1 to 4 y were also run. The 2- and 3-y lag was found to be significant at the p = 0.05 level (Table 2; Fig. 22).

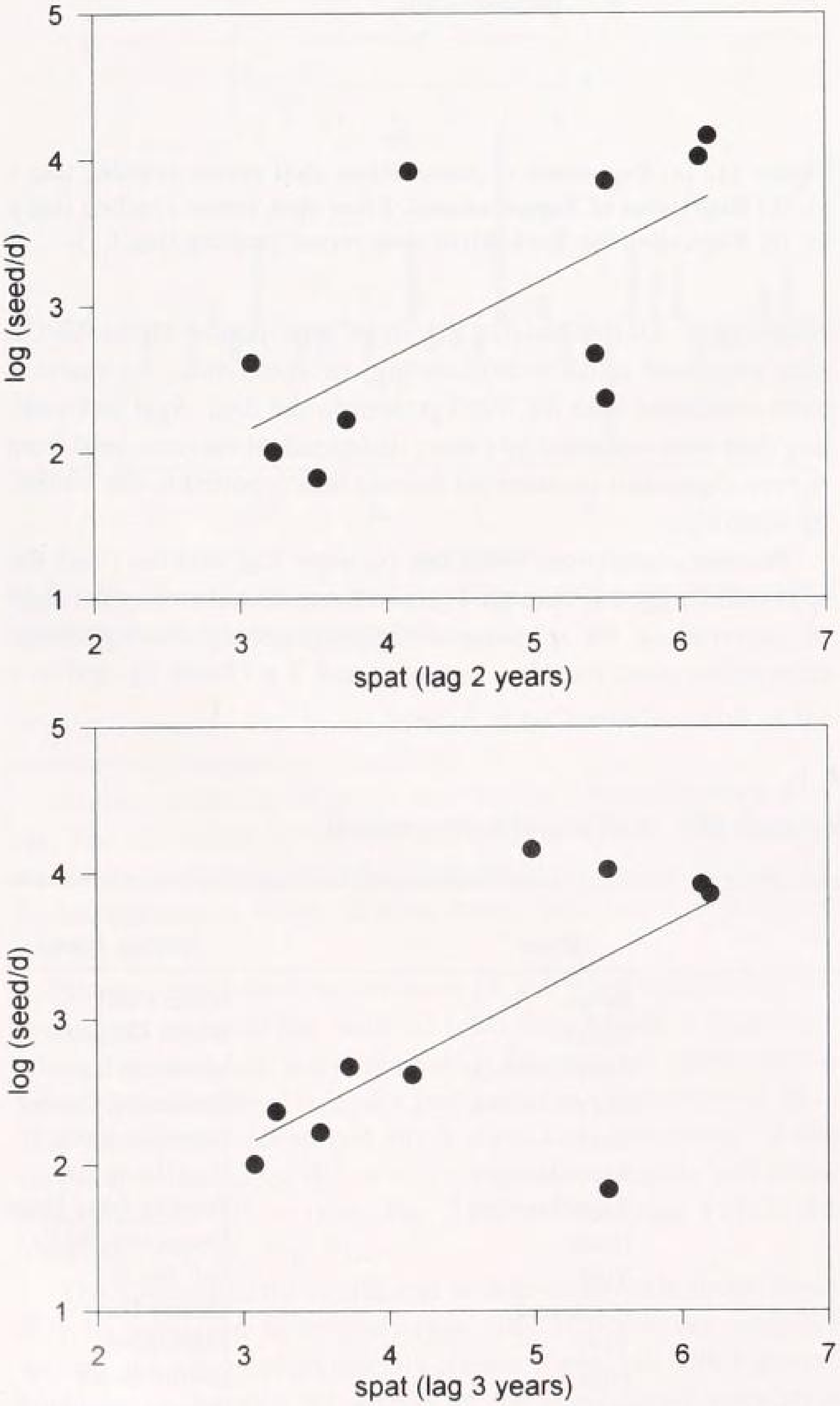


Figure 22. Regression for James River spat (lagged 2 and 3 y) versus James River market oysters.

Spat Versus Market Oysters

The relationship between James River spat and subsequent years' market oyster landings was examined. As with the spat/seed analysis, only James River spat/market was examined because the James River landings are not "contaminated" by oyster repletion and because the spat and market/day are from the same river. The short CPUE data series (market/day) precluded differencing. Pearson correlations were run for spat against market/day 1–4 y later. None were significant (Table 3), although there was a negative correlation between market/day and spat 2 y earlier, which is probably an artifact of the short, nondetrended market data.

Krantz and Merritt (1977) found their best correlation between spat and commercial harvest at a lag of 6–8 y and cited this as further evidence to ". . . sustain the theory that a period of successive years of low spat set will require between six to eight years before the period of poor recruitment is reflected in the commercial harvest." Ulanowicz et al. (1982), using a multivariate analyses, found a correlation between spat and seed at a lag of 4 y, and using cross-correlation analyses, found a peak in the correlation between spat and commercial harvest at a 9-y lag. This period, they speculated, could be due to a ". . . possible natural oyster cycle . . ." or an ". . . unexplained environmental variable."

These 4-, 6-, 8-, and 9-y lags found by Krantz and Merritt and Ulanowicz et al. may be artifacts of the cross-correlation because ". . . interpretation of the sample cross-correlation function can be fraught with danger unless one uses the prefiltering procedure . . ." (Chatfield 1989). Neither study detrended the raw

TABLE 3.

Pearson correlation coefficients for James River market oysters/day versus spat lagged 1–4 y.

Lag Year	*r*
Spat1	−0.283
Spat2	−0.696
Spat3	−0.490
Spat4	−0.125

TABLE 4.

Pearson correlation coefficients and linear regression coefficients and equations for James River seed/day versus market/day.

Parameter	Pearson Correlations					Linear Regression	
	Log market/day	Seed1/day	Seed2/day	Seed3/day	Seed4/day	p	R^2 (%)
Seed1/day	−0.063						
Seed2/day	0.160	0.732					
Seed3/day	0.513	0.387		0.802			
Seed4/day	0.716	0.028		0.554	0.820		
Equations							
Log market/day = 1.53 + 0.238 log seed3/day						0.194	26.3%
Log market/day = 1.17 + 0.355 log seed4/day						0.071	51.2%

data, so it is quite possible that the 4- to 9-y lags that they found are artifacts of this lack of differencing.

Their multivariate analysis revealed that spat densities and seed planting accounted for 56% of the variation in commercial harvest. The removal of significant volumes of seed from the James River, and their transplantation to the Rappahannock and Potomac Rivers, has no doubt affected the statistical results of our spat versus seed and market analysis.

James River Seed Versus Market Oyster

The James River abundance of seed was analyzed relative to James River market oyster CPUE. Normally, one would expect that the market oyster catch is composed of several year classes or cohorts. This is true for the James (Mann, unpublished data); however, with the current level of fishing pressure, depleted stocks, small minimum size limit (3″, 76.2 mm), and slow variable growth rates, it is likely that the commercial harvest, although composed of several year classes, is supported primarily by only a year class or two, most probably, age four. Nevertheless, Pearson correlations were run on log(market/day) by log(seed/day) lagged 1–4 y (Table 4). Because of the short overlap period with effort (boat days, 1983–1994), the data were not differenced. There was a significant correlation between market oyster and seed, lagged by 3 and 4 y (0.513, 0.716), and a slightly significant regression ($p = 0.071$, $R^2 = 51.2\%$) with seek laged 4 y (Table 3; Fig 23). This relationship appears to be fortuitous and is probably due to the strong downward trend in seed after 1985 and the pulse of market landings in the later 1980s, also followed by a dramatic decline.

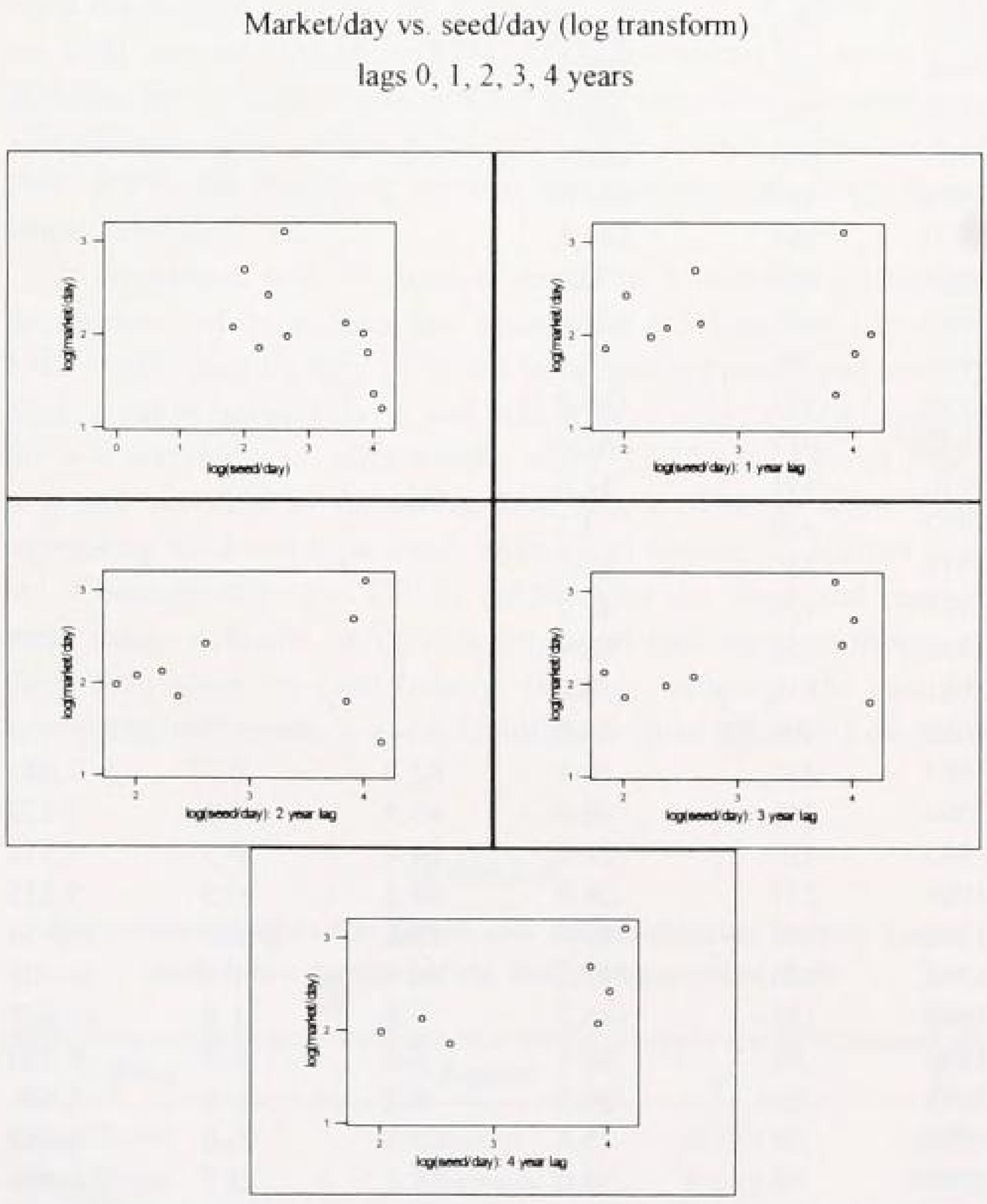


Figure 23. Regression for James River market/day versus lagged seed/day.

Predictions With Spat

Because spat (age "zero-plus") show a statistical relationship to seed (age two and three), intuitively, one might expect that there would be a relation between seed (2–3 y) and market oyster (age three and four) a year later. However, there is no significant relation between spat and any market size, and the seed-to-market relationship is between the age two and three seed and age six to seven market oyster.

It is our conclusion that spat abundance can be used to predict the abundance of subsequent yearling oyster abundance and can form the basis for a method of predicting abundance of seed

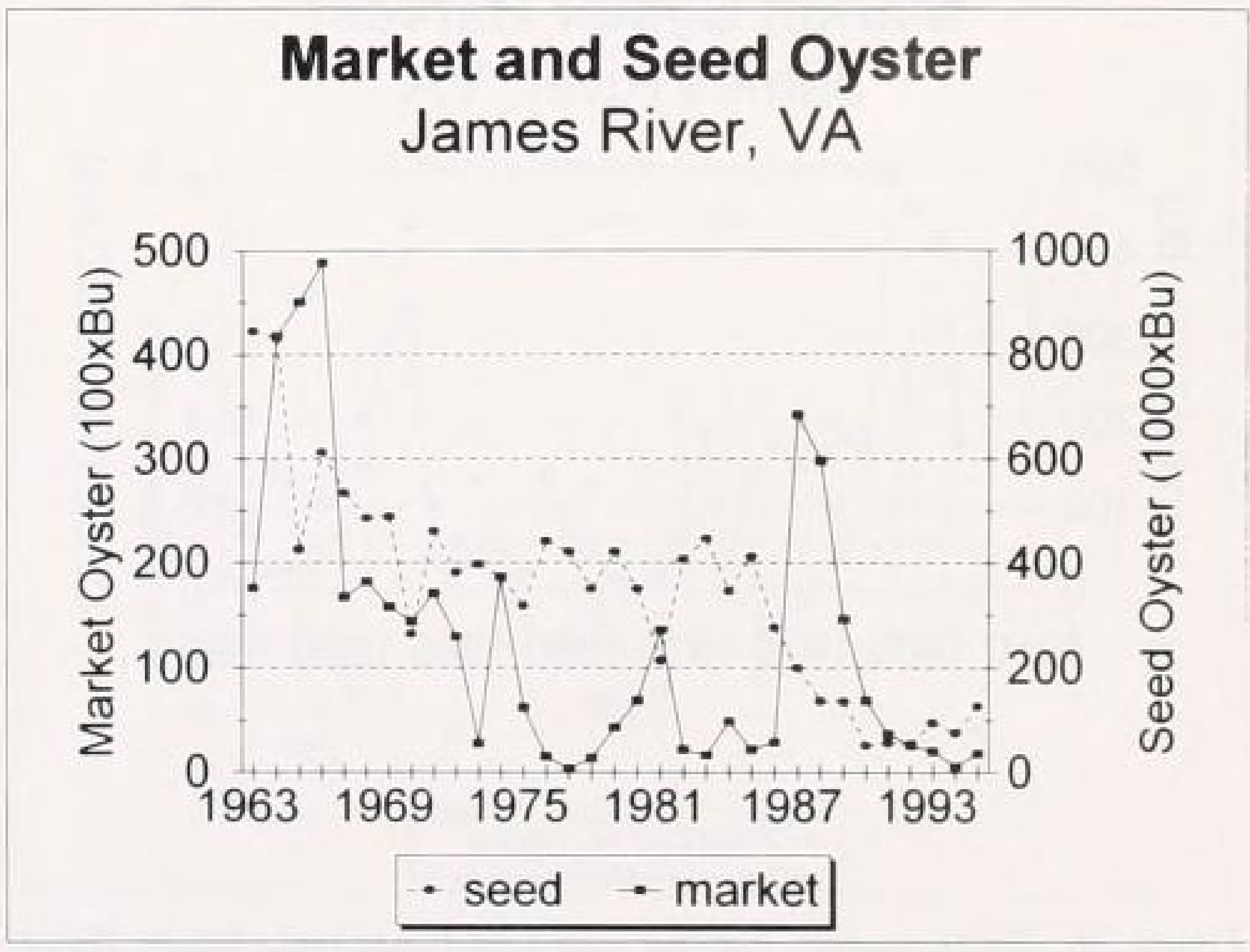


Figure 24. Total market and seed oyster harvest, James River, VA.

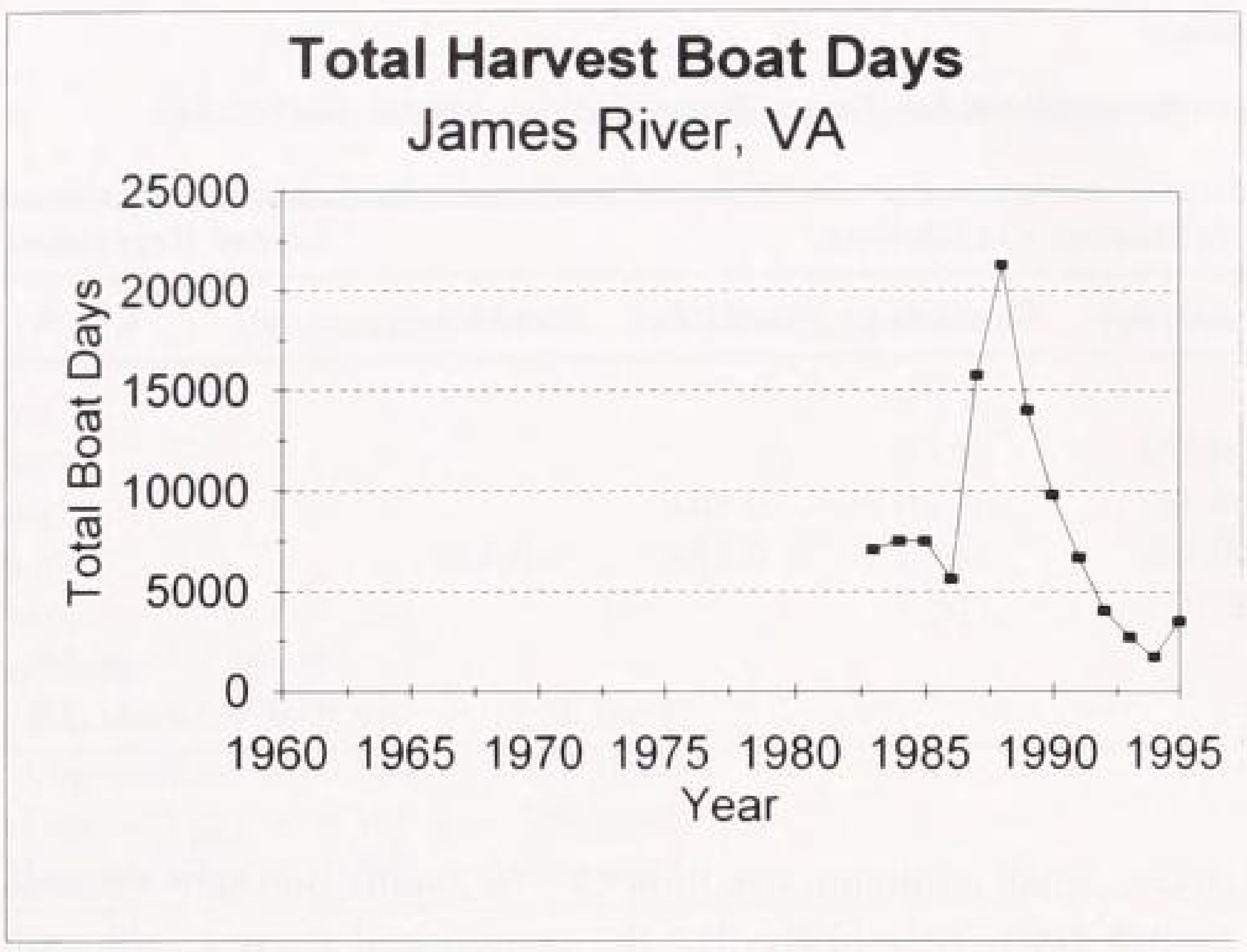


Figure 25. Number of boat days, James River, VA.

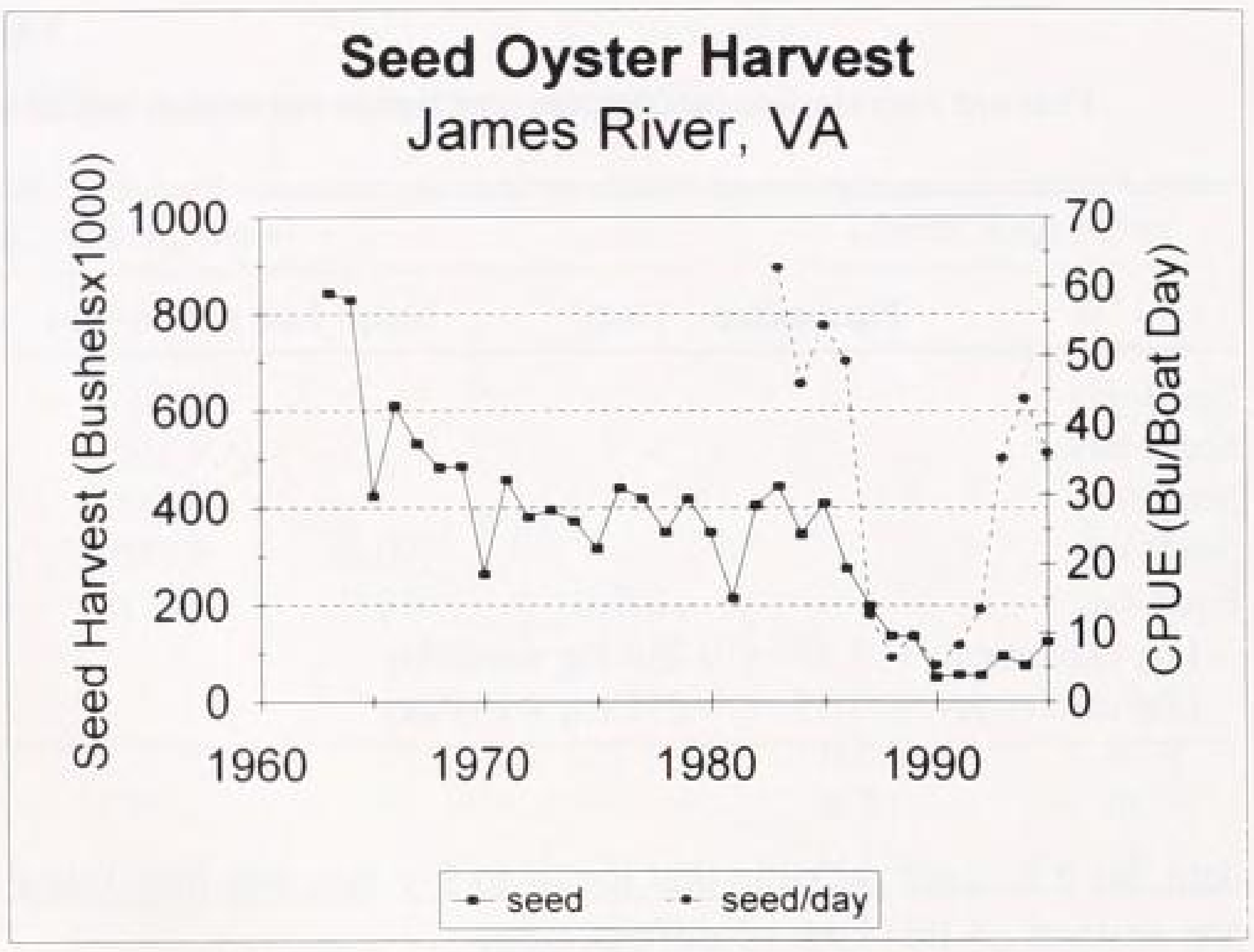


Figure 27. Seed oyster harvest and CPUE, James River, VA.

(CPUE) 2–3 y later. It does not appear, at this time, that spat can be used to predict future market oyster harvest. It may be that when the catch/day data set is longer, it will be possible to make a correlation after detrending. Further, although there is an apparent relation between seed CPUE and the market CPUE 4 y later, we feel that this may be due more to the overall trend of the data rather than to biologic cause and effect. Further, the multiple cohorts in the market catch and problems with CPUE data for seed and market oyster make this examination questionable. We will discuss the additional problems with seed and market data as to how they relate to CPUE when calculated with boat days. With this in mind, any examination of seed or market landings must be made with caution.

James River Seed and Market Harvest

The VMRC has maintained monthly harvest statistics since 1963 for seed, and market (currently, 3″, 76.2 mm) oyster, and since 1983 the number of boat days fished in the James. Figure 24 (Table 4) depicts the annual harvest of seed and market oyster in the James River since 1963. Figure 25 shows a dramatic increase in boat days (effort) in the James through, and peaking in, 1988 and an equally dramatic decline thereafter. This variation is due to the scarcity of oyster bay-wide, except in the James, a subsequent migration of the watermen from the less productive waters of the

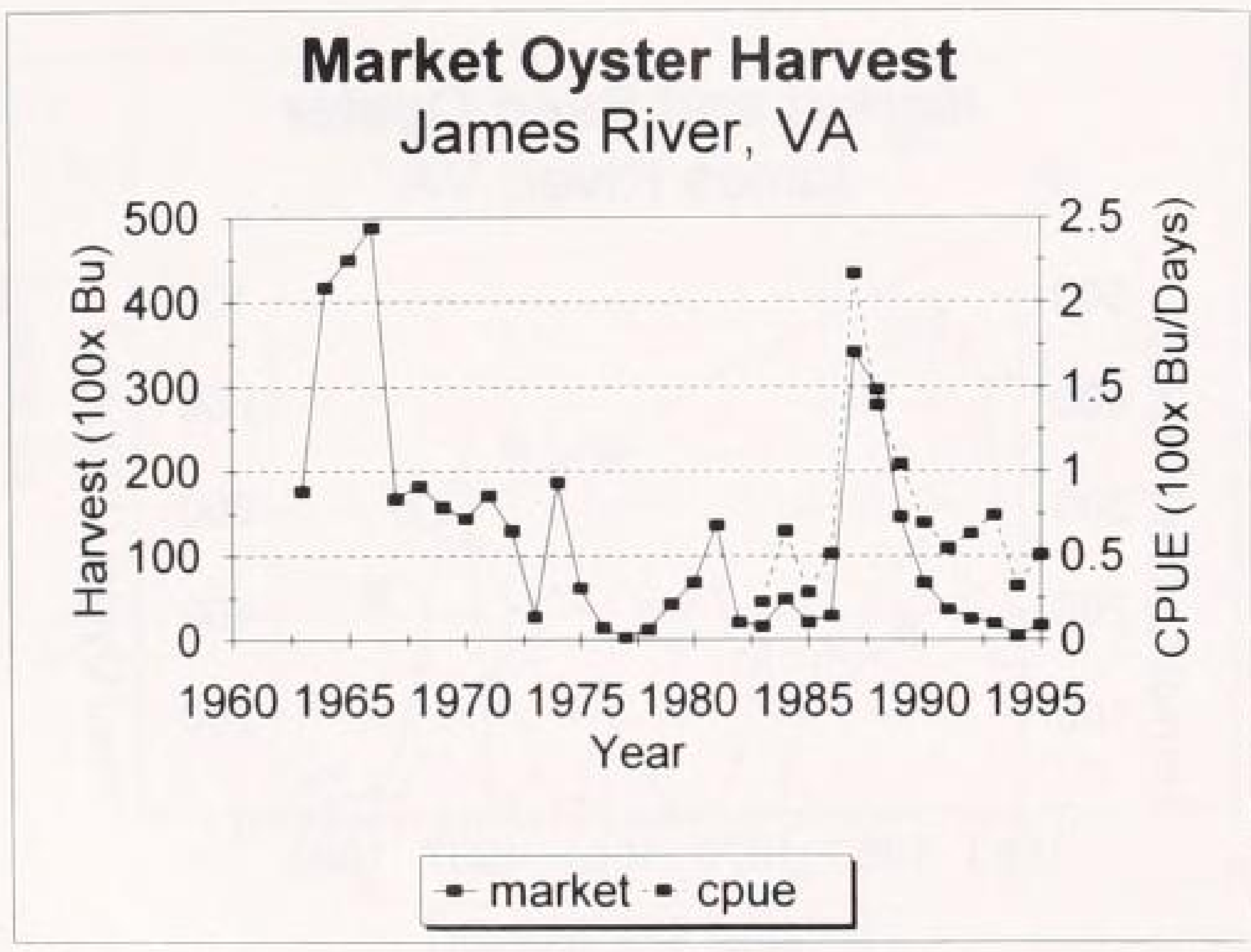


Figure 26. Total market harvest and CPUE harvest, James River, VA.

TABLE 5.

James River seed and market oyster harvest 1963–1995 (all data from VMRC).

Year	Seed (×1,000 Bu)	Market (×100 Bu)	Seed/Day	Market/Day	Boat Days
1963	844	175.7			
1964	830	417.4			
1965	424	450.0			
1966	611	487.9			
1967	533	167.0			
1968	484	182.0			
1969	487	157.7			
1970	264	143.8			
1971	459	170.8			
1972	381	129.7			
1973	396	27.4			
1974	373	186.3			
1975	317	61.6			
1976	441	14.6			
1977	420	3.3			
1978	350	13.2			
1979	420	42.7			
1980	350	68.4			
1981	214	136.0			
1982	406	21.5			
1983	445	16.1	62.8	0.2	7,087
1984	346	48.8	45.9	0.6	7,533
1985	410	21.5	54.4	0.3	7,537
1986	277	28.8	49.2	0.5	5,625
1987	199	341.4	12.6	2.2	15,754
1988	136	297.2	6.4	1.4	21,305
1989	135	146.2	9.6	1.0	14,027
1990	51	68.2	5.2	0.7	9,810
1991	55	36.5	8.2	0.5	6,698
1992	54	25.6	13.4	0.6	4,032
1993	95	20.0	35.2	0.7	2,698
1994	75	5.5	43.7	0.3	1,715
1995	126	17.7	36.0	0.5	3,500

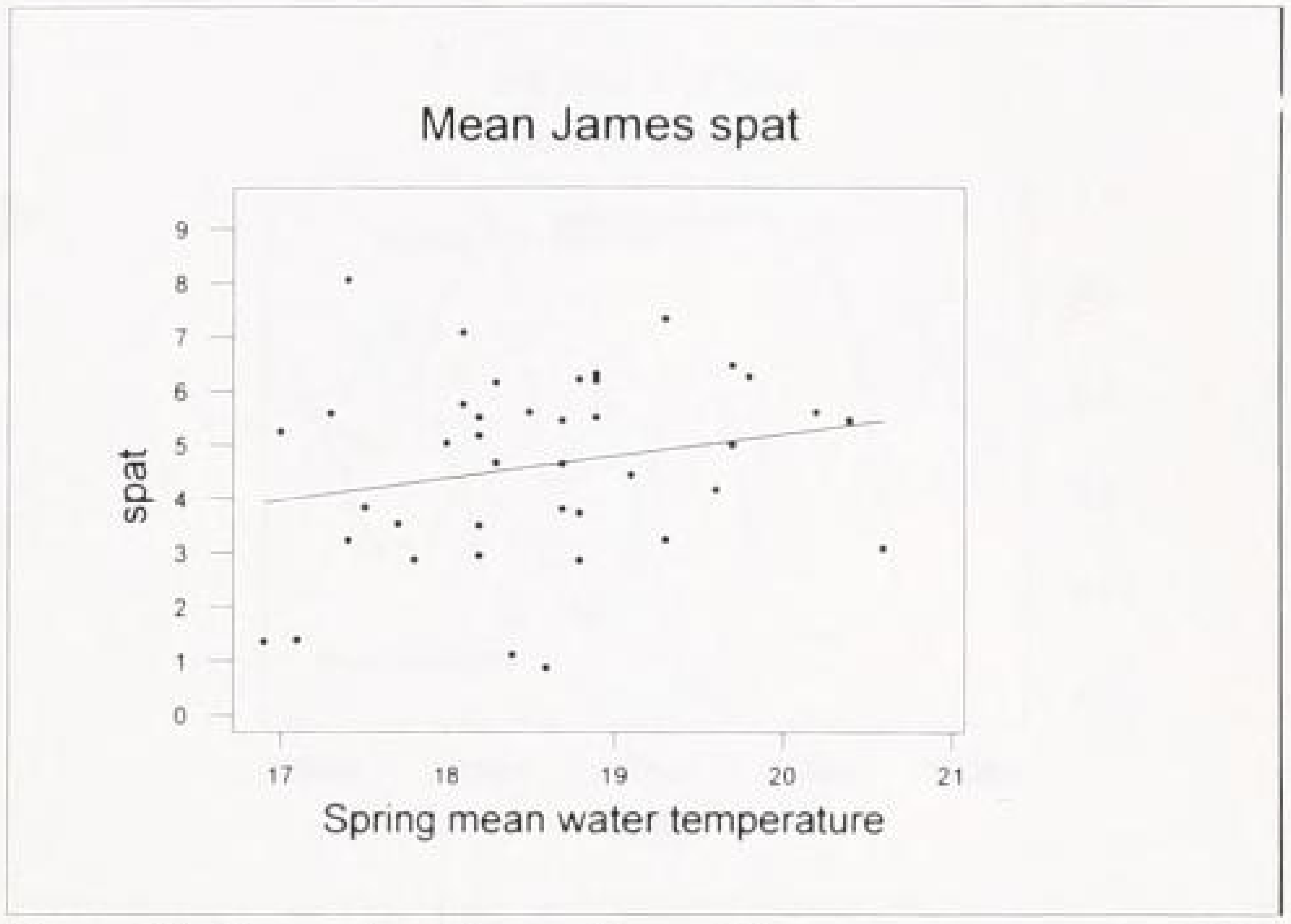


Figure 28. Regression of mean James River spat versus spring VIMS pier temperatures.

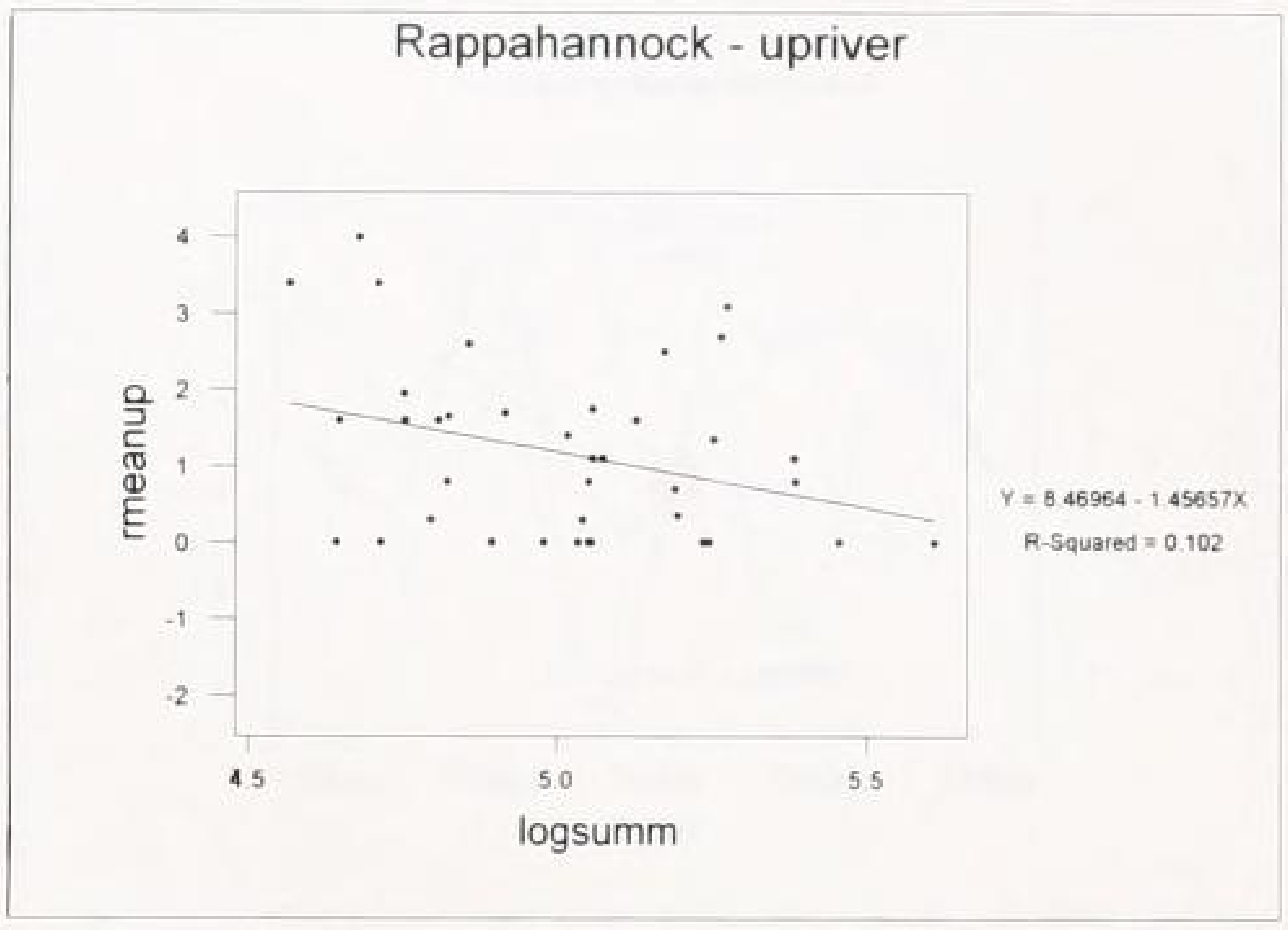


Figure 29. Regression of upper Rappahannock River spatfall versus summer river flow.

Rappahannock and Potomac Rivers into the James for both seed and market oysters, and a decline in effort as catch dropped off. Figure 26 depicts the market oyster and CPUE since 1983, with data derived from the market oyster harvest and both days (Bushels Market oyster/boat days). Reduced oyster stocks and active management by the marine Resources Commission combined to result in a post-1990 reduction in effort.

Both harvest of market oyster and CPUE of market oyster parallel boat days. This is because watermen would rather focus their efforts toward harvesting $30/Bu of market oyster, than $4/Bu of seed. After 1990, however, as stocks of market oyster became seriously depleted, significant effort was redirected toward the harvest of seed, the remaining resource. A quota system for seed was introduced in 1993–1994, permitting the harvest of 80 kBu, but the limit was increased at the watermen's insistence to 120 kBu in 1994–1995. Although CPUE for seed increased in 1993–1995, the total seed harvest has remained relatively stable since 1990 (Fig. 27).

A significant note of caution should be introduced. Although the number of boat days has been recorded monthly since the 1982–1983 season, they were not separated between seed harvest days, market harvest days, and which days were a split between the two activities. In other words, of the 5,625 boat days in 1986, it is not possible to determine how many of these were spent harvesting seed and how many were spent harvesting market oyster. Consequently, the CPUE calculations for seed and market were made with the unlikely assumption that equal numbers of days were spent on each fishery. In short, although the calculations have been made, we would not place great reliability on them because the data are so "spongy." This results in the Fisheries Management Axiom: Are "spongy" better than none?

Other factors may influence the results here in a way that cannot be estimated. The first is that the James River is the source of seed for the Virginia repletion program that transports seed oyster from the James to nonproducing areas of the Virginia tributaries. This movement of seed may result in changes in abundance both in the James (Downward) and the other rivers (upward) that are not reflected in our count data. The second factor is the spread of disease, which has been responsible for much of the mid- and late-1980s decline in market oyster (Bureson and Ragone Calvo 1996). After reaching 19–45 mm, when 2–3 y of age, the seed oyster in the lower, more saline regions of the James River become susceptible to the diseases MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*). Burreson and Ragone Calvo (1996) have found this to be particularly severe on Wreck Shoal in the James River, where mortality has been 100% for several years. The removal of seed and market oyster from the stock by either disease or repletion will obviously affect our results, but we are unable to estimate to what degree this has occurred. It is our conclusion that the seed and market CPUE data, as currently collected, cannot be used to examine the effect of seed abundance on subsequent market landings.

TABLE 6.

Regression analysis for James and Rappahannock upriver spat abundance versus spring and summer river flow.

River	Season	p	R^2
James River	Spring	0.089	0.034
James River	Summer	0.018	0.074
Rappahannock River	Spring	0.102	0.052
Rappahannock River	Summer	0.023	0.102

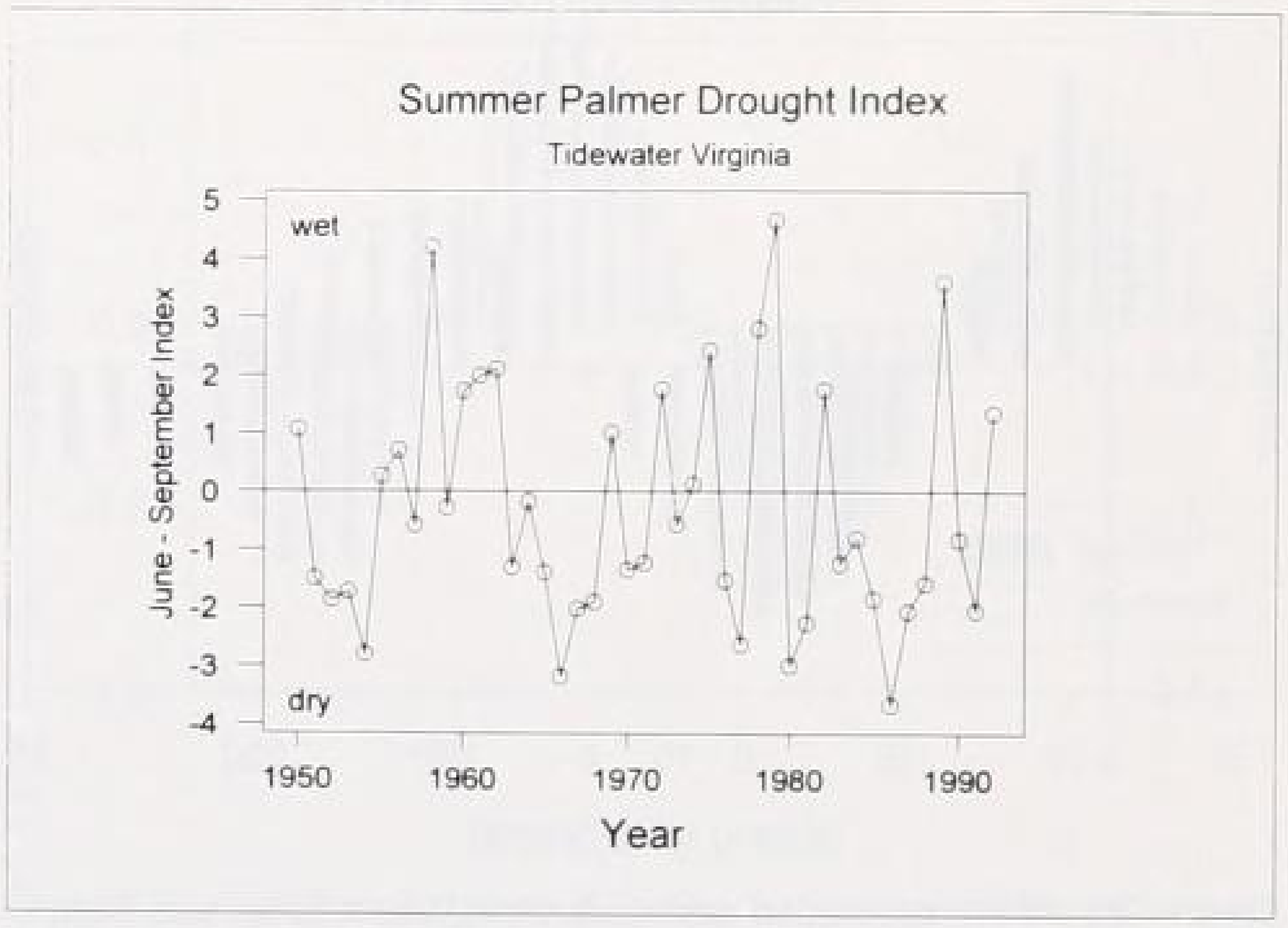


Figure 30. Summer PDI, Tidewater, VA.

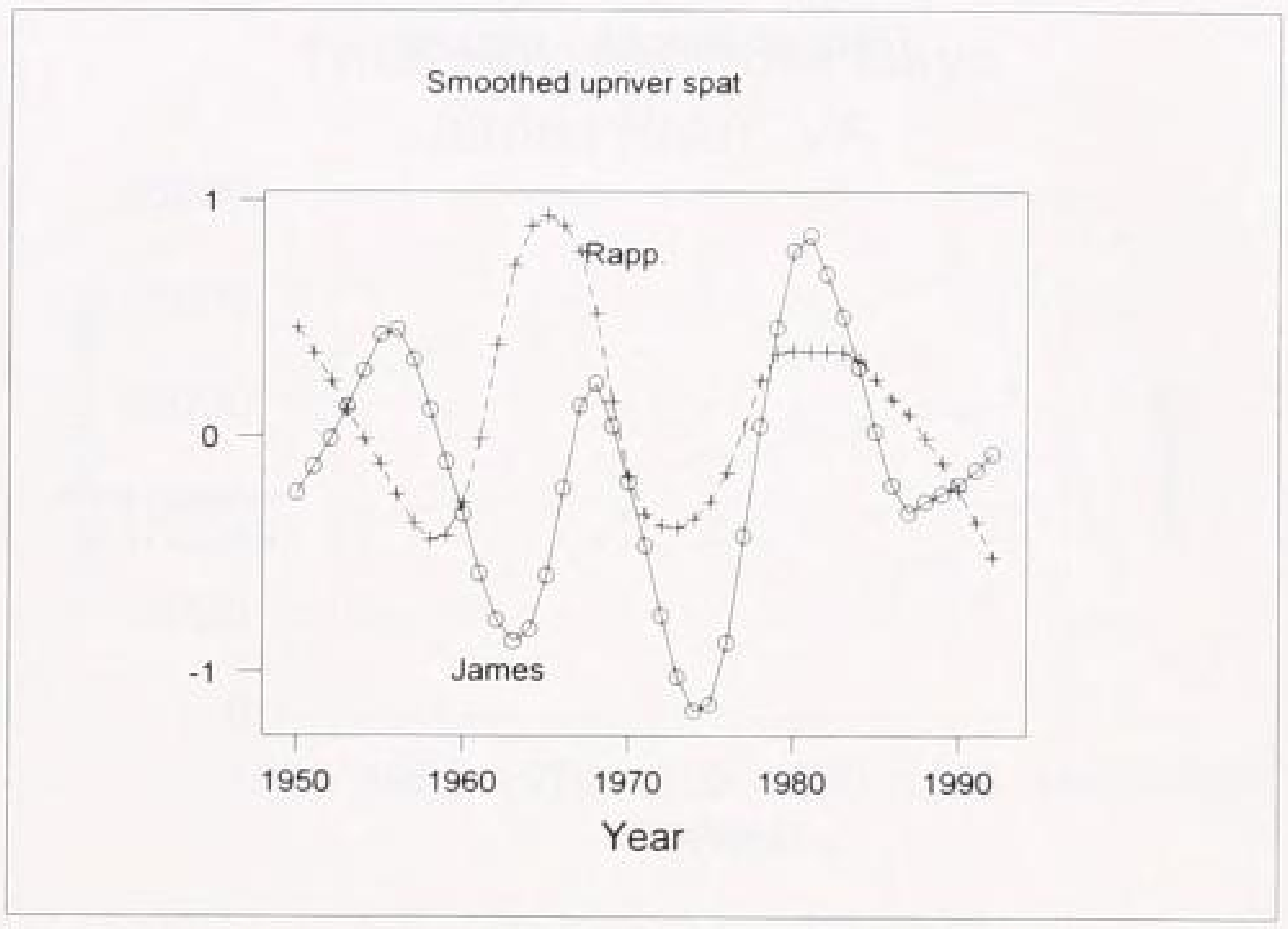


Figure 31. Detrended, smoothed upriver spatfall for James and Rappahannock (Rapp.) Rivers.

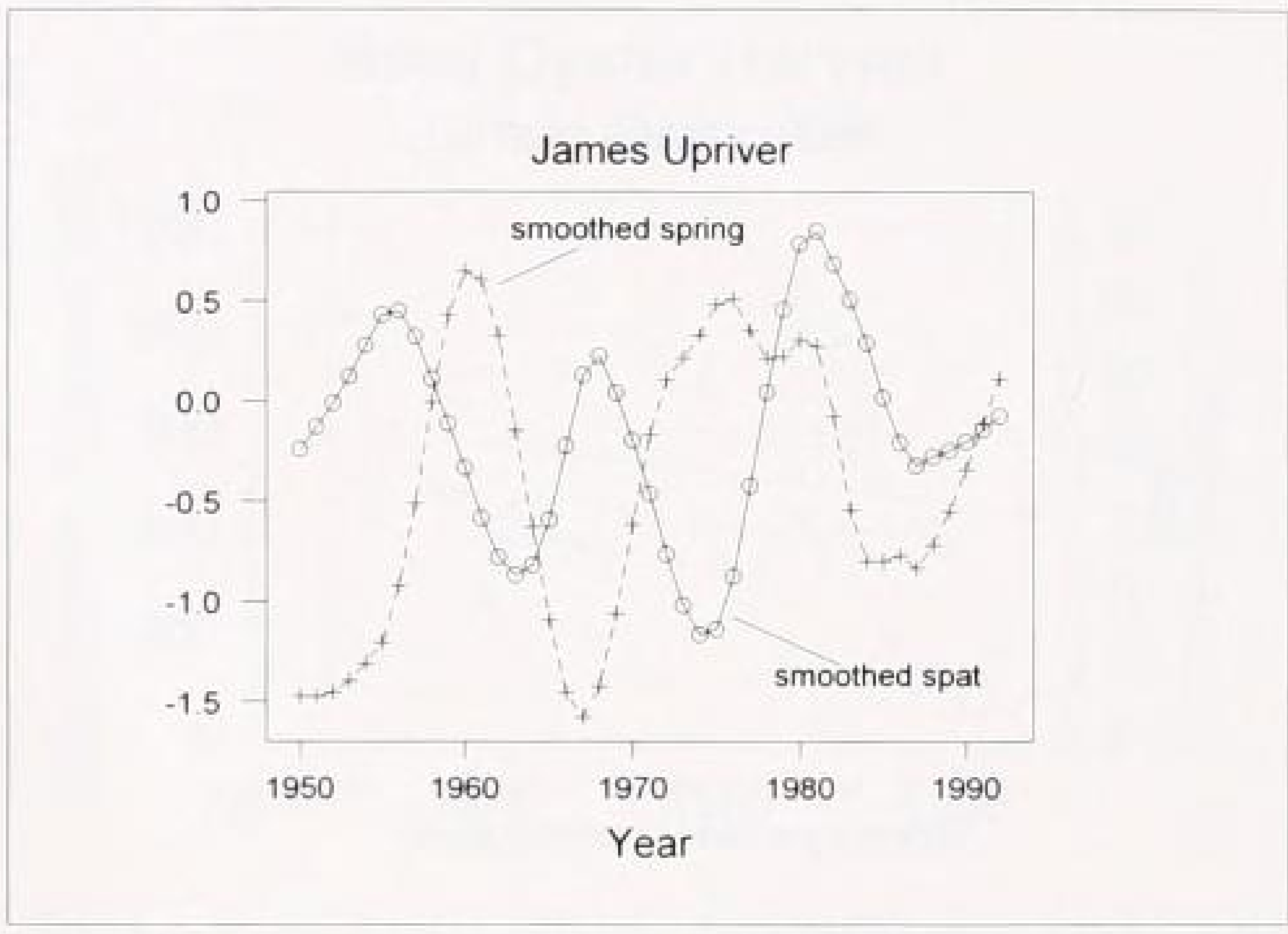


Figure 33. Detrended, smoothed upriver James spatfall and detrended, smoothed spring PDI.

Relation of Spat to Its Physical Environment

Most marine organisms, particularly those attached to the bottom, are susceptible to fluctuations in the physical environment. Numerous articles addressing these oyster-environment relationships have been published (Ulanowicz et al. 1980, Haven 1982, Chai 1988, Austin et al. 1993). Generally, they have pointed to temperature and salinity (or its proxy, river discharge) as the controlling physical variables.

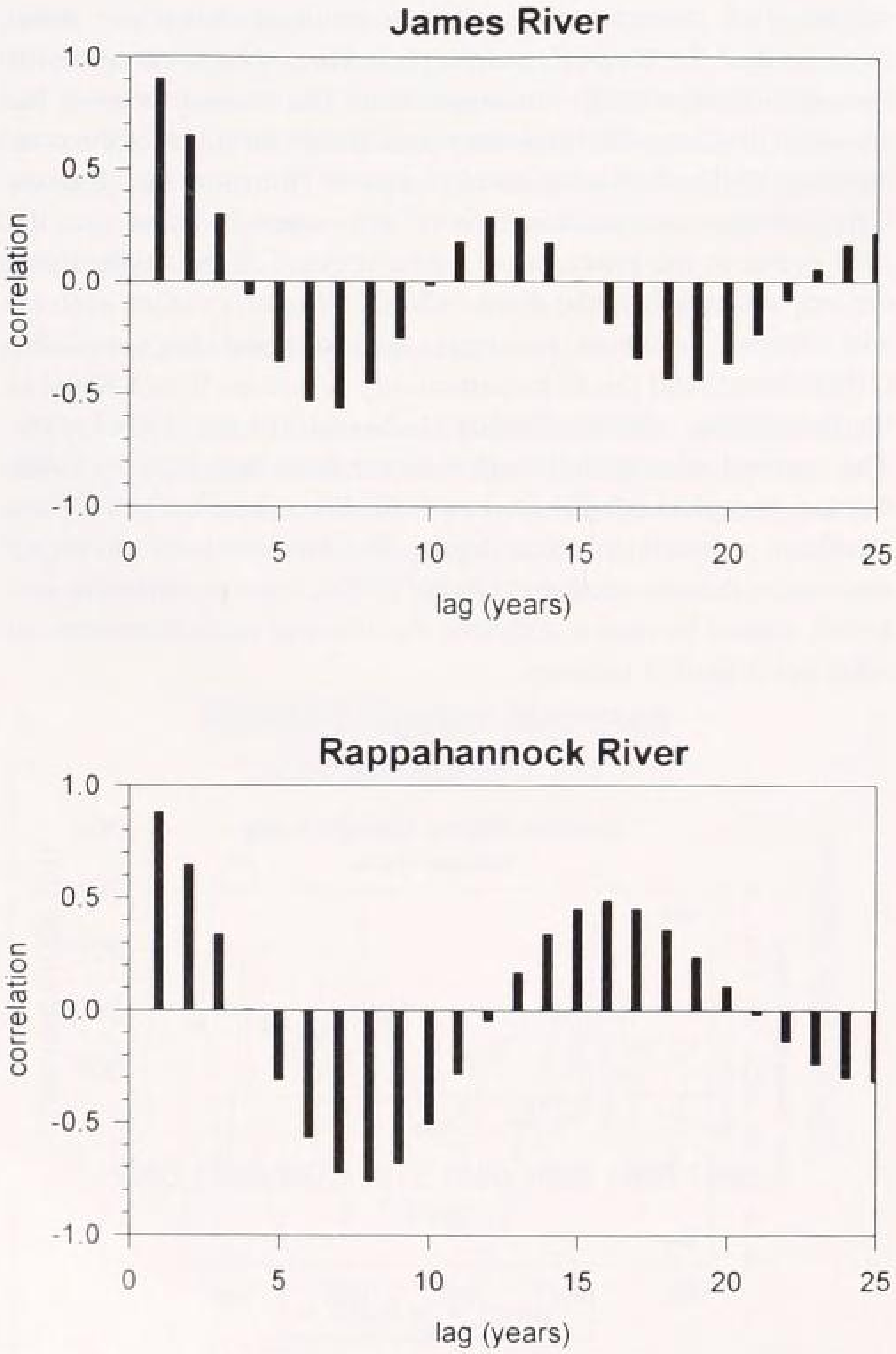


Figure 32. cff for detrended and smoothed James River and Rappahannock River spatfall.

Temperature Effects on Spat

The water temperature data measured at the VIMS pier at the mouth of the York River constitutes an almost continuous data set since 1952 and was used as surrogate data for all of the rivers. The effects were examined of mean spring temperature (May through July) and mean summer temperature (July through September) on the mean spat from the James and from the Rappahannock Rivers. In no case did the value of R^2 exceed 2.1%, and none of the regressions were significant (Table 5). As an illustration of the lack of relationship, the data and regression line for the "most significant" ($p = 0.18$) regression between James River spat and spring temperature are shown in Figure 28. The conclusion is that the water temperature during the spring and summer preceding the spat measurement has minimal effect on the spatfall.

River Discharge Effects on Spat

River discharge is monitored by the U.S. Geological Survey and the NOAA Office of Hydrology. We used data from the monitoring stations located on the fall line of the Rappahannock and

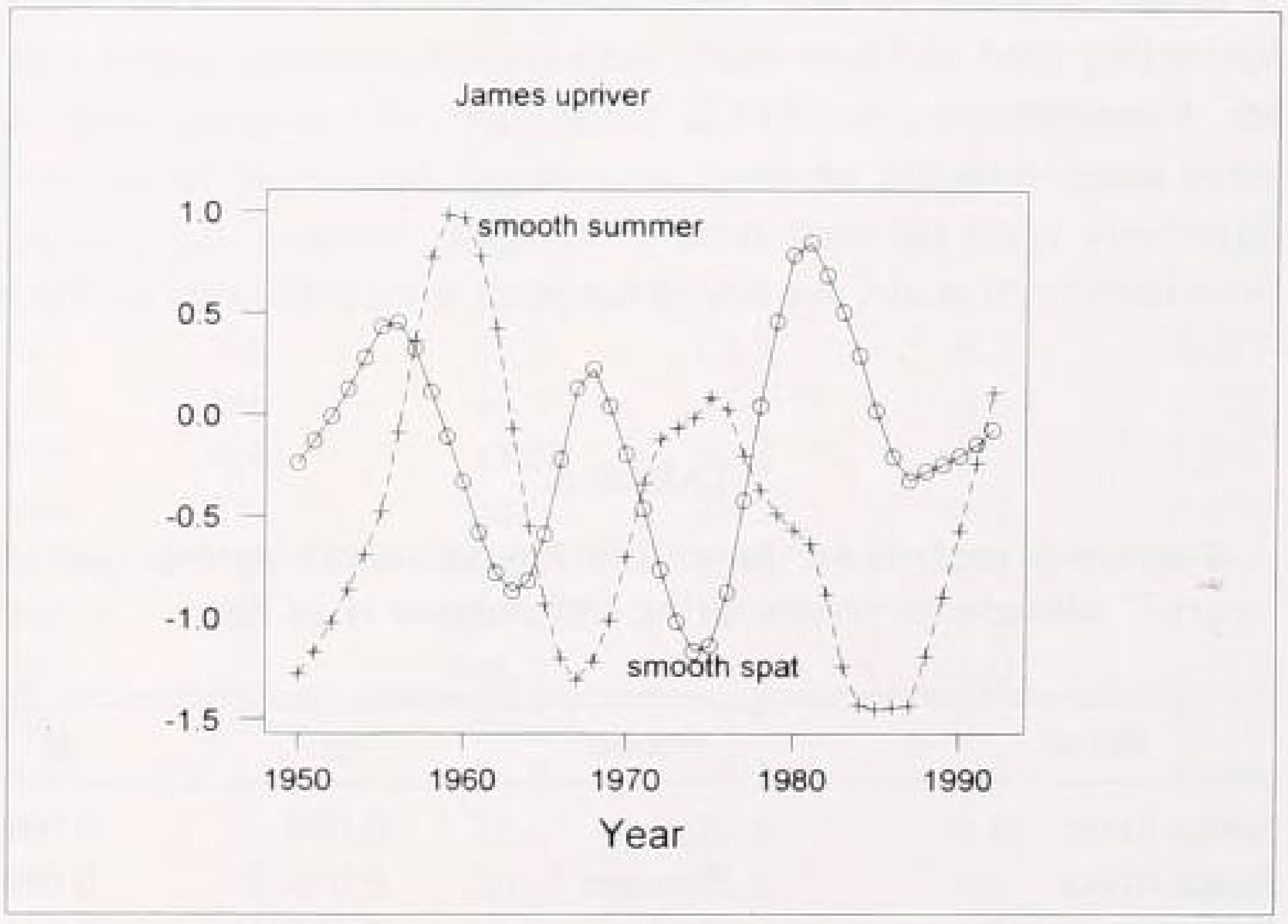


Figure 34. Detrended, smoothed upriver James spatfall and detrended, smoothed summer PDI.

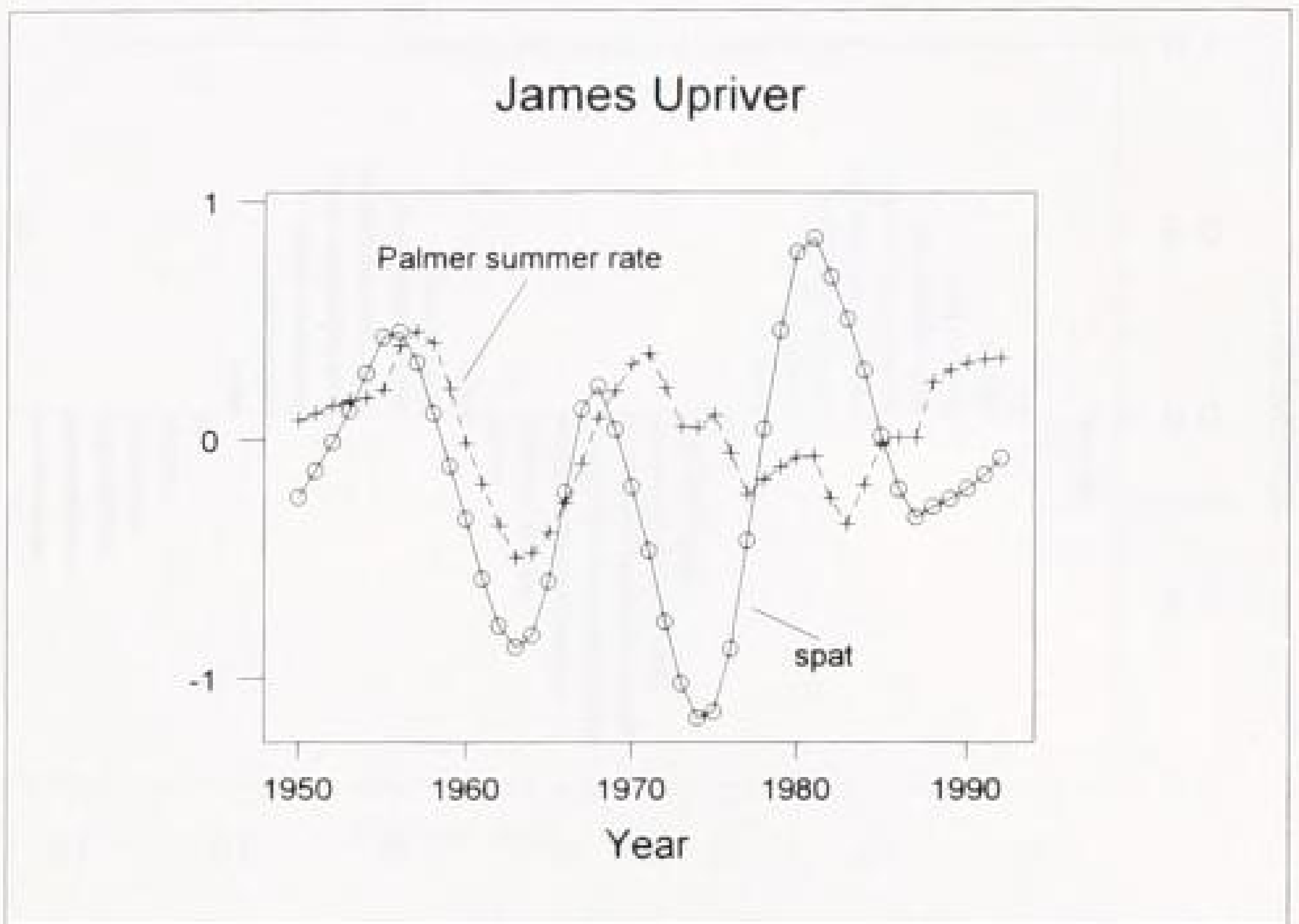


Figure 35. Detrended, smoothed upriver James spatfall and detrended, smoothed summer period of maximum rate of change in PDI.

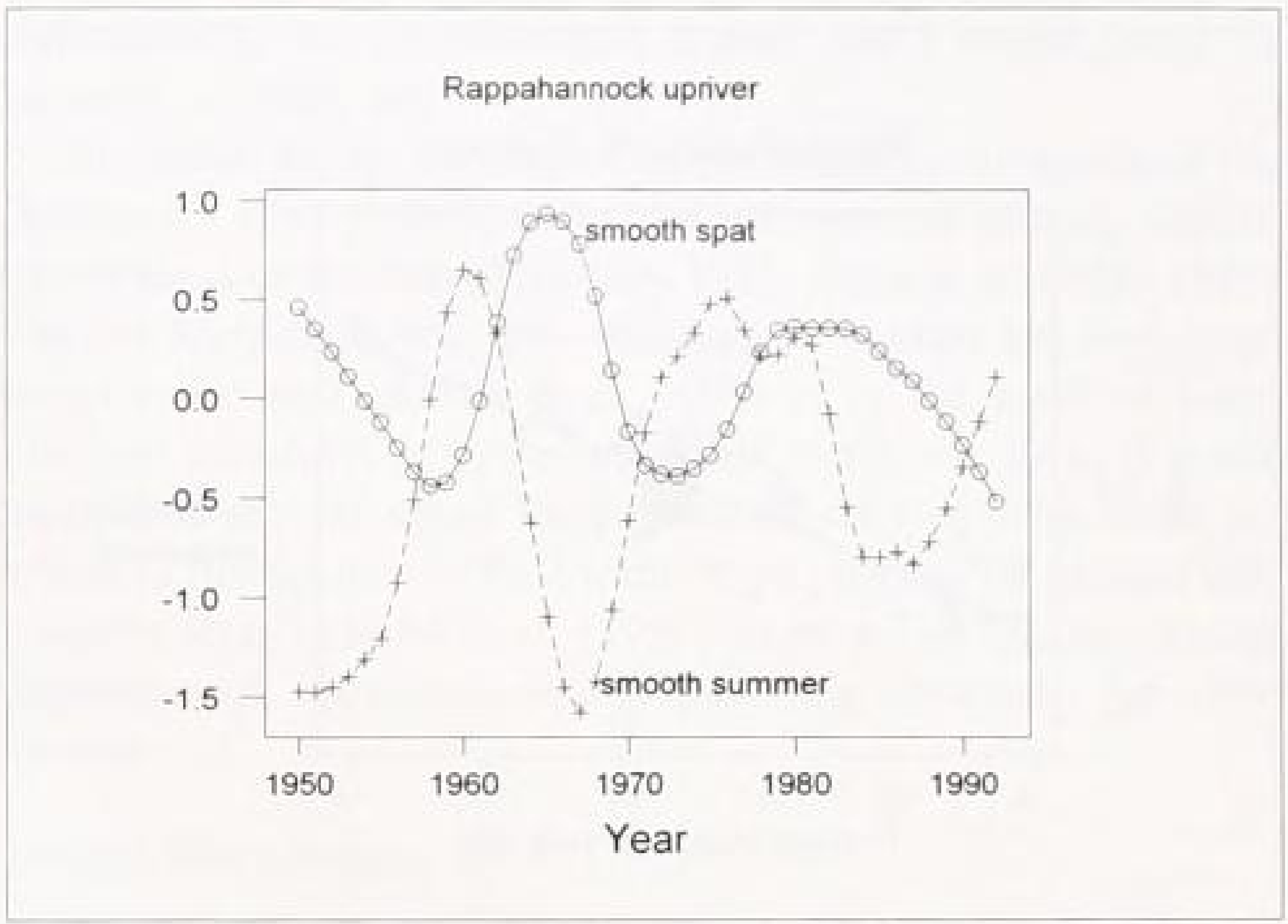


Figure 37. Detrended, smoothed upriver Rappahannock spatfall and detrended, smoothed summer PDI.

James Rivers and selected "upriver" stations by using agglomerative cluster analysis characterizations of the oyster reefs. It was expected that stations furthest up stream would be those most likely to reflect fluctuations in stream flow (Haven 1982). These included the Group I James River reefs (Deepwater Shoals, Horse head, and Point of Shoals) and both Morattico and Bowlers Reefs in the Rappahannock River.

We looked at both spring (May to July) and summer (June to September) mean discharge patterns for the James and Rappahannock Rivers and regressed them (log flow) against the mean spatfall abundance for the two upriver populations. It is obvious from the results in Table 6 that with the exception of the Rappahannock summer flow (Fig. 29), spring/summer river discharges alone did not produce a significant variation in spatfall patterns.

Andrews et al. (1959) noted that the significant 1957 spat set was largely wiped out during the 1958 winter-spring freshets. Although the fall survey count showed a large set in 1957, mortality was high during the following May to June period, when the previously overwintering dormant spat became active in the low-salinity James. They also reported that although this occurred in the James, they did not notice a similar effect in the Rappahannock. Haven (1982) reported that the prolonged periods of low salinity during the fall, winter, and spring of 1979–1980 produced extensive mortalities of the 1979 set in the James River. Yearling were affected to a lesser degree, and market size oyster exhibited the lowest mortality. This is reflected by a lower fall count of yearling oyster in the James River in 1980 (Fig. 4b).

PDI Relation to Spat Abundance

Neither temperature nor river discharge (proxy, salinity) data gave significant relationships with spat abundance, in spite of historic reports and an intuitive assumption that they should. In search of an alternative environmental variable, we considered the PDI, a combination of air temperature, precipitation, and soil type as a possible integrated environmental signature. The index is in standard usage by climatologists and is published monthly by the Office of the Virginia State Climatologist at the University of Virginia. Precipitation data alone do not always reflect river discharge and, consequently, salinity, because it is often the rate of the precipitation that influences the amount of runoff that ultimately results in river discharge. Rain soaks in, while rain showers often exceed the soil's absorption capacity and result in runoff to the creeks and rivers. The PDI is computed for four areas of the state, depending on the temperature, precipitation, and soil type regimens. We considered that the Tidewater index was appropriate for this study.

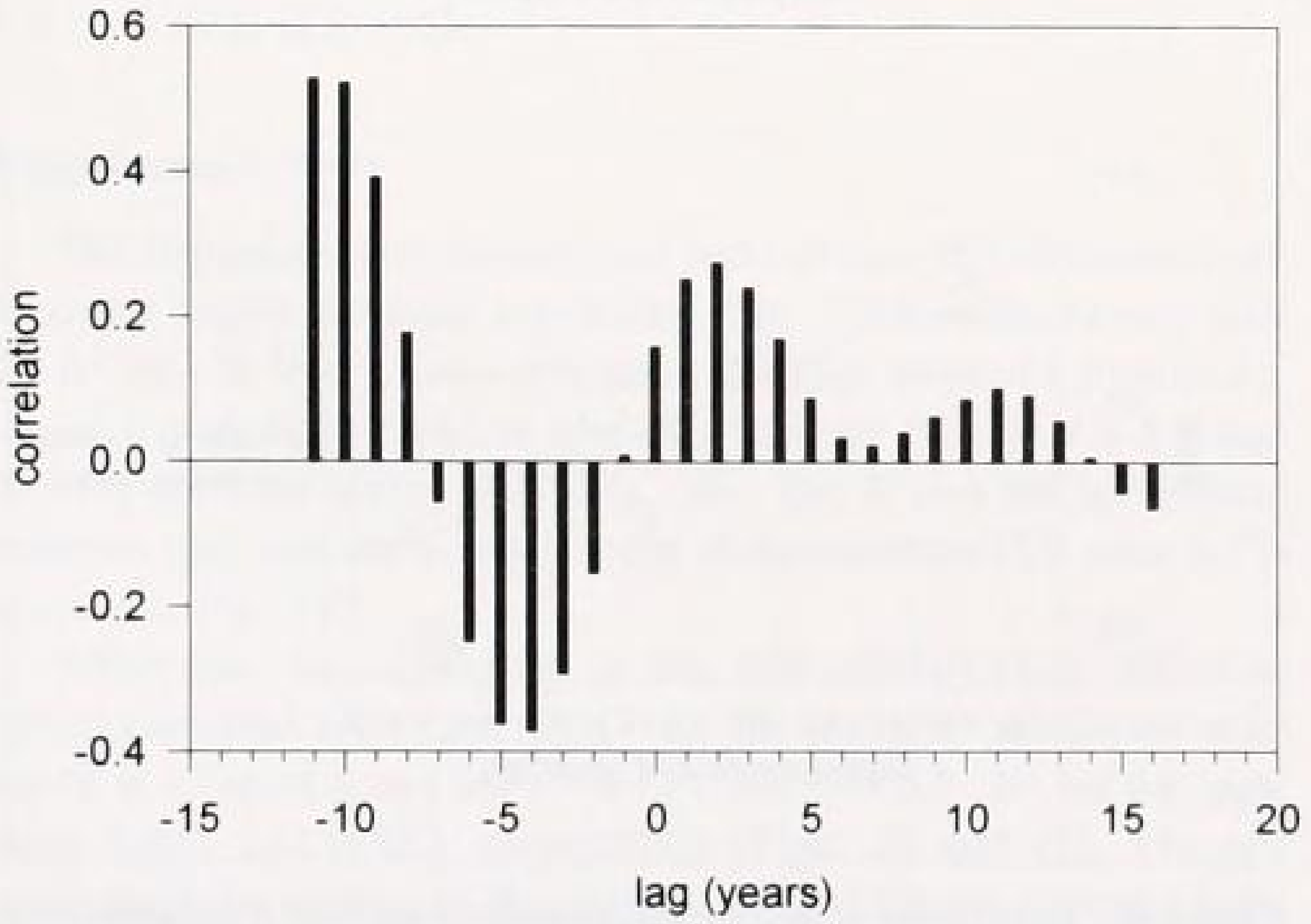


Figure 36. Cross-correlation of James River spat and smoothed summer period of maximum rate of change in PDI.

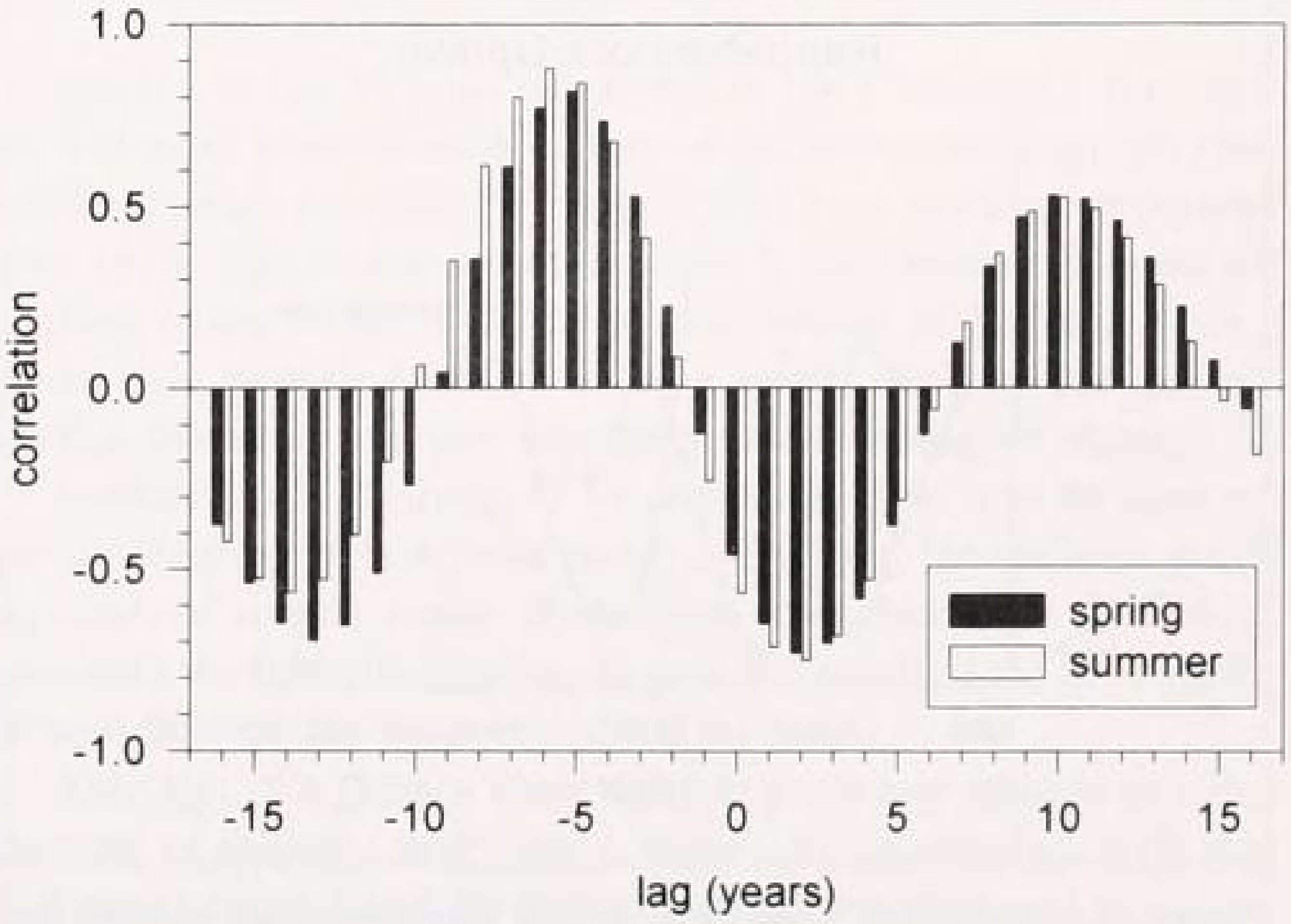


Figure 38. Cross-correlation of spring and summer Rappahannock River spat and PDI.

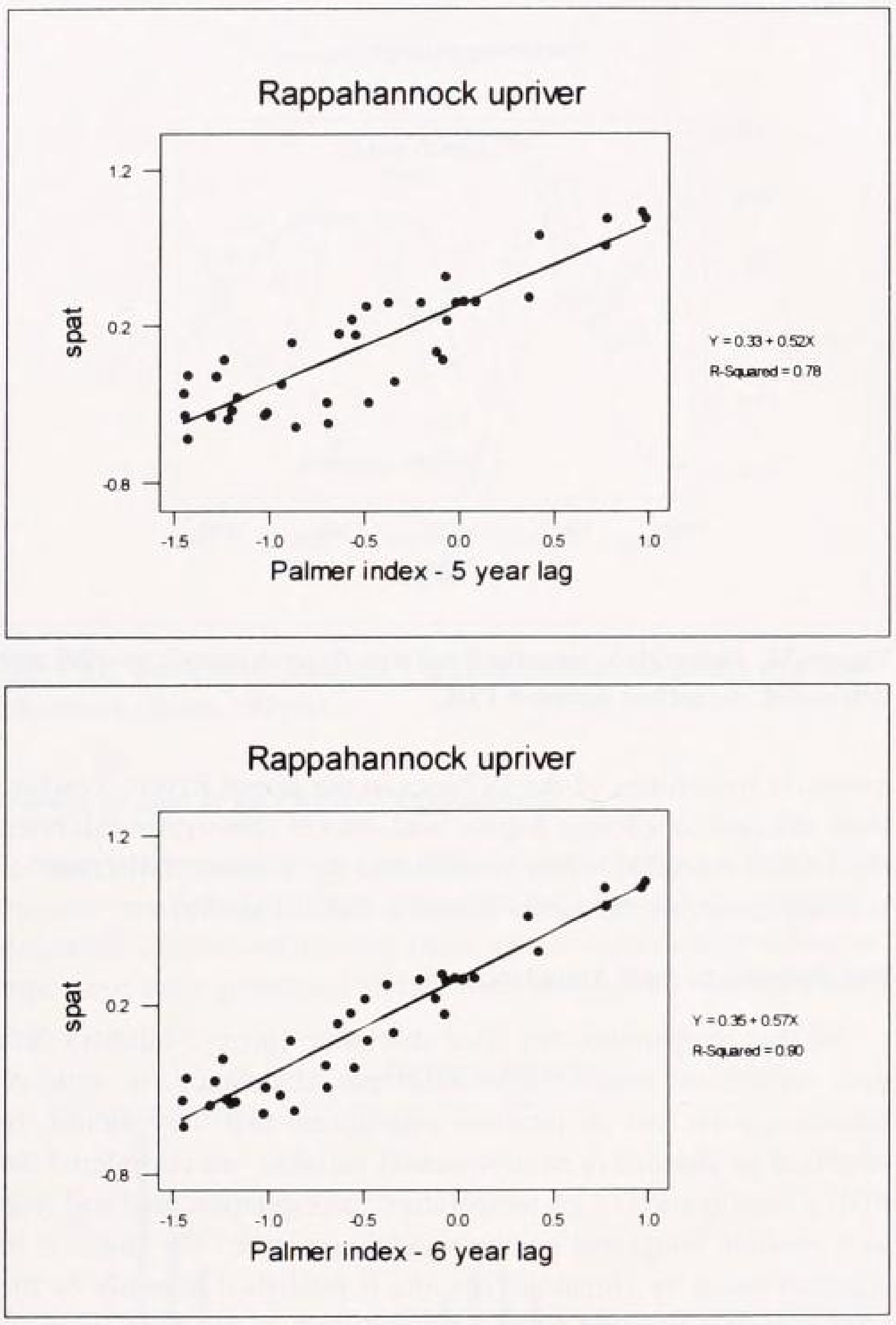


Figure 39. Regression of Rappahannock River spat and PDI lagged 5 and 6 y.

The PDI is a negative or positive deviation from normal. A positive index represents wet conditions (e.g., 1979, >4.0), and a negative index represents dry or drought conditions (e.g., 1986, >−3.5). Figure 30 depicts the summer index, which is reasonably representative of both the spring and the summer. The "dry" or drought conditions of the mid-1960s and mid-1980s are readily apparent, as is the trend away from drought to "wet" conditions during 1966 through 1979. There were no "wet" periods of over 2 y during the period of measurement, 1950 and 1994.

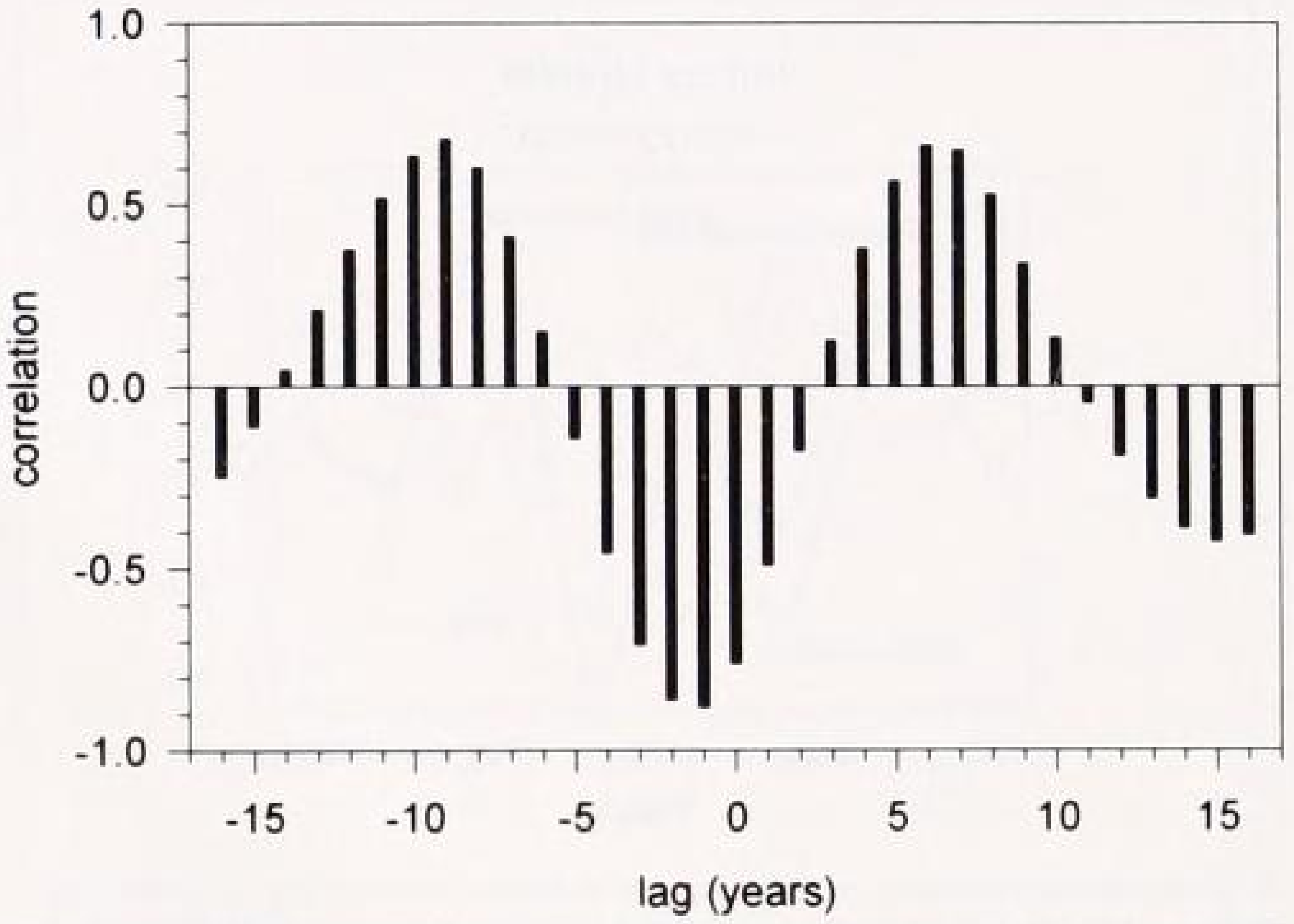


Figure 41. Cross-correlation between Rappahannock River spat and summer period of maximum Rate of change in PDI.

We computed a spring (May to July) and a summer (June to September) mean index. The ccf between the summer and spring PDI was 0.845, and the regression coefficient was 0.71.

As discussed above, if there is a relationship between fall spat-on-shell and river discharge (i.e., salinity) and/or temperature, it should be most readily apparent at the stations furthest upriver. Using the agglomerative cluster analysis characterizations of the oyster reefs, we picked the James and Rappahannock "upriver" groups for analysis. Strong long-term trends in spat data, particularly those following the post-1960 decline, were apparent (Figs. 4–7). Cross-correlation was the analysis tool planned for exploring the relationship between spat and river discharge. As we have observed earlier, the results of this type of analysis can be severely corrupted by the presence of long-term trends (Chatfield 1989). Such trends were therefore removed by use of the *loess* filter in MINITAB, with the adjustable parameter set to remove all but the lowest frequencies (parameter value = 0.7). The residuals from this smoothing constitute the detrended data. The random year-to-

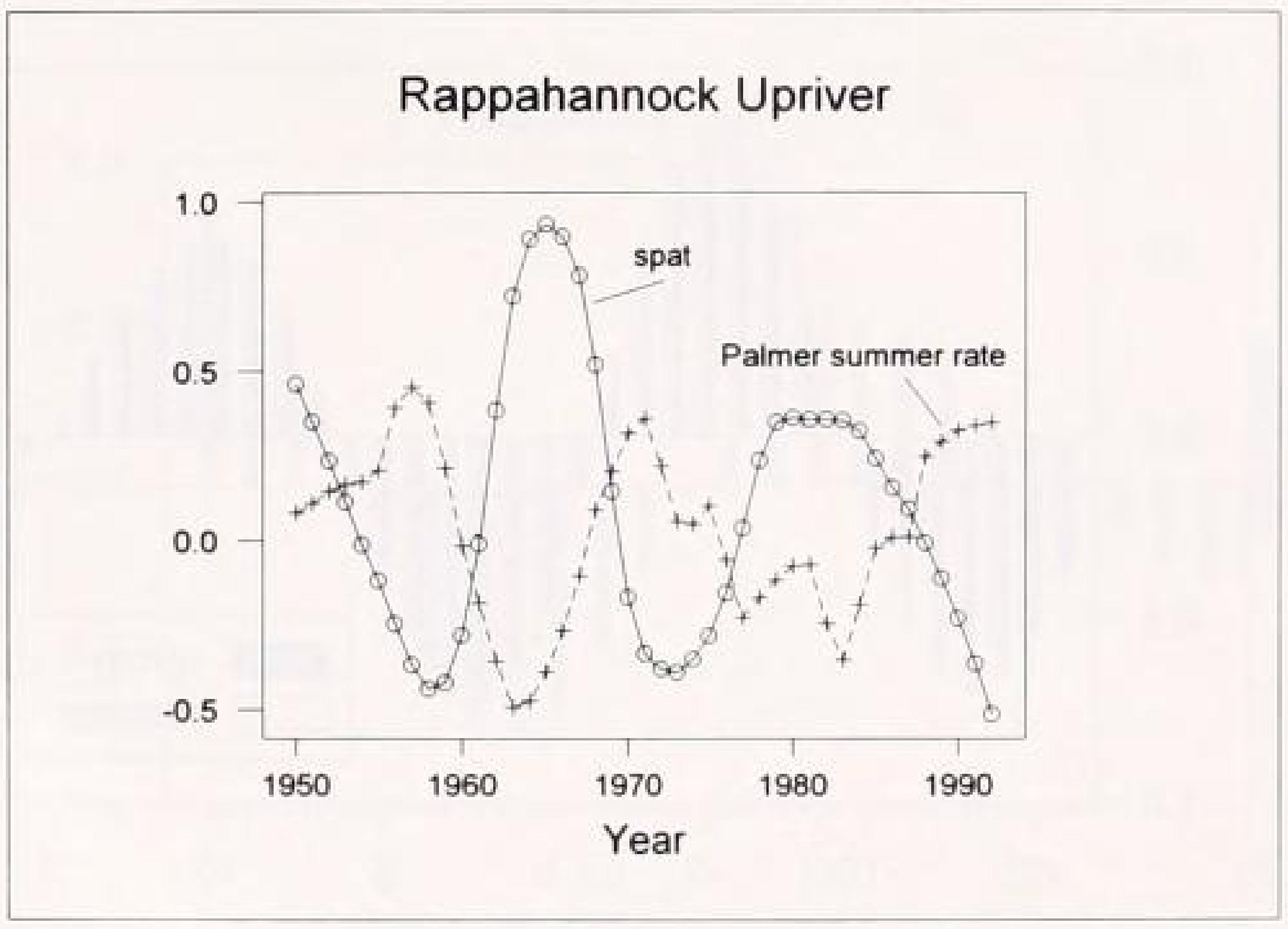


Figure 40. Detrended, smoothed upriver Rappahannock spatfall and detrended, smoothed summer period of maximum rate of change in PDI.

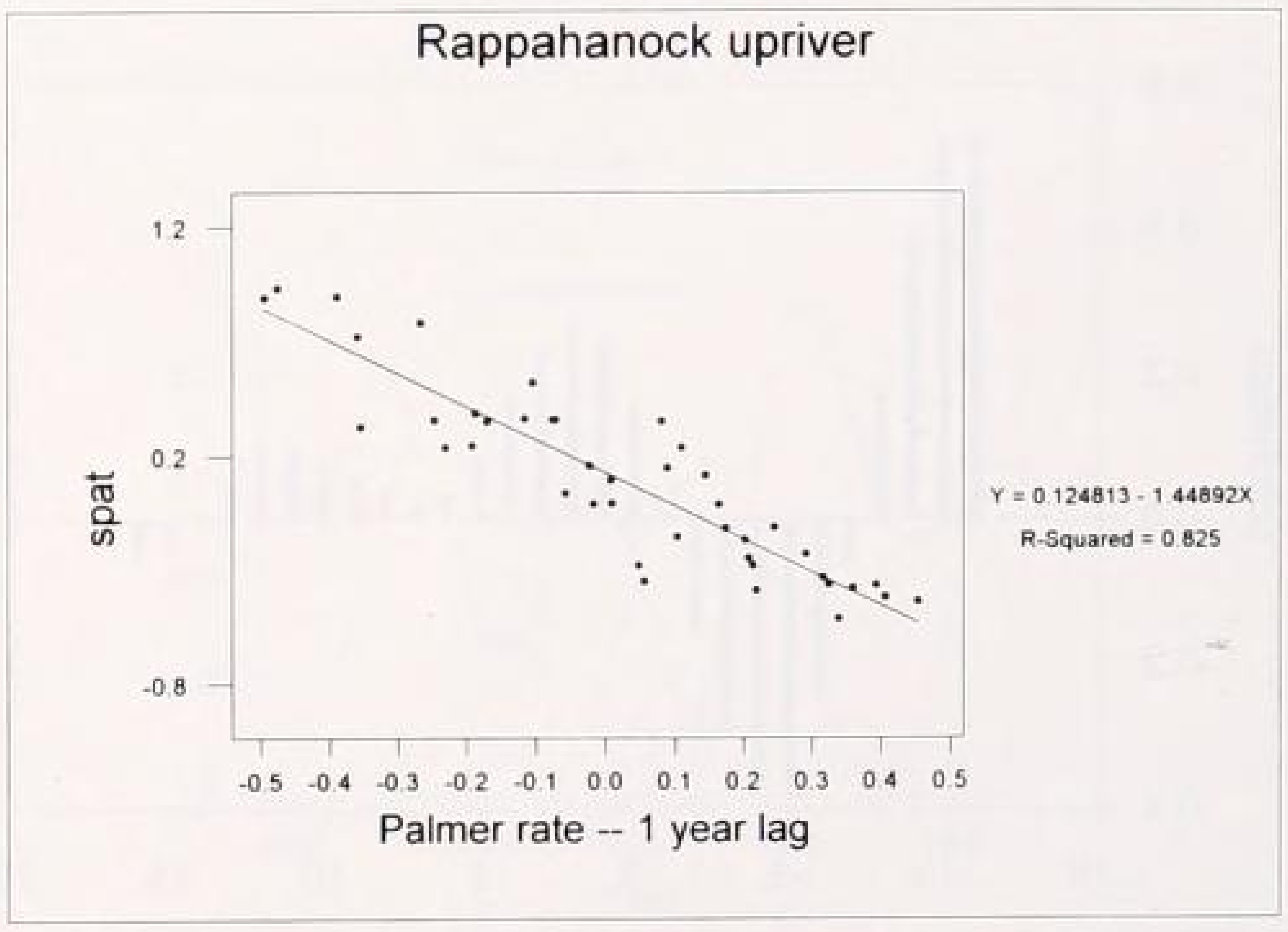


Figure 42. Regression of detrended, smoothed upriver Rappahannock spatfall versus detrended, smoothed summer period of maximum rate of change in PDI, lagged 1 y.

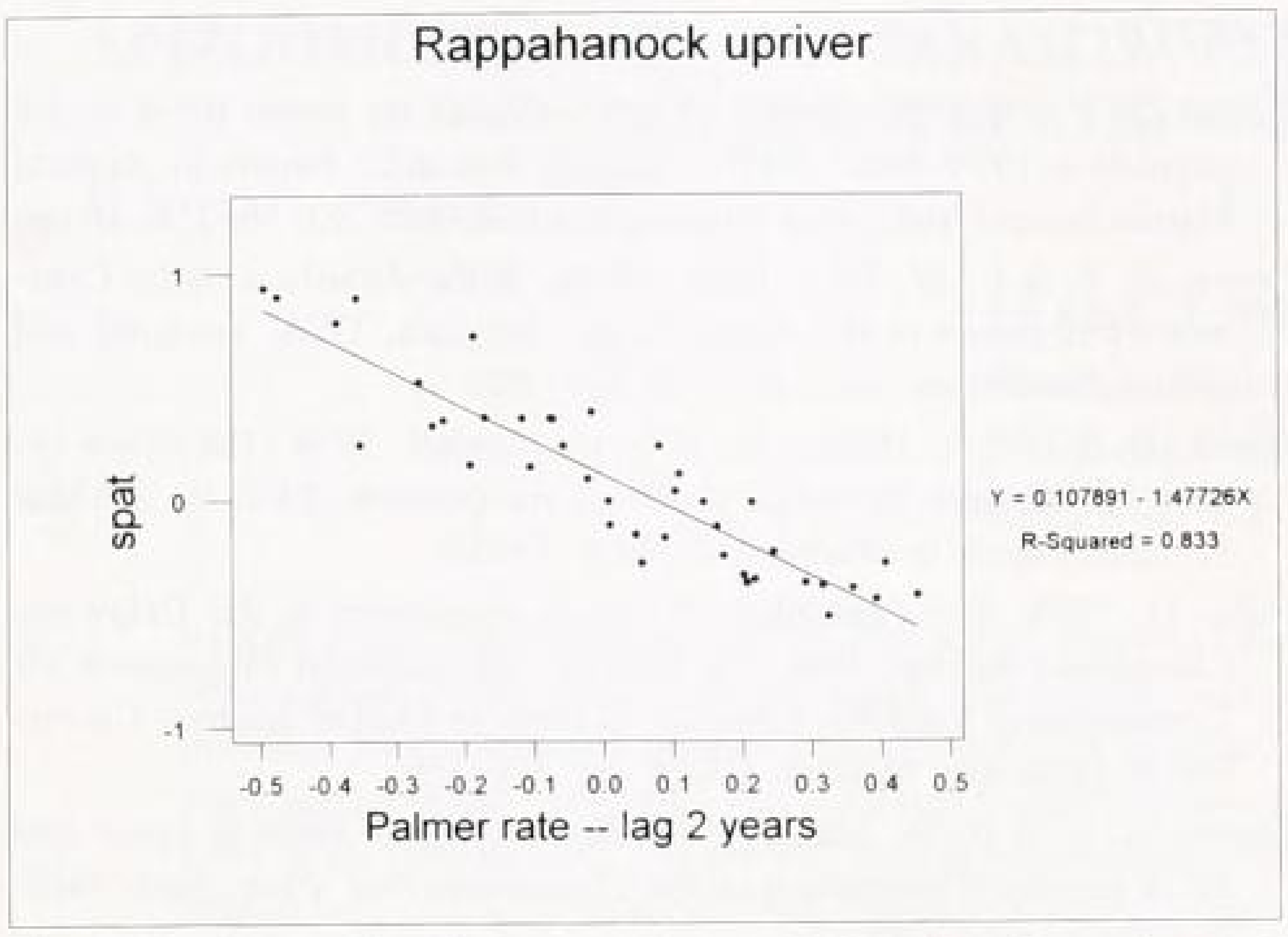


Figure 43. Regression of detrended, smoothed upriver Rappahannock spatfall versus detrended, smoothed summer period of maximum rate of change in PDI lagged 2 y.

year fluctuations in these data were smoothed by a further application of the *loess* filter with a parameter of 0.3. The overall effect of these procedures was a bandpass filtering of the original data whereby long-term trends and short-term fluctuations were removed. Figure 31 shows these smoothed data for both rivers through time. By visual inspection, the James River spat exhibited an 11- to 12-y cycle and the Rappahannock exhibited a 15-y cycle. This observation is confirmed by an inspection of the ccf (Fig. 32).

James River

Figure 33 shows the James upriver smoothed spat and spring PDI, and Figure 34 shows the spat and summer PDI. In each case, it is apparent from inspection that the summer precipitation deficits are more profound than the spring, but that both seasons move in synchrony. Also, visual inspection shows that spat and PDI fluctuate out of phase. If, however, one considers the period of greatest change in PDI (ΔPDI), as opposed to the actual values, it is apparent that they are in phase (Fig. 35). The peaks and valleys of the spat data are in phase with the periods of greatest ΔPDI. Regression of the summer ΔPDI against spat yielded an R^2 of only 14.2%. However, when the period of greatest ΔPDI was cross-correlated with spat, the greatest correlation was found at a lag of 4 y (−0.372) (Fig. 36).

Rappahannock River

The Rappahannock smooth spat and summer PDI demonstrated a greater degree of visual synchrony (Fig. 37) than the James, and the R^2 was 26.9%. Cross-correlation analyses showed a significant lag of 6 y (0.880) between spat and summer PDI, and a 5-y lag (0.817) with the spring PDI (Fig. 38). The R^2 for the regression between spat and the 5- and 6-y lag of the summer PDI were 0.77 and 0.90 (Fig. 39).

When the rate of change in the PDI (ΔPDI) (Fig. 40) was cross-correlated with spat (Fig. 41), the greatest correlation was found at a lag of 1 and 2 y (−0.881 and −8.62). R^2 for the lags were 0.825 and 0.833, respectively (Figs. 42 and 43). The responses of the spatfall to the changes in the PDI are reflected both in the 1960s, as conditions evolved from "damp" to "drought," and in the more prolonged "drying" period of the mid-1970s to mid-1980s, as the spatfall reflect a short and a longer period of increased set (Fig. 40).

The James River, because of its proximity to the mouth of the Chesapeake Bay, is more under the influence of oceanic-salinity gravitational circulation (Pritchard 1952, Neilson and Kuo 1989) than the Rappahannock. This circulation regimen has been suggested in the past (Austin et al. 1993) to be the cause of some interriver variations in oyster condition index. As such, it is not unexpected that the upper Rappahannock showed the greatest response to fluctuations in freshwater input. It must be pointed out, however, that Andrews et al. (1959) found no such James versus Rappahannock differences when examining extremely low flow patterns.

Spat and PDI Linkages

Statistically, high cross-correlations and/or regression coefficients between PDI and spatfall at 7 or 8 y do not make ready biologic sense. Yet, it is coincidence that this is the same lag period found to be statistically significant by Krantz and Merritt (1977) and Ulanowicz et al. (1980) for spat to harvest? Stepwise multiple regression by Ulanowicz et al. also showed that "drought episodes," cumulative (sustained) excessive salinity, extreme rainfall during the previous season, and harvest all caused direct variations in spat density. In this study, however, the "depth of the drought" or "peak period of rainfall/runoff" might not be expected to show a direct cause and effect with spatfall because the long lag is unexplained biologically. On the other hand, if one considers the period of greatest PDI change (ΔPDI), that period when the environment passes from one temperature/precipitation regimen to another, it makes biologic sense that the populations, after a lag, will begin to show change; then, change will occur rapidly as the population shifts toward equilibrium with the "new" environment. The cyclic nature of the physical (PDI) results in rapid and cyclic changes in the spatfall. Only during the extended drought of the early- to mid-1980s did the spatfall rates have a chance to equilibrate. Allen et al. (1977) and Legendre et al. (1985), looking at succession of species within a community, said that ecological succession evolves in steps, instead of smoothly, shifting from one structure to another, produced by intermittent shifts in the environmental structure.

CONCLUSIONS

Spatfall in the Virginia tributaries to the Chesapeake Bay and the Potomac River show a pattern of declining set from the late 1949's through the early 1970s, followed by a moderate recovery after 1975. The decline is not apparent in the Potomac. Counts of yearling oyster follow a similar pattern, except in the York River, where they increased, followed by a steady decline. Patterns of spatfall tended to partition into upriver and downriver clusters.

Spatfall levels, as indexed by counts-on-shell, can be used to predict the abundance of seed oyster 2–3 y later, but are not a good predictor of market oyster abundance. This lack of a predictive spat-market capability may be, in part, the result of the movement of seed through the oyster repletion program.

Although spat did not show a direct statistical relation to temperature or salinity, there was a significant relationship with the PDI, particularly when the index was shifting from wet to dry or vice versa. We attribute this to a shift in the environmental structure of the rivers and the response of the oyster recruitment.

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