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DECADAL SCALE CHANGES IN SEASONAL PATTERNS OF OYSTER RECRUITMENT IN THE VIRGINIA SUB ESTUARIES OF THE CHESAPEAKE BAY

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ABSTRACT Reproductive periodicity of sessile estuarine invertebrates reflects local seasonality of environmental (temperature, salinity) and biologic (food) parameters. Estuaries are ephemeral features in geologic time but considered somewhat constant in the course of recent human history (decadal time scales). Analyses of long-term trends in eastern oyster (*Crassostrea virginica*) settlement periodicity since 1960 in three major Chesapeake Bay rivers (James, Piankatank and Great Wicomico Rivers) of the Chesapeake Bay show marked changes within the 4-decade time frame. The 50th percentile of cumulative recruitment occurs between day 194 and 250 of the year depending on year and location. Significant coherence in interannual variation is observed across a wide range of sites. These patterns are related to pre and post disease (both *Haplosporidium nelsoni* and *Perkinsus marinus*) events, periods characterized by high and low river flow, varying harvest pressure, and trends arguably associated with directed climate change.

KEY WORDS: eastern oyster, *Crassostrea virginica*, settlement, recruitment, climate change, Chesapeake Bay

INTRODUCTION

Sessile marine invertebrates are suitable candidates to examine long-term changes in climate and anthropogenically induced changes in local environments. Recruitment intensity and periodicity are annual signals of the integrated impact of local perturbations superimposed on long-term (geological scale) changes. Commercially valuable species have been the focus of quantitative annual monitoring programs in support of fishery management, but have been examined in a limited manner with respect to combined impacts of climate change and fishing pressure (Allen & Turner 1989, Kim & Powell 1998). Estuarine environments are particularly susceptible to stress from cyclical changes on time scales ranging from tidal to annual. Long-term data on marine invertebrate communities in estuaries are limited, especially so in regions subject to increasing watershed development, water quality degradation, habitat destruction and/or diseases, and parasites. Temperate estuaries are natural laboratories where cumulative impacts of human societal growth are highly visible. Eastern oysters, *Crassostrea virginica*, are considered sentinel organisms in estuaries on the North American Atlantic seaboard in terms of biologic and geologic (habitat) function. Their loss in such environments predicates significant changes in ecosystem function and food chain dynamics with trickle down effects on nutrient cycling, species richness and complexity, stability of food webs, and production to support commercial fisheries.

The eastern oyster has long been recognized for its ecologic and commercial importance in the Chesapeake Bay, but the species has suffered numerous insults over the past century. Over fishing of oysters in the Chesapeake Bay has long been recognized. Maryland's harvests have been in decline since about 1885 and Virginia's since about 1904 (Hargis & Haven 1995). Recent catches are less than 1% of what they were 100 years ago. In addition to the continuous removal of market and seed oysters, uncounted millions of tons of shell have been removed for use in road building, chemical processing, and poultry husbandry. This essential habitat loss has resulted in the gradual replacement of 3-dimensional intertidal reefs, with 2-dimensional, subtidal reefs that are highly susceptible to siltation and burial (Hargis & Haven 1995). The onset of *Perkinsus marinus* in 1950 (Andrews 1996) and the arrival of the non-native disease *Haplosporidium nelsoni* (MSX) in 1959 (Burreson et al. 2000) caused further decline in the already seriously depleted oyster populations. Despite efforts of replenishment, beginning as early as 1924 in Maryland and 1928 in Virginia, oyster stocks have continuously declined. In response to these accumulating problems, monitoring efforts increased and became routine starting in the late 1940s and early 1950s in both Maryland and Virginia (Andrews 1982).

Early studies on oyster settlement (spat or young of the year oysters undergoing metamorphosis and attaching to the bottom) and recruitment (those oysters that survive post settlement to become part of the population) in Virginia focused on seasonal patterns in onset, duration, intensity, and cessation of oyster settlement (Andrews 1951, Andrews 1954). With the onset of the diseases, *P. marinus* and *H. nelsoni*, in the late 1950s and 1960s these patterns changed. Population studies from 1946 to 1967 in the James River showed that post *H. nelsoni* settlement was of lower intensity and occurred during a shorter period when compared with pre *H. nelsoni* settlement (Andrews 1982).

There have been two other long-term studies of oyster settlement and recruitment in the Virginia portion of the Chesapeake Bay. Haven and Fritz (1985) focused on the temporal and spatial distribution of oyster settlement. They examined weekly settlement in the James River from 1963 to 1980. They separated the river into three distinct settlement zones related to water circulation and found that settlement was synchronous at stations within a zone, but occurred 1 to 2 weeks earlier at stations in the upriver zones compared with the downriver zones. They also found that post *H. nelsoni* settlement intensity was lower and occurred in discrete pulses, 1 to 2 weeks in duration, instead of the continuous settlement pattern seen in pre *H. nelsoni* conditions. Austin et al. (1996) performed a time series analysis of recruitment from 1946 to 1993 in the four major sub estuaries of the Virginia portion of the Chesapeake Bay. The data used were from the Virginia Institute of Marine Science's (VIMS) annual fall dredge survey. They found a relationship between spat (young of the year, recently settled oysters) and subsequent seed at 2- and 3-years post settlement, but no relationship between recruitment numbers and spring and summer water temperatures and river discharge. Their study provided an overall picture of interannual variation in recruitment,

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but did not provide any information on interannual variation in the onset and duration of oyster settlement. Whereas both of these studies provide insight into oyster settlement and recruitment in the larger rivers of the Virginia portion of the Bay, relatively little effort has been devoted to critical examination of changes in settlement patterns in some of the smaller rivers. VIMS provides a descriptive monitoring report of settlement and recruitment in both small and large rivers in Virginia (summaries available at http//: www.vims.edu/mollusc) on an annual basis. Oyster settlement in these smaller systems and the overall health of resident oyster populations has become increasingly important over the past decade, primarily due to increasing restoration efforts in these smaller systems. The Piankatank and Great Wicomico Rivers in particular have served as important building blocks in a long-term plan for oyster restoration in Virginia (Bartol & Mann 1997, Southworth & Mann 1998).

In this study, we examine long-term changes in the Chesapeake Bay oyster population in response to the cumulative effects of the previously described stressors. We report the long-term trends in periodicity of oyster settlement in 3 rivers, namely the James, Piankatank, and Great Wicomico. These systems offer contrasting watershed drainage areas, river flows, and basin morphologies. We use duration of settlement period and mean date of settlement as indicators of environmental quality within a single year for each location. Comparisons were made within and between river systems over a 40-year period, to examine the relative roles of large-scale climatic events, local physical functions, and biologic stressors in driving the settlement patterns.

The value of historical long-term data sets, such as the VIMS shellstring survey used in this study, is in the consistency and length of data collection. Due to this longevity, the data can provide valuable insight into long-term trends (on a decadal or longer time scale) that most experiments do not afford. However, given that the initial data collection often has a different objective (i.e., was not designed to examine long-term trends) we have adopted caution in the analysis and interpretation of the data. As such we provide an overview of oyster settlement timing based on the long-term data set in a largely descriptive manner, using statistics that are appropriate to the data set.

MATERIALS AND METHODS

The James River (Fig. 1) has a large watershed, (approximately 27,000 km^2, Chesapeake Bay Program; http://www.chesapeakebay.net) with yearly average stream flow ranging from 4,400 to 21,500 ft^3/sec (United States Geological Survey data; http://nwis.waterdata.usgs.gov). Historically it was a major seed-producing river, with the seed area extending approximately from the Nansemond River up to Deep Water Shoal (Fig. 1), that supplied Virginia and Maryland planters with an average of 2 million bushels each year (Andrews 1982). The Piankatank and Great Wicomico Rivers (see Fig. 1) are relatively small watersheds (approximately 575 and 337

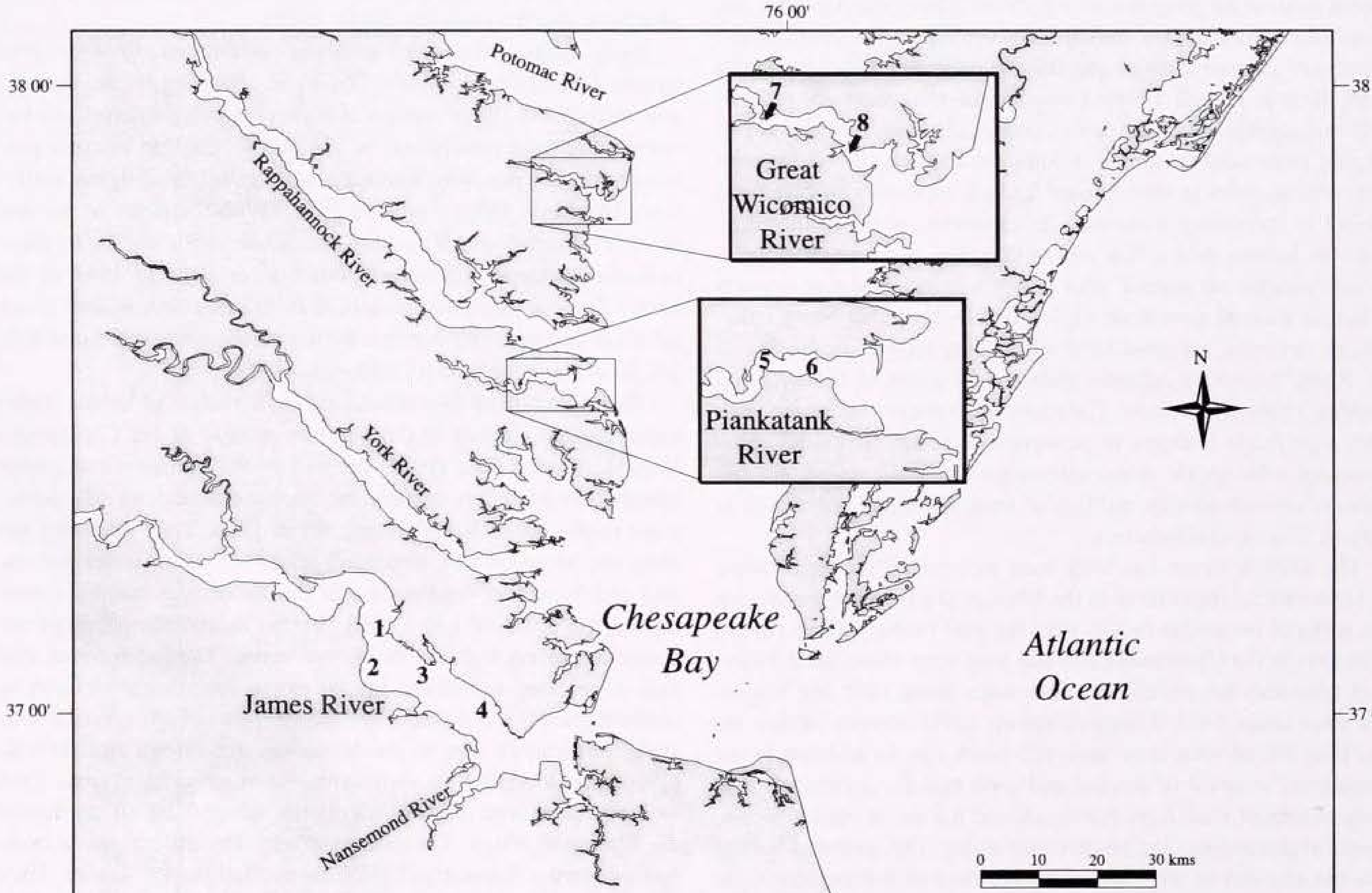

Figure 1. Map of the Chesapeake Bay showing the locations of the James, Piankatank, and Great Wicomico Rivers and the location of the 8 study sites (numbering system used throughout figures): (1) Deep Water Shoal, (2) Point of Shoal, (3) Wreck Shoal, (4) Miles Watch House, (5) Ginney Point, (6) Palace Bar, (7) Glebe Point, (8) Hudnall.

km^2, respectively, Chesapeake Bay Program; www.chesapeakebay.net) with a yearly average stream flow ranging from 50 to 460 ft^3/sec in the Piankatank River and 57 to 266 ft^3/sec in the Great Wicomico River (U.S. Geological Survey data; http://nwis.waterdata.usgs.gov). Both rivers have been termed trap-type estuaries by Andrews (1979) and are characterized by gyre-like circulation in their lower reaches. Historically, these rivers were used for oyster seed production and grow-out to market size on leased grounds. More recently, these rivers have become important in restoration efforts, with both rivers receiving shell plants and artificial oyster reefs (Southworth et al. 2002, Berman et al. 2002).

VIMS monitors oyster settlement annually using shellstring substrates from late May to early June through October. A shellstring consists of 12 oyster shells of similar size (standard length ?76 mm,) drilled through the center and strung (inside of shell facing substrate) on heavy gauge wire (Fig. 2). Throughout the monitoring period, shellstrings were deployed approximately 0.5 m off the bottom at each station. Shellstrings were usually replaced after a 1-week exposure. The number of spat that attach to the smooth underside of the middle 10 shells during the exposure period were counted under a dissecting microscope. An estimate of the mean number of spat shell^{-1} for the exposure period was obtained by dividing the total number of spat observed by the number of shells examined (10 shells in most cases). This estimate was then standardized on a per week basis (day 1 of the year = January 1) to allow for comparison between years and calculation of cumulative spat shell^{-1} estimates for each year.

TABLE 1.

Summary of the Virginia Institute of Marine Science oyster settlement monitoring stations in the James, Piankatank, and Great Wicomico Rivers, Virginia.

Station # (from Fig. 1)	River System	Station	Years Covered by Survey	Total Number of Years
1	James	Deep Water Shoals	64–72, 74–02	38
2	James	Point of Shoals	68–02	35
3	James	Wreck Shoal	68–02	35
4	James	Miles Watch House	63–97	35
5	Piankatank	Ginney Point	65–02	38
6	Piankatank	Palace Bar	67–02	36
7	Great Wicomico	Glebe Point	65–02	38
8	Great Wicomico	Hudnall	65–02	38

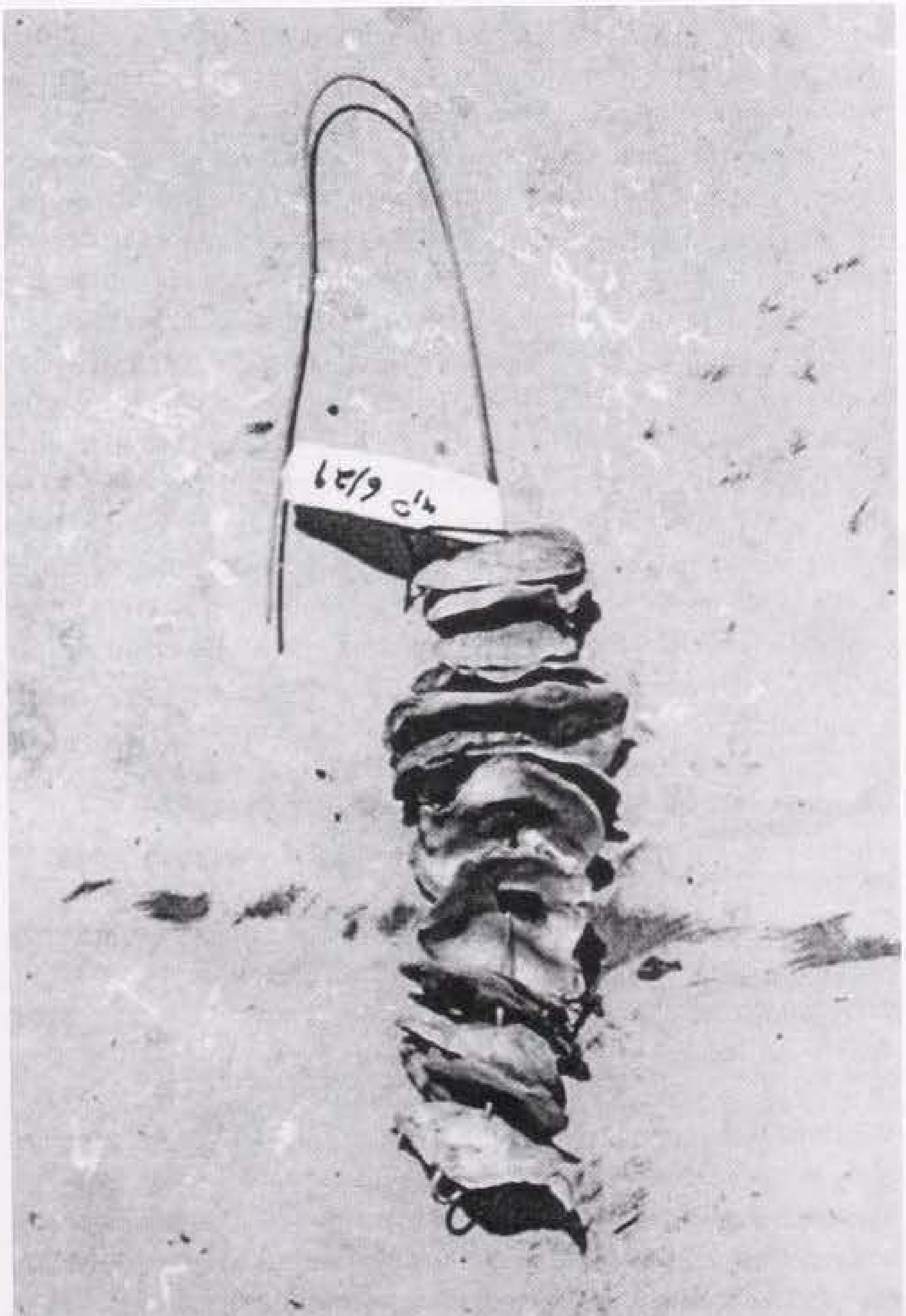

Figure 2. Picture of a typical shellstring used by the Virginia Institute of Marine Science Molluscan Ecology Program to monitor oyster spat settlement in Virginia estuaries, 1946 to present.

A total of 8 sites were selected for the study, 4 in the James River and 2 each in both the Piankatank and Great Wicomico Rivers with 34 to 38 years of data per site (Table 1). Figure 1 shows the location of the sites in their respective rivers. Sites were chosen based on their location in the river and consistency of collection of data. Data analyses were as follows. A sigmoid curve was produced for each year at each site using the formula:

$$Y = \frac{a}{1 + e^{\frac{-(x - x_0)}{b}}}$$

Where:

a = the maximum y (i.e., the total number of spat shell^{-1} in a given year).

b = the maximum slope of the line.

X_o = 50th percentile of cumulative recruitment (i.e., the day of the year when 50% of "a" has been obtained).

Examinations of temporal trends in X_o were made by plotting site-specific values of X_o for the multiyear duration of the data set. A common characteristic of time series data sets is the illustration of different features and patterns over different time scales. For example, there may be large interannual variation in a particular data set, but the overall trend on a larger decadal scale may show a steady decline. Smoothing is a tool available to identify trends within long-term data sets. One such smoothing technique, developed by Cleveland (1979), is Loess (originally LOWESS or LOcally WEighted Scatterplot Smoothing), which applies the tricube weight function to weight the data. A weighted regression is performed for each point along the smooth curve. Loess obtains each point along the smooth curve by performing a regression on the data points close to the curve point where the closest points are more heavily weighted. The user determines the amount of smoothing, which affects the number of points in the regression. This technique is robust and sufficiently well accepted to be included in most statistical packages (Cleveland 1979, 1993).

Temperature is generally considered to be an important ecological parameter influencing reproductive periodicity and larval development rates in oyster populations (Thompson et al. 1996).

We sought to examine the influence of temperature on periodicity and intensity of oyster settlement in the long-term data sets. Whereas temperature data goes back to the early 1980s for the James River and the early 1990s for the Piankatank River, consistent data for all three systems was only available from 1998 through 2002. Therefore, we limited comparisons and analysis to those 5 years. Temperature residuals were calculated by subtracting the temperature in the James River from that in the Piankatank and Great Wicomico Rivers for each day throughout the spawning season. A positive result can be interpreted as that system being warmer than the James River, whereas a negative result means the system is colder than the James River. The sum of the residuals for a particular river throughout the spawning season describes the magnitude of the difference between the river of interest and the James River.

Records of salinity over the time period examined in the three systems are also very limited; however, there are comprehensive river flow data near Richmond in the James River and near Dragon Swamp in the Piankatank River for the entire time period and in Bush Mill Creek (which flows into the Great Wicomico River) from 1963 through 1986, from the United States Geological Survey (http://nwis.waterdata.usgs.gov) records. Whereas river flow data does not give us a direct measure of salinity, it can be used as a measure of relative salinity in that there is an inverse relationship between river flow and salinity (Mann & Evans 1998).

RESULTS AND DISCUSSION

The relationship between day of the year and the cumulative sum of spat shell^{-1} was accurately described using the fitted sigmoid curve (R^2 values >0.92) and an example curve from each river is shown in Figure 3. There was a wide range in X_0 over the period examined in all three rivers. Over the 40-year period there was as much as a 60 to 90 day difference in the timing of oyster settlement between years and between river systems (Fig. 4). This plot demonstrates variability in oyster settlement timing between systems and years, but fails to identify any trends that may exist in the data. Therefore the data was smoothed using Loess and the resulting curves are shown in Figure 5.

The smoothed curves still illustrate the large range in the timing of oyster settlement observed over the 40-year period. Aside from the early years (through 1970) in the James River, settlement timing between sites within the same river was similar (usually within 1 week of each other). The Great Wicomico River shows the largest variation in timing, whereas the Piankatank River was fairly consistent in terms of settlement timing, especially compared with the other two systems. Prior to the mid 1970s, settlement was consistently earlier in the Great Wicomico and Piankatank Rivers than in the James River and there was a large difference in settlement timing between the systems. Settlement in the James River tended to be late in the year with the majority of oyster settlement occurring from late August into early September. There was a trend toward earlier settlement in both the James and Great Wicomico Rivers throughout the late 1970s and 1980s. Beginning in the early 1990s settlement timing in all three systems was increasingly later in the year and has remained similar (within 3 to 4 weeks of each other) since then. In particular, oyster settlement in the James River appears to have undergone the largest change such that current settlement patterns are similar to the other two systems; however, settlement in the Great Wicomico remains about 2 weeks earlier than in the other two systems.

There are many environmental factors that have the potential to affect both the timing and magnitude of oyster settlement. Among these are single large-scale meteorologic events, which may temporarily but fundamentally alter the conditions in a system, such as tropical storms or hurricanes (Haven et al. 1974), temperature (Medcof 1939), salinity (Butler 1949), disease (Ford & Figuereas 1988, Choi et al. 1989), and location of broodstock in a system (Haven & Fritz 1985). One or all of these factors may explain the variability in oyster settlement timing observed over the past 35 to 40 years in these rivers.

Throughout the duration of the study, the most significant meteorologic event to occur during a settlement season was Hurricane Agnes that entered the Chesapeake Bay in June of 1972 and resulted in record amounts of flooding in most of the major sub estuaries (Andersen et al. 1973, Schubel et al. 1974). This flooding had a major effect on oyster populations in the Bay causing 2 to 70% mortality in adult oysters (Haven et al. 1974). The mortality was mostly limited to the shallower systems and the upper bay and upriver sites. Mortality in the James River was as high as 85% at the more upriver sites, but was relatively low and similar to normal years at the more downriver sites, where the majority of the broodstock was located (Haven et al. 1974). Hurricane Agnes was responsible for almost complete recruitment failure in 1972 and severely reduced settlement in 1973 (Haven et al. 1974). Despite these short-term effects, Hurricane Agnes seems to have had little effect on the long-term trends in timing of the set in the Virginia portion of the Chesapeake Bay (Fig. 5).

Temperature and salinity affect every aspect of an oyster's biology, including gonadal development and timing of the spawn. Temperature in particular is viewed as the single most important factor controlling when the eastern oyster spawns (Shumway 1996). Figure 6 shows the daily temperature residuals for the 1998 to 2002 period for the Piankatank and Great Wicomico Rivers compared with the James River. In general, the temperature in the Great Wicomico River tends to be 1 to 2 °C warmer than the James River, whereas the temperature in the Piankatank River tends to be about 1 °C cooler than the James River. Both smaller rivers exhibit similar early season increases of 2 to 4 °C over a short (2 to 3 weeks) time period when compared with the James River. Further exploration of this temperature relationship can be examined by observing the cumulative day degrees as shown in Figure 7. The cumulative day degree is a sum of all of the temperature residuals for a particular year and system and demonstrates that the Great Wicomico River is, on average, warmer than the James River whereas the Piankatank River is, on average, cooler than the James River.

The difference in temperature between the three systems may explain several aspects of the observed settlement trends (see Fig. 5). Throughout the observed time span, spawning in the Great Wicomico tended to occur 1 to 2 weeks earlier than in the other two systems. Whereas both the Piankatank and the Great Wicomico Rivers showed a pronounced increase in temperature early in the season when compared with the James River (see Fig. 6), the Great Wicomico River also was on average several degrees warmer than the other two systems. Several studies have found that the rate of temperature change can be as important in inducing spawning in oysters as some "critical" level being obtained (Medcof 1939, Butler 1949). If we assume the temperature residuals in these systems have remained relatively consistent over the past 40 years then the increase in temperature observed in the Great Wicomico River early in the season combined with the overall

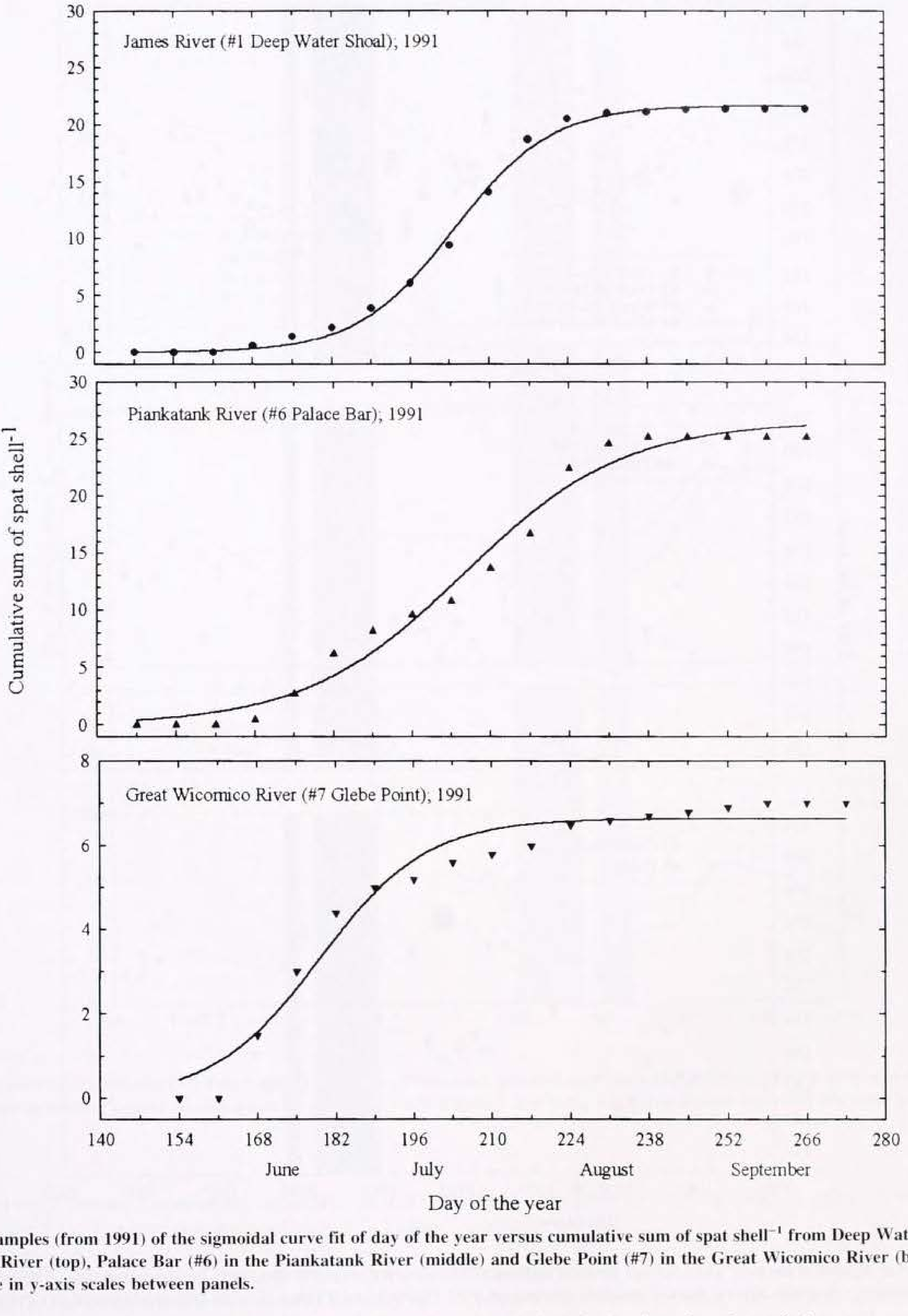

Figure 3. Examples (from 1991) of the sigmoidal curve fit of day of the year versus cumulative sum of spat shell^{-1} from Deep Water Shoal (#1) in the James River (top), Palace Bar (#6) in the Piankatank River (middle) and Glebe Point (#7) in the Great Wicomico River (bottom). Note the difference in y-axis scales between panels.

higher temperatures obtained throughout the spawning season may explain the earlier settlement observed in that system. The Piankatank River seems to warm at a similar rate to the Great Wicomico early in the spawning season, but may take longer to reach that "critical" temperature necessary to induce spawning.

Salinity, while not as important as temperature in determining the timing of spawning, can still affect gametogenesis, especially in flood conditions. Butler (1949) found that gametogenesis was delayed in salinities less than 6 ppt. Laboratory examination of gonads from field collected animals from May to August showed a 2-month lag in gametogenic development in about 90% of the oysters from a low salinity site (0–6 ppt) when compared with a high salinity site (6–15 ppt; Butler 1949). Whereas a few oysters did undergo normal gametogenesis and spawn at low salinity, the majority of them failed to produce gametes until salinity rose above 8 ppt (Butler 1949).

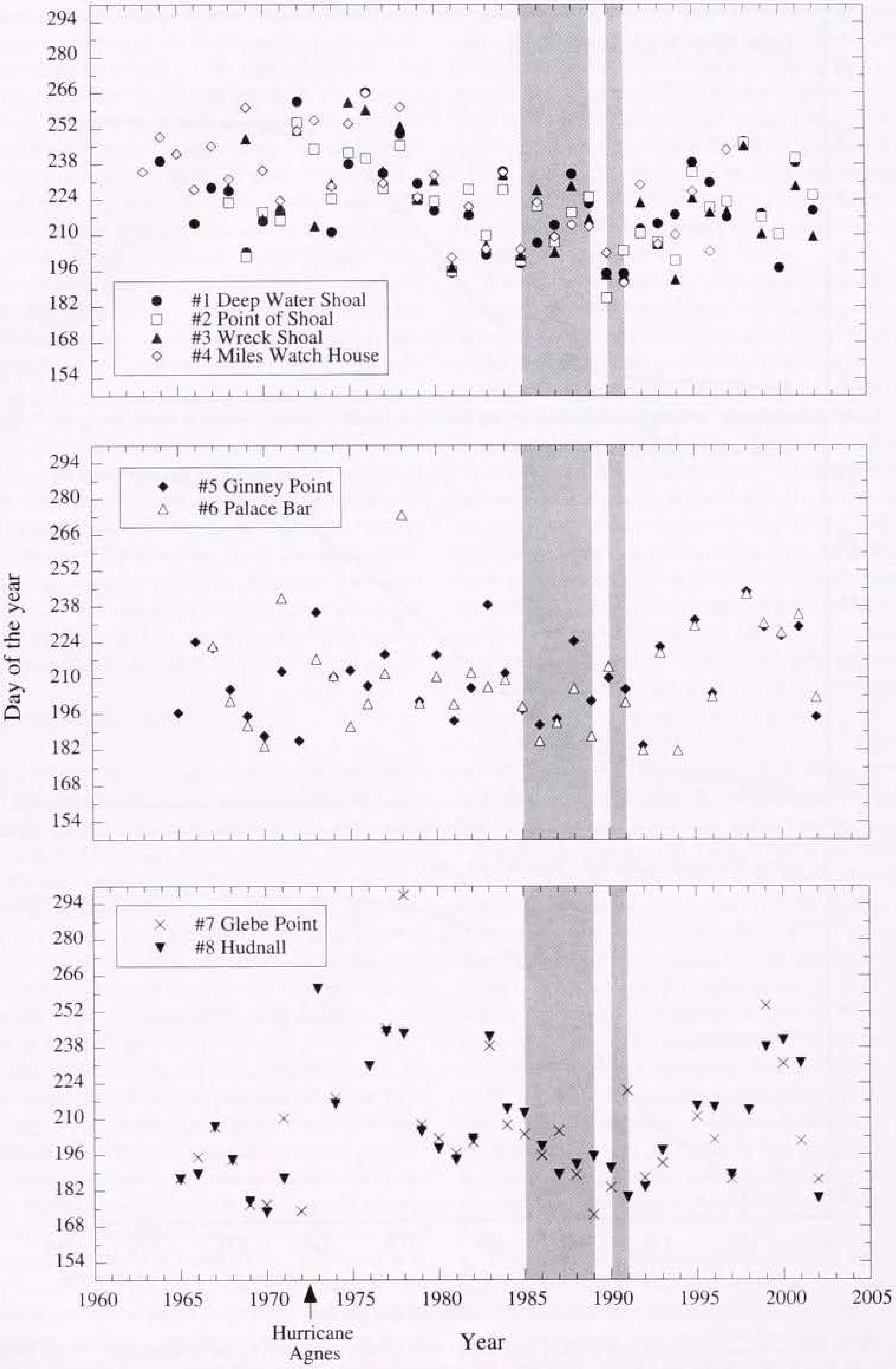

Figure 4. Plot of X_o (day of the year when 50% of the total settlement has occurred) over the 40-y study for the James (top), Piankatank (middle) and Great Wicomico (bottom) Rivers. Station numbers correspond with Figure 1 and Table 1. Shaded regions represent dry years as discussed in text.

River flow has been shown to have an inverse relationship with salinity (Mann & Evans 1998). Figures 8, 9, and 10 show average monthly water flow residuals (difference from the long-term average) from USGS records for May through September from 1960 through 2002 in the James and Piankatank Rivers and from 1964 through 1986 in the Great Wicomico River respectively. The water stations where data was obtained for each system drain approximately 65%, 45%, and 5% of the total watershed of the James, Piankatank and Great Wicomico Rivers, respectively. Applying corrections to the reported raw data for watershed area and the percentage of watershed reflected in the raw data we note that the run-off in the Piankatank and Great Wicomico Rivers are in the

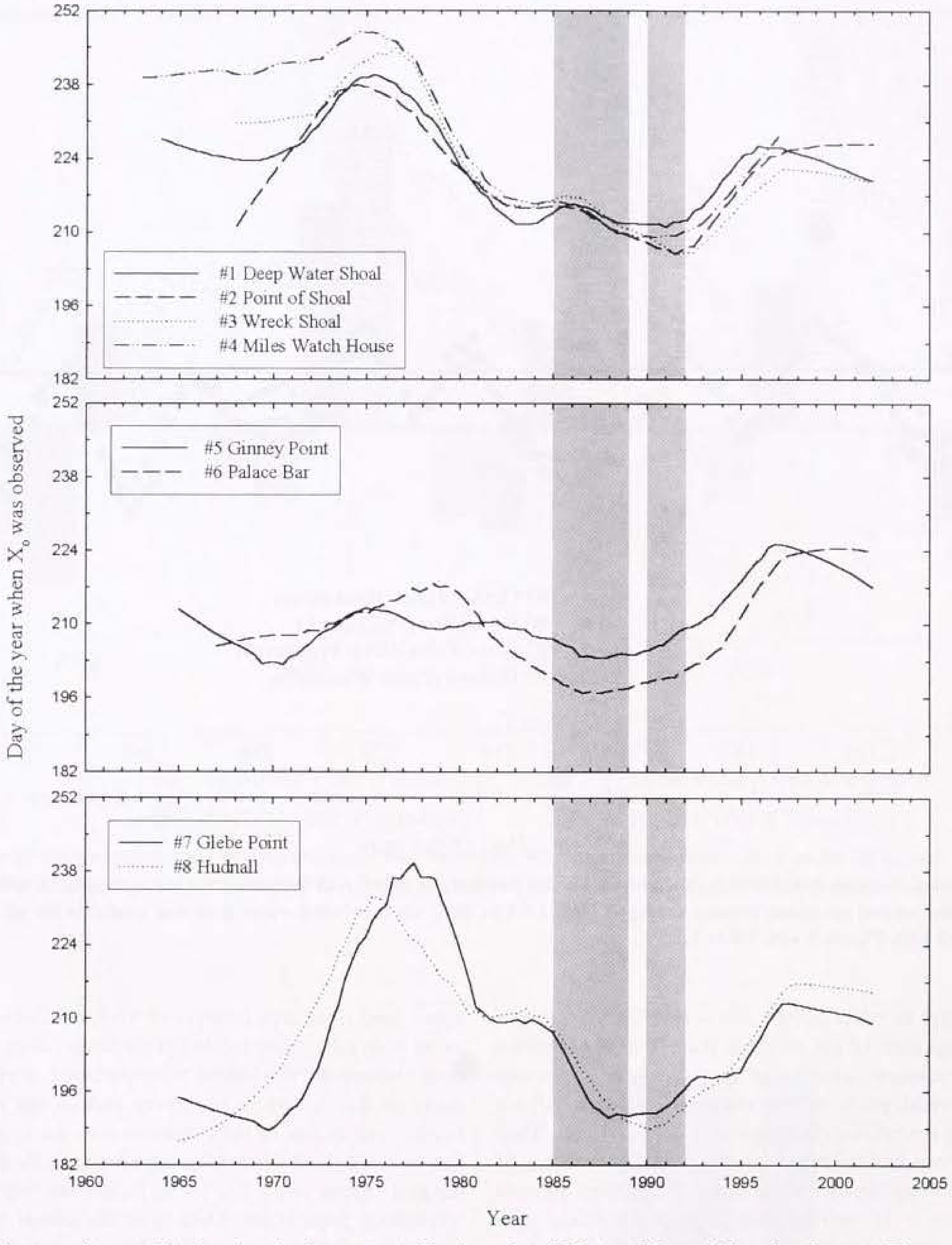

Figure 5. Cumulative recruitment (X_0) data for the James (top), Piankatank (middle) and Great Wicomico (bottom) Rivers, smoothed with the Loess technique in relation to year. Station numbers correspond with Figure 1 and Table 1. Shaded regions represent dry years as discussed in text.

10s to100s of cubic feet sec^{-1} whereas the James is in the 1,000s to 10,000s cubic ft sec^{-1}, at least two orders of magnitude higher. All three systems were characterized by low flow during the 1960s. Hurricane Agnes (June, 1972) appeared to have disproportionate impact in the James River compared with the other two systems. During the 7-year period from 1985 through 1991, only 1989 was considered a wet year for the Chesapeake Bay as a whole (Burreson & Ragone Calvo 1996). The 1985 to 1991 drought was more apparent in the James River where 5 of the 7 years had a net flow lower than average whereas only 3 out of the 7 years showed a net flow lower than average in the Piankatank River. Further examination of the relationship between oyster settlement and year (see Fig. 5) for the drought conditions of the late 1980s and early 1990s shows that the oysters spawned earlier in the year than during wetter years.

Salinity can have an indirect effect on oyster spawning through its influence on oyster diseases. Two oyster pathogens, *Haplosporidium nelsoni* and *Perkinsus marinus* were present in varying intensities in all three systems throughout the 40-year time frame of the study. Both diseases have been shown to have a detrimental effect on development of the gonad, especially in heavily infected animals (Choi et al. 1989, Ford & Figuereas 1988). Therefore we examined the option that the heavier the infection, the greater effect that infection would have on the animals. The distribution and abundance of both diseases is primarily controlled by salinity (Burreson & Andrews 1988). *H. nelsoni* requires a salinity of

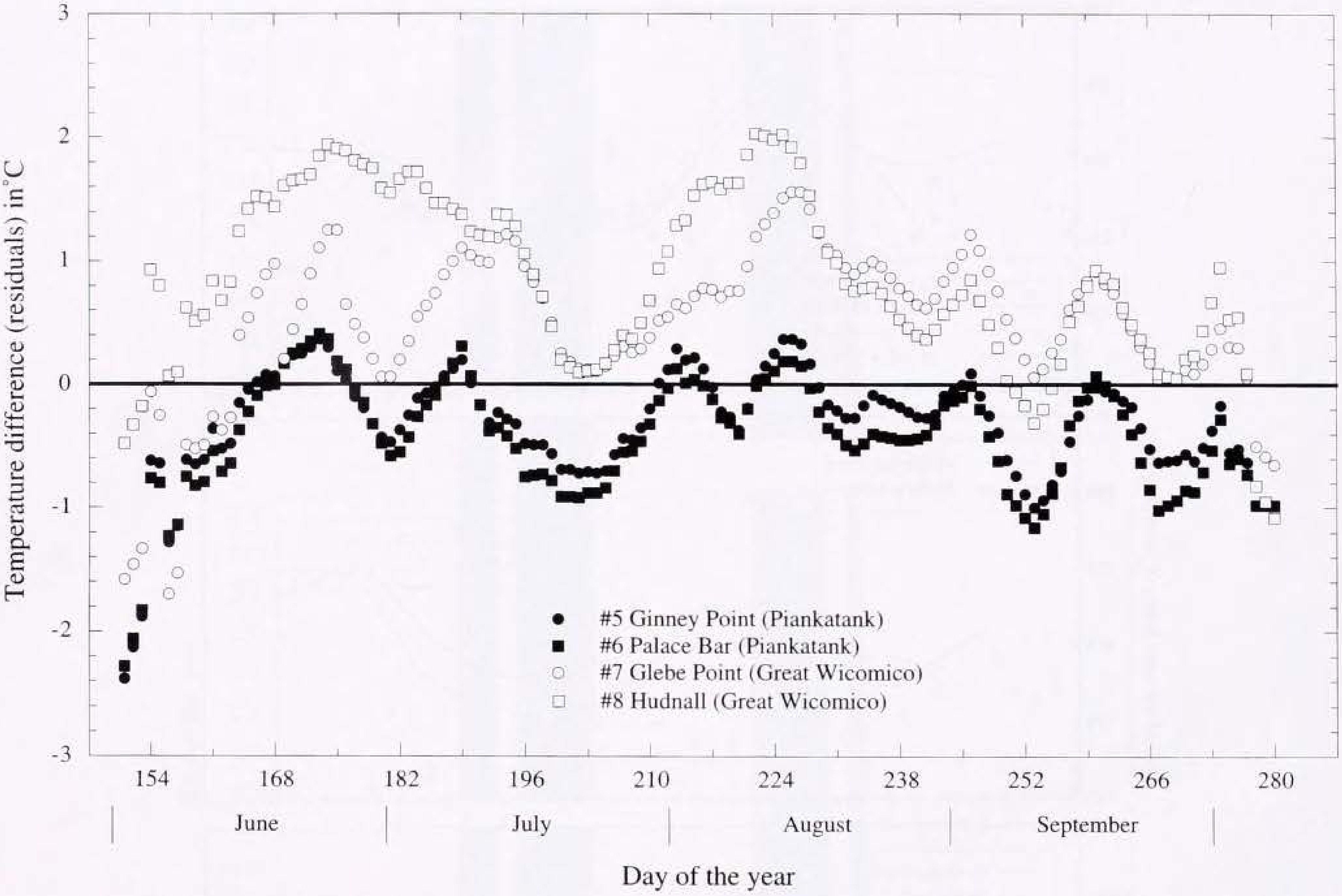

Figure 6. Daily average temperature differences (residuals) in the Piankatank and Great Wicomico Rivers as compared with the James River over the course of the annual spawning season; averaged from 1998 to 2002 when detailed water data was available for all 3 systems. Station numbers correspond with Figure 1 and Table 1.

approximately 15 ppt to infect oysters and is expelled in spring if salinities remain less than 10 ppt for more than 10 days (Andrews 1988). *P. marinus* requires salinities of approximately 12 ppt and can persist for several years at low seasonal salinities without causing substantial mortalities (Burreson & Andrews 1988). Thus *H. nelsoni* only moves into the upper bay and the upper reaches of the sub estuaries during drought conditions. *P. marinus* showed similar distributions to *H. nelsoni* until drought conditions persisted for the 7-year period in the late 1980s and early 1990s (see Figs 1 and 2 in: Burreson & Ragone Calvo 1996). Since that time *P. marinus* has persisted in the upper James River and throughout the Piankatank and Great Wicomico Rivers even though salinities returned to normal (compared with the long-term means) during the mid to late 1990s.

The effect that the two diseases have on oyster spawning, especially that of *P. marinus,* may explain the observed changes in settlement timing in the James River during the late 1980s. As disease became more prevalent throughout the James River, the difference in settlement timing between the most upriver (Deep Water Shoals) and downriver (Miles Watch House) stations decreased (see Fig. 5). The observed differences between the 3 rivers have also decreased as disease prevalence has increased.

The change in settlement timing in the James River may be related to the location of the broodstock oysters in that system and how that location has changed over the study period. It has been suggested that, historically, the majority of the settlement on the upper seed river area (upriver of Wreck Shoal, see Fig. 1) originated from the oysters located in the lower, more saline, part of the river (Haven & Fritz 1985). With the onset of *H. nelsoni* in 1959 many of the oysters in the lower part of the river were killed. Further excursions of both diseases into the upper reaches of the James, throughout the seed area and especially that observed over the past fifteen years, has led to further decline of the downriver broodstock populations. Data from the annual VIMS fall dredge survey (http//:www.vims.edu/mollusc) show that the percentage of broodstock upriver of Wreck Shoal (Fig. 1 for location in river) has been steadily increasing, whereas the broodstock downriver of Wreck Shoal has been decreasing (Fig. 11). We suggest that, historically, the oysters in the upper seed area provided the first smaller settlement pulse, whereas the more downriver oysters provided the larvae for the major settlement events that typically occurred in late August and early September. With the decline of these downriver populations, the majority of the settlement event increasingly originates from the upper seed area, with an accompanying earlier settlement peak.

In summary, the trends in oyster settlement timing observed over the past 40 years in the James River can be attributed to several interacting factors. There are anthropogenic inputs in the form of watershed influences and over harvesting that have been occurring in the river for the past century (Hargis & Haven 1995) and, despite continuing depleting stocks, some harvesting still occurs in the system (James Wesson, Virginia Marine Resources

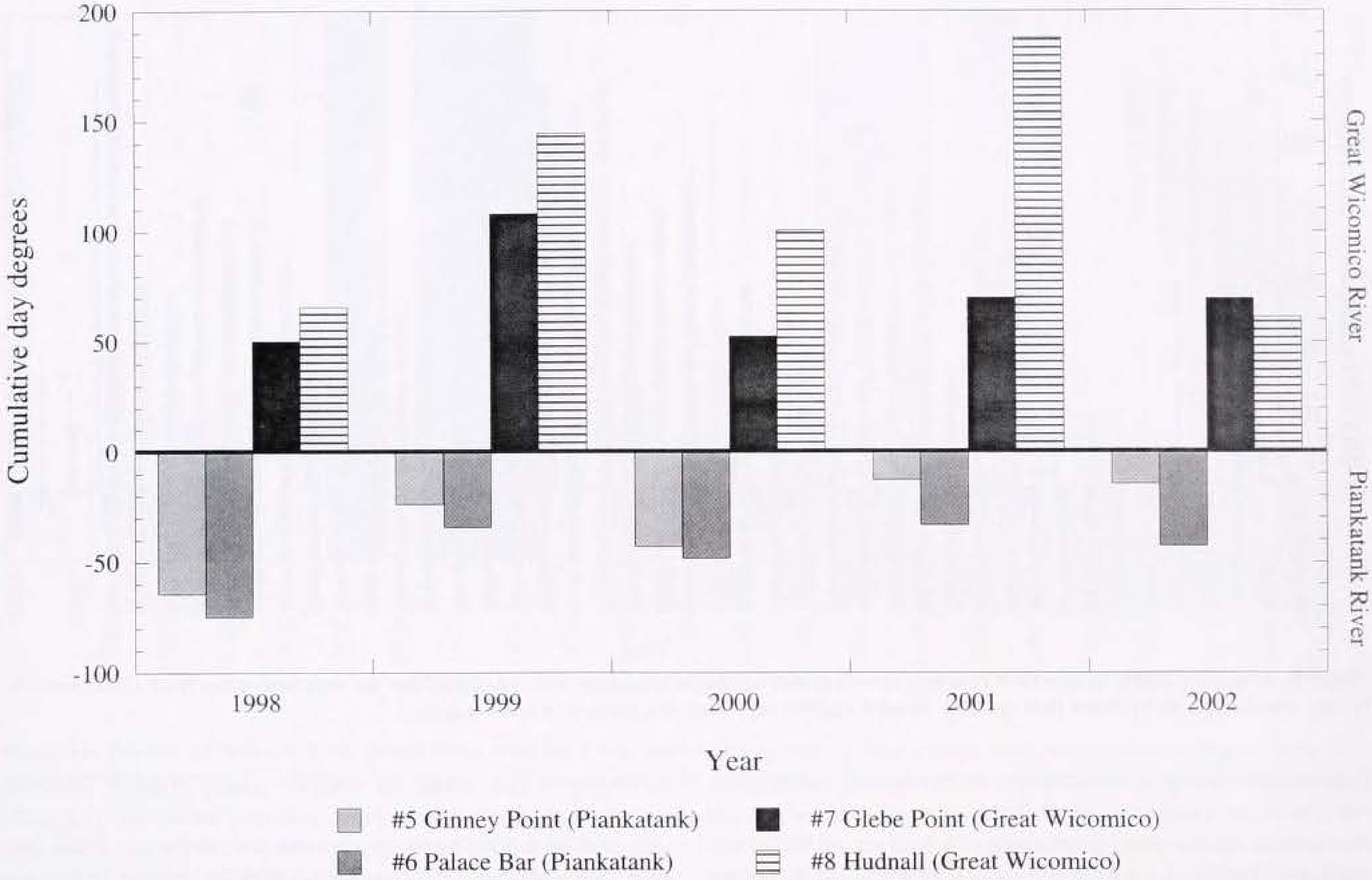

Figure 7. Cumulative day degrees for the Piankatank and Great Wicomico Rivers using the James River as the zero mark for the period 1998 to 2002 when detailed water data was available for all 3 systems. Station numbers correspond with Figure 1 and Table 1.

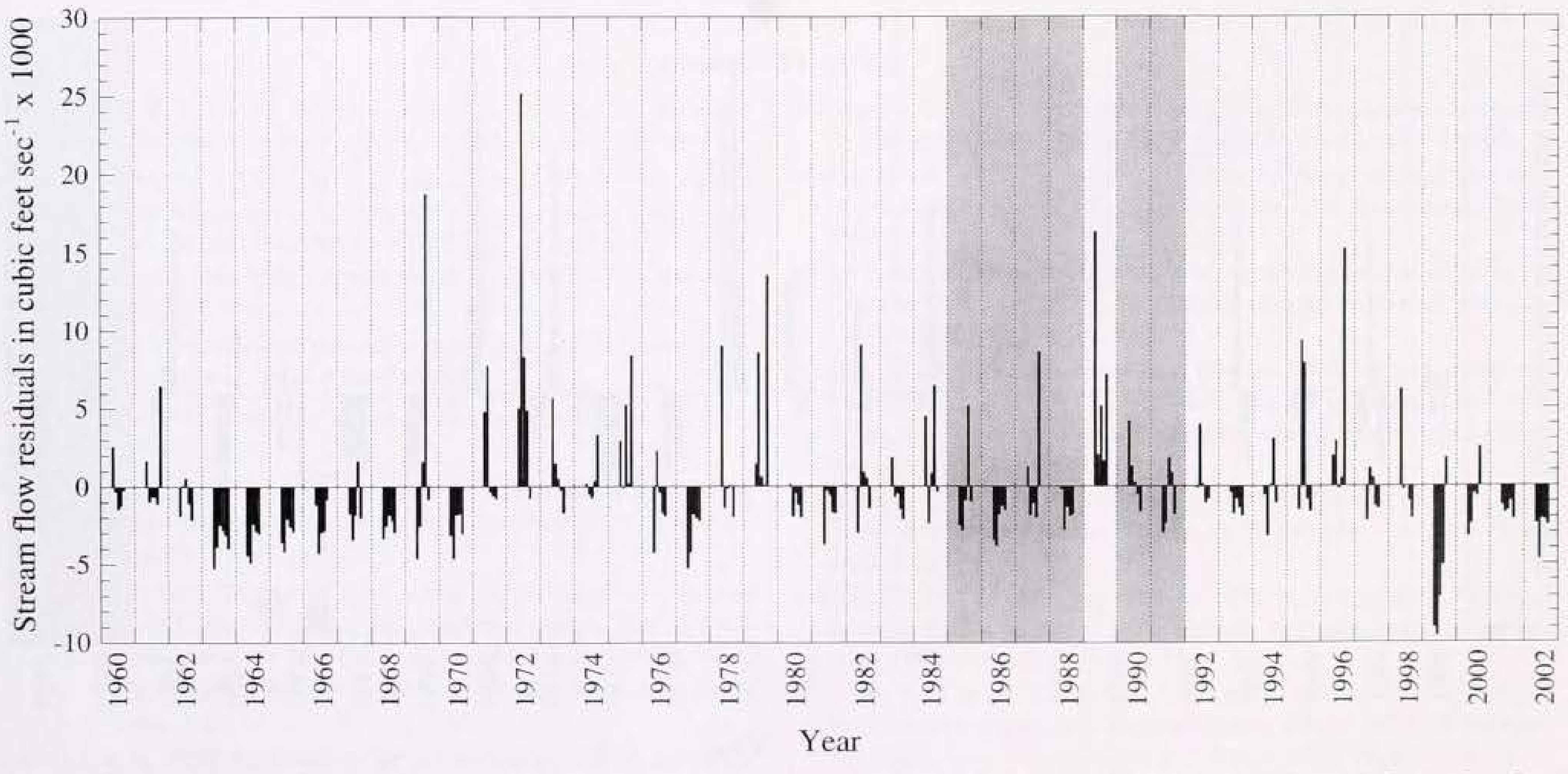

Figure 8. Average monthly stream flow residuals (monthly average minus long-term monthly average) from May through September from USGS records for the James River from 1960 to 2002. Shaded regions represent dry years as discussed in text.

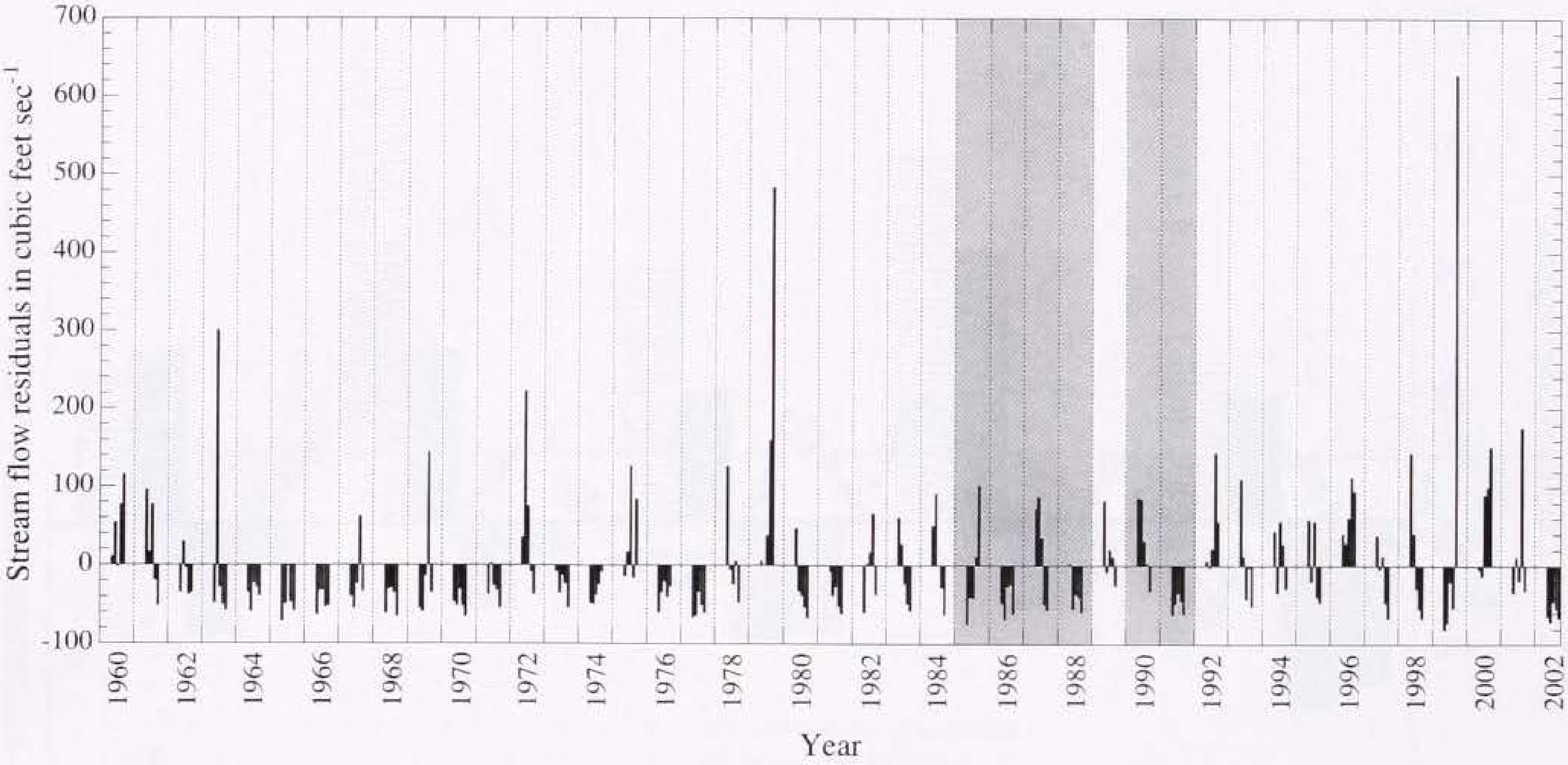

Figure 9. Average monthly stream flow residuals (monthly average minus long-term average) from May through September from USGS records for the Piankatank River from 1960 to 2002. Shaded regions represent dry years as discussed in text.

Commission, Newport News, VA 23607; personal communication). With the added insult of the 2 disease species, *H. nelsoni* and *P. marinus* and the subsequent change in location of the broodstock populations, the present distribution of oysters in the James River is very different from what was observed several decades ago. Overall there has been very little change in the timing of oyster settlement in the Piankatank River, especially compared with the changes observed in the James and Great Wicomico Rivers. Unlike the James River, there are very few anthropogenic influences in the Piankatank River, there has been no commercial harvesting in the system for decades (James Wesson; personal communication) and there are few watershed influences. The small change in settlement timing that we observed in the late 1980s and early 1990s are most likely associated with the drought of the late 1980s when *P. marinus* infections moved into the upper portion of the estuary (Burreson & Ragone Calvo 1996). Throughout the duration of the study, the Great Wicomico has exhibited the largest interannual variation in settlement timing. The drought of the late 1980s did not really alter the location of disease-infected oysters (Burreson & Ragone Calvo 1996), and given the small size and

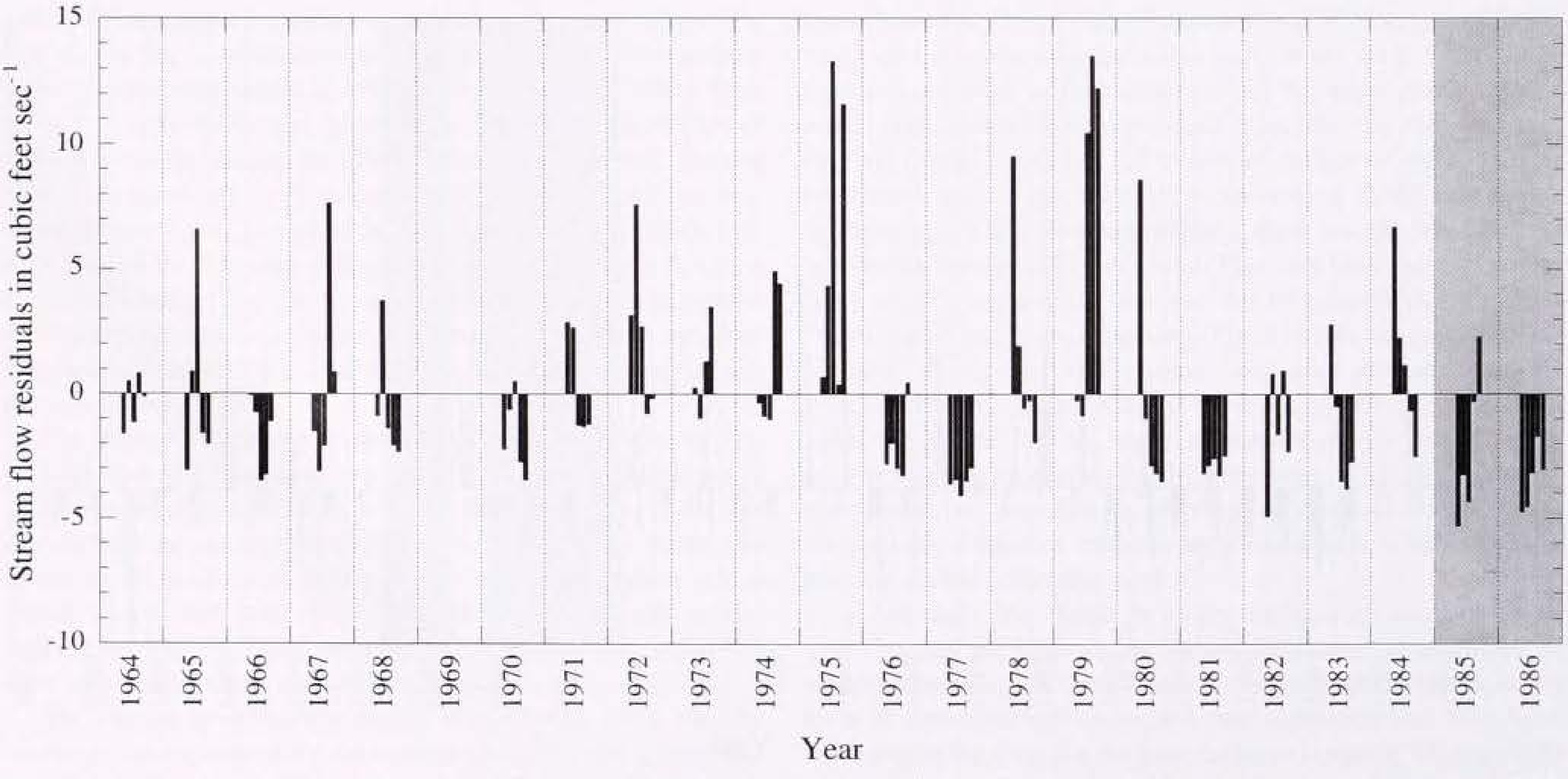

Figure 10. Average monthly stream flow residuals (monthly average minus long-term average) from May through September from USGS records for the Great Wicomico River from 1964 to 1986. Shaded regions represent dry years as discussed in text.

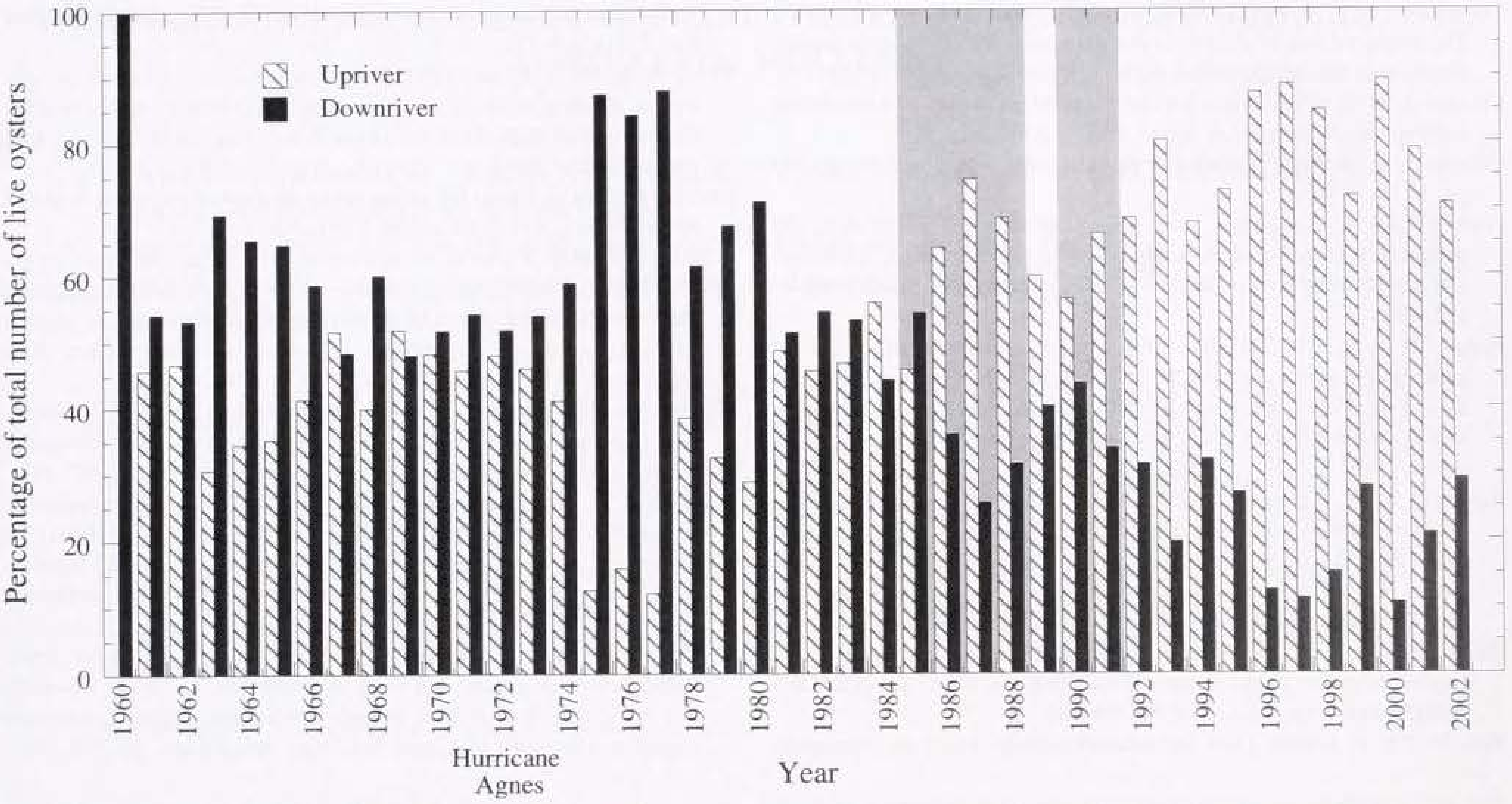

Figure 11. Broodstock location in the James River from the VIMS annual dredge survey from 1960 to 2002: sites upriver of Wreck Shoal (#3) versus sites downriver of Wreck Shoal. See Figure 1 for location within the James River. Shaded regions represent dry years as discussed in text.

gyre-like nature of the sub estuary, location of broodstock has no effect on the timing of oyster settlement. The combination of low run-off and higher temperatures (compared with the other two systems) is implicated and is arguably an effect of directed climate change.

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