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PALEOECOLOGY OF SUBMERGED MACROPHYTES IN THE UPPER CHESAPEAKE BAY

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Abstract. Fossil seed distributions of submerged aquatic vegetation (SAV) from dated sediment cores in tributaries of the upper Chesapeake Bay show prehistoric changes in species composition and abundance and reflect the response of SAV species to human disturbance since European settlement. The interval of time spanned by the cores includes several centuries prior to, and three centuries following, European settlement. Species diversity is greatest in the low-salinity northern and upper tributaries, while areas of higher salinity and extensive salt marshes are characterized by low diversity or absence of SAV. Mapped distributions of seed abundances show the migration from upstream to downstream in some tributaries of the brackish species *Potamogeton perfoliatus, Zannichellia palustris,* and *Ruppia maritima* following deforestation. The largest increase in SAV, represented by the highest abundance of fossilized seeds, occurred during the 1700s after Europeans first cleared the land for farms, and the largest and most widespread decline took place in the 1960s and 1970s after most of the watershed had been at one time or another cleared and heavily fertilized for agriculture. Distributions of SAV are highly variable both temporally and spatially, reflecting the dynamic nature of estuarine habitats. Despite high environmental variability, local and regional extinctions occurred only in the most recent decades, indicating a threshold response to land use changes and nutrient loading which had begun at least two centuries earlier and intensified in the mid- to late 19th century.

Key words: Chesapeake Bay; estuary; European settlement; fossil seeds; land use; species diversity; species extinction; submerged aquatic vegetation.

INTRODUCTION

A catastrophic decline in submerged aquatic vegetation (SAV) occurred throughout much of the Chesapeake Bay in the late 1970s, concurrent with declines in other areas of North America as well as Europe and Australia (Batuik et al. 1992). The northern Chesapeake Bay was affected more severely than southern areas, with local extinctions reported in the upper stretches of some tributaries. SAV is an important component of estuarine systems, providing food and shelter for many organisms including commercially important shellfish and finfish, as well as being a primary source of food for some waterfowl. In addition SAV removes toxins from the water column and stabilizes sediment (Sculthorpe 1967, Stevenson and Confer 1978, Davis and Brinson 1980). The precipitous decline of SAV was therefore an important economic as well as ecological event. The abruptness of the decline is particularly perplexing, because impacts on water quality, such as sediment loading and nutrient inputs, had been occurring for at least two centuries. A lack of long-term records made identifying potential causes difficult. Prior to 1958, historical information on SAV distributions was restricted primarily to data available from herbarium specimens collected since the late 19th century and from anecdotal information (Stevenson and Confer 1978). There were no records indicating whether the recent decline in SAV populations was unprecedented or a natural periodic fluctuation.

We reconstructed the prehistoric and historic distributions of SAV in upper Chesapeake Bay tributaries using the surrogate record of SAV seeds preserved in sediment, in order to determine whether there were previous reductions in SAV populations. Fossil seeds and pollen in lake sediments have been used to reconstruct long-term records of macrophyte populations in relation to changing climate and water quality (e.g., Watts and Winter 1966, Stark 1971, Birks and Birks 1980, Jackson et al. 1988, Jackson et al. 1997). They have also been used to reconstruct the post-European history of submerged macrophytes in an embayment and two tributaries of the Chesapeake Bay (Brush and Davis 1984, Davis 1985, Hilgartner 1995).

The study was designed to answer the following questions: (1) have there been widespread disappearances of SAV previous to the 1970s, and how did SAV communities fluctuate in prehistoric time compared with historic time? (2) what were the causes for the recent disappearance of SAV?

The seed record was selected rather than pollen, because SAV seeds, unlike SAV pollen, are abundant and well preserved. Also, seeds are easily identified to species, whereas pollen grains can usually be designated only to genus or family. In this paper, the term seed

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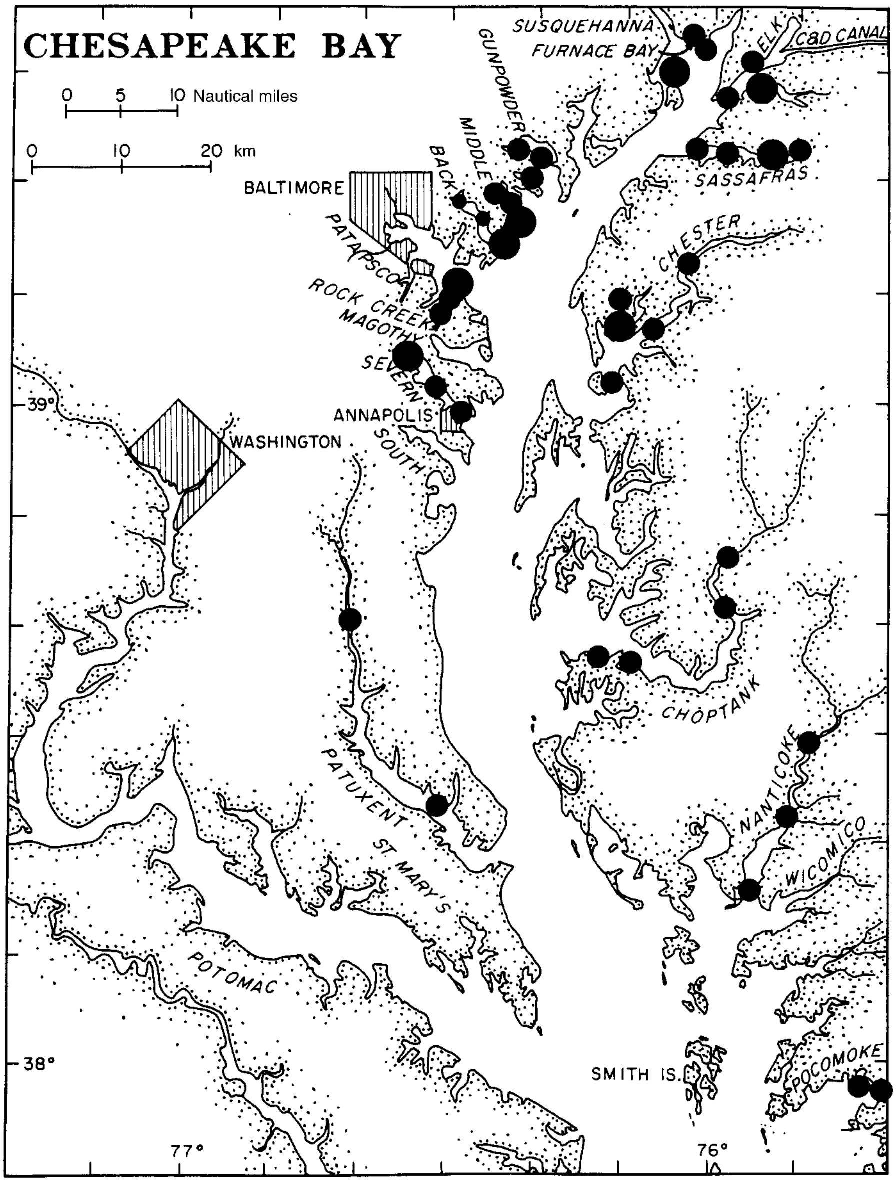


FIG. 1. Area of study, the upper Chesapeake Bay. Black circles show locations of coring sites. Large black circles are locations of core profiles shown in Figs. 4–7.

refers to the fruiting structure of the plant and includes endocarpal and exocarpal structures as well as the seed proper.

Representation of SAV by seeds in sediment can be affected by differential production of seeds among species, distance of transport of seeds from parent plants, and differential preservation of seeds once deposited and buried in the sediment. With respect to differential production, annual plants, such as *Zannichellia palustris,* are represented by more seeds in sediment than are perennials, such as *Potamogeton* spp. Laboratory and field studies on the distance seeds are transported in a river or estuary show that they are deposited preferentially in nonchannel sediments within a distance of 500 m, and most abundantly within 10–40 m (Davis 1985; W. Hilgartner, *unpublished data*). Seeds of 13 of the 25 extant species in the Chesapeake Bay were found in the top 2–4 cm of sediment, indicating that the fossil record represents about one-half of the total SAV.

STUDY AREA

The area of study includes the upper Chesapeake Bay from the head (latitude 39°34′ N) to the Pocomoke River (latitude 38°00′ N) (Fig. 1). SAV beds mapped in 1989 from aerial photography (Orth and Nowak 1990) show that SAV was extremely rare throughout the study area. Except for the mouth of the Susquehanna River and Eastern Bay between the Chester and

Choptank Rivers, SAV occurred only as a few strands at various locations. Table 1 lists the water depth, sediment type, salinity, shoreline characteristics, and living SAV observed at each core site.

Chesapeake Bay and tributaries are partially mixed estuaries, characterized by vertical, lateral, and longitudinal salinity gradients, controlled by freshwater inflows and tidal currents. Freshwater flows, and hence salinity gradients, are influenced by precipitation, which varies throughout the estuary. From early spring until winter, vertical differences in salinity result in water column stratification. Additionally, tides create a zone of sediment resuspension at the bottom of the estuary, the concentration of which varies throughout a tidal cycle (Schubel 1968). Sediment is also more concentrated where the wedge of higher salinity water interfaces with the fresh water. This zone, called the turbidity maximum, may move upstream or downstream seasonally or during storms and, when moving upstream, it can increase turbidity in shallow waters where SAV grows. Winds, associated with storms and hurricanes, are also variable, thus scouring and redepositing sediment locally. Hence, at any given time, there may be considerable spatial variability in water clarity and salinity throughout the estuary.

Land Use History

Soil eroded from fertilized land in the Chesapeake watershed influences turbidity and water quality, because it contributes sediment and nutrients to estuarine waters. The rate of soil erosion is related to land use, which has a long and varied history in the Chesapeake region. Prior to European colonization, the Chesapeake watershed was forested except for serpentine barrens, small Indian clearings, and tidal wetlands (Bruce 1896, Stetson 1956). Following European settlement, land use can be divided into four major periods (Brush 1989, Brush and Brush 1994) (Table 2). The periods are not synchronous as settlement proceeded from south to north, and agricultural practices were influenced by soil type.

1630–1720.—The Coastal Plain was first settled by Europeans in the early 1600s. Colonization of the Piedmont began in the late 1600s to early 1700s. Early agriculture centered first on subsistence farming and then tobacco. Tobacco was first grown on fertile loams and clay-rich soils of the Coastal Plain. The majority of farms were situated along tributaries where transport was accessible. Early farming entailed clearing small areas using an axe and planting tobacco seedlings with a hoe (Walsh 1989). Tobacco was grown on the same plot of land for about two to three years followed by corn and grain for another two to three years, when decreasing soil fertility led to abandonment (Earle 1992). A new plot was then cleared for cultivation, while the original plot laid fallow for ~20 yr. By that time, the soil was believed to have regained fertility and was put back in cultivation. Because of the long fallow required for tobacco, <20% of the land was cleared at any one time from the late 17th to early 18th century (Froomer 1980, Walsh 1989). In the early 18th century, the long fallow, scarcity of fertile soils, declines in the overseas tobacco market, and population pressure resulted in a shift to more grain crops and less tobacco. Grain, particularly corn (maize) and wheat, could be grown on the sandy, less fertile soils of the Coastal Plain. By this time, agriculture extended into the Piedmont, where both tobacco and grain were grown. In order to accommodate export trade, ports were established on the upper stretches of most tributaries by the 1700s (Gottschalk 1945, Brugger 1988).

1720–1880.—Grain farming necessitated the use of the plow rather than the hoe. By the late 1700s the plow was in general use (Brugger 1988). Between 1783 and 1820, the wooden plow, which cut into the soil ~6 inches (~15 cm), was succeeded by the iron plow, which cut to a depth of 8–10 inches (20–25 cm). After 1840, wooden and iron plows were replaced by the steel plow, which cut deep into the subsoil (Craven 1965). During this period, agriculture consisted mainly of individual small farms where both grain and some tobacco were grown, and livestock was raised (Walsh 1989). Grist mills were established along the Fall Zone, where waterfalls provided power to run the mills. As crops were grown farther inland, they had to be transported overland. Wheat, the largest export crop, was shipped as flour to the West Indies and South America. Whereas shipping to Europe was relatively safe because of English convoy protection, Caribbean waters were unprotected from piracy. Smaller, highly maneuverable, fast ships, rather than the larger boats used for the tobacco trade, were necessary for transport. This led to the development of a large shipbuilding industry in several counties adjacent to the Chesapeake (Brugger 1988).

Land transport required that forests be cleared for additional roads. Demand for wood resulted in additional deforestation. By the middle of the 18th century, the deep-water channels of the upper tributaries were clogged with eroded soil from deforested land, necessitating the movement of established ports downstream. The port of Baltimore located on the Patapsco River in 1706, was moved downstream in 1768, and to its present location in 1799, where it has been periodically dredged since 1815 (Gottschalk 1945). In 1870, the U.S. Army Corps of Engineers began deepening tributaries from the Elk to the Pocomoke River (Brugger 1988). Since European settlement, there has been shown a two- to tenfold increase in sedimentation rates related to land use (Brush et al.1982, Brush 1984, Brush 1989).

In the early 19th century, crop rotation and the application of burnt marl and lime to worn out fields eliminated fallow farming. Guano, introduced as a fertilizer in 1832, was widely used by the 1850s, allowing cultivation of infertile soils and erodible slopes not

TABLE 1. Descriptions of core locations.

Tributary	Core site	Water depth (m)	Sediment type	Average salinity (g/kg)	SAV observed	Shoreline description
Furnace Bay	embayment	<1.8	silty sand	<1	*Myriophyllum spicatum*	forested and residential
Gunpowder River	upper	1.4	fine organic silt	<5	none	residential with piers
	lower	1.2	fine organic silt	<5	none	*Phragmites, Quercus*
Middle River	upper	2	fine organic silt	<3	none	residential with *Quercus*
	middle	2.5	silt, fine sand	6	*Zannichellia palustris, Myriophyllum spicatum*	scattered residences and marina
	lower	2.6	fine organic silt	6	*Myriophyllum spicatum, Vallisneria americana* several hundred meters north of site	residential; some *Typha*
Back River	upper		sand	<3	none	*Typha* marsh and large landfill
	middle	1.5	fine organic silt	6	none	*Typha* marsh
	lower		fine organic silt	6	none	*Phragmites* marsh
Rock Creek	upper	1.2	sand and silt	<1	none	residential, deciduous forest
	middle	3	fine organic silt	5	none	residential
	lower	2	fine organic silt	5	none	dense residential
Severn River	upper	1	fine organic silt	<1	none	residential; Cyperaceae marsh; *Quercus* forest
	middle	2.2	fine organic silt and sand	6	none	deciduous forest; *Juncus*
	lower	2.2	fine organic silt	6	none	disturbed deciduous forest; *Phragmites*
Patuxent River	upper	1	fine organic silt	<1	none	fresh water tidal marsh
	lower	?	sand and mud	13	none	
Elk River	middle	1.3	mud	<3	none	deciduous forest; *Phragmites*
	middle–lower	0.6	fine organic silt and peat	<1	*Vallisneria americana*	fresh water tidal marsh; *Zizania, Pontederia* dominant
	lower	1.6	fine organic silt	<3	*Myriophyllum spicatum*	sandy beach; deciduous forest
Sassafras River	upper	1.1	fine organic silt	<1	none	deciduous forest
	middle	1.3	fine organic silt	<3	none	deciduous forest; *Scirpus americanus* and *Phragmites*
	lower middle	1.4	fine organic silt and sand	<3	none	deciduous forest; *Phragmites*
	lower	3	fine organic silt	<3	*Myriophyllum spicatum, Potamogeton crispus*	deciduous forest
Chester River	upper	1.5	fine organic silt	<1	none	freshwater wetland; *Pontederla cordata*
	middle	1	sand and peat	8	*Potamogeton perfoliatus, Ruppia maritima*	*Quercus-Pinus* forest; *Spartina-Acnida* marsh
	lower	1.6	fine organic silt	10	*Zannichellia palustris, Ruppia maritima*	*Phragmites* marsh
Langford Creek (lower Chester River)	upper	?	fine organic silt	6	none	
	lower (mouth)	1	fine organic silt	9	*Zannichellia palustris*	*Quercus-Acer* forest
Choptank River	upper	?	fine organic silt			
	middle	?	fine organic silt			
	lower	?	fine organic silt and fine sand			
Nanticoke River	upper	1.5	fine organic silt	<3	none	brackish-fresh tidal marsh; *Scirpus* and *Phragmites*
	middle	2.2	fine organic silt	13	none	marsh
	lower	2.2	fine organic silt	13	*Ruppia maritima*	extensive marsh; *Spartina alterniflora, Iva frutescens*

TABLE 1. Continued.

Tributary	Core site	Water depth (m)	Sediment type	Average salinity (g/kg)	SAV observed	Shoreline description
Pocomoke River	lower	1	peat and fine organic silt	15	none	Cyperaceae marsh
	mouth	1.6	peat and fine organic silt	17	none	*Spartina* marsh
Pocomoke Sound	bay	2.2	sand and fine organic silt	17	*Ruppia maritima*	*Phragmites, Pinus taeda*

previously farmed (Earle 1992). During this period, the amount of land under cultivation increased from 20% to 40–50% (Froomer 1980, Brush 1989, Walsh 1992).

1880–1930.—By the late 19th century, techniques to increase soil fertility using guano, processed bones, and imported phosphate, and steadily increasing populations, led to cultivation of 60–80% of the region (U.S. Census Data 1850–1975). Many small farms were combined into large commercial operations. The widespread use of heavy machinery and a deep plow zone of 12 inches (~30.5 cm) led to greater soil erosion and the highest sedimentation rates in Chesapeake Bay and its tributaries (Brush et al. 1982, Brush 1989, Cooper 1995; G. Brush, *unpublished data*). Guano continued to be used as the main fertilizer, until chemically produced nitrogen fertilizers became available after World War I. From 1920 on, chemical fertilizers were used extensively, except during World War II when compost and animal manure were used as substitutes (Stevenson et al. 1999).

1930.—From the turn of the century until after the 1930s, farms were abandoned mainly in the Piedmont because of depressed economic conditions, and forests began to regenerate. At the same time, wetlands were drained on the Eastern Shore for arable land. Today 30% of the Eastern Shore of Maryland and 40% of the eastern Piedmont are forested (Powell and Kingsley 1980, Robbins et al. 1989). Soil conservation, such as no-till farming, has been practiced since the 1940s. Fertilizers continue to be used extensively, and pesticides were introduced in the 1950s. DDT was banned in 1972, but chemicals such as 2–4D are still used on agricultural land and urban/suburban lawns.

TABLE 2. Major periods of land use in the study area.

Dates	Description
Pre-1630	Area entirely forested except for serpentine barrens, tidal marshes, and small Indian clearings; <1% land cleared
1630–1720	Initial European settlement; <20% land cleared
1720–1880	Developing agriculture; 20–40% land cleared
1880–1930	Intensive agriculture; 60–80% land cleared, mechanized agriculture resulted in deep plow zone
1930–present	Farm abandonment; 40% land under cultivation; wetlands drained; soil conservation practices begun (Afforestation has resulted in about 40% of area forested today.)

Increased sediment loading was detrimental not only to navigation, but the resulting turbidity also impacted estuarine ecology. Chemicals from fertilizers attached to small sediment particles increased turbidity, eutrophication, and anoxia (Officer et al. 1984, Cooper and Brush 1991, Smith et al. 1992, Cooper 1995); resulting in a shift from a predominantly benthic–pelagic to a planktonic and heterotrophic system (Brush and Davis 1984, Boynton 1997, Brush 1997)

In addition to regional agricultural land use, local activities also affected estuarine water quality. Charcoal, produced in the northern Bay area for the manufacture of iron from the early 18th to 19th century, resulted in high sedimentation rates in tributaries draining those areas (Brush 1989). Chrome and iron were mined both on the Western and upper Eastern shores throughout the 19th century (Vokes and Edwards 1974). Canneries were established in the northern Bay in the mid-1800s (Gardner et al. 1988). Newspapers at the time reported that discharge from canneries were contributing to pollution. Gravel was quarried in the upper Chesapeake in the mid- to late 20th century (Davis 1985, Brush 1989). Railroad and road building contributed increased sediment loads to the estuary (Khan and Brush 1994, Pasternack and Brush 1998), and initial urbanization prior to paving and asphalting resulted in sediment peaks in receiving waters associated with changing hydrographs (Wolman 1967).

METHODS

Thirty-six sediment cores, from the upper, middle, and lower stretches of eight tributaries were collected in 1987, using a hand-operated piston corer. The cores are 5.4 or 6.6 cm in diameter and range in length from 0.3 to 2 m. Core locations (Fig. 1) were chosen where SAV was reported (Orth et al. 1985) or where it was observed growing at the time the cores were collected. If, as was generally the case, none was reported or observed, cores were collected close to shore in soft, silty sediments suitable for plant growth. Cores were transported in their plastic liners to the laboratory where they were stored at 4°C until extruded. Once extruded from the liner, each core was split in half

TABLE 3. Pollen horizons used for dating sediments in the Chesapeake region (Brush 1984).

Time horizon	Change in land use/vegetation	Indicator in sediment core
1930 (1923–1937)	demise of American chestnut	absence of chestnut pollen
1910 (1908–1912)	decline of American chestnut because of disease	significant decrease in chestnut pollen
1840 (1820–1860)	40–50% land cleared	ragweed pollen >10%; oak to ragweed pollen ratio <5 (generally <1)
1780 (1760–1800)		
1700 (1720–1740)	<20% land cleared (generally <5% of land cleared for initial and tobacco farming)	ragweed pollen >1% to <10%; oak to ragweed pollen ratio >5 (generally >10)
1730 (1720–1740)		
1650 (1640–1660)		
1634 (1620–1640)		
pre-European	Indian agriculture	ragweed pollen <1% or absent

Notes: The history of land use differed geographically, so that the date assigned to a horizon with a particular concentration of ragweed is not similar for all cores throughout the region. The history of land use was obtained from U.S. Bureau of Census data, U.S. Bureau of Agricultural Census data, tax assessment records, land grant records, early maps, aerial photographs (since 1937), and miscellaneous historical studies. The history of chestnut decline and demise also differed from place to place as the disease spread (Anderson 1974).

lengthwise and described. Each half was cut into 2-cm samples; one sample was used for seed analysis and the other for pollen dating. Samples were sealed in ziploc bags and stored at 4°C until analyzed.

Comparisons were made with 20 cores from four previously studied areas: Furnace Bay (Davis 1985), Patuxent River (Brush and Davis 1984), Choptank River (G. Brush, *unpublished data*), and the Susquehanna Flats (F. Davis, *unpublished data*).

Seed and pollen extractions

Seeds were extracted from sediment by soaking one-half of the 2-cm sample (8.5 or 10.4 cm depending on the core diameter) in 10% nitric acid, and running the disaggregated sample through a column of nested 0.8-mm and 0.25-mm sieves. All seeds in the residue were placed in water in a petri dish and examined under 15×–40× magnification. Influxes of seeds (the number of seeds deposited per 100 square centimeters per year) were computed by multiplying the concentration of seeds by the appropriate sedimentation rate.

Pollen was extracted from the sample by washing 1.5 mL of sediment in hydrochloric acid, hydrofluoric acid, and a mixture of sulfuric acid and acetic anhydride in order to remove carbonates, silicates, and organic material. The residue was washed in glacial acetic acid, distilled water, and alcohol, and stored in 25 mL of tertiary butyl alcohol. After careful mixing, 0.1-mL aliquots were extracted from the 25-mL mixture of pollen residue and tertiary butyl alcohol. All pollen were counted in an aliquot, and the concentration (number of pollen grains per millilter of sediment) calculated. Percentages of ragweed and oak pollen, based on the total pollen sum, and the ratio of ragweed to oak pollen were also calculated.

Dating sediment cores

Sediment layers within cores were dated by identifying the agricultural horizons, recognized by changes in ragweed and oak pollen (Table 3). At least one agricultural horizon was identified in all cores. The chestnut horizon, dated from the historical record of the demise of American chestnut due to a blight (Anderson 1974), was identified in one core. The basal sediment was radiocarbon dated for one core in each tributary.

Calculating influxes

Cores with both agricultural and carbon-14 dated horizons (Table 4) provide average sedimentation rates between dated horizons for calculating influx values (number of seeds deposited per unit area per unit time) for pre- and post-European time. However, because sediment deposition in the shallow estuary is highly variable both spatially and through time, it was necessary to estimate sedimentation rates for individual layers in order to obtain realistic estimates of seed influxes. This was done by adjusting average sedimentation rates between dated horizons using the total pollen concentration in each sample (Brush 1989). The method is based on both pollen and silt particles having similar hydrodynamic properties (Brush and Brush 1974, Brush and Brush 1994), most pollen being introduced into the estuary atmospherically while silt enters through river discharge (Brush 1989), and the assumption that during periods of similar vegetation cover, the influx of pollen is more or less uniform, at least within the time resolution of the cores. Thus a high pollen concentration in a core sample signifies lower sediment deposition, and conversely a low pollen concentration signifies high sedimentation. Sedimentation rates for individual layers of the core also allow each layer to be dated by dividing the length of the increment of sediment by the sedimentation rate (Fig. 2). However, whether dating is based on isotopic or pollen analysis, caution must be exercised in the interpretation of chronologies in shallow estuaries because of scouring and redeposition of fine sediments. These processes are not always visible in the stratigraphy, although aberrations in the ragweed profile indicate discontinuities in sedimentation (G. Brush, *unpublished data*).

It was necessary to determine an average sedimentation rate for presettlement time in cores with no basal

TABLE 4. Pollen and carbon-14 dated horizons for sediment cores.

Location	Core	Depth (cm)	Age (ybp)§	Method
Back River	BR3B	40–42	300 ± 40	ragweed
Back River	BR3B	74–80	1020 ± 110	carbon-14
Chester River	CHR6C	66–68	300 ± 40	ragweed
Chester River	CHR6C	80–88	600 ± 220	carbon-14
Choptank River†	HP3	79–80	300 ± 40	ragweed
Choptank River†	HP3	100–103	1030 ± 130	carbon-14
Elk River	ER6A	24–26	300 ± 40	ragweed
Elk River	ER6A	58–60	1420 ± 120	carbon-14
Furnace Bay‡	FB2	44–46	60 ± 10	chestnut
Furnace Bay‡	FB2	118–120	210 ± 40	ragweed
Furnace Bay‡	FB2	130–132	260 ± 40	ragweed
Furnace Bay‡	FB2	200–210	1820 ± 100	carbon-14
Middle River	MR6	16–18	260 ± 40	ragweed
Middle River	MR6	156–160	2150 ± 100	carbon-14
Rock Creek	RC10	66–68	210 ± 20	ragweed
Rock Creek	RC10	108–110	260 ± 40	ragweed
Rock Creek	RC10	142–146	1030 ± 140	carbon-14
Severn River	SR1A	62–64	260 ± 40	ragweed
Severn River	SR1A	102–106	1690 ± 60	carbon-14
Sassafras River	SAS2	30–32	300 ± 40	ragweed
Sassafras River	SAS2	74–79	1570 ± 90	carbon-14

Note: The pollen horizons are described in Table 3.
† (Brush 1987)
‡ (Davis 1985)
§ Dates obtained by carbon-14 dating are means ± 2 SE; dates obtained by chestnut or ragweed dating are means ± a range derived from the first order propagation of error. Dates are expressed as years before present (ybp).

carbon-14 date. Years before present (ybp) were plotted against depth for all cores with a basal carbon-14 date (Fig. 2). Dates obtained from pollen-derived sedimentation rates (solid line) for each level of a core follow for the most part a straight line connecting carbon-14 and ragweed dated depths (squares). Based on these age–depth curves, an average presettlement sedimentation rate of 0.1 cm/yr was used to estimate pre-European influxes of seeds for those cores lacking a basal carbon-14 date, which were used in compilation of the maps. Post-European influx values are based on sedimentation rates between agricultural horizons, identified in all cores, and the time the core was collected.

RESULTS

Present SAV bed and SAV seed distributions

During collection of cores, SAV was observed growing at only a few locations (Table 1). The most common species were *Zannichellia palustris, Myriophyllum spicatum,* and *Ruppia maritima.* Distributions of seeds in the top 2–4 cm of the sediment cores (surface sediments) (Fig. 3) are consistent with our field observations as well as with mapped beds from aerial photography (Orth and Nowak 1990). Both mapped SAV beds and SAV seeds show *Vallisneria americana, Elodea canadensis, Najas gracillima,* and most species of *Potamogeton* occurring in the upper, fresher tributaries; *Potamogeton perfoliatus, Najas guadalupensis,* and *Zannichellia palustris* in the mesohaline areas; and *Ruppia maritima* and *Zostera marina* in the more saline areas.

Twelve native and one introduced species of SAV are represented in the fossil record (Table 5). Seeds of *Ceratophyllum demersum* and some species of *Potamogeton,* both important native taxa, are absent in the sediment cores. Several exotic species that have become widespread also are not present in the seed record, such as *Potamogeton crispus* introduced in the 1800s, *Najas minor* in 1930, and *Hydrilla verticillata* in 1982.

Past SAV seed distributions

Species richness.—Histograms of the presence of SAV seeds in each sediment core show species richness with depth in the different tributaries through time (Fig. 3). The greatest number of species occurs in the low salinity northern tributaries and upstream reaches of all tributaries. Furnace Bay and the upper Patuxent River are the freshest areas and contained the highest number of species, 10 and 8, respectively. The Choptank River with highest salinity has fewest species. *Zannichellia palustris* is the most common species, followed by *Najas guadalupensis.* Both species occupy fresh and brackish areas. *Vallisneria americana, Elodea canadensis,* and *Najas gracillima* are restricted generally to fresh water environments, while *Ruppia maritima* is limited to mesohaline water, and *Zostera marina* to near sea water salinity. There are no fossil or historical records of SAV in the marsh-surrounded Nanticoke and Pocomoke Rivers, except for a few very recent occurrences in the Pocomoke.

Tributary profiles.—Profiles of seed influxes and sedimentation rates for one core in each of eight tributaries plotted against depth and time (Figs. 4–7) show

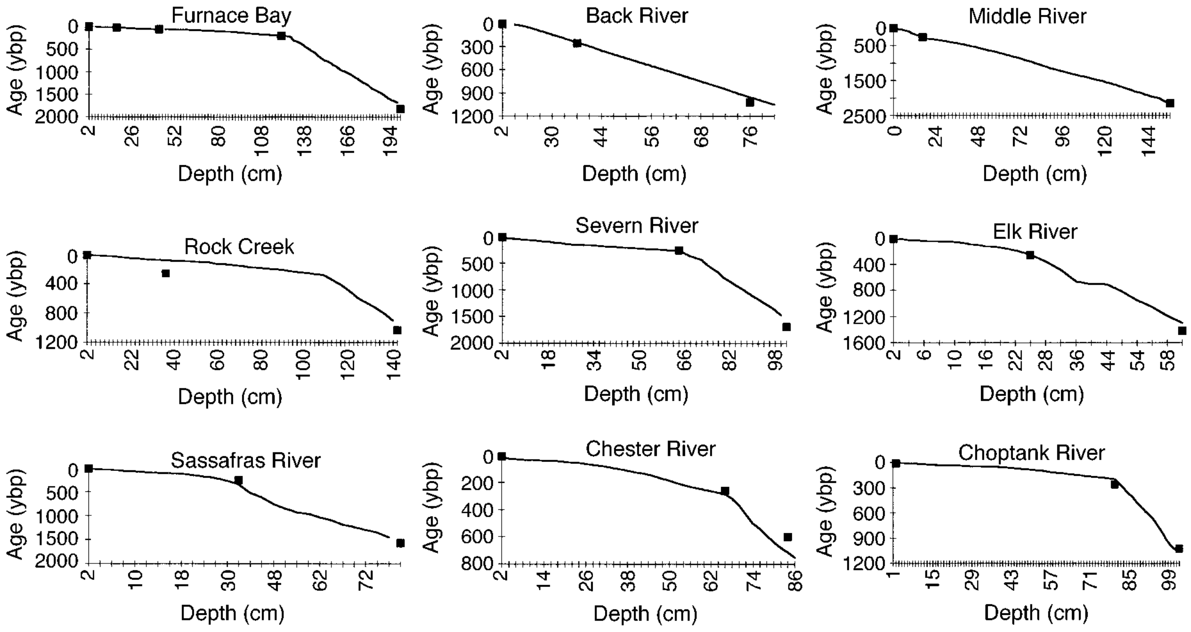


FIG. 2. Age–depth curves for sediment cores with a pollen-dated horizon and a basal carbon-14 date. Black squares indicate pollen and carbon-14 dated horizons. The lines indicate dates determined from pollen-derived sedimentation rates (Brush 1989). Dates (years before present, ybp) are given in Table 4.

temporal changes in numbers of species and their abundances. Core locations within tributaries (Fig. 1) vary, some being upstream and others downstream, because the basis for selection was a long time span and intact stratigraphy. The area drained by different tributaries ranges from 27 to 955 km. The surface layer of each core is dated 1987, the time of collection, except for Furnace Bay, which was collected in 1980. Seed profiles were graphed and zoned by optimal splitting of the data set using the psimpoll 3 program (Bennett 1998). The sedimentation rate profile was not zoned.

There is a great deal of variation among tributaries. In general, SAV communities are dominated by a single species; occasionally there is a codominant. *Zannichellia palustris* is dominant in all tributaries except the low salinity Furnace Bay, where *Vallisneria americana* is dominant. The Sassafras River, also in the fresher part of the Bay, is characterized by five species, four of which are more or less equally abundant.

1. Furnace Bay.—Furnace Bay (Fig. 4a), a small freshwater (salinity < 1g/kg) embayment in the upper Chesapeake Bay, slightly northeast of the Susquehanna River, drains 57 km. A 2-m core spanning 1800 yr is divided into six zones. Of seven species retrieved from the sediment, the number present at any one time varies between none and six. Pre-European time is contained in zone F-1 and about half of F-2. None of the species are abundant, but *Vallisneria americana* is dominant most of the time. A large decline in *Najas gracillima* followed by sporadic occurrences of *Najas guadalupensis* separates F-1 from F-2. Local deforestation for charcoal production from 1716 to 1887, along with piecemeal farming, contributed to higher sedimentation during initial European settlement (upper part of F-2). However, there was no obvious change in SAV. Sedimentation continued to increase from ~1880 until the 1900s (F-3), augmented by the construction of a railroad, completed in 1880, that crossed a creek in the drainage area. From 1900 to the mid-1930s (F-4), still in the period of most intensive agriculture, sedimentation rates reached their highest levels. A sewage treatment plant began discharging wastewater into a creek draining into Furnace Bay in 1920 (Davis 1985). Beginning ~1870 and extending to ~1930 (F-3 and F-4), *V. americana* peaked and declined three times. *N. gracillima*, the only other species present at the time of the first large rise in *V. americana* (F-3), was later replaced by *E. canadensis* (F-4). No other species were

→

FIG. 3. Histograms of the occurrence of seeds for each species in all cores analyzed plotted against depth. Black portions indicate the depths in the sediment cores at which seeds were present. Within tributaries, histograms are arranged from the upper (fresh) stretch on the left to lowermost (brackish) stretch on the right. The Nanticoke and Pocomoke Rivers are not included because no seeds were present in those sediments; Susq. Fls. = Susquehanna Flats. Species are listed in order from those that occupy freshwater habitats, starting with *Vallisneria americana,* to those that occupy brackish habitats, ending with the saline *Zostera marina.*

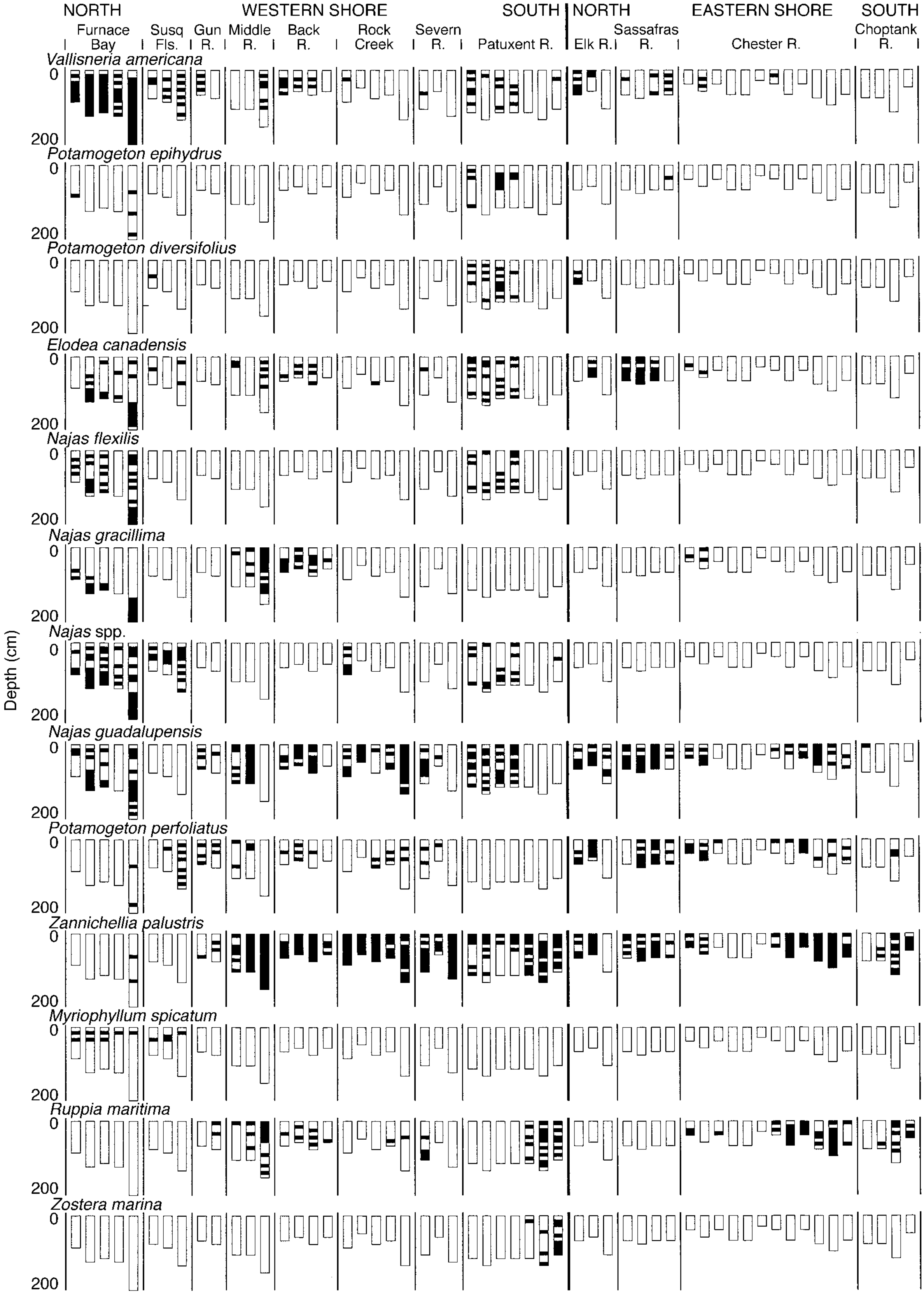

NORTH
WESTERN SHORE
SOUTH
NORTH
EASTERN SHORE
SOUTH
Furnace Bay
Susq Fls.
Gun R.
Middle R.
Back R.
Rock Creek
Severn R.
Patuxent R.
Elk R.
Sassafras R.
Chester R.
Choptank R.
Vallisneria americana
Potamogeton epihydrus
Potamogeton diversifolius
Elodea canadensis
Najas flexilis
Najas gracillima
Najas spp.
Najas guadalupensis
Potamogeton perfoliatus
Zannichellia palustris
Myriophyllum spicatum
Ruppia maritima
Zostera marina
Depth (cm)
0
200

TABLE 5. Species of SAV (submerged aquatic vegetation; all seed-producing angiosperms) found in Chesapeake Bay.

Species name	Common name	Salinity range
Native species		
Ceratophyllum demersum	coontail	tidal fresh
Heteranthera dubia	water stargrass	tidal fresh
Najas muenscheri	(no common name)	tidal fresh
Potamogeton amplifolius	large-leaved pondweed	tidal fresh
P. diversifolius	variable pondweed	tidal fresh
P. epihydrus	floating pondweed	tidal fresh
P. gramineus	grassy pondweed	tidal fresh
P. nodosus	long-leaved pondweed	tidal fresh
Elodea canadensis	common waterweed	tidal fresh–oligohaline
Najas flexilis	northern naiad	tidal fresh–oligohaline
N. gracillima	slender naiad	tidal fresh–oligohaline
Potamogeton pusillus	slender pondweed	tidal fresh–oligohaline
Vallisneria americana	wild celery	tidal fresh–oligohaline
Potamogeton pectinatus	sago pondweed	tidal fresh–mesohaline
Najas guadalupensis	southern naiad	oligohaline–mesohaline
Potamogeton perfoliatus	redhead grass	oligohaline–mesohaline
Zannichellia palustris	horned pondweed	oligohaline–polyhaline
Ruppia maritima	widgeon grass	mesohaline–polyhaline
Zostera marina	eelgrass	mesohaline–polyhaline
Exotic species (time of introduction)		
Egeria densa (mid-1900s?)	waterweed	tidal fresh
Najas minor (1930)	(no common name)	tidal fresh
Hydrilla verticillata (1982)	hydrilla	tidal fresh–oligohaline
Potamogeton crispus (mid-1800s)	curly pondweed	tidal fresh–oligohaline
Trapa natans (mid-1800s)	water chestnut	tidal fresh–oligohaline
Myriophyllum spicatum (~1900)	Eurasian watermilfoil	tidal fresh–mesohaline

Notes: The four salinity range categories are: tidal fresh (0–0.5 g/kg); slightly brackish or oligohaline (0.5–5 g/kg); moderately brackish or mesohaline (5–18 g/kg); high salinity polyhaline (18–30 g/kg). Species are arranged in alphabetical order as native or exotic according to increasing salinity tolerance. Sources are Hurley (1990) and Batuik et al. (1992). Species found as seeds in the fossil record are listed in bold type.

present during this time. Beginning ~1930 and continuing to 1960 (F-5), regional farm abandonment and soil erosional conservation practices resulted in decreased sedimentation rates. The completion of Route 40 in 1940 also meant a decrease in sedimentation from the previous period of construction. Although more species were present in Furnace Bay during F-5 than at any other time, *V. americana* decreased in abundance by about one-fourth, while *N. guadalupensis* reached maximum abundance. The exotic *Myriophyllum spicatum* appeared in the seed record, consistent with its reported entry into the upper estuary (Stevenson and Confer 1978). *V. americana,* which is more turbidity tolerant than most SAV (Stuckey 1971), was probably able to outcompete other species during the period of high sedimentation. However, when sediment decreased, all species could thrive in the less turbid waters that were also being enriched with nutrients from sewage effluent. Local stone and gravel quarrying begun in 1952, and the construction of Interstate 95 completed in 1960, led to increased sedimentation rates during the last few decades (F-1). In 1972, Hurricane Agnes impacted salinities and sedimentation in the upper Bay. Seeds of *V. americana* disappeared around 1960. Seeds of all other species disappeared in the 1960s and 1970s, consistent with the historical record of the disappearance of SAV in the upper Chesapeake Bay.

2. Middle River.—Middle River (Fig. 4b), a small tributary close to Baltimore City, drains an area of 38 km, all in the Coastal Plain. A 1.5-m core collected at the mouth of the river, where the average salinity is 6 g/kg, spans 2150 yr. The SAV seed profile is divided into eight zones. Because of low sedimentation rates, variations that may have occurred in SAV over the last two centuries, related to land use, are not seen. Significant changes in SAV seed abundances, particularly in *Zannichellia palustris,* occurred throughout pre-European time (M-1 through M-5), with a spike in *Z. palustris* ~1300 ybp. At the time of European settlement (M-6), there was a sharp rise in *Z. palustris* and *Najas guadalupensis.* From the mid-1700s to the 1900s (M-7), sedimentation rates decreased and species declined in abundance or disappeared. After 1900 (M-8) *Z. palustris* peaked and all species increased, except

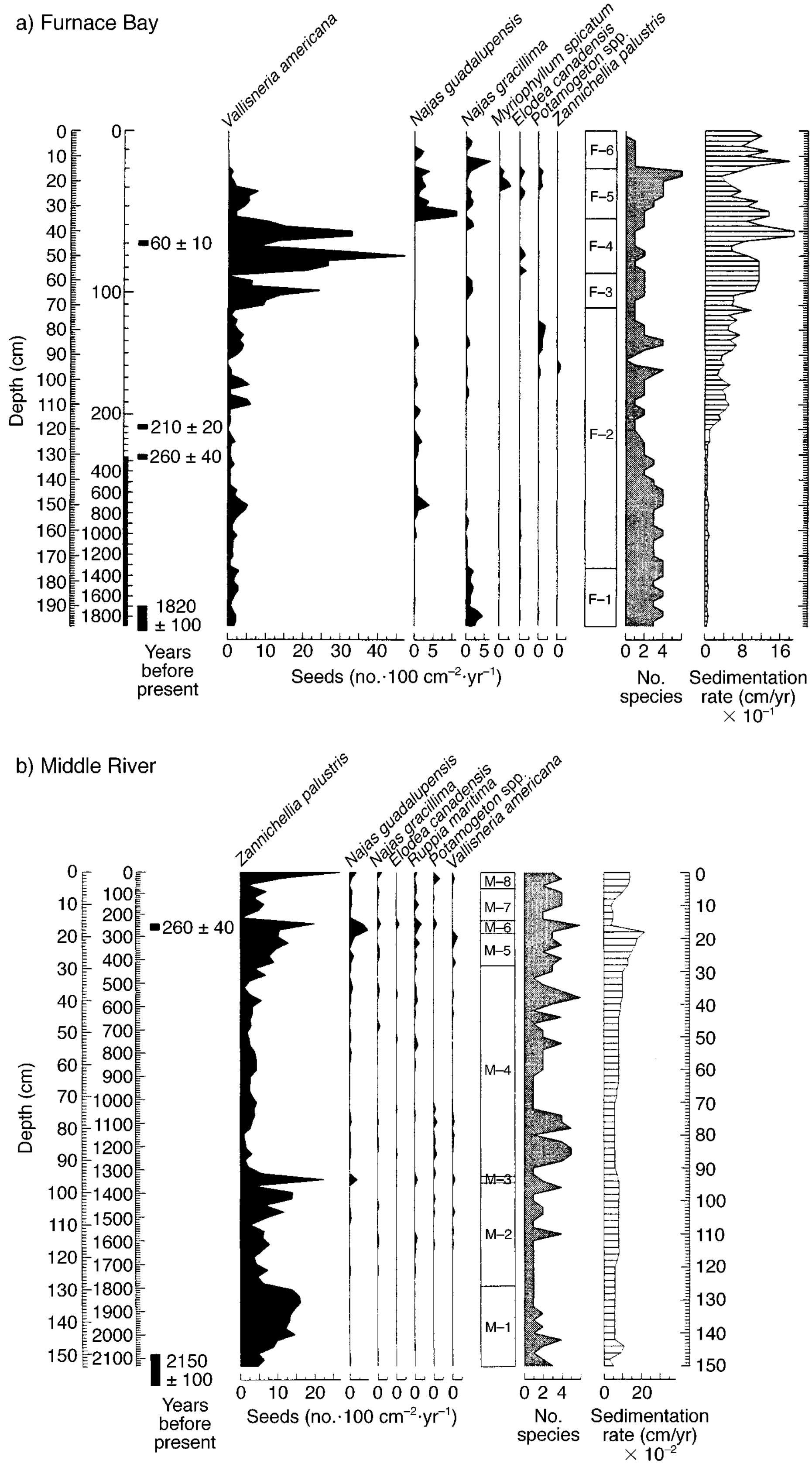


FIG. 4. Seed influxes plotted against depth and time for (a) Furnace Bay and (b) Middle River. Values are for one core from each tributary.

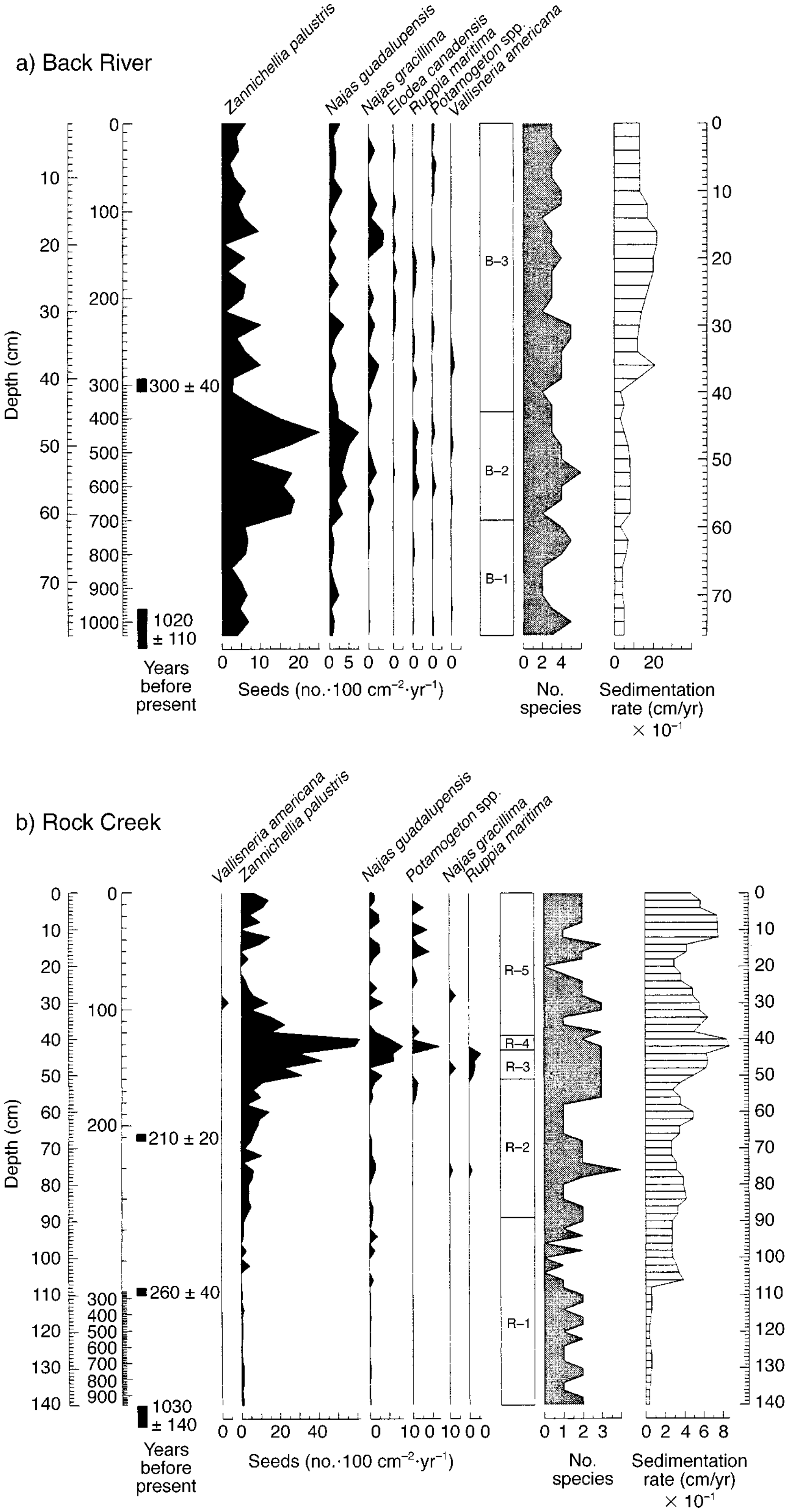


FIG. 5. Seed influxes plotted against depth and time for (a) Back River and (b) Rock Creek. Values are for one core from each tributary.

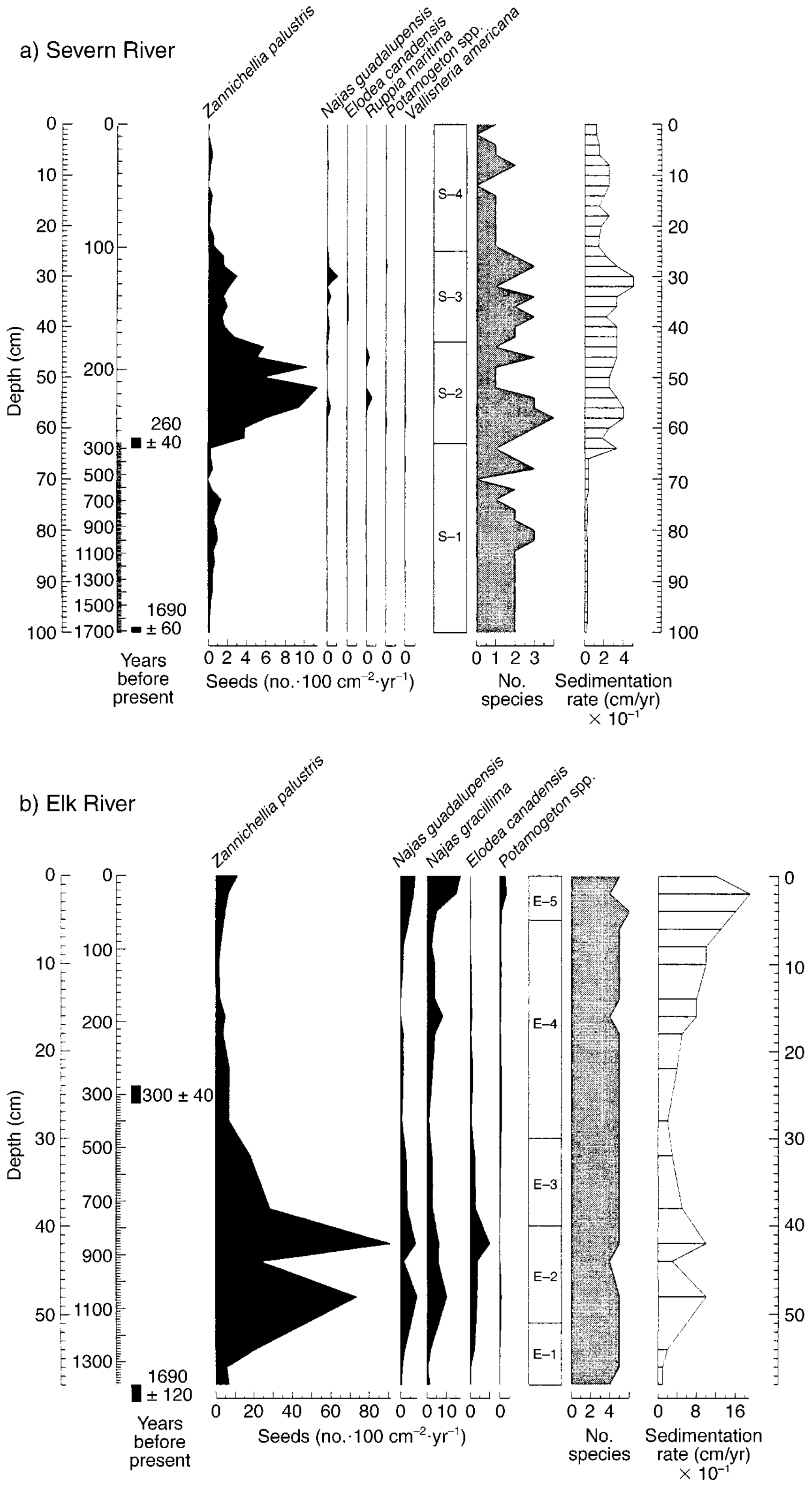


FIG. 6. Seed influxes plotted against depth and time for (a) Severn River and (b) Elk River. Values are for one core from each tributary.

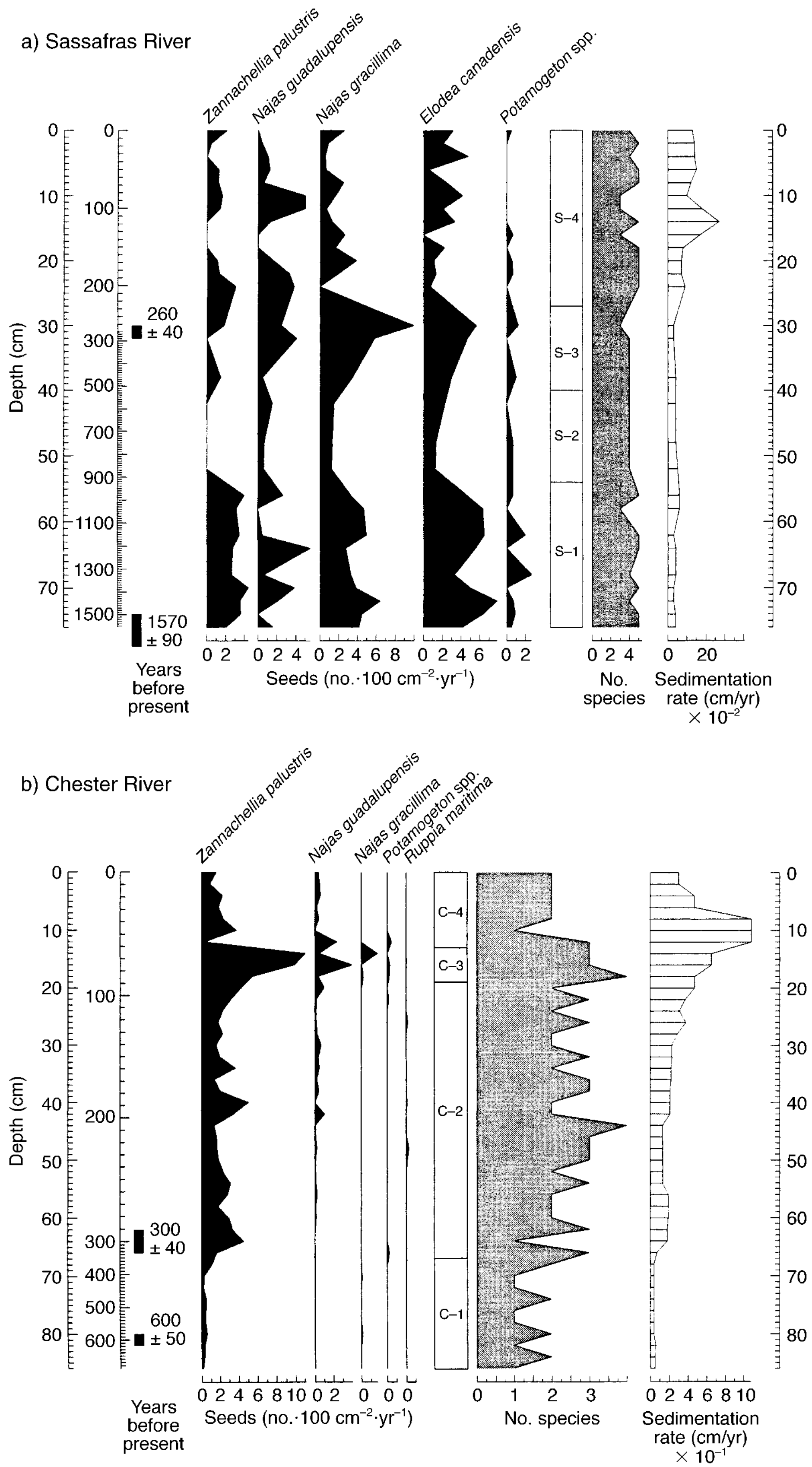


FIG. 7. Seed influxes plotted against depth and time for (a) Sassafras River and (b) Chester River. Values are for one core from each tributary.

Elodea canadensis which disappeared at the time of European settlement.

3. Back River.—Back River (Fig. 5a), located close to Baltimore City, drains 158 km, and extends into the Piedmont. The core, collected at the mouth where the average salinity is 6 g/kg, is 78 cm long, and covers >1000 yr. The seed profile is divided into three zones, with a total of seven species fluctuating between two and four. All species increased in abundance from 700 to 350 ybp (B-2). The entire period since European settlement is contained in B-3, extending from ~350 ybp to 1987. At the beginning of European settlement, there are large decreases in *Zannichellia palustris* and *Najas guadalupensis.* The zone is similar throughout except for an increase in *Najas gracillima* from about 1830 to 1880.

Back River watershed became heavily industrialized and urbanized in the 20th century. The Back River Sewage Treatment Plant, serving metropolitan Baltimore, is situated 2 km downstream from the headwaters. In 1912, it began discharging secondarily treated effluent into the river. Sediment cores collected downstream from the plant show the disappearance of all SAV after the early 1900s (Fig. 3). However, cores close to the mouth are unaffected. Chlorophyll measurements made along transects of the river at various times since the plant has been in operation show highest concentrations in the upper and middle estuary, and lowest at the mouth. A black, gelatinous, highly organic layer of sediment from 40- to 70-cm thick occurs in the vicinity of the plant and diminishes toward the mouth (Brush 1984). Hydrodynamic studies of Back River, using rhodamine dye, showed that even with rapid lateral and vertical mixing, 14 d were required for the center of mass of the dye field to move to the mouth of the estuary (C. Flynn and L. M. Brush, *unpublished data*). Thus the hydrodynamics of the river protect the downstream stretch from eutrophication and anoxia related to nutrient input from an upstream source.

4. Rock Creek.—Rock Creek (Fig. 5b), a small tributary off the Patapsco River (Baltimore Harbor), drains 27 km of Coastal Plain, the smallest catchment in the study area. The core, collected close to the mouth of the river where the average salinity is 5 g/kg, is 140 cm long. The seed profile consists of five zones, with six species fluctuating between none and five. Pre-European and early post-European time are included in R-1. Sedimentation rates increased with initial European settlement 260 ybp, but SAV populations did not change. During this time, abundances of *Zannichellia palustris* and *Najas guadalupensis*, the only species in the river, were sparse. From the mid 1700s until around 1820 (R-2), sedimentation rates remained more or less unchanged, *Z. palustris* gradually increased, and other species appeared at different times. From the early to mid-1800s (R-3), sedimentation rates began to rise, and all species increased. From the mid- to late 1800s (R-4), a peak in sedimentation rates was accompanied by peaks in *Z. palustris, N. guadalupensis,* and *Potamogeton spp. Ruppia maritima* dropped out and did not return. From the end of the 1800s to 1987 (R-5), SAV declined in abundance. Sedimentation rates decreased until about the 1950s, and then increased until 1987. In addition to being impacted by regional patterns of agriculture, suburban development, begun along Rock Creek after World War II (U. S. Census data), contributed to higher sedimentation rates in the top 15 cm of the core. Recent historical evidence, not recorded in the core, indicate increased anoxia and the loss of most SAV in the river (Maryland Department of the Environment, *unpublished data*).

5. Severn River.—The Severn River (Fig. 6a), located on the Western shore of the Chesapeake, drains 209 km and extends into the Piedmont. The core, 1 m in length and spanning 1700 yr, was collected in the upstream fresh water (salinity < 1 g/kg) part of the tributary. The seed profile is divided into four zones. Six species, varying between none and four, are preserved in the sediment. During pre-European time (S-1), sedimentation rates were low and uniform. *Zannichellia palustris* occurred in small numbers, accompanied by rare occurrences of one to two other species. Sedimentation rates quadrupled at the beginning of European settlement (S-2) and *Z. palustris* increased tenfold, followed by a large decrease from the late 1700s to late 1800s (S-3). By the mid-1800s, sedimentation rates reached their maximum, accompanied by increases in *Z. palustris* and *Najas guadalupensis.* From the late 1800s to 1987 (S-4), sedimentation rates decreased, and *Z. palustris* was reduced to pre-European numbers. The decline in SAV seeds during post-European time was higher than in any other tributary studied, except for Furnace Bay where all species disappeared from the seed record within the last two decades. The intensity of agricultural activity surrounding the Severn River during the 18th century is reflected in the considerable trading out of Annapolis as early as 1740 (Brugger 1988), and would most certainly have impacted SAV populations in the upstream part of the tributary.

6. Elk River.—Elk River (Fig. 6b), located in the upper Eastern shore where the average salinity is <3 g/kg, drains ~323 km, extending into Delaware. The core, located at the confluence of a tributary and the lower Elk River is 62 cm long and covers 1400 yr. The seed profile consists of five zones representing changes in five SAV species. Species numbers changed little over time. Zone E-2, extending from ~1200 to 800 ybp, shows large increases in all species over the preceding zone E-1. Sedimentation rates were also high. From 800 to ~450 ybp (E-3), all species declined, with the greatest decline in *Zannichellia palustris.* Sedimentation rates also decreased and remained low until ~250 yr ago. Following European settlement, sedimentation gradually increased reaching its highest rate about 1960. From 450 ybp to the mid-1900s (E-4) *Z. palustris, Najas guadalupensis*, and *Elodea canadensis* were greatly reduced. There was little change in *Najas gracillima*. From 1940 to 1987 (E-5), increasing sedimentation rates were accompanied by an increase in all SAV seeds, with the exception of *E. canadensis*, which never recovered since before European settlement. European settlement began in the Elk River around the end of 17th and beginning of 18th century, synchronous with the long decline in SAV abundance. Since European settlement, the watershed has been impacted by a number of local activities. In the early 18th century, charcoal was produced for the Piedmont iron industry and by mid- to late 18th century, Elkton had become a prominent port. In the early 19th century, canneries were established and shipbuilding was important (Brugger 1988). Chrome was mined from local serpentine rocks from 1830 to 1900 (Vokes and Edwards 1974). In 1820, there were newspaper reports of decreased fishing, and in the mid-1800s the water was polluted from cannery wastes and sawdust (M. Jarosewich, *unpublished data*). Construction of the Chesapeake and Delaware Canal connecting Delaware to the Chesapeake Bay was completed in 1829, and later enlarged in 1935 and 1954 (Brugger 1988). Human impact lessened somewhat in the early 20th century as chrome mining ended, state parks were established in the 1950s, and forest growth was encouraged on the peninsulas.

7. Sassafras River.—The Sassafras River (Fig. 7a), located on the Eastern shore, drains 250 km originating in Delaware. The core, 76 cm long and extending over 1570 yr, was collected in the middle to upper part of the river, where the average salinity is <3 g/kg. The seed profile is divided into four zones. Five species are present in the core; four are codominant. All species were present in the pre-European zones S-1 from 1500 to 950 ybp and S-3 from 550 to 250 ybp. *Zannichellia palustris* disappeared in S-2, from 950 to 550 ybp, and all other species decreased. Sedimentation rates were uniformly low in pre-European time. After settlement (S-4), *Najas guadalupensis* dropped out from about 1810 to 1830, as did *Z. canadensis* from 1810 until about 1850. *Potamogeton spp.* disappeared about 1830 and returned about 1960. Sedimentation rates began to increase ~250 yr ago, peaked 150 yr ago, declined 100 yr ago, and have remained more or less unchanged since that time. There are slight decreases in SAV abundance since European time. Land use surrounding the Sassafras River was similar to that for the upper Eastern shore. However, the headwaters of the river extend into Delaware, where dikes and dams built along most of the tributaries since European settlement (Orson et al. 1992) could have offset the full impact of agriculture on the upper part of the Sassafras River, where this core was collected.

8. Chester River.—The core was collected at the mouth of a small tributary draining into the lower Chester River on the Eastern shore (Fig. 7b). The tributary drains 323 km, all in Maryland. The core, collected where the water has a mean salinity of 6 g/kg, is 84 cm in length, spans 600 yr, and is divided into four zones. Five species fluctuate frequently between one and four. During pre-European time, restricted to 300 yr in this core (C-1), species abundances were very low. From European settlement until the 1900s (C-2), sedimentation rates doubled to tripled and *Zannichellia palustris* quadrupled in abundance. About 200 yr ago, *Najas guadalupensis* doubled in abundance. From 1900 until the 1930s (C-3), *Z. palustris* and *N. guadalupensis* more than doubled. *Najas gracillima* appeared, became fairly abundant and dropped out. *Potamogeton spp.* were also present. Sedimentation rates gradually increased. From the 1930s to 1987 (C-4), when sedimentation rates were highest, *Z. palustris* and *N. guadalupensis* decreased, and *Potamogeton* spp. dropped out. The history of land use around the Chester River is similar to the upper Eastern Shore in general. However, proceeding south along the Chesapeake, marshes become more extensive and SAV less abundant.

Species maps.—In order to summarize differences in histories of different tributaries, spatial patterns of species abundance for five different time intervals are shown on maps (Figs. 8 and 9). All cores (Fig. 3) were used in compiling the maps. The time intervals signify different periods of land use (Table 2), except that the most recent interval, 1930–present, was divided into 1930–1970 and 1970–1987, because of the historical records of SAV disappearance after 1970. Seed abundances are shown by different size circles representing average influxes for each time period at each location. Occurrences of the different species in the tributaries are summarized in Table 6.

Zannichellia palustris (Fig. 9b) was the most abundant species with the widest range both in pre- and post-European time. The freshwater species *Vallisneria americana* (Fig. 8a) and *Elodea canadensis* (Fig. 8b) suffered the greatest loss over time, disappearing in all but two and three tributaries, respectively, while *Najas gracillima* (Fig. 8c) showed the least change. *Najas guadalupensis* (Fig. 8d) and *Potamogeton perfoliatus* (Fig. 9a) increased in abundance after 1700. After 1880, *Ruppia maritima* (Fig. 9c) occurred only in the lower brackish parts of the tributaries except for reoccupying the completely brackish Middle River after 1930.

Species extinctions.—The number of years since the last occurrence of seeds for each species at each locality is presented in Table 7. There are only three periods over the last 1000 to 2000 yr when several species disappeared at approximately the same time. Seven species disappeared from three localities in Back River in the very early 20th century, at the time the Baltimore sewage treatment plant began discharging effluent into the upper river. Another three species disappeared from two localities in the same river in the mid-1950s. More

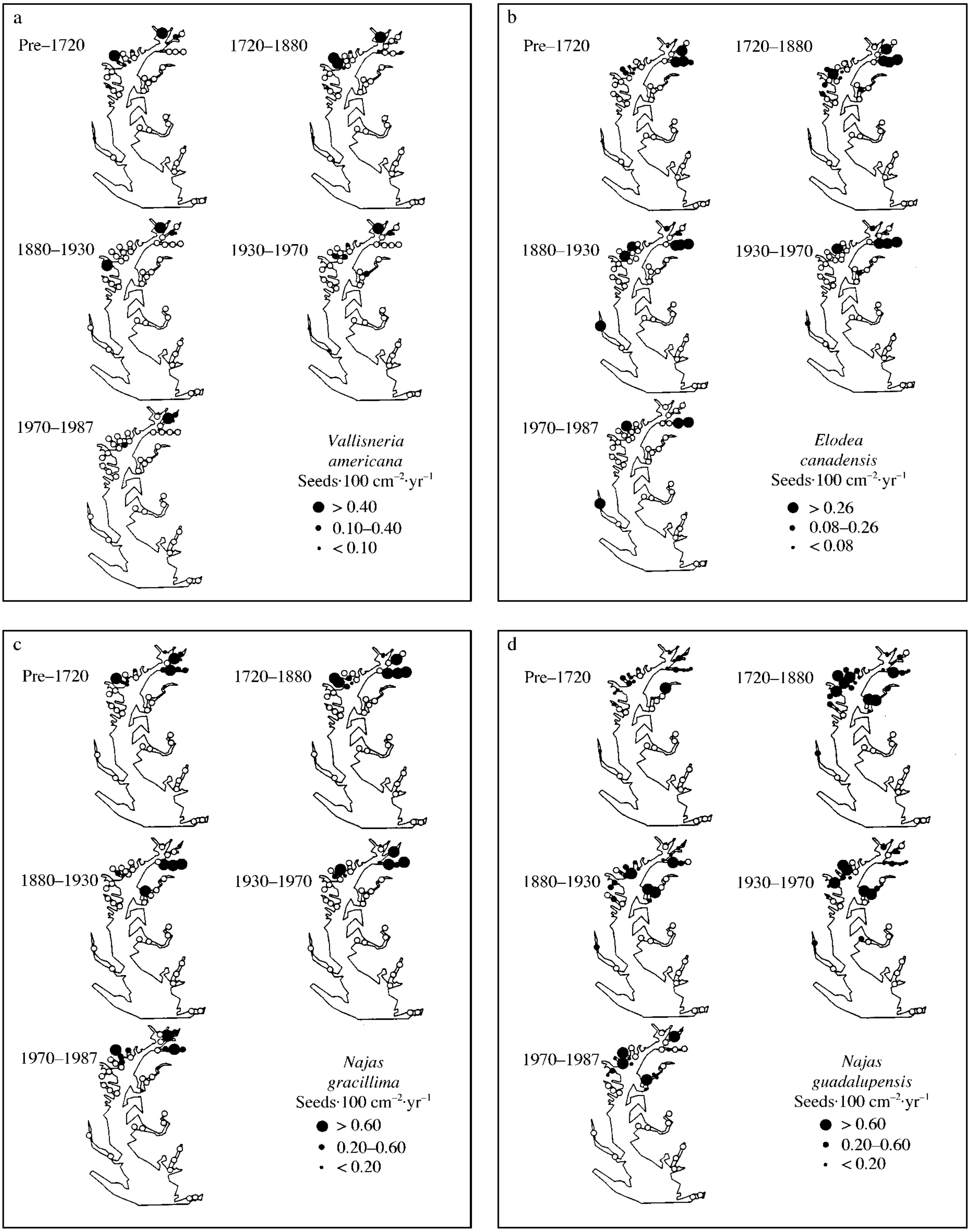
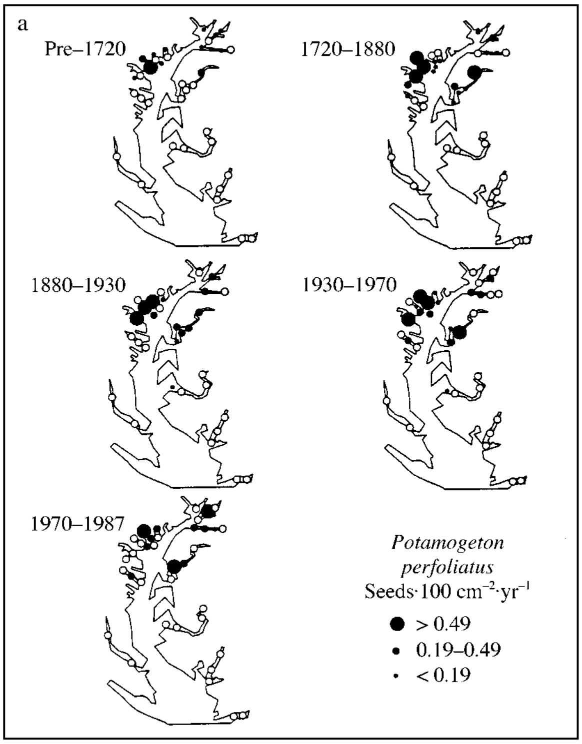
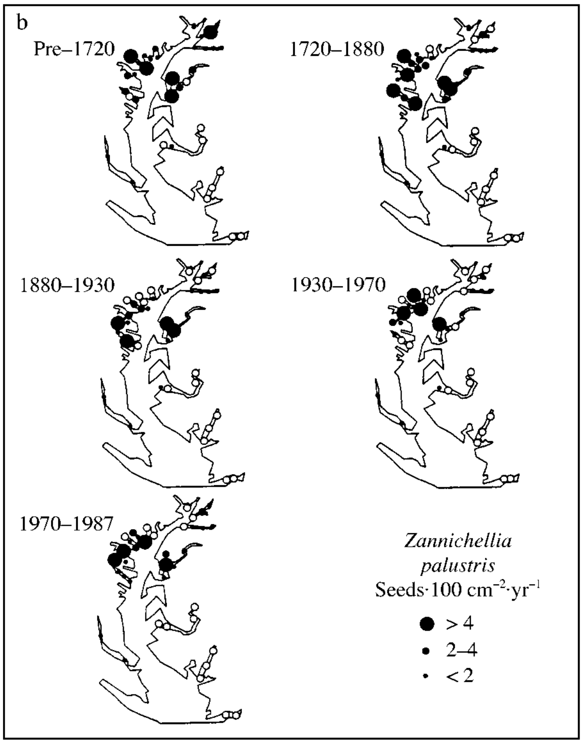


FIG. 8. Maps of seed distributions of seven species for five land use categories. Solid black dots indicate the occurrence of the seeds, and the size of the dot indicates abundance (mean values for all cores for each time period for each new species). Open circles are the locations of cores where seeds were absent. Seed distributions from the Susquehanna Flats location are not placed on the map because it was impossible to date these sandy cores. However, the seed distributions are shown plotted against depth for this area in Fig. 3. Species are: (a) *Vallisneria americana*; (b) *Elodea canadensis*; (c) *Najas gracillima*; and (d) *Najas guadalupensis*.





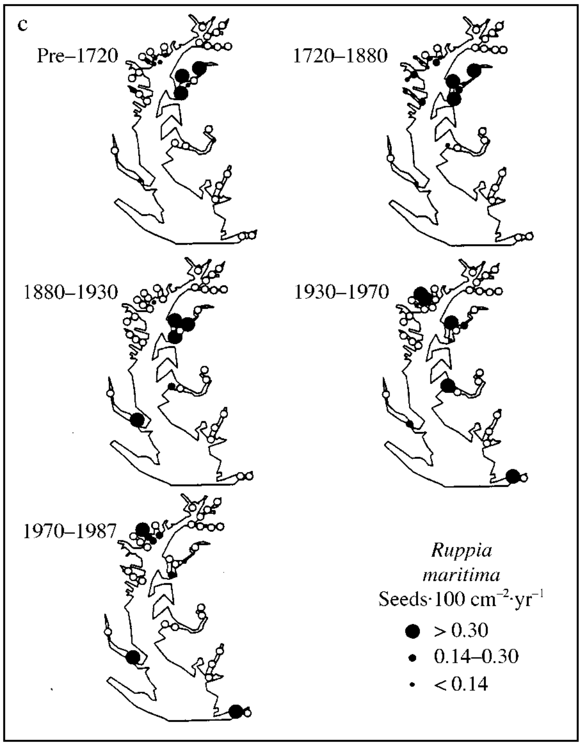


FIG. 9. Maps of seed distributions of seven species for five land use categories. Solid black dots indicate the occurrence of the seeds, and the size of the dot indicates abundance (mean values for all cores for each time period for each new species). Open circles are the locations of cores where seeds were absent. Seed distributions from the Susquehanna Flats location are not placed on the map because it was impossible to date these sandy cores. However, the seed distributions are shown plotted against depth for this area in Fig. 3. Species are: (a) *Potamogeton perfoliatus*; (b) *Zannichellia palustris*; and (c) *Ruppia maritima*.

TABLE 6. Number of tributaries occupied by SAV at different time periods.

Species	Time period				
	pre-1700	1720–1880	1880–1930	1930–1970	1970–1987
Vallisneria americana	8	6	3	6	2
Potamogeton perfoliatus	8	8	8	9	7
Elodea canadensis	7	8	6	6	3
Najas gracillima	6	5	4	4	5
Najas guadalupensis	10	10	9	9	6
Zannichellia palustris	11	11	9	9	8
Ruppia maritima	7	7	4	6	5

widespread extinctions took place during the early 1970s, when eight species disappeared from 18 different locations in eight tributaries, coincident with the historical descriptions of a vast decline in SAV throughout the upper Chesapeake.

DISCUSSION AND CONCLUSIONS

The composition of SAV in the upper Chesapeake Bay varied both spatially and temporally, with more frequent and abrupt changes occurring in some tributaries than in others. *Zannichellia palustris* is the dominant species and *Najas guadalupensis* the codominant in all tributaries except the freshwater embayment at the head of the estuary, where *Vallisneria americana* is dominant. Differences within and among tributaries and changes over time are expressed in species richness and population abundances. Changes have consisted primarily of variations in the abundance of *Z. palustris*, which was absent for a single extended period, in the Sassafras River from ~900 to 600 ybp. There has been no replacement of one dominant species by another and no trends in species richness. Prior to European settlement, SAV was abundant in some tributaries and sparse in others. However, over the last century, there has been a general trend to decreased abundances. The post-European successional history of SAV differs from that of diatoms in the Chesapeake Bay. Since European settlement, benthic diatoms have been replaced by planktonic diatoms, species diversity has been greatly reduced, and abundance has increased dramatically (Brush and Davis 1984, Cooper 1995).

SAV is comprised of species adapted morphologically, physiologically, and phenologically to estuarine dynamics, which vary among tributaries depending on depth of water, freshwater flow, exposure to Atlantic storms and changing sea level. Therefore, the spatial and temporal distributions of SAV depend on local changes in water quality and substrate characteristics. For example, salinity gradients vary with changes in precipitation and runoff. The amount of light in the water column is determined by the amount of material in suspension. In the shallow estuary, fine material suspended from bottom sediments increases during storms. Deforestation and the conversion of land to impervious surfaces also affect runoff and loadings (Wolman 1967, Jones and Grant 1996). Eroded soil from various land uses is transported by streams to the estuary where it increases the amount of suspended material in estuarine waters.

Two major periods of drought, one in the late 16th to early 17th century and another from ~1000 to 1200 A.D. are documented in tree ring records for the mid-Atlantic region (Stahle et al. 1988, Stahle et al. 1998), and in pollen and seed records for the upper Chesapeake Bay (Khan 1993, Hilgartner 1995). During those periods of climate variation, when the watershed was mostly forested, there is no corresponding change in species richness or abundance in the submerged macrophytes.

The paleoecological record shows decreasing abundances in post-European SAV populations. In five tributaries, SAV abundances increased after European settlement before declining. Populations decreased after settlement in Back River and never increased. After a long decline in the Elk River, there has been a slight increase in recent years. Low sedimentation rates in Middle River obscure changes that may have occurred. The brackish species, *Ruppia maritima*, shows a shift since the late 19th century to presently brackish areas from presently fresh areas, possibly indicating that the tributaries have become fresher in the upstream reaches with deforestation. Although species disappeared and did not reappear at a locality, as in the upper Back River in the early 20th century, only in the last 15–20 yr has there been a widespread disappearance of SAV species and a failure to reappear throughout the upper Bay.

The post-European increase, decline, and eventual disappearance of SAV coincide with major changes in regional and local land use and estuarine water quality. As more land was cultivated and fertilized, the amount of sediment and nutrients from fertilizers entering the tributaries increased, enriching the waters and increasing turbidity (Brush 1984, Fisher et al. 1988, Cooper and Brush 1991, Cooper 1995). Sedimentation rates increased two- to tenfold throughout the Bay and tributaries after European settlement (Brush et al. 1982, Cooper and Brush 1991). Total annual nutrient loading of nitrogen into the Bay, including that coming from shore erosion as well as the tributaries, increased sixfold from 24.6×10^6 kg in pre-European time to 152 $\times 10^6$ kg in 1985, and there was a 17-fold increase in

TABLE 7. Local extinctions of species from longest period of extinction to shortest.

Years since last occurrence	Species	Tributary
740	*Potamogeton epihydrus*	lower Sassafras
680	*Potamogeton diversifolius*	middle Elk
680	*Potamogeton perfoliatus*	middle Elk
285	*Potamogeton perfoliatus*	upper Rock Creek
265	*Elodea canadensis*	upper Chester
245	*Elodea canadensis*	upper Rock Creek
245	*Najas gracillima*	upper Chester
205	*Ruppia maritima*	upper Severn
175	*Ruppia maritima*	upper Chester
175	*Potamogeton perfoliatus*	middle Rock Creek
165	*Elodea canadensis*	upper Severn
155	*Ruppia maritima*	lower Back
140	*Vallisneria americana*	upper Sassafras
135	*Najas guadalupensis*	upper Severn
110	*Potamogeton epihydrus*	Furnace Bay
105	*Ruppia maritima*	lower Rock Creek
100	*Najas gracillima*	lower Rock Creek
90	*Najas guadalupensis*	upper Chester
85	*Elodea canadensis*	lower Chester
85	*Elodea canadensis*	upper Back
85	*Elodea canadensis*	middle Back
85	*Najas gracillima*	upper Back
85	*Najas guadalupensis*	upper Back
85	*Najas guadalupensis*	middle Severn
85	*Potamogeton perfoliatus*	upper Back
85	*Zannichellia palustris*	upper Back
85	*Ruppia maritima*	upper Back
85	*Vallisneria americana*	upper Back
70	*Potamogeton perfoliatus*	upper Chester
65	*Najas guadalupensis*	upper Severn
55	*Vallisneria americana*	middle Back
35	*Elodea canadensis*	lower Back
35	*Najas gracillima*	middle Back
35	*Najas gracillima*	lower Back
35	*Potamogeton perfoliatus*	middle Gunpowder
30	*Elodea canadensis*	Elk (Bohemia)?
20	*Vallisneria americana*	upper Gunpowder
20	*Elodea canadensis*	middle Sassafras
20	*Potamogeton epihydrus*	upper Patuxent
20	*Najas guadalupensis*	middle Rock Creek
20	*Potamogeton perfoliatus*	upper Gunpowder
20	*Potamogeton perfoliatus*	middle Middle
15	*Vallisneria americana*	Furnace Bay
15	*Elodea canadensis*	Furnace Bay
15	*Elodea canadensis*	upper Middle
15	*Potamogeton diversifolius*	Furnace Bay
15	*Potamogeton diversifolius*	upper Patuxent
15	*Najas gracillima*	upper Middle
15	*Najas guadalupensis*	upper Sassafras
15	*Potamogeton perfoliatus*	lower Chester
15	*Potamogeton perfoliatus*	middle Back
15	*Potamogeton perfoliatus*	lower Rock Creek
15	*Ruppia maritima*	lower Chester
15	*Ruppia maritima*	middle Back

phosphorus from 0.66×10^6 kg before settlement to 11.3×10^6 kg in 1985 (Boynton et al. 1995). Because most of the sediment and nutrients are delivered to the estuary by runoff, turbidity differed among the tributaries at different times, depending on the effect of local climate on the hydrology and hydrodynamics of each tributary. SAV species, particularly *Z. palustris* and *N. guadalupensis*, known to grow well in eutrophic waters (Wentz and Stuckey 1971, Jupp and Spence 1977, Van Vierssen 1982) increased in abundance in several tributaries following European settlement. As more land was cleared and fertilized for agriculture, turbidity increased and light became limiting for benthic populations. Eventually, the majority of the benthic flora, including SAV, disappeared due to light limitation, and the Bay shifted to a predominantly planktonic system (Brush and Davis 1984, Smith et al. 1992, Cooper 1995, Boynton 1997).

In addition to agriculture, local activities also influenced SAV populations in the affected tributaries. Charcoal production, stone and gravel quarrying, and road building increased soil erosion in the upper Bay drainage area, and sediment loads in those tributaries draining the affected areas. Sewage treatment plants and livestock production introduced increased nutrient levels into the water. In Back River in the early 1900s, the introduction of nutrient-rich water from a local sewage treatment plant resulted in the demise of SAV, because of increased turbidity mainly due to excessive phytoplankton growth rather than sedimentation (Brush 1984). This effect was confined to the upper part of the tributary because of the long retention time in Back River. The effect was also immediate because of continuous discharge from the sewage treatment plant of large volumes of soluble nutrients into a relatively small receiving system. This contrasts with discontinuous runoff of particulate nutrients from agricultural fields into the entire Chesapeake system.

Simultaneous with the decline of SAV, phytoplankton growth in the upper enriched water column where light is not limiting, exceeded the nutrient needs of higher levels of the food web. Excess phytoplankton biomass deposited to the bottom sediment increased the demand for oxygen in the lower stratified waters. Oxygen as well as light became limited in benthic habitats (Smith et al. 1992). As anoxia intensified and became more widespread, efficient bacterial recycling of nutrients from the sediment resulted in still greater phytoplankton growth. Many parts of the estuary shifted from a coupled benthic–pelagic system consisting of populations of large metazoa to a planktonic system, which in many parts of the upper and middle Bay is primarily heterotrophic (Boynton 1997). Benthic populations were further depleted by overharvesting. Eventually, bottom dwelling fish disappeared. Oysters were also greatly stressed, and their populations declined precipitously. Recently, the crab populations have also decreased.

Initial attempts at reversing this series of events were targeted toward decreased use of fertilizers on agricultural land, particularly nitrogen. (U.S. Environmental Protection Agency 1983, 1992). Recently, these efforts have been augmented by removal of nitrogen from point sources, control of animal wastes, reduction of atmospheric nitrogen emissions, and other management practices designed to reduce nutrient inputs (L. Lenker, *personal communication*). Annual loadings of nitrogen and phosphorus differ among tributaries, and vary with flow, but over the past 10 yr there is no general trend in reduction of either nitrogen or phosphorous, and in many cases there is an increase. The total nitrogen annual load into the Chesapeake from the Susquehanna River basin was 57×10^6 kg in 1985 and in 1996 it was 99×10^6 kg. The loading for total phosphorus was 2×10^6 kg in 1985 and 3×10^6 kg in 1996 (Darrell et al. 1999). Loadings from the Patuxent River basin remained essentially the same over the same time period, but increased from the Potomac River basin, and quadrupled from the Choptank River basin. Suspended sediment loadings from the different river basins into the Chesapeake have also increased, but less so from the Potomac than elsewhere (Darrell et al. 1999).

There is no clear trend of recovery of SAV or other benthic organisms in the Bay. There is also no indication from the paleoecological record of how long such a recovery would require, since the recent widespread reductions are a unique phenomenon. The question of whether or not the bottom-up management practice of removing nutrients is most effective in restoring the ecology and economy of the Bay continues to arise. But the alternative top-down approach, where nutrients are removed by benthic organisms such as filter feeders, is not feasible until benthic sites are made habitable, by increasing light and decreasing anoxia in bottom waters.

The conversion of an entirely forested landscape to a highly productive arable landscape from 20% to 40% forested was accomplished through continuous massive disturbance and nutrient inputs. These changes in the land, which took place over a few hundred years, resulted in an unforeseen loss of a highly productive, naturally subsidized estuarine food resource. The paleoecological record shows that the decrease in SAV abundance has taken place over at least two centuries, and is not a late 20th century occurrence. The paleoecological record also shows that SAV populations in different tributaries have varied over pre- and post-European time. No two tributaries are similar. Strategies designed to restore SAV must consider the characteristics, including the history, of individual tributaries and their watersheds. What works for one tributary will not necessarily work for all.

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