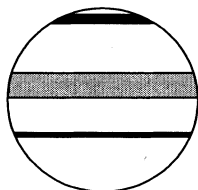


Prehistoric habitat stability and post-settlement habitat change in a Chesapeake Bay freshwater tidal wetland, USA

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Abstract: Analyses of fossil seeds and pollen grains preserved in seven sediment cores and borings were combined with historical land-use records to reconstruct an 1800-yr history of Otter Point Creek (OPC), a freshwater tidal deltaic wetland in the upper Chesapeake Bay. The objectives of the study were to document the role of natural and anthropogenic disturbance on habitat development at different sites within the wetland. Fossil seeds revealed a 1500-yr period (AD 230 to 1700) of subtidal habitat stability characterized by the aquatic macrophytes *Zannichellia palustris*, *Najas gracillima*, *N. guadalupensis*, *Elodea canadensis* and *Vallisneria americana*. Natural disturbance had little or no impact on the estuarine habitat during this time. By the early 1700s, forest clearance for agriculture and lumber during European settlement led to higher erosion rates in the watershed. This led to rapid sediment efflux and broad habitat changes along a hydrologic gradient within the estuary. The aquatic macrophytes disappeared when estuarine sedimentation rates increased from a pre-1700 mean of 0.05 cm/yr to 0.60 cm/yr after 1730–1750. As the estuary continued to fill behind a prograding delta from AD 1750 to 1950, sub-tidal species were replaced sequentially by increasingly less flood-tolerant dominants of low marsh (*Zizania aquatica*), middle marsh (*Typha angustifolia* or *Leersia oryzoides*), high marsh (*Acorus calamus*), shrub marsh (*Typha latifolia* and *Salix nigra*) and riparian forest (*Acer negundo*, *Fraxinus pennsylvanica* and *Betula nigra*). Habitat change progressed in pulses followed by periods of habitat stasis. The most rapid and extensive period of change occurred between 1840 and 1880, synchronous with the period of highest sedimentation rates, mid-century storms and intensive land use in the watershed. The rate and pattern of community change differed among sites where position relative to the watershed, local disturbance, and channel shifts at or adjacent to the site influenced different community pathways. A conceptual model is proposed to describe the spatial and temporal development of eastern US freshwater tidal wetland habitats, reflecting the importance of the impact of colonial deforestation.

Key words: Chesapeake Bay, deforestation, freshwater tidal wetland, human impact, plant macrofossils, sedimentation, wetland habitat development.

Introduction

Freshwater tidal wetlands (FTW) lie at the interface between upland watersheds and tidal rivers along the Atlantic and Gulf Coasts of the eastern USA. These biologically diverse and economically important systems are particularly vulnerable to human activities associated with major East Coast cities as well as watershed disturbance (Simpson *et al.*, 1983;

Hershner and Wetzel, 1987). Palaeoecological and geomorphological reconstructions have shown that over the past 350 years human impact, particularly sediment efflux from deforestation and hydrologic change through channelization, have been important factors in initiating FTW and estuarine marsh and wetland forest development in the central Chesapeake Bay region (Gottschalk, 1945; Froemer, 1980; Khan and Brush, 1994), Delaware River (Orson *et al.*, 1992) and New York (Heusser *et al.*, 1975; Pederson *et al.*, 2005). In some Delaware River FTWs, marsh development was generated by natural disturbance such as changing flooding regimes from sea-level rise (Carmichael, 1980; Orson *et al.*, 1992), while at two river sites in Delaware dominant species have persisted for

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> 1000 years with no change (W.B. Hilgartner, unpublished data, 1990–91). While some of these studies have documented spatial and temporal shifts in marsh and forest habitat little is known about the details and patterns of habitat change at various locations within a FTW. It is not known whether species characteristic of modern habitat zones distributed along an increasing elevation and decreasing flood frequency gradient (ie, subtidal, low marsh, middle marsh, high marsh and riparian forest) follow this sequence at particular sites through time. Disturbances might also have different effects at different locations. Hence the influence of human and natural disturbance on rates of change and trajectories at different wetland sites over centuries needs to be explored.

This study uses palaeoecological and land-use records to evaluate the relative influence of human and natural disturbance on the 1800-yr history of habitats in a FTW delta in the upper Chesapeake Bay. The objectives of the study were to address the following questions: (1) How long have the present habitat patterns and species associations existed? (2) How have habitats and species associations changed spatially in prehistoric time compared with historic time? (3) How are these changes related to human activity and natural disturbance?

FTWs contain a high diversity of plant species arranged as vegetation zones along an elevation gradient. Each zone is characterized by one or two dominant species (Simpson *et al.*, 1983; Leck and Simpson, 1995; Mitsch and Gosselink, 2000; Pasternack *et al.*, 2000). Elevation and hydrology are the primary factors governing plant patterns because they dictate the depth and duration of flooding imposed on species assemblages. Therefore, any factor or disturbance producing a change in elevation and hydrology, either by increasing or decreasing the substrate level or by altering the hydrologic regime, will affect species composition (Leck and Simpson, 1987, 1995; Niering 1989; Pasternack *et al.*, 2000). Although

biotic or internal factors may be important in altering the substrate and initiating habitat change in coastal wetlands, most evidence supports the role of abiotic or external factors, such as shifts in sediment or hydrology by storms (Niering and Warren, 1980; Serodes and Troude, 1984; Clark and Patterson, 1985; Clark, 1986; Shaffer *et al.*, 1992; Mitsch and Gosselink, 2000).

As we were interested in examining local site differences within the wetland, we utilized seeds, fruits and other macrofossils in the stratigraphic record. These can be identified to species level with greater precision than microfossils such as pollen and are not transported far from parent plants. Thus macrofossils provide virtually an *in situ* record of vegetation over centuries. (Watts, 1978; Allen and Huntley, 1999; Birks and Birks, 2000; Birks, 2003; Van der Putten *et al.*, 2004; Wasylikowa, 2005). In this study, the area of the seed species assemblage circumscribed by the term *in situ* is 1 m² for marsh samples and 80–100 m² for sub-tidal and forest samples, based on surface sample analyses in Otter Point Creek and other Chesapeake Bay tributaries (Davis, 1985; Hilgartner, 1995). Seed bank studies along the Delaware River (Leck and Simpson, 1994, 1995) and similarity between seed bank and macrofossil depositional processes (Wasylikowa, 1986) are further evidence that macrofossils are a reliable surrogate of local vegetation in FTWs.

The site

Physical setting and vegetation

Otter Point Creek (OPC) is a freshwater tidal delta containing a series of distributary channels flowing into the Bush River, a tributary of the upper Chesapeake Bay, Maryland (Figure 1). The areal extent of OPC is approximately 1.4 km². Winters Run, the main river flowing into OPC, drains a watershed of

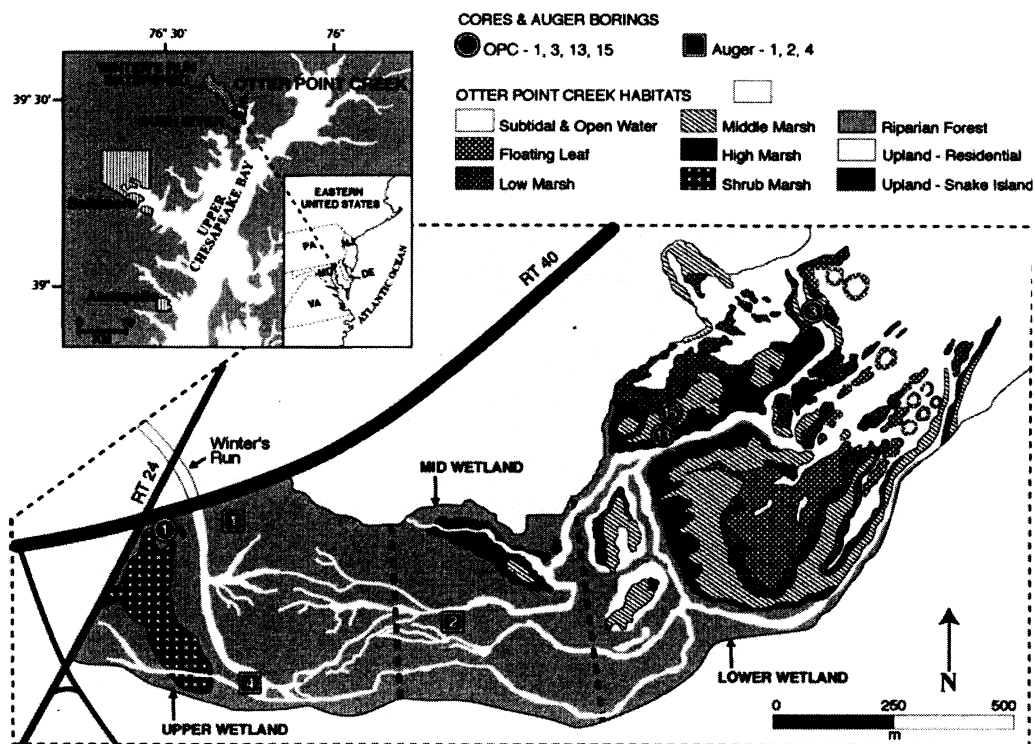


Figure 1 Location of Otter Point Creek study area in the Winters Run watershed in the upper Chesapeake Bay, Maryland, USA, showing vegetation zones, wetland subdivisions and the location of seven cores and borings. Vegetation (habitat) zonation was constructed by combining low aerial photography with ground surveillance and quadrat analysis. The map was originally created from GIS software (MIPS program), by D. Bleil, Department of Natural Resources of Maryland in collaboration with W. Hilgartner, and adapted for this paper by M.S. Hilgartner

150 km², producing a ratio of area of watershed to wetland of 108. Most of the watershed is within the Piedmont province and underlain by soils weathered from Precambrian and early Palaeozoic schist, granite, gneiss, gabbro and serpentinite. OPC lies at the base of the Piedmont (Fall Line), within the Coastal Plain, a province underlain by Quaternary lowland gravel, sand, silt and clay deposits, with some unconsolidated Cretaceous gravel and sand on the uplands (Cleaves *et al.*, 1968). Geomorphic and hydrometeorological analyses of modern sedimentation rates and water-level controls in the wetland are reported in Pasternack and Brush (1998), Pasternack *et al.* (2000) and Pasternack and Hinnov (2003). Pasternack *et al.* (2001) propose a diffusion model reflecting historic depositional patterns of delta progradation and land-use history. The Chesapeake Bay Foundation and the Izaak Walton League of America own most of the OPC wetland, which in 1990 was designated a component of NOAA's National Estuarine Research Reserve.

OPC wetland contains a mosaic of eight habitat zones occurring in general along a gradient of increasing elevation and decreasing flood levels (Table 1, Figure 1). Floating leaf and marsh zones are characterized by six dominant or indicator species associations, based on cluster analysis of 115 1-m² quadrats of herbaceous marsh and levee vegetation (Pasternack *et al.*, 2000). Shrub marsh vegetation was determined from analysis of 22 1-m² quadrats and the riparian forest from seven 100-m² belt transects (Hilgartner, 1995). Although the subtidal environment is relatively barren of plants, the introduced *Myriophyllum spicatum* and *Potamogeton crispus* occur in scattered patches. Dominant species that define the habitats comprise generally 60–80% relative cover. Important associated species represent those with >20% relative cover.

While the wetland contains fragments of interspersed habitats, the general pattern from the delta front to the delta head and channel levee is a progression from subtidal to floating leaf to low marsh to middle or high marsh to forest, with an area of shrub marsh at the western end of the wetland and along channel banks (Figure 1). Similar habitat zones and indicator species have been described from other freshwater tidal wetlands in the mid-Atlantic region (Simpson *et al.*, 1983; Parker and Leck, 1985; Leck *et al.*, 1988; Leck and Simpson, 1994, 1995). The tidal riparian forest habitat, dominated by *Acer negundo* and its codominants *Fraxinus pennsylvanica* and *Betula nigra* is an association also found along numerous non-tidal riparian systems in the region (Brush *et al.*, 1980).

Disturbance history

The history of natural disturbance in the OPC watershed and estuary includes long-term climate changes and episodic storm events. Alternating dry and wet periods over the past 2000 years have been identified from pollen, charcoal, diatom, dinoflagellate cysts and macrofossil analyses of sediment cores in the mid-Atlantic seaboard region (Brush, 1986; Fletcher *et al.*, 1993; Khan and Brush, 1994; Kellogg and Custer, 1994; Willard *et al.*, 2003; Pederson *et al.*, 2005). Extended dry periods occurred during the seventh century, between 1000 and 1250, 1400, and 1580–1610. Wet periods prevailed during the tenth and fourteenth centuries and between 1610 and 1750. Prehistoric storm events are unknown in the study area but seven intense hurricanes (≥ Category 3) over the past 700 years have been identified in cores from southern coastal New England (Donnelly *et al.*, 2001). Landsberg *et al.*, (1968) recorded four major storm events during the 1850s in the Philadelphia area, 100 km northeast of the study area. Particularly notable hurricanes and tropical storms in the upper Chesapeake Bay during the past century include the Hurricane of 1933 (15 cm precipitation), Hurricanes Hazel of 1954 (12.5 cm), Connie of 1955 (25 cm) and Agnes of 1972 (25 cm). These storms produced high-impact floods from heavy rainfall and significant sedimentation (Vokes and Edwards, 1974; Gross *et al.*, 1978).

Human disturbance before European settlement in the seventeenth century was minimal (Custer, 1986). Populations of no greater than 6000 along the entire Maryland coastline of Chesapeake Bay (Ubelaker and Curtin, 2001) cleared <1% of forests (Brush, 1984). Anthropogenic fire within the uppermost reaches of Winters Run watershed may have been important in producing 'grasslands or grassland savannahs' (Marye, 1955a, b). A charcoal peak found in sediments deposited during the thirteenth century in OPC suggests increased wildfire or human-set fires during that time (Hilgartner, 1995).

Human disturbance accelerated after 1658, when the first European settlers moved into the OPC region (Wright, 1967). Population growth in Harford County (which includes the entire Winters Run and Bush River watersheds) increased slowly, from 12 700 people in 1775 to 35 000 around 1925. Population growth accelerated after 1925; by 2000 the population had reached 218 590 (US Census Bureau, 2000, retrieved 26 January 2006 from http://factfinder.census.gov/home/saff/mail.html?_lang=en).

A detailed sequence of historical land-use changes in the upper Chesapeake Bay (Hilgartner, 1995; Brush and Hilgart-

Table 1 Zonation of habitats (defined by dominant species) along an increasing elevation gradient at Otter Point Creek

Habitat	Habitat gradient position	Dominant species	Important associated species
Subtidal	1	None	<i>Myriophyllum spicatum</i> <i>Potamogeton crispus</i>
Pioneer mudflat	2	None	None
Floating leaf	3	<i>Nuphar advena</i>	None
Low marsh	4	<i>Zizania aquatica</i> <i>Peltandra virginica</i>	<i>Peltandra virginica</i> <i>Typha angustifolia</i>
Middle marsh	5	<i>Typha angustifolia</i> <i>Leersia oryzoides</i>	<i>Eleocharis ambigens</i>
High marsh	6	<i>Acorus calamus</i>	
Shrub marsh	7	<i>Typha latifolia</i>	<i>Salix nigra</i> , <i>Saururus cernuus</i>
Shrub levee	7	<i>Cornus amomum</i>	<i>Polygonum sagittatum</i> , <i>Alnus serrulata</i>
Riparian forest	8	<i>Acer negundo</i>	<i>Fraxinus pennsylvanica</i> <i>Betula nigra</i>

Dominance and associated species were determined from quadrat and transect analyses. *Myriophyllum spicatum* and *Potamogeton crispus* were observed but not recorded in quadrats.

ner, 2000) is briefly summarized here. Deforestation in the watershed began to accelerate in the early eighteenth Century, so that by 1730 forest cover had declined to between 95 and 80%, by 1800 to 80 and 50%, by 1850 to 50 and 40%, and by 1900 to 40 and 20%. Thus the period that witnessed the most rapid and extensive loss of forest was 1730–1800 (30%). Forests were first cleared for tobacco agriculture, a labour intensive, low-impact crop. Farms were abandoned because of lost fertility and forest regeneration was common before 1730. By the late eighteenth century, a shift to grain crops requiring more open land had taken place. The Chesapeake Bay began to experience eutrophic conditions for the first time in at least 2500 years, evidenced by increased nitrogen and planktonic diatoms and a decline in benthic diatoms and overall diversity (Cooper and Brush, 1993). In the mid-1800s, more land was brought under cultivation, accompanied by increased fertilizer use and deep plough farming. The latter increased upland erosion, intensifying eutrophication and sedimentation in the estuary. Increased sedimentation resulted in heavy siltation of ports and embayments in numerous Chesapeake Bay watersheds and wetlands (Gottschalk, 1945; Brush 1989, 1994). Deforestation and agriculture peaked in the late 1800s. After 1910, an increasing number of farms were abandoned, resulting in greater forest cover over subsequent years. Afforestation resulted in 48% forest cover in Harford County by 1975. Although some recent decline in forest cover has occurred since 1975, most of the population growth and residential development has taken place on previously cleared land at low elevations and has not resulted in forest clearance. Major construction within the watershed and adjacent to the wetland include the B&O Railroad in 1885, Route 40 in 1938, Atkisson and Van Bibber Dams in 1944–45, Route 24 in the early 1970s and several housing developments between 1970 and 2000. Construction can cause sharp spikes in sediment input because of exposed erosional surfaces (Wolman, 1967; Groffman *et al.*, 2003). The housing developments of the 1980s and 1990s have followed county regulations by constructing sediment trap ponds between the development and the estuary, thus reducing estuarine deposition. Within the upper portion of the lower wetland, two sewage lagoons were excavated in 1967–1968 and subsequently abandoned in 1970.

Methods

Sediment cores

Four cores, 6.6 cm in diameter and ranging in length from 110 to 212 cm (OPC1, OPC3, OPC13, OPC15) and three soil auger borings, ranging in length from 224 to 304 cm (Augers 1, 2 and 4) were collected from four different habitats throughout the wetland (Table 2; Figure 1). A mini-vibrocoring system (Smith, 1987) was used to extract cores from marsh peat. Cores were extruded from aluminum or plastic tubes, cut in half length-

wise and sampled at 1 cm intervals. A selection of 55 1-cm levels from OPC3 and 52 levels from OPC13 were examined, roughly half above and half below the dated AD 1730 level. In the two post-AD 1780 dated cores, 29 samples from OPC1 and 17 samples from OPC15 were analysed. Auger borings were extracted from forested sediment because the sediment was too compacted for penetration by vibrocoring equipment. Auger borings were sampled in 16-cm sections and a segment from each section was examined. Core and auger samples were stored at 4°C until processed for analysis.

Stratigraphy and dating of sediments

Colour (Munsell Soil Colour Chart), sediment texture and plant content of each core and auger boring were described visually (Figure 2). Bulk sediment samples containing silt, clay and organics from bottom levels within cores OPC1, OPC3 and OPC13 and soil auger borings Auger1 and Auger2, were radiocarbon-dated at Beta Analytic Laboratories, Florida (Table 3). Pollen-dated horizons (Table 4) were differentiated on the basis of the ratio of oak (*Quercus*) to ragweed (*Ambrosia*) pollen (O:R), which reflects the history of regional land use (Brush, 1984). Pre-European levels contain <1% ragweed and a dominance of oak and pollen of other arboreal taxa. Dates of AD 1730 were assigned to the level where the O:R decreases to ≤ 5.0 , and AD 1780 when O:R drops below 1.0.

Sedimentation rates

Average sedimentation rates (R) for OPC3, OPC13 and Auger2 were calculated between radiocarbon and pollen-dated horizons. Each sample was then dated by adjusting the average sedimentation rate between dated horizons according to pollen concentrations in each sample (Brush, 1989). This method is based on an inverse relation between pollen concentration and sediment accumulation. The sedimentation rate for a given sample (R_{0-n}) is calculated using the following equation:

$$R_{0-n} = (N/n_{0-n})R_{\text{avg}} \quad (1)$$

where N is the average number of pollen grains per area in a given time period, n_{0-n} is the number of pollen grains per area in interval 0– n , and R_{avg} is the average sedimentation rate. Once sedimentation rates were calculated for each sample, a chronology was established by determining the number of years represented by each sample. Starting at the top of the core a date is assigned to each sample based on the number of years represented by each sample. In cores where bottom sediment was deposited after 1700 (OPC1, OPC15, Auger1, Auger4) O:R ratios and stratigraphic similarities to dated cores were used to estimate dates. In addition, in OPC1 sand and gravel layer anomalies were linked with two road construction events adjacent to the site at years 1938 (Rt 40) and 1972 (Rt 24) (see Figure 1).

Table 2 Core habitat and wetland elevations

Core name	Wetland subdivision	Elevation range (m) above s.l.	Dominant vegetation	Habitat	Habitat no.
OPC3	Lower	0–1.0	<i>Typha angustifolia</i>	Middle marsh	5
OPC15	Lower	0–1.0	<i>Typha angustifolia</i>	Middle marsh	5
OPC13	Lower	0–1.0	<i>Acorus calamus</i>	High marsh	6
Auger2	Mid	1.1–2.0	<i>Acer negundo</i> , <i>Fraxinus pennsylvanica</i>	Riparian forest	8
OPC1	Upper	2.1–3.2	<i>Typha latifolia</i> , <i>Salix nigra</i>	Shrub marsh	7
Auger4	Upper	2.1–3.2	<i>Acer</i> / <i>Fraxinus</i>	Riparian forest	8
Auger1	Upper	2.1–3.2	<i>Acer</i> / <i>Fraxinus</i>	Riparian forest	8

Wetland subdivisions based on increasing elevation range (elevations from Harford County Planning and Zoning, MD).

Table 4 Pollen-dated age determinations in OPC cores and auger borings

Core	Dated depth (cm)	O/R	Date (yr AD)	Range of O/R within depth (cm)	O/R range	N
OPC3	116–117	0.4	1780	1–117	0.14–0.63	18
	164–165	2.8	1730	118–165	2.4–2.86	7
	210–212	30.0	230*	166–210	15.0–59.0	5
OPC13	124–125	0.35	1780	1–125	0.05–1.0	12
	157–158	1.1	1730	126–158	1.1–5.1	5
	206–209	78.0	540*	159–206	11.0–78.0	7
Auger2	208–224	0.8	1780	1–224	0.11–0.54	5***
	240–256	4.0	1730	224–256	1.5–22.0	3
	272–288	+9.0	1290*	256–288	9.0	1
OPC15	109–110	**	post-1780	–	–	–
OPC1	95–100	0 (0/5)	post-1860	1–100	0–0.9	5
Auger4	224–240	2.8	1730	224–240	2.8	1
Auger1	192–208	no pollen				

The dated depth is the first time the O/R value drops below 5.0 (1730) and 1.0 (1780) when advancing from the bottom to the top of the core. O/R is the *Quercus: Ambrosia* or Oak to Ragweed pollen ratio. N is the number of pollen samples examined within depth levels indicated.

*Refer to Table 3 for radiocarbon dates and calibrations.

**No pollen count was made.

*** Sixteen samples analysed between 16 and 160 cm contained no pollen.

from other tributaries and have been used in previous studies (Brush and Hilgartner, 2000). The floating leaf habitat (Habitat 3) represented only by *Nuphar advena* was not identified in samples because this species leaves a poor macrofossil record. In the case where a macrofossil could not be assigned confidently to species, the closest taxonomic level was assigned as in *Carex* sp. or Cruciferae type. 'Rootlets' was assigned to *Acer negundo*, and associated forest dominants *Fraxinus pennsylvanica* and *Betula nigra*. These three arboreal species characterize the riparian forest in 100-m² belt transects with relative densities of 46–75%, 25–46% and 9–20%, respectively (Hilgartner, 1995). These rootlets, while not differentiated to species level, were treated as a proxy for the riparian forest.

Species shown in macrofossil profiles were those represented by ≥ 2.0 seeds/15 ml sample or > 7.0 seeds/100 ml. These are species that are generally locally dispersed and provide greater precision in interpreting local vegetation changes (Hilgartner,

unpublished data, 1998–2000). Species represented by only one seed in a typical 15 ml sample can be deposited many tens of metres away from their parent plants and thus may not represent local vegetation. For this reason, 'one-seed species' were not included in the analysis, except in several instances when they were present in consecutive stratigraphic samples. The software Psimpoll was used to produce the macrofossil profiles.

Results

Fossil species, sediment and habitat history

Ninety-two macrofossil taxa were recovered from 195 samples in seven cores and borings (Table 6). Of the 62 taxa identified to species, 54 (87%) occur in the modern vegetation, while eight species represent local extinctions. The following core analyses are presented in increasing wetland elevation from the lowest site at the delta front to the highest site at the delta head.

Lower wetland cores, OPC3 (present habitat: *Typha angustifolia* middle marsh)

A subtidal estuarine habitat, characterized by six species of aquatic macrophytes persisted for 1500 years from AD 230 to 1730 (Figure 3). At AD 230 the community was comprised of *Elodea canadensis*, *Najas gracillima* and the most abundant species *Zannichellia palustris*. A natural levee in proximity to the subtidal habitat appeared \sim AD 800, as indicated by *Scirpus* (*Schoenoplectus*) *validus* and *Acnida cannabina*. During this period sedimentation rates (SR) ranged between 0.02 and 0.05 cm/yr. *Acnida* disappeared by the 1500s. By the early 1700s, five submerged macrophyte species and *Scirpus* disappeared after SR increased to 0.52 cm/yr. *Z. palustris* disappeared by 1780 as SR rose to 0.60 cm/yr. A transitional period of rapid mud accumulation interbedded with sand layers, mica and allocthonous leaves and twigs, produced nearly 1.0 m of sediment between 1750 and 1870. The transitional sediment plus the presence of *Phalaris arundinacea*, *Betula nigra*, *Salix nigra*, *Rubus* sp. and *Sambucus canadensis* indicate fluvial deposition and/or a prograding delta that included clastic particles and plant fragments transported from the watershed. Around 1870 a low marsh characterized by *Zizania aquatica* became established and

Table 5 Important macrofossil habitat indicators from surface samples at Otter Point Creek. These species are generally restricted to, or only abundant in the habitat indicated

Subtidal ^a (1)	High marsh (6)
<i>Zannichellia palustris</i>	<i>Acorus calamus</i>
<i>Najas</i> spp.	<i>Scirpus cyperinus</i>
<i>Ruppia maritima</i>	<i>Aster simplex</i>
<i>Potamogeton perfoliatus</i>	Shrub marsh and levee (7)
Floating leaf (3)	<i>Carex crinita</i>
none	<i>Carex lurida</i>
Low marsh (4)	<i>Typha latifolia</i>
<i>Zizania aquatica</i>	<i>Saururus cernuus</i>
Middle marsh (5)	<i>Polygonum sagittatum</i>
<i>Typha angustifolia</i>	<i>Alnus serrulata</i>
<i>Eleocharis ambigens</i>	<i>Cornus amomum</i>
<i>Leersia oryzoides</i>	<i>Salix nigra</i>
<i>Bidens laevis</i>	Riparian forest (8)
<i>Scirpus</i> (<i>Schoenoplectus</i>) <i>validus</i>	<i>Acer negundo</i> ,
<i>Sagittaria latifolia</i>	<i>Fraxinus pennsylvanica</i> ,
<i>Polygonum arifolium</i>	<i>Betula nigra</i>
	<i>Viola papilionacea</i>

Macrofossils from the subtidal habitat were recovered from Robin Cove, an embayment adjoining the Chester River, a tributary of the Chesapeake Bay.

Table 6 Species and taxa from Otter Point Creek cores

Scientific name	Common name	A	B	C	D	E	F	G
Herbaceous species								
<i>Acnida cannabina</i>	water hemp	+						
<i>Acorus calamus</i>	sweetflag		+	+				
<i>Alisma subcordatum</i>	small water plantain		+	+	+	+		+
<i>Apios</i> type	none		+					
<i>Asclepias incarnata</i>	swamp milkweed			+				
<i>A. syriaca</i>	common milkweed			+				
<i>Aster simplex</i>	panicked aster			+				
<i>Bidens laevis</i>	large bur marigold	+		+	+	+		+
<i>Boehmeria cylindrica</i>	false nettle							+
<i>Cardamine</i> type	cress					+		+
<i>Carex comosa</i>	none		+	+				
<i>C. crinita</i>	none			+				
<i>C. lurida</i>	none	+		+		+		
<i>C. scoparia</i>	none	+	+	+	+	+		
<i>C. stipata</i> type	none			+				
<i>C. stricta</i> type	tussock sedge		+			+		
<i>C. vulpinoidea</i>	none				+			
Cyperaceae (7 spp.)	sedges	(4)	+	(2)	(5)		+	
Caryophyllaceae type	none			+				
<i>Cicuta maculata</i>	water hemlock	+		+				
<i>Claytonia caroliniana</i>	carolina spring beauty				+			
Compositae sp.	none	+						
<i>Cyperus</i> sp. A	sedge			+				
<i>Cyperus strigosus</i>	umbrella sedge		+					
<i>Dulichium arundinaceum</i>	three-way sedge		+	+		+		
<i>Eleocharis ambigens</i>	spike rush	+	+					
<i>E. obtusa</i>	spike rush	+			+	+		+
<i>Elodea canadensis</i>	common waterweed	+	+	+	+			
<i>Glyceria striata</i>	fowl manna grass				+			
Gramineae sp.A	none	+		+	+			
Gramineae (2 spp.)	none		+					
<i>Hypericum</i> type	none	+						
<i>Impatiens capensis</i>	jewelweed	+	+	+			+	
<i>Juncus effusus</i>	smooth rush							+
<i>Leersia oryzoides</i>	rice cutgrass	+	+	+	+	+		+
<i>Lycopus americanus</i>	water horehound			+				
<i>L. uniflorus</i>	northern bugleweed			+				
<i>Lysimachia</i> type	none			+				
<i>Mikania scandens</i>	climbing hemp	+	+	+	+			+
<i>Mollugo verticillata</i> type							+	
<i>Najas gracillima</i> (E)	slender naiad	+	+	+	+			
<i>N. guadalupensis</i> (E)	southern naiad	+	+	+	+			
<i>Oxalis</i> cf. <i>stricta</i> (E)	yellow wood sorrel						+	
<i>Oxalis</i> sp.	wood sorrel			+				
<i>Panicum</i> type	panic grass					+		
<i>Phalaris arundinacea</i>	reed canarygrass	+		+				
<i>Polygonum arifolium</i>	halberd-leaved tearthumb	+	+	+		+		+
<i>P. persicaria</i> type	ladies thumb type	+						
<i>P. punctatum</i>	dotted smartweed	+		+	+	+		+
<i>P. sagittatum</i>	arrow-leaved tearthumb	+	+	+	+	+		
<i>Polygonum</i> sp.	none	+					+	+
<i>Potamogeton diversifolius</i>	variable pondweed	+		+	+			
<i>P. epihydrus</i> (E)	floating pondweed		+	+				
<i>P. perfoliatus</i> (E)	redhead grass	+		+				
<i>Sagittaria latifolia</i>	broad-leaved arrowhead	+	+	+				
<i>Saururus cernuus</i>	lizardtail							+
<i>Scirpus cyperinus</i>	woolgrass			+				
<i>S. fluviatilis</i> (E?)	river bulrush			+				
<i>S. maritimus</i>	bulrush	+						
<i>S. validus</i>	bulrush	+	+	+				
<i>Sium suave</i> type	water parsnip type		+	+				
Solanaceae type	none	+				+		+
<i>Sparganium americanum</i>	American burweed	+						
<i>Typha angustifolia</i>	narrow-leaved cattail	+	+	+		+		
<i>T. latifolia</i>	broad-leaved cattail							+
<i>Vallisneria americana</i>	wild celery	+	+	+				
<i>Vernonia novaboracensis</i>	New York ironweed				+			
<i>Vernonia</i> type	none							+

continued

Table 6 (continued)

Scientific name	Common name	A	B	C	D	E	F	G
<i>Viola papilionacea</i>	common blue violet		+	+	+			+
<i>Zannichellia palustris</i> (E)	horned pondweed	+	+	+				
<i>Zizania aquatica</i>	wild rice	+	+	+				
Woody species								
<i>Acer negundo</i>	box elder							+
<i>Alnus serrulata</i>	smooth alder	+	+	+	+	+		
<i>Betula nigra</i>	river birch	+			+	+		+
<i>Cephalanthus occidentalis</i>	buttonbush			+				+
<i>Cornus florida</i>	flowering dogwood		+	+				
<i>Liriodendron tulipifera</i>	tulip tree	+	+		+	+		
<i>Lyonia ligustrina</i> (E)	maleberry					+		
<i>Platanus occidentalis</i>	sycamore	+	+		+			
<i>Rosa palustris</i>	swamp rose					+		
<i>Rubus cf. occidentalis</i>	black raspberry	+	+	+	+	+	+	+
<i>Salix nigra</i>	black willow	+	+	+				+
<i>Sambucus canadensis</i>	black elderberry	+	+	+	+	+		+
<i>Vaccinium</i> sp.	blueberry				+			
(<i>Acer-Fraxinus-Betula</i>)	Rootlets type A		+		+	+	+	+
Total macrofossil taxa/core		44	36	52	31	23	7	23
Total macrofossil taxa richness = 92								
Other species listed in text, but not found in cores or augers								
<i>Amphicarpa bracteata</i>	hog peanut							
<i>Fraxinus pennsylvanica</i>	green ash							
<i>Myriophyllum spicatum</i>	Eurasian milfoil							
<i>Nuphar advena</i>	spatterdock							
<i>Peltandra virginica</i>	arrow arum							
<i>Potamogeton crispus</i>	crisped pondweed							

Plus sign (+) indicates macrofossil presence within a core or auger boring, listed in increasing wetland elevation from left to right. Abbreviations are: A, OPC3; B, OPC15; C, OPC13; D, Auger2; E, Auger4; F, Auger1; G, OPC1. (E) next to a species means species not found in modern vegetation surveys and which may represent a local extinction.

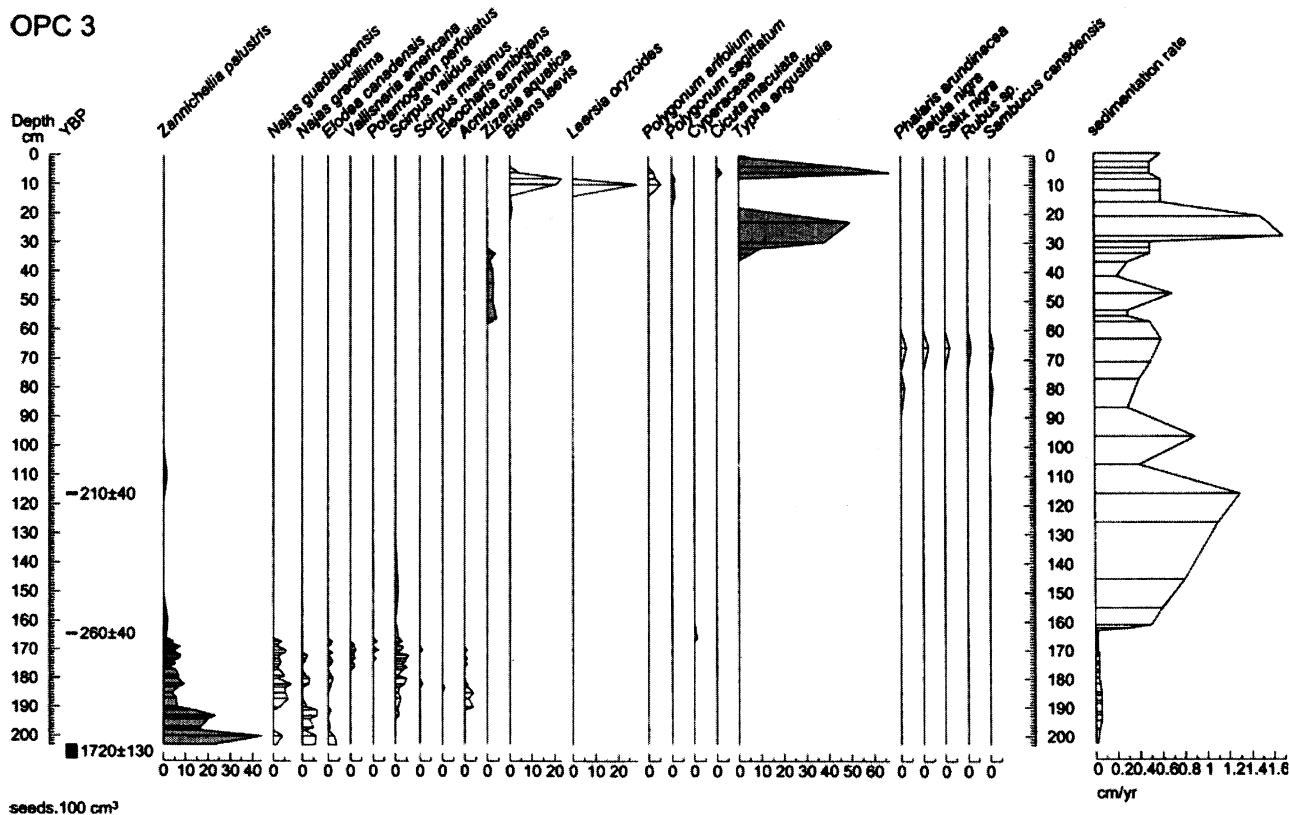


Figure 3 Macrofossil species in OPC3. Read from left to right species and habitats are listed from most flooded to least flooded. Habitats are defined by the following species: subtidal (*Zannichellia palustris*), low marsh (*Zizania aquatica*) and middle marsh (*Typha angustifolia* and *Leersia oryzoides*)

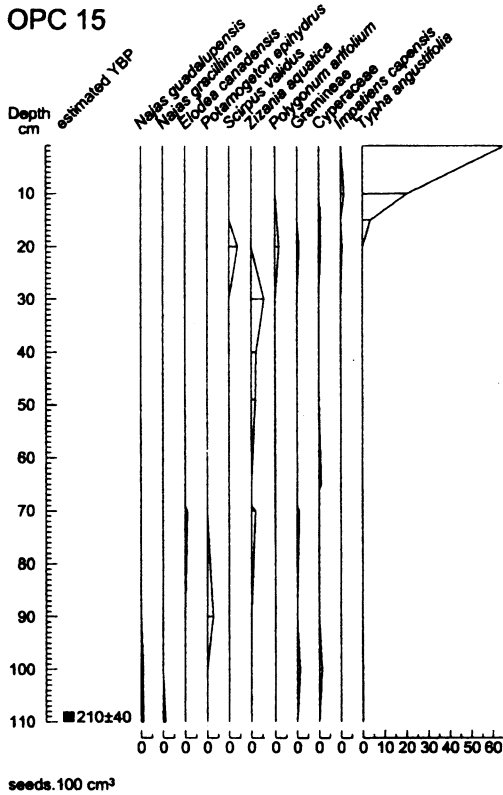


Figure 4 Macrofossil species in OPC15. Read from left to right species and habitats are listed from most flooded to least flooded. Habitats are defined by the following species: subtidal (*Najas guadalupensis*), low marsh (*Zizania aquatica*) and middle marsh (*Typha angustifolia*). A bottom date of 1780 at 110 cm is estimated based on similar age/depth levels in OPC3 and OPC13

persisted until 1945. During this low marsh period SR fluctuated between 0.18 and 0.70 cm/yr. A *Typha angustifolia*-dominated middle marsh followed when SR reached 1.7 cm/yr. *Typha* disappeared for a period of 20 years and was replaced by *Bidens laevis* and *Leersia oryzoides*, signifying slightly wetter conditions. *Typha angustifolia* returned around 1980 when other species declined or disappeared. This species has remained dominant to the present, encompassing as much as 80% of the vegetation cover.

OPC15 (present habitat: Typha angustifolia middle marsh)
The core provided a record of ~200 years. *Najas guadalupensis* and *Najas gracillima* were present at 110 cm (~1780), representing a subtidal habitat (Figure 4). *Potamogeton epihydrus* replaced *Najas* spp. at 90 cm (~1810–1830). *Potamogeton* disappeared when a period of fluvial deposition, similar to that which occurred in OPC3, follows from 87 cm to 50 cm (~AD 1815–1870). A low marsh dominated by *Zizania aquatica* became established after 49 cm (~1870). The low marsh persisted until 30 cm (~1950), when a middle marsh represented by *Scirpus validus* and *Polygonum arifolium* appeared. This habitat shifted to a *Typha angustifolia*-dominated middle marsh at 15 cm (~1960) where it has remained to the present.

OPC13 (present habitat: Acorus calamus high marsh)
A sub-tidal habitat characterized by *Elodea canadensis*, *Najas gracillima*, *Najas guadalupensis* and *Zannichellia palustris* persisted for 1150 years from ~AD 550 until the early 1700s (Figure 5). SR varied narrowly between 0.03 and 0.07 cm/yr during this period. *Z. palustris* and *N. guadalupensis* declined and *Elodea* and *N. gracillima* disappeared around 1300. *Elodea* reappeared around the mid-1500s. The subtidal community shifted in composition from the mid-1700s to the mid-1800s;

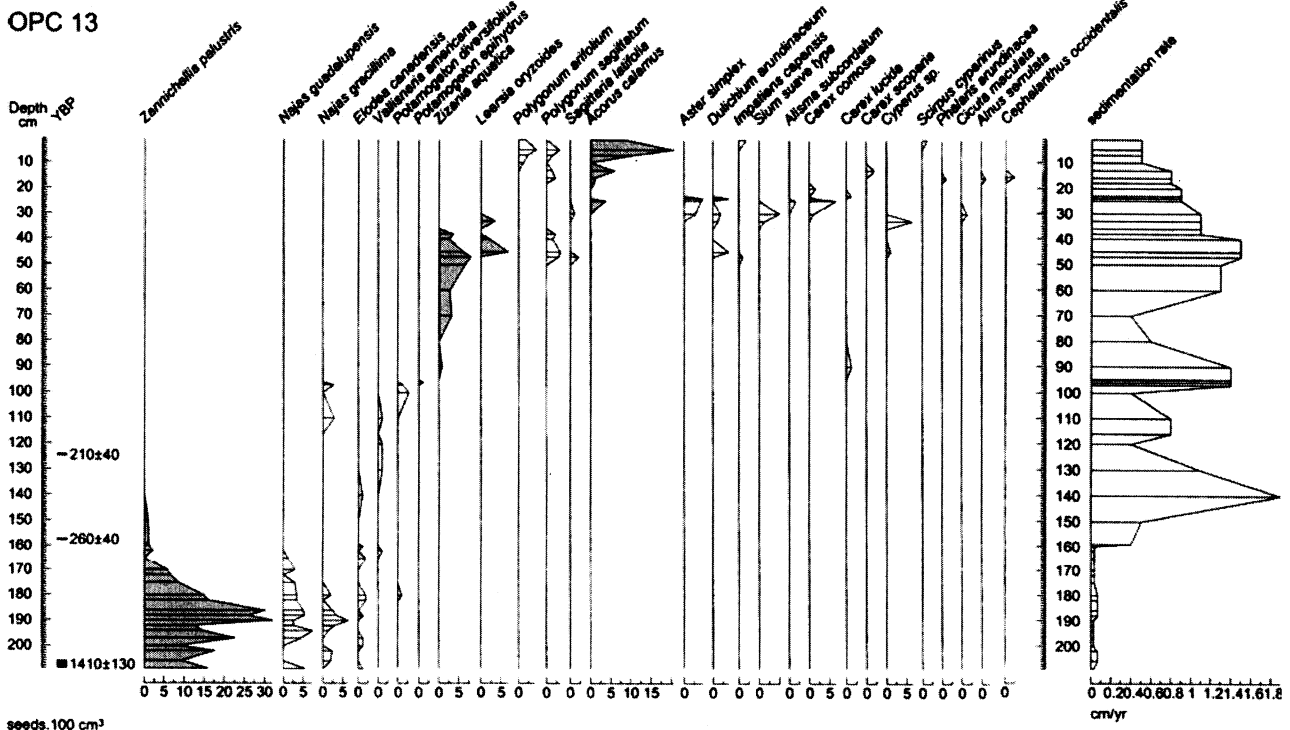


Figure 5 Macrofossil species in OPC13. Read from left to right species and habitats are listed from most flooded to least flooded. Habitats are defined by the following species: subtidal (*Zannichellia palustris*), low marsh (*Zizania aquatica*), middle marsh (*Leersia oryzoides*) and high marsh (*Acorus calamus*)

Z. palustris disappeared around 1750 when SR had reached 0.47 cm/yr and *Vallisneria americana* appeared shortly afterwards when SR had risen to 1.07 cm/yr. *N. gracillima* returned in the early 1800s and two other aquatic macrophytes, *Potamogeton diversifolius* and *P. epihydrus*, became established for a brief period in the mid-1800s. Soon afterwards all subtidal species disappeared. Clays interspersed with sand layers and higher sedimentation rates between 1860 and 1950 indicate increased upland erosion and deltaic deposition. A *Zizania aquatica* low marsh became established around 1860 after SR increased from 0.4 to 1.35 cm/yr. From 1860 until about 1935 *Z. aquatica* was virtually the only species present. In 1935 the habitat shifted to a middle marsh dominated by *Leersia oryzoides*, *Polygonum sagittatum*, *Sagittaria latifolia* and sedges as SR peaked at 1.5 cm/yr. Within 10 years or so an assemblage of herbaceous species with no modern analogue became established including *Aster simplex*, *Dulichium arundinaceum*, *Sium suave*, *Alisma subcordatum* and *Carex* spp. *Sium* has not been found at OPC, *Dulichium* occurs in Haha branch, a small delta adjacent to OPC, and *Alisma* is common in the higher elevation shrub marsh habitat but not at lower elevations. This assemblage shifted to high marsh when *Acorus calamus* became established around 1950. Numerous species immigrated and emigrated for brief periods while SR declined from 0.92 to 0.47 cm/yr. The modern *Acorus calamus* high marsh present at this site became established by the early 1970s.

Mid Wetland. Auger2 (present habitat: *Acer negundo* riparian forest)

A subtidal habitat consisting of five species of aquatic macrophytes persisted from ~1300 until the late 1700s (Figure 6). Up to this time SR ranged between 0.07 and 0.09 cm/yr. While *Elodea canadensis* disappeared around AD 1540 the remaining four species, *Najas gracillima*, *N. guadalupensis*, *Potamogeton diversifolius* and *Zannichellia palustris*, disappeared after SR increased to 0.61 cm/yr by ~1775. During the early 1800s the habitat changed to a shrub marsh dominated by sedges, when *Eleocharis obtusa* and other sedges

became established as SR rose to between 0.8 and 1.4 cm/yr. The presence of *Eleocharis obtusa* indicates shrub marsh habitat, based on its modern occurrence in OPC (W.B. Hilgartner, personal observation, 1996), although no shrub fossils were recovered. By 1850 these species disappeared and were replaced by a maturing riparian forest of *Acer negundo*, *Fraxinus pennsylvanica* and *Betula nigra*, identified by the presence of 'Rootlets'. The disappearance of the sedges in 1850 indicates the closing of the forest canopy and reduced sunlight. The presence of 'Rootlets' before 1850 probably represents root penetration into lower stratigraphic levels. Hence, the modern closed canopy riparian forest at this location became established about 1850. During the last half of the nineteenth century SR varied widely from 0.5 to an exceptional episode when 48 cm was deposited. Poor macrofossil preservation in forest sediment prevents interpretation of minor changes within the vegetation over the past 150 years.

Upper Wetland. Auger4 (present habitat: *Acer negundo* riparian forest)

At 224–240 cm (~1730) a shrub marsh habitat is indicated by the presence of *Carex scoparia*, *Eleocharis obtusa* and *Alnus serrulata* (Figure 7a). This habitat persisted until 160–176 cm (~1840) when a closed canopy riparian forest became established as indicated by the dominance of 'Rootlets' and the disappearance of herbaceous species. At 112–128 cm (~1870), the forest canopy became more open and soil conditions wetter, as *Glyceria striata* and *Polygonum punctatum* became established. These herbaceous species disappeared at 48–64 cm (~1880) when the forest habitat again became a closed canopy forest. Sedimentation was extremely high at this time with as much as ~50 cm/yr deposited around 1880, possibly in one or several major storms. Sometime during the mid to late twentieth century, the forest canopy opened up as *Leersia oryzoides* and *Polygonum sagittatum* became established. This may have been 1972 when flooding from Hurricane Agnes killed many trees in a basin 100 m distant from the site.

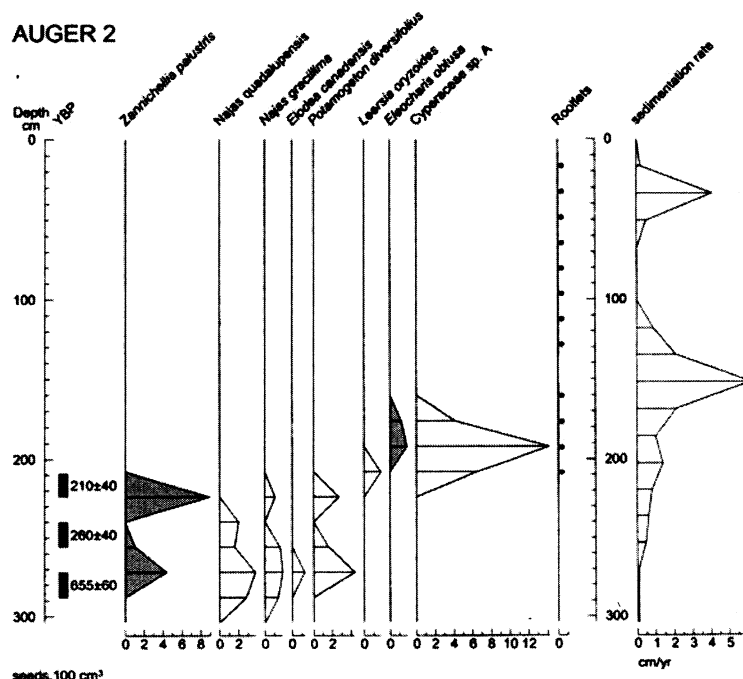


Figure 6 Macrofossil species in Auger2. Read from left to right species and habitats are listed from most flooded to least flooded. Habitats are defined by the following species: subtidal (*Zannichellia palustris*), shrub marsh (*Eleocharis obtusa*) and riparian forest (rootlets)

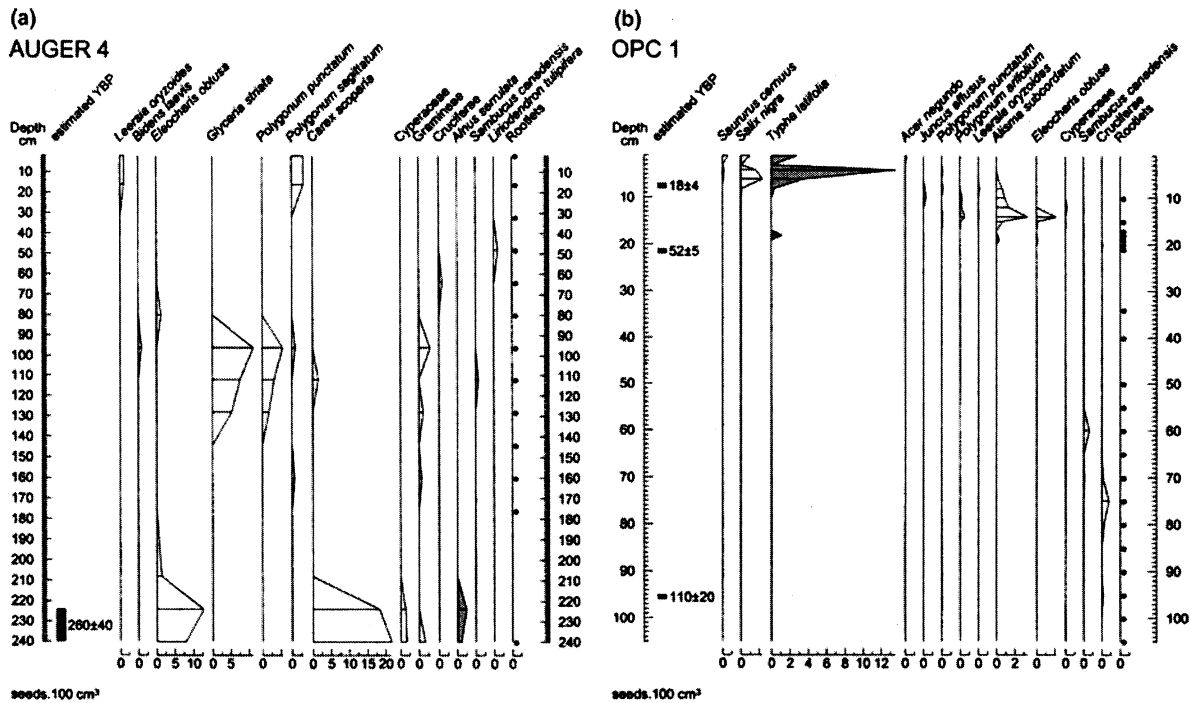


Figure 7 Macrofossil species in (a) Auger4 and (b) OPC1. Read from left to right species and habitats are listed from most flooded to least flooded. Habitats are defined by the following species: shrub marsh (*Alnus serrulata* and *Typha latifolia*) and riparian forest (rootlets). In Auger4 a bottom date of 1730 at 224–240 cm is estimated based on a 2.8 *Quercus: Ambrosia* pollen ratio and similar dated levels in Auger2, the nearest auger boring within the riparian forest. In OPC1 a bottom date of ~1860–1880 at 96–100 cm is estimated based on the absence of *Quercus* pollen and a similar age/depth level to Auger2

Auger1 (present habitat: *Acer negundo* riparian forest)

A bottom date of ~1750 at 208–224 cm is estimated based on similar age/depth levels in Auger2 and Auger4. No pollen was recovered and the ^{14}C date appears too young. No profile is presented because only seven macrofossil taxa were recovered from this auger boring. The continuous presence of 'Rootlets' throughout the boring from 192–208 cm to the core apex indicates that the present riparian forest of *Acer negundo*, *Fraxinus pennsylvanica* and *Betula nigra* was established at least by the late 1700s at this site. A species of *Oxalis*, possibly *O. stricta* was present for a brief period in the early to mid-1800s. This species has not been found in forest transects or surveys and may represent a local extinction. It is also possible that it may be a non-native *Oxalis* sp. introduced during disturbance.

OPC1 (present habitat: *Salix nigra*-*Typha latifolia* shrub marsh)

A riparian forest habitat, based on the presence of 'Rootlets' was established in the bottom sediment (Figure 7b). A species of Cruciferae and *Sambucus canadensis* were important from 85 cm to 60 cm (~1890–1910). The forest persisted until around 1938, when an opening in the forest canopy and increased flooding occurred, based on the presence of *Alisma subcordatum*, *Eleocharis obtusa*, *Polygonum arifolium* and, for a brief period, *Typha* cf. *latifolia*. This date is estimated, based on the timing of road construction of Route 40, the edge of which lies within 20 m of the coring site (Figure 1). The road embankment is believed to have initiated hydrologic alteration of this portion of the wetland. In the early 1970s, the above species (except *Typha*) disappeared as flooding depth increased and *Salix nigra*, *Typha latifolia* and *Saururus cernuus* became dominant. Again completion of the nearby road construction of Route 24 (1971–1972) impeded drainage and, combined

with flooding from Hurricane Agnes (1972), is believed to be the reason for the habitat shift to greater flooding depth (Figure 1). Sequential aerial photographs support this argument (Hilgartner, 1995).

Discussion: The cause and pattern of habitat change

We infer from the palaeoecological record that an aquatic macrophyte habitat in an estuarine basin remained relatively stable for 15 centuries. A prehistoric, undisturbed, forested watershed acting as a storm buffer in flood and erosion control, released sediment into the estuary at a mean rate of only 0.05 cm/yr during this extended period. Major storms must have occurred with regular frequency during this time, based on documentation of seven major storms within the past 700 years in coastal Rhode Island (Donnelly *et al.*, 2001) and historical records of hurricanes and tropical storms in the upper Chesapeake Bay within the past 100 years. Yet no stratigraphic evidence of storms appears in sediments deposited prior to European settlement. Stratigraphic evidence for storm and flooding events within a core would include the appearance of thin laterally accreted sand layers, increased sedimentation rates, and/or the occurrence of macrofossils transported from upland plants (Watts, 1978; Birks and Birks, 1980; Cotton *et al.*, 1999; Donnelly *et al.*, 2001). This storm buffer effect of forested watersheds is well-documented elsewhere from recent and long-term watershed studies as well as from geomorphologic reconstructions (Bormann *et al.*, 1974; Jacobson and Coleman, 1986; Freedman, 1995; Goudie, 2000).

The centuries-long dry and wet periods identified in the region had a minor effect on the subtidal habitat at OPC. *Zannichellia palustris* increased in abundance around the

seventh century and tenth to twelfth centuries dry periods at one site (OPC13), but other species showed no response. Higher salinity as a result of dry conditions may have favoured *Zammichellia*, but it would have depressed or negatively affected *Najas gracillima*, which is less salinity-tolerant (Brush and Hilgartner, 2000). If dry conditions reduced water levels, some marsh or pioneer species such as *Zizania aquatica* might have appeared for a brief period but this did not happen. The appearance of the marsh species *Scirpus validus* in OPC3 appears to be independent of climate changes since it became established 200 years after the seventh century dry period and persisted from 800 to 1730. The decline or disappearance of four species around 1300 in OPC13 is coincident with the onset of the fourteenth-century wet period but the habitat remained intact as *Zammichellia* and *Najas guadalupensis* persisted.

The absence of any shift in habitat and dominant species in 1500 years indicates that autochthonous or biological factors, as well as Mediaeval and 'Little Ice Age' climate change, were not important in initiating habitat change during a time spanning 1000–2000 years. Habitat change proceeded only after the sedimentation rate increased during the eighteenth century. This result is supported by other studies showing that rapid accretion of infilling silt, sand and clay from anthropogenic disturbance is the primary factor forcing major changes in species assemblages in coastal wetlands (Cole, 1994; Khan and Brush, 1994).

Beginning in the early 1700s sedimentation rates increased sharply. The initial influx of sediment was synchronous with European settlement and land clearance, as populations migrated into and began to cultivate the steeper slopes of the Piedmont between 1730 and 1780. Erosion steadily increased as forests were cleared and agriculture became more extensive. The subtidal habitat that had persisted for centuries tolerated this initial phase of sediment increase with shifts in species abundances as sedimentation rates increased from 0.05 cm/yr up to 0.60 cm/yr. However, aquatic macrophytes disappeared when a mean sedimentation rate reached 0.60 cm/yr. This rate appeared to be a critical threshold, because habitat change

proceeded as rates continued to exceed 0.60 cm/yr during the nineteenth century and the first half of the twentieth century. The period of peak accretion rates ranging from 3.9 cm/yr to an exceptional 48.0 cm/yr occurred between 1840 and 1880. Bain (2003) identified this same peak sedimentation period (1840–1880) in the Red Run watershed in the Maryland Piedmont 45 km inland from OPC, thus providing independent evidence of this highly erosive period in local watersheds. During the same period forest cover in the watershed was reduced from 40% to 20% and new settlement occurred on steep, marginal slopes that previously had been inaccessible or unfavourable for agriculture (Earle, 1992). Increased storm water runoff on a deforested landscape comprised of steep, marginal slopes would certainly have resulted in increased erosion rates and sediment deposition in the estuary. Hydrographic data show that flow rates following storms in a deforested or urbanized watershed can be five to ten times greater than flow rates from a forested watershed, and the rate of sediment yield appears to double for every 20% loss in forest cover (Goudie, 2000). Stratigraphic evidence of storms after AD 1700 (levels of 65–80 cm in OPC3 and OPC13) is present in the form of thin laterally accreted layers of sand, mica and allochthonous seed and leaf fragments. These levels (65–80 cm) include the mid-1800s, when four major storms impacted the region and habitat change in the estuary was most extensive. During this period the subtidal habitat disappeared at all sites while low marsh and riparian forest expanded.

Between 1750 and 1950 habitat communities shifted throughout the estuary (Figures 8 and 9). Habitats changed at five sites from wetter to drier, one changed from drier to wetter, and another did not change. Using a Chi-Square test from a probability matrix of the numbered habitat sequences shown in Figure 8, the null hypothesis that habitat changes were independent of one another after AD 1700 was rejected at $p < < 0.001$ ($\chi^2 = 226.3$, $df = 49$). This indicates that the sequence of habitat change was non-random. The trajectory of temporal change reflects the physical position of modern

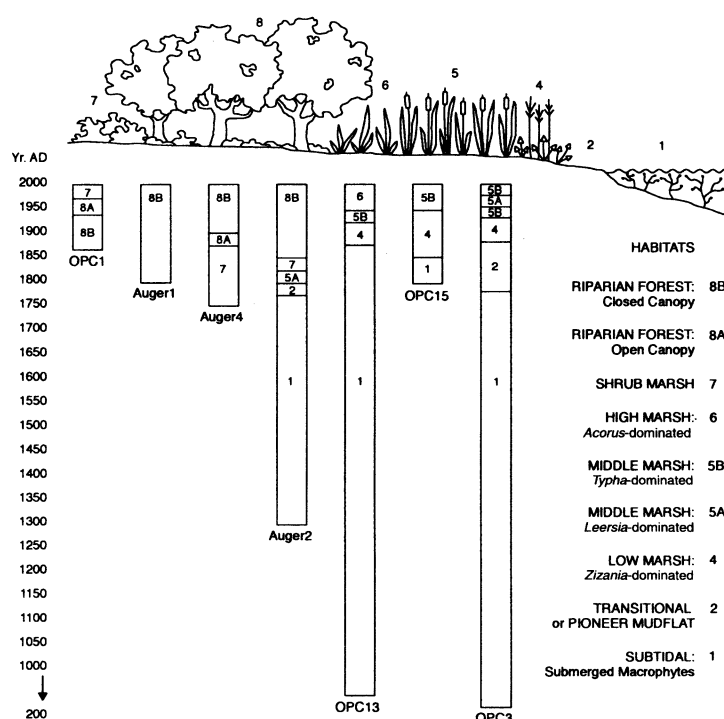


Figure 8 Sequence of habitat changes in seven cores and borings in Otter Point Creek

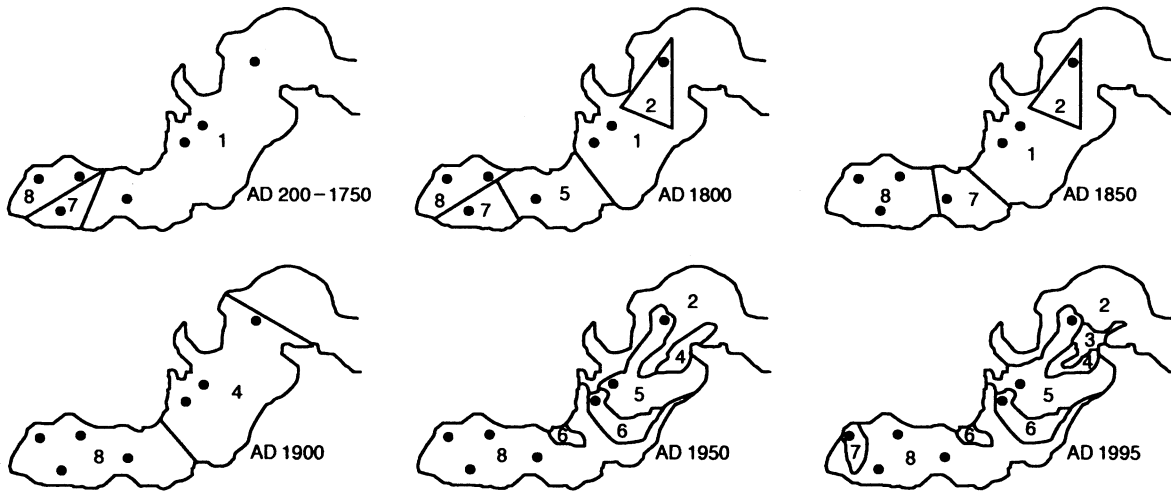


Figure 9 Spatial habitat distribution within the OPC wetland for pre-European period (AD 200 to AD 1750) and 50-yr increments since 1750. Dots represent coring locations. Habitats numbers follow Figure 6 and Table 1: 1, subtidal; 2, pioneer mudflat; 3, floating leaf; 4, low marsh; 5, middle marsh; 6, high marsh; 7, shrub marsh; 8, riparian forest

habitats relative to subtidal and channel margins; ie, from the most flooded (subtidal) to least flooded (riparian forest).

However, the sequence, rate of change and species composition at each coring site varied considerably, demonstrating the influence of local site characteristics on spatial variability within and between habitats. The most rapid series of changes occurred at the Auger2 site; subtidal habitat shifted to middle marsh, shrub marsh and riparian forest within 75 years 'skipping over' the low marsh and high marsh sequences. This site received the highest post-settlement sedimentation of 240 cm. The sites receiving less deposition (OPC3 and OPC13) experienced roughly equal levels of post-settlement sedimentation of 165 cm and 160 cm, respectively, and shifted more gradually from subtidal to marsh habitats. In addition to differential sediment deposition between sites, minor changes in species composition could be caused by local, physical

differences in hydrology and nutrients (Gosselink and Turner, 1978; Mitsch and Gosselink, 2000), or biological factors including herbivory, competition, seed dispersal, colonization, seed bank dynamics or channelization by beavers (Connell and Slatyer, 1977, van der Valk, 1981; Simpson *et al.*, 1983; Huston and Smith 1987; Leck 1989; Crawley 1997; Pasternack *et al.*, 2000).

The data demonstrate that marsh and forest habitat development did not happen gradually over the past 300 years, but proceeded in alternating periods of stasis bounded by periods of change. The periods of change, or pulses, were a response to high yields of sediment input. The pulse timing varied somewhat with each core, depending on its proximity to the watershed or distributary channel. New habitats established equilibrium within a new range of elevation and sedimentation rates. This stasis-pulse-stasis model is similar to the equili-

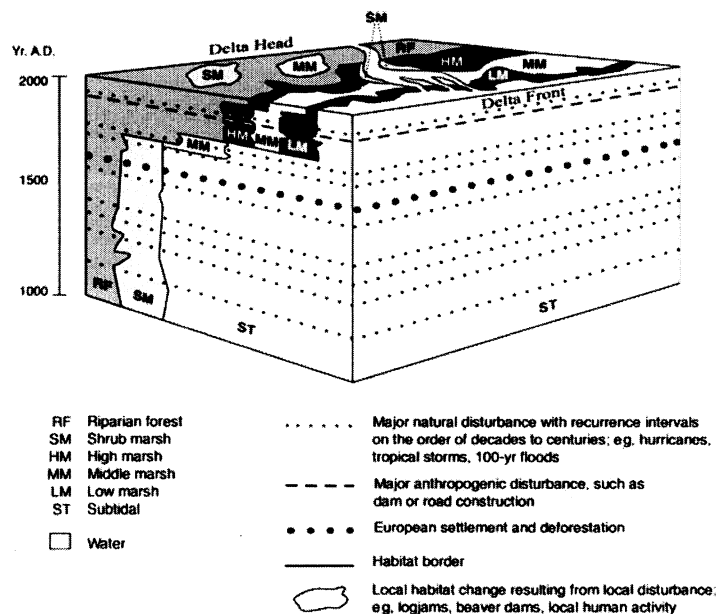


Figure 10 Conceptual model of habitat change in a freshwater tidal wetland delta. The model hypothesizes that stability prevails in estuaries with forested watersheds for many centuries before European settlement. Large disturbances such as 100-yr storm events do not impact wetland habitats while the watershed is > 98% forested. After deforestation erosion increases and combined with storm water, sediment efflux produces a prograding delta away from the delta head and the main channel bank with accompanying habitat change. Habitat change occurs after sediment pulses. A period of habitat stasis follows until interrupted by the next storm pulse or major watershed disturbance.

brum-disequilibrium model derived from palaeoecological studies of habitat development in kettle-hole peatlands in Wisconsin and Ontario (Winkler, 1988; Campbell *et al.*, 1997). In these instances habitat change is produced by dramatic shifts in hydrology resulting from climate change spanning centuries. By contrast, habitat response at OPC occurred within decades because of changes in sedimentation rates as a result of human-induced soil erosion.

No significant change in wetland configuration or broad habitat change has occurred since the early 1950s. There have been no extensive changes since completion of Route 40 (1938) and the Atkisson and Van Bibber Dams (1944–45). The Atkisson Dam traps sediment supplied from the upper two-thirds of the watershed. Thus, while high sedimentation rates during dam and road construction appear to have contributed to habitat change before 1950, a substantially reduced sediment load reached the estuary after 1950. Low post-construction sediment yields have been shown to follow up to a tenfold increase in sedimentation during construction (Wolman, 1967; Groffman *et al.*, 2003). The coincidence of reduced sediment yields from the watershed since 1950 (mean rate of 0.52 cm/yr) and the reduction or cessation of delta progradation and habitat change in the estuary, further identifies human disturbance of the watershed as the primary influence on wetland habitat development and configuration.

While the macrofossil record clearly shows a sequential replacement of vegetation assemblages, it may not provide an accurate record of successional processes at each coring site, because important, subtle successional changes that would occur within 1–20 yr periods would be obscured or lost. We agree with the caution proposed by Hughes and Dumayne-Peaty (2002) that macrofossils spanning hundreds of years probably cannot address particular processes or mechanisms inherent in the term 'succession'.

We propose a conceptual model to describe the history of disturbance and habitat change in an upper estuary that results in freshwater tidal wetlands (Figure 10). We believe the model describes the development of freshwater tidal wetlands in most subestuaries along the western shore of the Chesapeake Bay for historical and geographical reasons. Virtually the entire Chesapeake watershed has been deforested in the 380 years since European settlement (Brush, 1994), and much of the western shore of the Bay adjoins the steep Fall Line. The model may be applied more broadly to describe the development of any FTW that forms in the basin of a forested watershed with steep topography, since watershed slope is an important factor in sediment supply (Goudie, 2000; Pasternack, *et al.*, 2001). Refinement of the model could be accomplished through further study of the relationships between watershed slope, ratio of watershed area to basin area, dominant vegetation, and varying human and natural disturbance regimes.

Conclusion

The results of this study emphasize the strong relationship that exists (or existed) between a fully forested watershed and a stable estuarine habitat. A forested watershed ameliorates the effect of major storms by absorbing runoff and reducing erosion, so that sediment efflux into the estuary remains low for centuries. Once this buffering effect was reduced by up to 80% deforestation during the eighteenth and nineteenth centuries, erosion in conjunction with storm events produced increased accretion of inorganic sediment in the estuary, burying the pristine aquatic macrophyte habitat. The most extensive and rapid change occurred from 1840 to 1880, when

human disturbance was the only factor initiating habitat change. Major storms or construction in conjunction with a deforested landscape produced pulses of habitat change, followed by periods of habitat stasis. During the period of stasis, minor fluctuations in species composition and abundance occurred within habitats. Hence, scale is important in understanding local habitat change since large-scale watershed disturbance over 300 years produced different wetland habitats, while individual habitats responded to local site variations. The macrofossil record in freshwater tidal wetlands is useful in shedding light on the sequential replacement of vegetation communities at various spatial and temporal scales.

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