

## Coastal Wetlands of Chesapeake Bay

ANDREW H. BALDWIN, PATRICK J. KANGAS, J. PATRICK MEGONIGAL,  
MATTHEW C. PERRY, and DENNIS F. WHIGHAM

Chesapeake Bay is the largest estuary in the United States. It occupies 5,700 km<sup>2</sup>, has 6,400 km of shoreline, and is fed by about 50 major and thousands of minor tributaries (Fig. 3.1) (US EPA 1982, 2004; White 1989). Its location entirely within the flat topography of the Atlantic Coastal Plain has favored the development of vast areas of wetlands, including tidal freshwater, oligohaline (intermediate), and brackish (mesohaline) marshes (dominated by herbaceous plants), tidal freshwater swamps (dominated by woody plants), submersed macrophyte ("seagrass") beds, and tidal mudflats lacking vascular plants (Fig. 3.2a–g). We estimate that about 160,000 ha of these types of coastal wetlands occur in the Bay, based on several sources (Wass and Wright 1969; McCormick and Somes 1982; Tiner and Burke 1995; Tiner, Berquist, et al. 2001).

Coastal wetlands of Chesapeake Bay experience a range of tidal amplitudes and salinity regimes. Mean amplitude is 0.9 m at the Bay mouth and generally lower along major subestuaries such as the Patuxent (0.37–0.73 m), Potomac (0.43–0.85 m), Rappahannock (0.37–0.79 m), and Nanticoke (0.67–0.73 m), but can be higher, for example, up to 1.16 m on the upper tidal reaches of the York River (Fig. 3.1) (Hicks 1964). Although tidal amplitude decreases moving north across the Bay proper, within subestuaries the maximum amplitude often occurs near the upper reach of tidal influence, i.e., in the tidal freshwater zone (Hicks 1964). Tidal amplitude of Bay wetlands is small relative to those of the rest of the East Coast (WWW Tide and Current Predictor, <http://tbone.biol.sc.edu/tide>), and in this respect Bay wetlands are more similar to Gulf Coast than to other Atlantic Coast wetlands. Salinity regimes range from tidal freshwater (< 0.5 ppt salinity) at the upper reaches of the Bay and its subestuaries to polyhaline (18–30 ppt) near the mouth, although most of the Bay is below 20 ppt and brackish water predominates (US EPA 2004). During summer months, particularly during droughts, salinity in typically freshwater areas may increase to 5–7 ppt (Baldwin 2007). Salinity can also fluctuate daily at a given location by as much as 5 ppt due to tidal exchange (White 1989). The diversity and size of Chesapeake Bay coastal wetlands provide a unique natural laboratory to examine the influence of global, regional, and local changes caused by humans on estuarine structure and function.

### Hydrogeology and Biogeochemistry

Chesapeake Bay is a drowned river valley that formed in the late Pliocene (Hobbs 2004) and began filling with water 10,000 years ago as sea level rose due to Holocene warming. Sediment originating in both the 166,500-km<sup>2</sup> catchment and the continental shelf has since filled the Bay (Hobbs, Halka, et al. 1992) to an average depth of about 7 m. Soil erosion and subsequent sediment deposition in streams and estuaries accelerated dramatically in the 17th century as European settlers converted forests to agriculture (Brush 1984), with consequences for both tidal and nontidal wetlands.

Prior to the 17th century, Chesapeake Bay streams supported extensive nontidal wetlands with relatively organic-rich soils (Walter and Merritts 2008), reflecting their low rates of sediment deposition and capacity to accumulate carbon. Many of these fluvial presettlement wetlands were buried in the 17th and 18th centuries by fine upland sediments deposited behind tens of thousands of mill dams constructed for water power (Walter and Merritts 2008). The 17th-century spike in soil erosion is also apparent in sediment cores from Bay tidal wetlands (Pasternack, Brush, et al. 2001). For example, sediment deposition at Jug Bay on the Patuxent River, Maryland, increased fivefold from an apparent pre-European rate of < 1 mm yr<sup>-1</sup> to a 19th-century rate of 5 mm yr<sup>-1</sup> (Khan and Brush 1994). Because of this sharp increase in sediment loading, it is possible that European settlement initially increased the area of Bay tidal wetlands, particularly the area of tidal freshwater wetlands at the head of tide, where the channel is relatively narrow and shallow. The high suspended sediment loads of the present-day Chesapeake Bay and its tributaries are a legacy of soil erosion that began with European settlement and is ongoing today (Schenk and Hupp 2009).

Rates and patterns of sediment deposition influence wetland ecosystem attributes such as soil organic matter content, nutrient availability, and soil surface elevation, and spatiotemporal variation in sediment deposition is the source of structural and functional differences among and within wetlands (Pasternack 2009). Deposition rates in both tidal (Jordan, Pierce, et al. 1986) and nontidal (Noe and Hupp 2009) fluvial

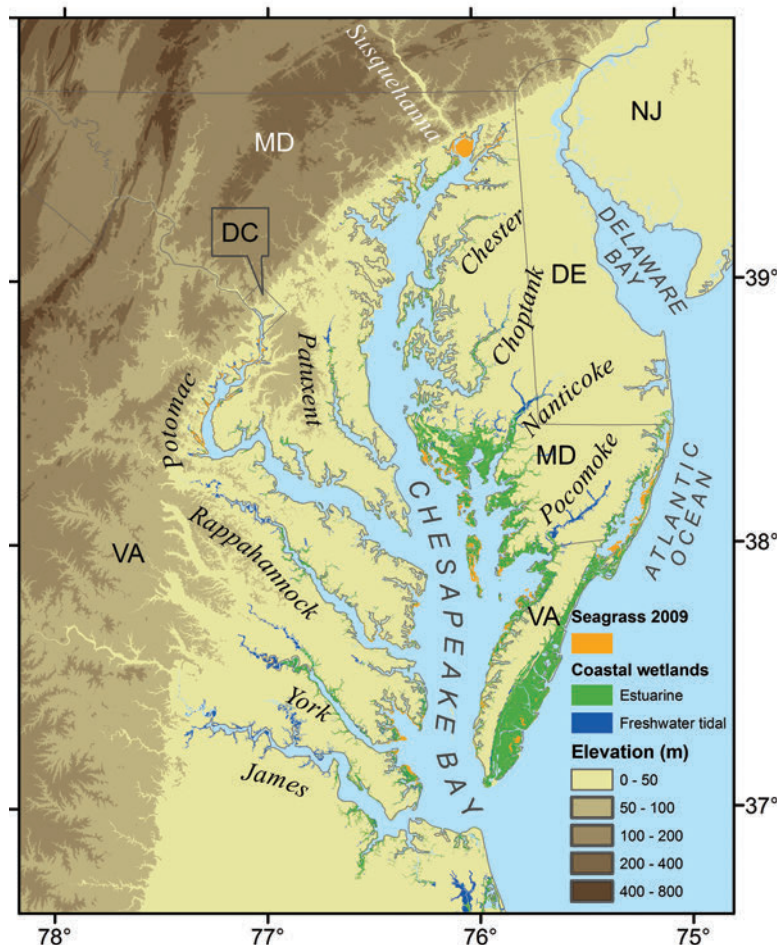


FIG. 3.1. Major tributaries and coastal wetlands of Chesapeake Bay. The location of estuarine and freshwater tidal wetlands is based on U.S. Fish and Wildlife National Wetlands Inventory geospatial data and includes wetlands with emergent vegetation, unvegetated intertidal areas (mudflats), and vegetated shallow-water areas (seagrasses or algae). “Seagrass 2009” is the distribution of submersed aquatic vegetation (SAV) beds determined in 2009 by the Virginia Institute of Marine Science Submerged Aquatic Vegetation program (<http://web.vims.edu/bio/sav/sav09/>). Map prepared by A. H. Baldwin.

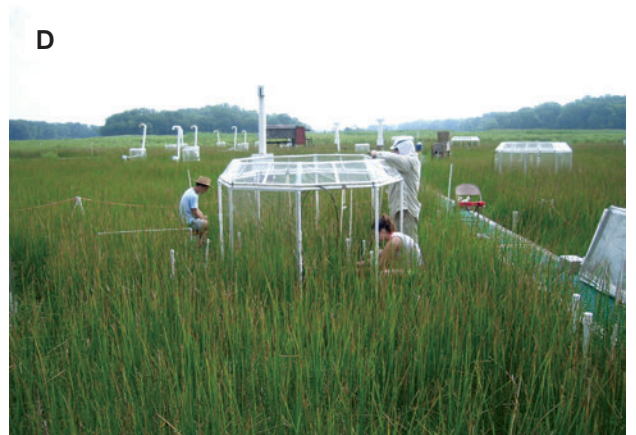
Chesapeake Bay wetlands are related to the suspended sediment load of the floodwater. In a comparison of two sites separated by 19 km on the Mattaponi River, Virginia, rates of sediment deposition were up to tenfold higher at the site farthest downstream and closest to the turbidity maximum (Darke and Megonigal 2003). The turbidity maximum is a dynamic feature of Chesapeake Bay that coincides roughly with the freshwater-saltwater interface (Schubel 1968) and responds to variation in the discharge of the Susquehanna River (Schubel and Prichard 1986). At the site scale, deposition rates in both tidal and nontidal wetlands (Ross, Hupp, et al. 2004) decline rapidly with distance from the fluvial source and increasing elevation (i.e., decreasing frequency of inundation). Such factors contribute to the observation that tidal low-marsh soils near fluvial sources are relatively low in organic matter and mineral rich compared to high-marsh or interior marsh soils (A. Bald-

win pers. obs.). Many Bay tidal high marshes have peat soils (sapric histosols) with profiles up to 5 m deep composed of > 70% soil organic matter (P. Megonigal pers. obs.).

The productivity and composition of vegetation can regulate sediment deposition rates in tidal wetlands, provided that suspended sediment does not limit the process. Plant density and height were highly correlated with sediment deposition rates in a tidal freshwater wetland located near the turbidity maximum of the Mattaponi River, but not at a site 19 km upstream, where sediment concentrations were much lower (Darke and Megonigal 2003). In other Chesapeake Bay tidal freshwater wetlands, sediment deposition was strongly correlated to plant community type (Pasternack and Brush 2001) and creek bank deposition was higher in vegetated than in unvegetated areas (Neubauer, Anderson, et al. 2002). The seasonal dynamics of vegetation contribute to intra-annual varia-

FIG. 3.2. (opposite) Examples of Chesapeake Bay wetland ecosystems. A. Jug Bay in the freshwater tidal portion of the Patuxent River subestuary. B. Freshwater tidal marsh, showing zonation into low and high marsh plant communities. C. Brackish marsh, showing *Spartina cynosuroides* (foreground), *S. patens* (middle), and *Juncus roemerianus* (background). D. Chambers for the CO<sub>2</sub> elevation experiment at the Smithsonian Environment Research Center. E. Freshwater tidal swamp. F. Landsat mosaic of the Choptank and Nanticoke River subestuaries and adjacent eastern Chesapeake Bay shoreline. G. Restored freshwater tidal marsh on the Anacostia River, Washington, DC. (Photo credits: A: A. Luckenbach; B, C, E, G: A. H. Baldwin; D: J. P. Megonigal. Used with permission.)







tion in sedimentation, with peak deposition coinciding with peak plant biomass (Leonard 1997; Pasternack and Brush 2001; Neubauer, Anderson, et al. 2002; Darke and Megonigal 2003); however, there are exceptions (Kastler and Wiberg 1996).

Chesapeake Bay tidal wetlands must periodically increase soil mass in order to rise in elevation at a pace coincident with sea-level rise, a process that many extant Bay wetlands have maintained for the past 6,000 years over an approximately 5 m increase in sea level. Plant-enhanced sediment deposition is one mechanism for adding soil mass, but many Bay wetland soils are composed almost entirely of decaying plant matter. In comparison to sediment deposition, there is relatively little known about how organic processes such as wetland plant productivity and decomposition govern the gain or loss of soil organic matter and elevation in tidal wetland soils.

Wetlands are sinks, sources, and transformers of matter that cross the upland-aquatic interface. Sediment deposition is an important vehicle for importing allochthonous particulate organic carbon and nutrients into wetland soils (Morse, Megonigal, et al. 2004). For example, at Sweet Hall Marsh, a Chesapeake Bay tidal freshwater wetland, one-third of organic carbon inputs are imported with sediment, with the remainder from in situ production (Neubauer, Anderson, et al. 2002). Seven nontidal Bay Coastal Plain rivers deposit a large fraction of their annual load of nitrogen (24%) and phosphorus (59%) in the adjacent floodplain (Noe and Hupp 2009). Tidal wetlands also appear to be efficient nutrient traps, sequestering 35% of the nitrogen and 81% of the phosphorus load in the upper reaches of the Patuxent River by one rough estimate (Merrill and Cornwell 2000).

Tidal wetlands can be either sources or sinks of particulate and dissolved matter, depending on factors such as tidal range, subsystem area, and distance to the ocean (Childers, Day, et al. 2000), all of which vary across Chesapeake Bay. There has been relatively little work on energy and nutrient exchange in the Bay. Studies of the brackish Rhode River subestuary concluded that brackish tidal wetlands acted mainly to transform nutrients from particulate to dissolved forms, and identified mudflats as the most important nutrient sink (Jordan, Correll, et al. 1983). Net export of ammonium has been observed in both brackish and tidal freshwater wetlands (Jordan and Correll 1991; Neubauer, Anderson, et al. 2005), but the direction of nitrate exchange differed between the low marshes at these sites. Both denitrification (Hopfensperger, Kaushal, et al. 2009) and dissimilatory nitrate reduction to ammonium (Tobias, Macko, et al. 2001) are sinks for nitrate in Bay tidal wetlands.

Early work on carbon export in tidal marshes was motivated by the hypothesis that these systems export energy (as carbon) to aquatic food webs. Recent work on dissolved organic carbon (DOC) has been motivated by the effects of light-adsorbing forms of DOC (i.e., chromophoric dissolved organic matter, or CDOM) on ultraviolet light penetration and the possibility of using the CDOM signature to trace the flux of estuarine compounds into coastal oceans. Both brackish and freshwater tidal wetlands of the Bay are net sources of CDOM to the estuary (Tzortziou, Neale, et al. 2008; Megonigal and Neubauer 2009). There is limited evidence that tidal wetlands are dominant sources of dissolved inorganic carbon to Chesapeake Bay (Neubauer and Anderson 2003).

The biogeochemical factors that control specific pathways of microbial respiration are important for understanding the wetlands as simultaneous sinks of carbon dioxide (CO<sub>2</sub>) and sources of methane (CH<sub>4</sub>), a powerful greenhouse gas. Methane emissions are typically higher in nontidal than tidal wet-

lands (Bridgman, Megonigal, et al. 2006) because sulfate-reducing microbes outcompete methanogens for organic carbon, an effect that varies predictably with salinity (Poffenbarger, Needelman, et al. 2011). Methane production in Chesapeake Bay wetlands is also regulated by iron availability (Neubauer, Givler, et al. 2005) and possibly humic acid availability (Keller, Weisenhorn, et al. 2009).

## Plant Communities

Wetland plant communities of Chesapeake Bay are species rich; a total of 286 emergent vascular plant species were recorded at 9 tidal wetland sites spanning salinities of about 0.5–22 ppt in the James River estuary (Fig. 3.1) (Atkinson, Bodkin, et al. 1990). *Emergent plants*, as used in this chapter, means those having stems or leaves protruding above the water. Furthermore, benthic microalgae are important primary producers in emergent marshes, seagrass beds, and mudflats, and macroalgae are also common in shallow open water where attachment substrate occurs (White 1989).

## Emergent Plants

Salinity is the most important environmental variable controlling emergent plant species composition across estuaries. In general, the number of plant species within plots or distinct wetlands increases as average salinity decreases, proceeding from areas near the confluence of Chesapeake Bay and the Atlantic Ocean and the upper reaches of the tide, where the Susquehanna River discharges into the Bay. Within individual subestuaries, salinity also varies from the confluence with the Bay to the upper extent of the tide (Anderson, Brown, et al. 1968). Oligohaline wetlands may have species richness similar to or higher than that of tidal freshwater wetlands farther upstream (Anderson, Brown, et al. 1968; Sharpe and Baldwin 2009), possibly due in part to periodic salinity intrusions that promote coexistence of brackish and freshwater species.

Only a few species can establish and grow in the brackish wetlands and salt marshes that occur at the downstream end of the salinity gradient (see estuarine wetlands in Figs. 3.1 and 3.2c), including the graminoids *Spartina alterniflora*, *S. patens*, *S. cynosuroides* (Fig. 3.3h), *Juncus roemerianus*, *Schoenoplectus americanus*, and *Distichlis spicata* and the shrub *Iva frutescens* (Anderson 1972; Sharpe and Baldwin 2009). A few forbs also occur in higher-salinity wetlands, such as the annual *Pluchea purpurascens*. At the most saline sites, near the mouth of the Bay, obligate halophytes such as *Salicornia virginica* and *Limonium carolinianum* occur (Perry and Atkinson 1997). Within a given brackish wetland, spatial patterns in plant community composition are due primarily to elevation-related differences in inundation.

The tidal freshwater and oligohaline wetlands of Chesapeake Bay (tidal freshwater wetlands are shown in Figs. 3.1 and 3.2a–b) include many species common in nontidal wetlands, but often at different relative abundances. Although a given wetland site may contain 50 or more species, among the most widespread and dominant perennials are *Peltandra virginica*, *Leersia oryzoides*, *Acorus calamus*, and *Nuphar lutea* (Fig. 3.3e) (Doumlele 1981; Perry, Bilcovic, et al. 2009; Sharpe and Baldwin 2009). These low-salinity wetlands differ considerably from brackish and salt marshes in that annuals, such as *Polygonum arifolium* (Fig. 3.3j), *P. sagittatum*, *Impatiens capensis*,

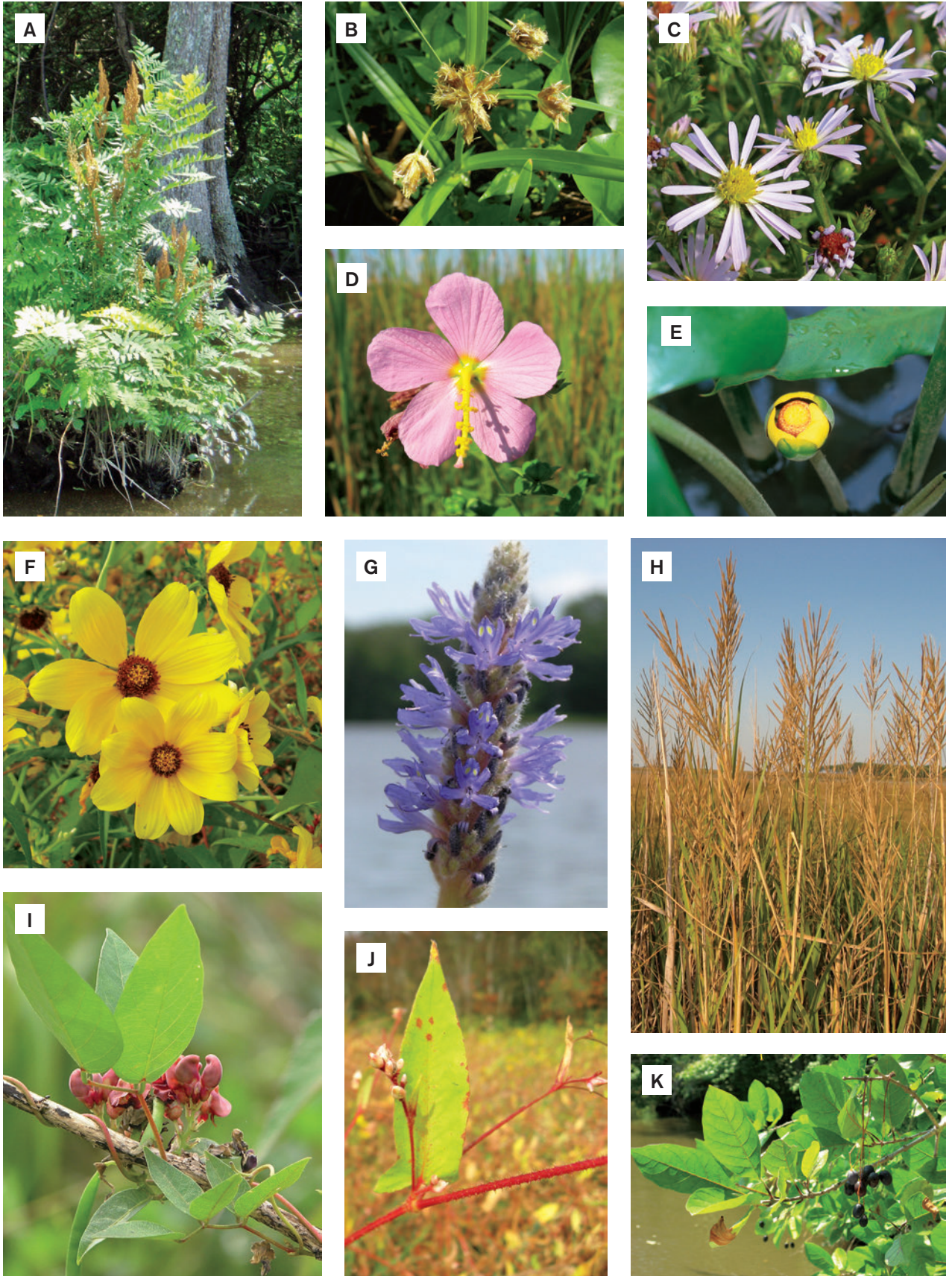


FIG. 3.3. Plant species of Chesapeake Bay wetlands. A. Royal fern, *Osmunda regalis*. B. River bulrush, *Schoenoplectus fluviatilis*. C. Purple-stemmed aster, *Symphyotrichum puniceum*. D. Saltmarsh mallow, *Kosteletzkya virginica*. E. Spatterdock, *Nuphar lutea*. F. Bur-marigold, *Bidens laevis*. G. Pickerelweed, *Pontederia cordata*. H. Big cordgrass, *Spartina cynosuroides*. I. Ground nut, *Apios americana*. J. Halberd-leaved tearthumb, *Polygonum arifolium*. K. Swamp tupelo, *Nyssa biflora*. (Photo credits: A–F, H, J–K: A.H. Baldwin; G, I: K. Jensen. Used with permission.)



and *Bidens laevis* (Fig. 3.3f), may make up half of the species in the community and, in some cases, most of the biomass (Baldwin, Egnotovich, et al. 2001; Baldwin and Pendleton 2003; Whigham 2009). These wetlands exhibit horizontal zonation, with the frequently flooded low marsh often a monoculture of *N. lutea* (Perry and Atkinson 2009) and most other species occurring in the high marsh (Leck, Baldwin, et al. 2009). Species composition varies seasonally, with *A. calamus* and *P. virginica* reaching their maximum abundance early in the growing season and annuals peaking later (Baldwin 2004; Perry, Bilcovic, et al. 2009; Whigham 2009). Saltwater intrusion may cause interannual variation in species composition: salt-tolerant species were abundant in a tidal freshwater wetland during low-flow, higher-salinity conditions, but freshwater species became dominant during wetter, fresher years (Davies 2004 in Perry, Bilcovic, et al. 2009).

Tidal freshwater and oligohaline swamps (Fig. 3.2e) are probably the most species-rich type of coastal wetland in the Bay, but also the least studied (Conner, Doyle, et al. 2007; Leck, Baldwin, et al. 2009). Although a few species of woody plants dominate the canopy, including *Fraxinus pennsylvanica*, *Acer rubrum*, and *Nyssa sylvatica* (Kroes, Hupp, et al. 2007), in plots at 24 sites along the Nanticoke River (Fig. 3.1), more than 40 species of trees and shrubs and over 100 herbaceous species were observed (Baldwin 2007). Similarly, on the Pamunkey River, a tributary of the York River, 20 canopy, 23 subcanopy, and 69 herbaceous species were recorded at 23 sites (Reinhardt 1992). The diversity of herbaceous plants is due in part to the hummock-hollow microtopography typical of these wetlands. Periodic salinity intrusions during droughts may also be a cause of high plant diversity in some swamps (Peterson and Baldwin 2004; Baldwin 2007).

## Seagrass Beds

Seagrasses are abundant in shallow waters across the Bay (Fig. 3.1), but species richness is higher in freshwater than in saline areas (Moore, Wilcox, et al. 2000). The spatial distribution of seagrass beds is also related to variables controlling light (depth, water turbidity, epiphytes on leaves, nutrients) and physiochemical factors including sediment grain size and organic matter content, porewater sulfide concentration, water currents (minimum need and maximum tolerance), and tolerance of individual species to waves (Koch 2001; Kemp, Batiuk, et al. 2004). Lower abundance of seagrasses is associated with higher agricultural and urban development (Li, Weller, et al. 2007).

About 20 species of submersed macrophytes occur in Chesapeake Bay, which can be divided into 4 species associations (Moore, Wilcox, et al. 2000; Moore 2009). An association dominated by *Zostera marina* predominates in the lower, most saline parts of the Bay, while an association dominated by *Ruppia maritima* is most widespread in the middle parts of the Bay. Farther upstream along the Bay and subestuaries is an association dominated by *Potamogeton pectinatus* and *P. perfoliatus*, and in the freshest parts of the Bay the most abundant type is a “freshwater mixed” association dominated by *Vallisneria spiralis* and two nonnative species, *Myriophyllum spicatum* and *Hydrilla verticillata*; this association contains more species (12) than the others (4 each for the *Ruppia* and *Potamogeton* associations and 2 for the *Zostera* association).

Changes in the abundance of seagrass beds in Chesapeake Bay over time have been both dramatic and well documented. In the 1930s, eelgrass (*Zostera marina*) populations, predomi-

nant in the lower, more saline parts of the Bay, were damaged by eelgrass wasting disease, a pandemic caused by the protist *Labyrinthula zosterae* (Orth and Moore 1984; Moore 2009). Another major change in Bay seagrass beds was an increase in the Eurasian water milfoil (*Myriophyllum spicatum*) in the fresher parts of the Bay in the late 1950s and 1960s (Orth and Moore 1984). Subsequent to these changes, an “unprecedented decline” in seagrass beds began (Orth and Moore 1983), perhaps exacerbated by high sediment and freshwater loading from Hurricane Agnes in 1972, but largely due to increases in nutrient concentrations associated with human population growth in the watershed, which promoted phytoplankton and epiphyte growth, shading leaves and reducing plant growth (Kemp, Boynton, et al. 2005). There has been a modest recovery of seagrasses in the Bay since about 1985, particularly in subestuaries where nutrient loading has decreased (Kemp, Boynton, et al. 2005).

## Micro- and Macroalgae

Benthic microalgae, or microphytobenthos, occur on the surface of marsh soils, mudflats, leaves and stems of emergent and submergent plants, and sediment surface in shallow waters, habitats that are widespread and abundant in Chesapeake Bay (Rizzo and Wetzel 1985).

Microalgal communities in Atlantic coastal wetlands are dominated by pennate diatoms, green algae (Chlorophytes) and blue-green algae (Cyanobacteria) (Pinckney and Zingmark 1993; Mitsch and Gosselink 2000). Subtidal oyster bars in the upper Bay supported 22 taxa of benthic algae (12 Chlorophyta, 2 Phaeophyta, and 8 Rhodophyta; Connor 1978). In the York River subestuary, no significant differences in benthic soil/sediment community metabolism and chlorophyll concentrations among habitats (marsh, mudflat, sandflat, eelgrass, and subtidal sand) were observed when data for the whole study were pooled (Rizzo and Wetzel 1985). The chlorophyll *a* concentration observed (16–23 mg m<sup>-2</sup>) was lower than that in marshes dominated by *Spartina alterniflora* or *Phragmites australis* on Kent Island, farther north in the Bay (Posey, Alphin, et al. 2003). Based on stable isotope measurements, benthic diatoms, C<sub>3</sub> plants, phytoplankton, and *S. alterniflora* together were important in supporting consumers in a low-salinity marsh system in the Bay (Stribling and Cornwell 1997).

Macroalgae are not normally observed in marshes, mudflats, or tidal forested wetlands of Chesapeake Bay because they require a hard substrate on which to attach via a holdfast, such as oyster shells, generally in shallow open waters (White 1989). However, they may also attach to fleshy sessile animals such as sponges and tunicates, submersed and emergent plants, and manmade structures including docks and rip-rap (Wulff and Webb 1969). Four classes of macroalgae occur in the Bay: Rhodophyceae, Phaeophyceae, Xanthophyceae, and Chlorophyceae (Orris 1980). Macroalgae have been observed to exhibit vertical zonation on pilings spanning the intertidal and shallow subtidal zones (Wulff and Webb 1969).

## Animal Communities

### Fish and Invertebrates

Tidal wetlands, seagrass beds, and adjacent shallow waters of Chesapeake Bay support diverse and productive fish and invertebrate communities (Fig. 3.4a–l). Invertebrate production in

a 140-ha seagrass bed in Virginia was estimated at 200 g dry weight  $\text{m}^{-2} \text{yr}^{-1}$ , or 4.8 metric tons (t) dry weight of invertebrates and 56 t of invertebrate production over the year for the whole seagrass bed (Fredette, Diaz, et al. 1990). Fish that rely on these habitats for spawning or nurseries include economically important species such as striped bass (*Morone saxatilis*) and yellow perch (*Perca flavescens*), while small fish such as killifishes (*Fundulus* spp.) and mosquitofish (*Gambusia affinis*) are abundant and important ecological links between benthic and pelagic species (Lippson 1973; White 1989). Crabs, shrimp, amphipods, snails, polychaete worms, clams, zooplankton, terrestrial insects and spiders, and a diverse array of other taxa vary widely between marsh, swamp, seagrass, and tidal-flat habitats and across salinity gradients (Lippson 1973; Odum, Smith, et al. 1984; White 1989; Swarth and Kiviat 2009).

Some of the most widespread and abundant wetland-dependent species are mummichog (*Fundulus heteroclitus*), naked goby (*Gobiosoma boscii*), grass shrimp (*Palaemonetes pugio*), and blue crab (*Callinectes sapidus*) (Fig. 3.4g), which occur in both fresh and saline habitats and use the surface of emergent wetlands (during tides or remaining in surface pools), seagrass beds, and near-shore shallow water devoid of vegetation (Ruiz, Hines, et al. 1993; Yozzo and Smith 1998). Use of the wetland surface during low tide may be promoted by microtopography resulting from dominant emergent vegetation such as *Peltandra virginica* or reduced if dense beds of seagrasses occur in the lower intertidal zone (Yozzo and Smith 1998). Historically, small species such as mummichog and grass shrimp were abundant in deeper seagrass beds, but the decline in area of seagrasses may have led to a restriction of these fish and crustaceans to shallow, unvegetated waters near shore (Ruiz, Hines, et al. 1993). Killifish were more abundant in Bay marshes dominated by *Spartina alterniflora* than those dominated by *Phragmites australis*, while the opposite was true for grass shrimp (Meyer, Johnson, et al. 2001). No significant difference in number of nekton species between habitats was observed, however. Colonization by *Phragmites* may ultimately greatly reduce killifish use of the wetland surface due to large increases in biomass and litter deposition, resulting in less standing water (Hunter, Fox, et al. 2006).

## Terrestrial Vertebrates

The coastal wetlands of Chesapeake Bay support hundreds of species of turtles, frogs, snakes, waterfowl, songbirds, birds of prey, and aquatic and terrestrial mammals (Fig. 3.4a–l; Odum, Smith et al. 1984; White 1989; Swarth and Kiviat 2009). The terrestrial fauna of tidal swamps and marshes is similar to that of nontidal freshwater wetlands and more diverse than that of brackish and salt marshes, seagrass beds, and mudflats (Odum, Smith et al. 1984). Fauna of these latter habitats are adapted for feeding, growth, or reproduction in saline or continuously flooded conditions (Mendelssohn and Batzer 2006). A few Bay species, such as diamondback terrapin (*Malaclemys terrapin*), swamp sparrow (*Melospiza georgiana*), clapper rail (*Rallus longirostris*), marsh wren (*Cistothorus palustris*), and meadow vole (*Microtus pennsylvanicus*), are restricted to coastal wetland habitats (Mitchell 1994; Robbins 1996; Greenberg and Maldonado 2006).

Nutria (*Myocastor coypus*), an exotic species introduced to Chesapeake Bay, has played an important ecological role via high grazing pressure in some brackish wetlands, as has been demonstrated using exclosures (Mitchell, Gabrey, et al. 2006;

Whigham, Baldwin, et al. 2009; G. M. Haramis pers. comm.). Nutria herbivory has positive effects on waterfowl and open-water species but negative effects on rails and marsh sparrows (Mitchell, Gabrey, et al. 2006). The removal of nutria has improved habitat for the native herbivore muskrat (*Ondatra zibethicus*). Nutria and muskrats feed extensively on three-square sedge (*Schoenoplectus americanus*) as well as the starch-rich tubers of cattail (*Typha latifolia* and *T. angustifolia*). Muskrat populations have traditionally been largest in the wetlands of Dorchester County, Maryland, especially during the 1920s to 1930s (Smith 1938; Harris 1952). In contrast with nutria, smaller muskrat “eat-outs” of vegetation can provide excellent habitat for rails (Meanley 1978), although larger eat-outs will result in habitat changes similar to that of nutria herbivory (Mitchell, Gabrey, et al. 2006).

American black duck (*Anas rubripes*), which historically has been the most numerous duck on the Bay (Perry 1988; Perry and Deller 1995), also benefit from limited nutria and muskrat eat-outs, where they feed on a variety of invertebrates and submersed macrophyte species. Seagrasses were important in the diet of black ducks in the past (Stewart 1962), but in more recent years seagrasses have declined and these ducks have moved into emergent plant habitats. Large numbers of black ducks nested on Bay islands in the 1950s (Stotts and Davis 1960). When these sites were resurveyed in the 1980s, many of the islands had disappeared or were greatly reduced in size by erosion (Stotts 1986). For example, Poplar Island was reduced from 400 ha in 1847 to only 2 ha in recent years. A major project by the Corps of Engineers is the restoration of wetland and upland habitats on Poplar Island with dredge material from the Baltimore Harbor shipping channel. Restoration of Poplar Island and other Bay islands should benefit the black duck by providing tidal brackish marshes for nesting habitat with minimal exposure to predators (Haramis, Jorde, et al. 2002; Erwin, Brinker, et al. 2010).

The Canada goose (*Branta canadensis*; fig. 3.4f) is a native species that occurs in Bay wetlands as a migratory bird and also as a resident nonmigratory species. Wintering populations of migratory Canada geese have historically occurred in the Chesapeake Bay region but actually increased with the decline of seagrasses, which led geese to become consumers of residue from the harvest of agricultural crops (e.g., corn). Exclosure studies demonstrated that expanding populations of nonmigrating Canada geese significantly reduced the populations of wild rice (*Zizania aquatica*) and other annual species in tidal freshwater wetlands in the Patuxent River (Baldwin and Pendleton 2003; Haramis and Kearns 2007). The negative impacts of goose grazing on seedling establishment occur in the spring, when juveniles and molting adults eat or trample seedlings. Effective management of goose populations and efforts to restore populations of wild rice have been successful on the Patuxent River (Haramis and Kearns 2007). Feeding by nonmigrating geese has also hindered tidal wetland restoration efforts on the Anacostia River (Hammerschlag, Baldwin, et al. 2006). Possible negative effects of exclosures include debris and sediment accumulation, animal exclusion and entrapment, and aesthetics (C. Swarth pers. comm.). Although four of the six species of North American rails can be found in Bay tidal freshwater wetlands (Meanley 1965), the sora (*Porzana carolina*) is the species most common in the Patuxent rice marshes and the species most impacted by loss of wild rice to goose grazing. Their migratory stopover occurs shortly after the wild rice and other seeds fall to the water, and these seeds form the bulk of their diet (Meanley 1965).



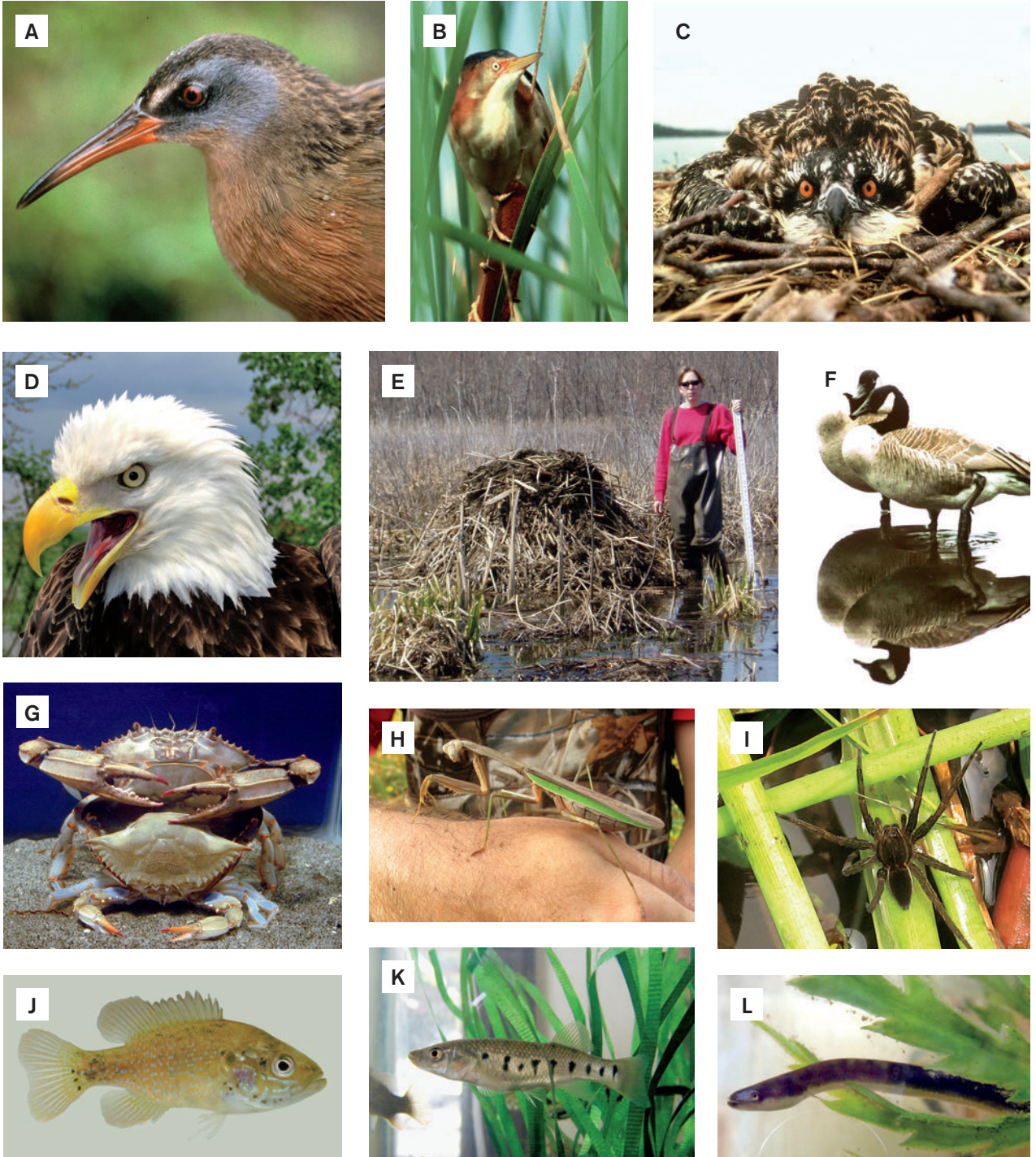


FIG. 3.4. Examples of Chesapeake Bay wetland fauna. A. Virginia rail, *Rallus limicola*. B. Least bittern, *Ixobrychus exilis*. C. Young osprey, *Pandion haliaetus*, in nest. D. Bald eagle, *Haliaeetus leucocephalus*. E. Den of muskrat, *Ondatra zibethicus*. F. Canada geese, *Branta canadensis*. G. Blue crabs, *Callinectes sapidus*. H. Praying mantis, Insecta: Mantodea. I. Fishing spider, *Dolomedes* sp. J. Green sunfish, *Lepomis cyanellus*. K. Striped killifish, *Fundulus majalis*. L. American eel, *Anguilla rostrata*. (Photo credits: A–D, F: G. Kearns; E, H–I: A. H. Baldwin; G: A. Young; J: R. Aguilar; K, I: M. Kramer. Used with permission.)

Although the species and life-history traits of reptiles and amphibians inhabiting Chesapeake Bay coastal wetlands are generally known (Harris 1975; White 1989; Mitchell 1994), few ecological studies or recent surveys exist. Diversity is much lower in saline than in tidal freshwater wetlands (Odum, Smith, et al. 1984), and the most common groups restricted to tidal marshes and estuaries are colubrid snakes and emydid turtles, for example northern water snake (*Nerodia sipedon*)

and diamondback terrapin (Greenberg and Maldonado 2006). In the Patuxent River, smaller terrapins, primarily males, were more abundant in shallow water than in deeper water, making them vulnerable to drowning in crab pots and susceptible to coastal development, while larger, primarily female, terrapins were more abundant in deeper water, where they are vulnerable to speedboats (Roosenburg, Haley, et al. 1999). Bycatch reduction devices on crab pots reduced terrapin bycatch but



had no effect on the size and number of crabs caught (Roosenberg and Green 2000). The Poplar Island restoration site provides excellent terrapin nesting habitat, due largely to a lack of nest predators such as foxes, raccoons (*Procyon lotor*), and otters (*Lutra canadensis*); 68 nests and 565 hatchlings were recorded during one year (Roosenburg, Allman, et al. 2003). These results suggest that island restoration will help offset nesting site losses due to development.

## Key Ecological Processes

### Productivity and Decomposition

Aboveground net primary production measurements for Chesapeake Bay wetlands generally range from about 1,000 to 1,500 g dry weight  $\text{m}^{-2} \text{yr}^{-1}$ , and the values fall within those expected for the East Coast (Turner 1976). However, aboveground productivity of a tidal freshwater marsh dominated by *Peltandra virginica* on the Pamunkey River in Virginia was only 780 g  $\text{m}^{-2}$  over one growing season (Doutle 1981). Oligohaline and mesohaline marshes on tributaries to the York River had even lower aboveground production (560–570 g  $\text{m}^{-2} \text{yr}^{-1}$ ; Mendelssohn and Marcellus 1976). In contrast, net aboveground productivity of *Hibiscus moscheutos* in a brackish marsh on the Choptank River was 1,210–1,220 g  $\text{m}^{-2} \text{yr}^{-1}$  over a two-year period, with peak aboveground standing crop of 550–590 g  $\text{m}^{-2}$  (Cahoon and Stevenson 1986). Belowground biomass of *H. moscheutos* was 1,060–1,320 g  $\text{m}^{-2}$ , about double the aboveground biomass. Mean live standing biomass in Patuxent River marshes varied across sites with different communities types, ranging on the low end from sites dominated by *P. virginica* and *Polygonum arifolium* (990 g  $\text{m}^{-2}$ ) up to sites dominated by *Phragmites australis* (1,990 g  $\text{m}^{-2}$ ), *Spartina cynosuroides* (2,160 g  $\text{m}^{-2}$ ), and *Typha* spp. (2,340 g  $\text{m}^{-2}$ ) (Flemer, Heinle, et al. 1978). Thus, Chesapeake Bay marshes demonstrate large variation in biomass production across plant communities, salinity regimes, and river systems.

The aboveground biomass of seagrass communities is lower than that of marshes: for example, in the range of 100–250 g  $\text{m}^{-2}$  in the York River (Moore 2009) and 60–100 g  $\text{m}^{-2}$  in unfertilized plots and 210–340 g  $\text{m}^{-2}$  in fertilized plots in seagrass beds near the Virginia portion of the Delmarva Peninsula (Orth 1977). Root and rhizome biomass in the unfertilized plots was higher (160–170 g  $\text{m}^{-2}$ ) than leaf biomass, and fertilization resulted in no significant effect on belowground biomass. Estimates of seagrass biomass across the entire Chesapeake Bay are that maximum summer biomass increased from 15,000 t (about 0.7 t  $\text{ha}^{-1}$ ) in 1985 and 1986 up to almost 25,000 t (0.9 t  $\text{ha}^{-1}$ ) from 1991 through 1993 (Moore, Wilcox, et al. 2000). Minimum biomass occurred in December and January 1996 (< 5,000 t).

Rapid rates of decomposition were reported for tidal freshwater wetland vegetation in a tributary of the York River in which 70 to 80% of plant mass was lost within two months (Odum and Heywood 1978). Other studies of decomposition have shown more typical loss rates of about 80% over an annual cycle (Kassner 2001; P. Kangas unpub.). Slower decomposition rates were observed in stems of *Hibiscus moscheutos*, which are somewhat woody: only 45% decomposed within two years (Cahoon and Stevenson 1986).

In a brackish marsh community on the western shore of Chesapeake Bay dominated by *Schoenoplectus americanus*, annual net ecosystem production (NEP) was estimated at

1.45–1.59 kg C  $\text{m}^{-2}$  during two years based on measurements of carbon (C) fluxes for gross primary production (GPP; 1.89–2.08 kg C  $\text{m}^{-2}$ ) and ecosystem respiration ( $R_e$ ; 0.44–0.49 kg C  $\text{m}^{-2}$ ) (Drake, Muehe, et al. 1996). Elevating atmospheric  $\text{CO}_2$  increased GPP by 30% and decreased  $R_e$  by 36–57%, resulting in an overall increase in NEP by 50–58% up to 2.17–2.51 kg C  $\text{m}^{-2}$ .

### Herbivory

Grazing by birds and mammals is important in some Bay coastal wetlands and seagrass beds. In a tidal freshwater wetland on the Patuxent River, low-marsh plots fenced to exclude Canada geese and other large animals had significantly higher peak total biomass (940 g  $\text{m}^{-2}$ ) than unfenced plots (350 g  $\text{m}^{-2}$ ), although biomass in high-marsh plots was not significantly affected (Baldwin and Pendleton 2003). In another study in the same part of the river, stalk density of *Zizania aquatica* was about 97 stalks  $\text{m}^{-2}$  but only 2.7 stalks  $\text{m}^{-2}$  in unfenced plots (Haramis and Kearns 2007). Herbivorous insects are also important in some Bay wetlands: they consumed about 15% of annual aboveground production of *Hibiscus moscheutos*, or about 30% of peak biomass (Cahoon and Stevenson 1986). The periwinkle snail, *Littoraria irrorata*, is an important grazer on *Spartina alterniflora* leaf tissue and fungal biomass, and snail density was found to be negatively related to stem density of *S. alterniflora* in a York River salt marsh (Long and Burke 2007). In experimental seagrass ecosystems, grazers have been found to reduce growth of epiphytic algae on macrophyte leaves, increasing macrophyte production (Neckles, Wetzel, et al. 1993). Some taxa also graze on macrophyte leaves, and grazing response varies between grazing organisms (Duffy, MacDonald, et al. 2001).

### Ecosystem Experiments

Global change experiments have been performed since 1986 at the Smithsonian's Global Change Research Wetland, a brackish marsh located on the Rhode River (on the western shore of the Bay, due east of Washington, DC). The site is operated by the Smithsonian Environmental Research Center. One of the experiments, which has been ongoing for more than 25 years, has reported that elevated atmospheric  $\text{CO}_2$  significantly increases the net primary productivity (NPP) of the  $\text{C}_3$  sedge *Schoenoplectus americanus* in both monoculture and mixed plots, but not the NPP of the  $\text{C}_4$  grasses *Spartina patens* and *Distichlis spicata* (Curtis, Drake, et al. 1989; Curtis, Drake, and Whigham 1989; Drake 1992; Erickson, Megonigal, et al. 2007). In a second ongoing experiment, which began in 2006 (Fig. 3.2d), the well-documented stimulation of ecosystem-level NPP by elevated  $\text{CO}_2$  added as a single factor was significantly reduced in treatments that crossed elevated  $\text{CO}_2$  and added nitrogen, simulating eutrophication (Langley and Megonigal 2010). This reduction in  $\text{CO}_2$  stimulation of NPP was caused by a nitrogen-induced shift in plant community composition that favored  $\text{CO}_2$ -indifferent  $\text{C}_4$  species. Collectively, these studies highlight the important role that plant community composition will play in determining ecosystem responses to multiple, interacting global change variables.

Another ecosystem tidal wetland experiment was conducted as part of a 10-year EPA-supported project entitled the Multi-scale Experimental Ecosystem Research Center (Petersen, Ken-

nedy, et al. 2009). As part of the study, experimental 6-m<sup>2</sup> salt marsh ecosystems containing a tidal inundation gradient were seeded with wetland plant species (high and low plant diversity) and several representative macroinvertebrates. Studies of nutrient fertilization and fire were also conducted in the mesocosms, and effects of fire in the small-scale mesocosms were similar to those observed in the field (Schmitz 2000). No significant differences in primary production or nutrient removal were found between high- and low-diversity mesocosms (Petersen, Kennedy, et al. 2009).

## Conservation Concerns

Wetlands in Chesapeake Bay, as in the rest of the country, suffered considerable losses between the late 1700s and 1980s (Tiner 1985; Baldwin 2009). Maryland lost more than 60% of its wetlands (Hayes 1996a), losses in Virginia were between 40–50% (Hayes 1996b), and only 10% of the original wetland area remained in the District of Columbia (Hayes 1996a). Losses have decreased, but efforts to restore and mitigate wetlands have offset only a small percentage of past wetland losses (Boesch and Greer 2003). Historically, intertidal wetland losses in the Bay were mostly due to direct human activities (dredging, filling, draining), but many current and future impacts are indirect, such as the effects of rising sea level in response to global warming, continued degradation of water quality, and invasive species. Sudden marsh die-back has not been widespread in the Bay but is plausible in the future, given the potential for increased temperatures as a result of global warming and changes in precipitation patterns (Alber et al. 2008).

## Sea-Level Rise

Sea-level rise arguably poses the single greatest threat to Bay intertidal wetlands. The rate of sea-level rise is projected to increase significantly in the Bay (Boesch and Greer 2003), resulting in an increased rate of erosion of coastal margins (Wood, Boesch, et al. 2002) and subsequent wetland loss. Significant wetland losses have already been documented, particularly in brackish marshes on the eastern shore of the Bay (Kearney, Grace, et al. 1988; Wray, Leatherman, et al. 1995). In low-lying areas where intertidal wetlands cannot migrate landward, losses of brackish and oligohaline wetlands are projected to be significant over the next half century (Larsen, Clark, et al. 2004).

Extensive tidal freshwater wetlands still occur in some Bay subestuaries (e.g., Nanticoke, Pocomoke, York, Patuxent), and tidal freshwater wetlands experienced less deterioration than did brackish wetlands in the Nanticoke subestuary (Kearney, Grace, et al. 1988). These wetlands are, however, likely to suffer significantly in response to increased rates of sea-level rise due to intrusion of brackish water (e.g., Perry and Hershner 1999). Tidal freshwater wetlands will also be threatened because they occur in geomorphic settings where there are limitations to upstream and horizontal migration due to steep slopes (western shore) and steep river gradients at the Fall Line between the Coastal Plain and Piedmont (Neubauer and Craft 2009; Whigham, Baldwin, et al. 2009).

Some Bay wetlands may not succumb as rapidly as others to sea-level rise. Wray, Leatherman, et al. (1995) projected that the three Bay upland islands they studied (Poplar, James,

and Barren) would disappear by 2010. However, Poplar Island is being restored using dredge material, and James and Barren Islands still exist and are also slated for restoration or shoreline protection ([www.nab.usace.army.mil/Factsheets/PDFs/Civil/MD-MidBayIsland-GI.pdf](http://www.nab.usace.army.mil/Factsheets/PDFs/Civil/MD-MidBayIsland-GI.pdf)). Wetlands dominated by the non-native genotype of *Phragmites australis* (Rooth and Stevenson 2000) have the potential to keep pace with sea-level rise due to high rates of root and rhizome production and a network of dense stems and litter that increase sediment accumulation.

## Eutrophication

Excess nutrients have been a persistent problem in Chesapeake Bay for decades, and most of the past, current, and future restoration efforts focus on a reduction of nutrient inputs from point and nonpoint sources (Boesch and Greer 2003). A primary impact of excess nutrients on Bay subtidal wetlands has been the decline in seagrasses (Orth 1994), but effects on intertidal wetlands may be no less important. One potential effect of increased nitrogen (N) is the rapid expansion of the non-native genotype of *Phragmites australis* since the 1980s (King, Deluca, et al. 2007; McCormick, Kettenring, et al. 2010a). The expansion of *Phragmites* subsequent to the onset of eutrophic conditions is likely an example of a lag effect that has been shown to be common for invasive species (Crooks and Soule 1999) and a threshold response associated with a critical change in the nutrient status of the Bay (King, Deluca, et al. 2007). Furthermore, seed production was greater in cross-pollinated plants fertilized with N (Kettenring, McCormick, et al. 2011), and the nonnative genotype was more productive than the native genotype under elevated N conditions (T.Mozder unpub.).

Increased N may exacerbate the effects of sea-level rise. The surface elevation of brackish wetlands increased at a rate that was almost twice the current rate of sea-level rise under conditions of elevated CO<sub>2</sub> (Langley, McKee, et al. 2009). However, N addition resulted in a smaller increase in substrate elevation, about equal to the current rate of sea-level rise, and was correlated with a decrease in belowground production. The observed decrease in belowground biomass was probably due partly to a shift in allocation from belowground to aboveground tissues and a shift from C<sub>3</sub> to C<sub>4</sub> species (Langley and Megonigal 2010).

## Invasive Plants

### NONNATIVE STRAIN OF *PHRAGMITES AUSTRALIS*

The nonnative strain has been responsible for a relatively recent expansion of *P. australis* in Chesapeake Bay intertidal wetlands (Saltonstall 2002; King, Deluca, et al. 2007) associated with human activities (development) at or near the shoreline (King, Deluca, et al. 2007; Chambers, Havens, et al. 2008). Recent research in Bay subestuaries has provided insight into the proximate causes for its expansion. McCormick, Kettenring, et al. (2010a,b) and Kettenring and Whigham (2009) sampled patches of *Phragmites* in Bay subestuaries that had upland watersheds dominated by different land uses (forests versus varying amounts of development). Their results indicate that patches with multiple genotypes produce more viable seeds than patches with lower genetic diversity and sug-



gest that disturbance in developed watersheds promotes colonization from seed, leading to multiple-genotype patches that cross-pollinate and produce more viable seed than low-diversity patches. Furthermore, *Phragmites* seeds occurred in the seed bank at much higher densities in patches producing viable seeds than patches that did not (Baldwin, Kettenring, et al. 2010).

The importance of seed dispersal and seedling recruitment may explain the observed invasion and expansion of *Phragmites* in part of the Rhode River subestuary where there has been no development in recent years (Kettenring, McCormick, et al. 2009). The potential consequences of the continued spread, primarily by seeds into wetlands that have not had any anthropogenic disturbances, of the nonnative strain are dramatic. All Bay brackish intertidal wetlands, other than low marshes dominated by *Spartina alterniflora*, potentially will be invaded, and *Phragmites* is also expanding in Bay freshwater intertidal wetlands. Although replacement of native plant communities and reduction of plant diversity (Chambers, Meyerson, et al. 1999) will result from continued expansion of the nonnative strain in Chesapeake Bay intertidal wetlands, effects on diversity of fauna and ecosystem function are complex and may not be disastrous (e.g., Findlay, Groffman, et al. 2003; Weis and Weis 2003).

## OTHER NONNATIVE PLANTS

*Hydrilla verticillata* and *Myriophyllum spicatum* are dominant in vast seagrass beds where the Susquehanna River flows into the upper Bay (Fig. 3.1). These species have shallower roots than the native species *Vallisneria spiralis*, which, when codominant with the two nonnative species, resulted in lower sediment porewater concentrations of phosphate than when it was absent (Wigand, Stevenson, et al. 1997). The leaves of *V. spiralis* may physically capture *H. verticillata* fragments, promoting colonization of the nonnative species, and *V. spiralis* does not inhibit growth unless nutrient supply is limited (Chadwell and Engelhardt 2008). The nonnative submersed macrophyte *Trapa natans* (water chestnut) is not widespread in Chesapeake Bay, but is common in other East Coast estuaries (Whigham, Baldwin, et al. 2009). The emergent herb *Lythrum salicaria* (purple loosestrife) is also not widespread in Bay coastal wetlands, although it does occur in some tidal freshwater marshes (Neff, Rusello, et al. 2009). *Murdannia keiskei* (marsh dewflower) is locally abundant in some tidal freshwater marshes (Baldwin and Pendleton 2003).

## Native and Nonnative Animals

In addition to nutria and nonmigrating Canada geese, snow geese (*Chen caerulescens*) eat-outs have been documented for wetlands on the Delmarva Peninsula (Sherfy and Kirkpatrick 2003). Mute swan (*Cygnus olor*), which increased from 5 to about 4,000 animals between 1962 and 1999, can have a significant and detrimental impact on seagrasses (Hindman and Harvey 2004; Tatu, Anderson, et al. 2007). However, mute swan numbers now have been reduced to under 500, and management plans will attempt to maintain the population near zero on public waters. Beaver activities in tidal wetlands appear to be restricted to the tidal freshwater portion of tidal rivers (Swarth and Kiviat 2009), where they can create non-

tidal ponds containing submersed macrophytes (A. Baldwin pers. obs.).

## Wetland Restoration

A goal of the 2009 Chesapeake Bay Executive Order (<http://executiveorder.chesapeakebay.net/>) is to restore 10,000 ha of tidal and nontidal wetlands. Current efforts in estuarine habitats are focused on living shorelines, tidal wetlands, seagrasses, and remote island habitats ([www.ngs.noaa.gov/PROJECTS/Wetlands/](http://www.ngs.noaa.gov/PROJECTS/Wetlands/)). Sediments that are used in the restoration of brackish tidal wetlands in at least two projects are dredged materials from Baltimore Harbor. Restoration of the Poplar Island complex includes approximately 220 ha of intertidal wetlands (Miller and Murphy 2002), and 4,500 ha of wetlands are proposed for Blackwater National Wildlife Refuge ([http://library.fws.gov/CCPs/CMC/cmc\\_index\\_final.html](http://library.fws.gov/CCPs/CMC/cmc_index_final.html)). Sediments dredged from the Anacostia River also have been used in efforts to restore tidal freshwater wetlands (Fig. 3.2g) (Hammerschlag, Baldwin, et al. 2006). There have been numerous efforts to restore eroded shorelines and wetlands throughout Chesapeake Bay (e.g., Garbisch and Garbisch 1994; Hardaway, Varnell, et al. 2002; Havens, Varnell, et al. 2002), and there are companies that specialize in wetland and shoreline restoration. Most restoration efforts are relatively small in scale, and although data on the area of intertidal wetlands restored in the Bay are lacking, the total is only a minor component of the area lost. For example, wetland losses in the Virginia portion of Chesapeake Bay between 1988 and 1998 were 124 ha per year compared to 0.07 ha of compensatory mitigation (Hardaway, Varnell, et al. 2002).

## Conclusions

Chesapeake Bay supports one of the greatest concentrations of coastal wetlands in North America. Hydrogeomorphic conditions that have developed since the last ice age have led to the formation of a diversity of coastal wetland types, including tidal freshwater wetlands, tidal brackish and salt marshes, mudflats, and submersed aquatic vegetation beds. These wetlands have high primary productivity and support a diverse array of vegetation types, algae, fish and invertebrates, and terrestrial wildlife.

However, the future of Chesapeake Bay wetlands is uncertain. Rising relative sea level has the greatest potential to reduce the area of Bay tidal wetlands. The second most important process affecting coastal wetlands is likely to be the spread of the nonnative genotype of *Phragmites australis*. The invasion of *Phragmites* has accelerated in recent years, and its spread, primarily from seed, appears to be self-perpetuating once patches with multiple genotypes have become established. Submersed aquatic vegetation beds, which have been impacted to a greater degree than emergent wetlands, will continue to be threatened by eutrophication, which reduces light available for photosynthesis. Restoration of coastal wetlands in Chesapeake Bay has had some success, but the area of restored wetlands is less than that lost and the persistence of restored wetlands under future sea-level and eutrophication scenarios is unknown.

The audience addressed in this chapter, which includes students, researchers, environmental managers and engineers, and policymakers, is critical to sustaining the wetlands of

Chesapeake Bay. Students and researchers must continue scientific discovery of the processes and actions that underlie changes in Bay ecosystems because ecological knowledge is the foundation for environmental management and policy-making. As noted in this chapter, many of the Bay's wetland habitats, their species interactions, and their hydrological and biogeochemical processes are poorly understood. Environmental managers and engineers need to base restoration activities on this ecological knowledge to avoid wasting resources on unsustainable or underperforming wetlands. Managers and engineers must also bear in mind the dynamic nature of these ecosystems and potential future changes due to sea-level rise, elevated CO<sub>2</sub>, invasive plants and animals, and eutrophication. Wetland restoration is a particularly challenging activity that has produced many failures; adopting an adaptive restoration approach based on monitoring and building knowledge of restoration techniques will lead to more successful restoration outcomes. Engineers and managers should also continue to explore and develop new techniques, such as thin-layer sediment application, to help wetlands keep pace with sea-level rise and accept nonnative species such as *Phragmites australis* if that is the only wetland plant community that will persist in, for example, a eutrophic environment with high rates of relative sea-level rise and nonresident herbivores. Finally, by introducing legislation and developing regulations and guidelines, policymakers at the local, state, and national levels can have a great positive impact on the sustainability of Chesapeake Bay wetlands. Locally, land use (for ecotourism, recreation, agriculture, or other activities that do not pose barriers to migration) in the flat Coastal Plain adjacent to coastal wetlands can be regulated to provide space for wetlands to migrate inland as sea level continues to rise. At the local and state level, improved management of runoff from agricultural and urban lands can be required to reduce nutrient and sediment loading; "living shorelines" (constructed wetlands) can be used to stabilize shores instead of rip-rap, bulkheads, and other erosion-control structures; and more wildlife sanctuaries can be created (Erwin, Haramis, et al. 1993). Requiring more stringency in avoiding wetland impacts in development projects and, if there is no realistic way to avoid such impacts, longer-term monitoring of mitigation sites are necessary to reduce the rate of net wetland loss and improve restoration techniques. Finally, at the national level, efforts to regulate greenhouse gas emissions should be expanded, not only because of their role in climate warming, but also because of their strong influence on plant community composition. Furthermore, the Chesapeake Bay Program, established by Congress in the 1980s to restore and protect the Bay, should be fully supported and expanded.

Impacts to Chesapeake Bay wetlands will continue, an unavoidable outcome due to the increasing human population density in the Bay watershed. Efforts to protect, manage, and restore Bay wetlands must be weighed against other pressing socioeconomic needs. Focusing on important wetlands or wetland-rich regions that are amenable to conservation, management, or restoration will ensure that humans and other organisms will continue to benefit from the ecosystem services provided by Bay wetlands into the foreseeable future.

## Acknowledgments

We are grateful to Greg Kearns of Patuxent Wetland Park for bird photos and to Margaret Kramer and other members of the Fish

and Invertebrate Ecology Lab at the Smithsonian Environmental Research Center for photos of fish and invertebrates.

## References

- Alber M, Swenson EM, Adamowicz SC, Mendelssohn IA. 2008. Salt marsh dieback: an overview of recent events in the US. *Estuar. Coast. Shelf Sci.* 80:1–11.
- Anderson RR. 1972. Submersed vascular plants of the Chesapeake Bay and tributaries. *Chesap. Sci.* 13 Supplement:S87–S89.
- Anderson RR, Brown RG, Rappleye RD. 1968. Water quality and plant distribution along the upper Patuxent River, Maryland. *Chesap. Sci.* 9:145–56.
- Atkinson RB, Bodkin NL, Perry JE. 1990. New county records collected in tidal wetlands of four coastal plain counties along the James River, Virginia. *Castanea* 55:56–64.
- Baldwin AH. 2004. Restoring complex vegetation in urban settings: the case of tidal freshwater marshes. *Urban Ecosyst.* 7:137.
- Baldwin AH. 2007. Vegetation and seed bank studies of salt-pulsed swamps of the Nanticoke River, Chesapeake Bay. In *Ecology of tidal freshwater forested wetlands of the southeastern United States*, Conner WH, Doyle TW, Krauss KW, editors. Dordrecht, The Netherlands: Springer, pp. 139–60.
- Baldwin AH. 2009. Restoration of tidal freshwater wetlands in North America. In *Tidal freshwater wetlands*, Barendregt A, Whigham DF, Baldwin AH, editors. Leiden, The Netherlands: Backhuys, pp. 207–22.
- Baldwin AH, Egnatovich MS, Clarke E. 2001. Hydrologic change and vegetation of tidal freshwater marshes: field, greenhouse, and seed-bank experiments. *Wetlands* 21:519–31.
- Baldwin AH, Kettenring KM, Whigham DF. 2010. Seed banks of *Phragmites australis*-dominated brackish wetlands: relationships to seed viability, inundation, and land cover. *Aquat. Bot.* 93:163–69.
- Baldwin AH, Pendleton FN. 2003. Interactive effects of animal disturbance and elevation on vegetation of a tidal freshwater marsh. *Estuaries* 26:905–15.
- Boesch DF, Greer J. 2003. *Chesapeake futures choices for the 21st century*. Edgewater, MD: Chesapeake Research Consortium.
- Bridgman SD, Megonigal JP, et al. 2006. The carbon storage of North American wetlands. *Wetlands* 26:889–916.
- Brush GS. 1984. Patterns of recent sediment accumulation in Chesapeake Bay. *Chem. Geol.* 44:227–42.
- Cahoon DR, Stevenson JC. 1986. Production, predation, and decomposition in a low-salinity *Hibiscus* marsh. *Ecology* 67:1341–50.
- Chadwell TB, Engelhardt KAM. 2008. Effects of pre-existing submersed vegetation and propagule pressure on the invasion success of *Hydrilla verticillata*. *J. Appl. Ecol.* 45:515–23.
- Chambers RM, Havens KJ, et al. 2008. Common reed *Phragmites australis* occurrence and adjacent land use along estuarine shoreline in Chesapeake Bay. *Wetlands* 28:1097–103.
- Chambers RM, Meyerson LA, Saltonstall K. 1999. Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquat. Bot.* 64:261–73.
- Childers DL, Day JW Jr, McKellar HN Jr. 2000. Twenty more years of marsh and estuarine flux studies: revisiting Nixon (1980). In *Concepts and controversies in tidal marsh ecology*, Weinstein MP, Kreeger DA, editors. Dordrecht, The Netherlands: Kluwer, pp. 391–423.
- Conner WH, Doyle TW, Krauss KW, editors. 2007. *Ecology of tidal freshwater forested wetlands of the southeastern United States*. Dordrecht, The Netherlands: Springer.
- Connor JL. 1978. Benthic algae in Chesapeake Bay, Maryland. *J. Phycol.* 14:20.
- Crooks JA, Soule ME. 1999. Lag times in population explosions of invasive species: causes and implications. In *Invasive species and biodiversity management*, Sandlund OT, Schei PJ, Viken A, editors. Dordrecht, The Netherlands: Kluwer, pp. 103–25.
- Curtis PS, Drake BG, et al. 1989. Growth and senescence in plant communities exposed to elevated CO<sub>2</sub> concentrations on an estuarine marsh. *Oecologia* 78:20–26.
- Curtis PS, Drake BG, Whigham DF. 1989. Nitrogen and carbon



- dynamics in C<sub>3</sub> and C<sub>4</sub> estuarine marsh plants grown under elevated CO<sub>2</sub> in situ. *Oecologia* 78:297–301.
- Darke AK, Megonigal JP. 2003. Control of sediment deposition rates in two mid-Atlantic coast tidal freshwater wetlands. *Estuar. Coast. Shelf Sci.* 57:255–68.
- Davies, SB. 2004. Vegetation dynamics of a tidal freshwater marsh: long-term and inter-annual variability and their relation to salinity. MS Thesis. Gloucester Point, VA: Virginia Institute of Marine Science, College of William and Mary.
- Doumlele DG. 1981. Primary production and seasonal aspects of emergent plants in a tidal freshwater marsh. *Estuaries* 4:139–42.
- Drake BG. 1992. A field study of the effects of elevated CO<sub>2</sub> on ecosystem processes in a Chesapeake Bay wetland. *Aust. J. Bot.* 40:579–95.
- Drake BG, Muehe MS, et al. 1996. Acclimation of photosynthesis, respiration and ecosystem carbon flux of a wetland on Chesapeake Bay, Maryland, to elevated atmospheric CO<sub>2</sub> concentration. *Plant Soil* 187:111–18.
- Duffy JE, MacDonald KS, et al. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82:2417–34.
- Erickson JE, Megonigal JP, et al. 2007. Salinity and sea level mediated elevated CO<sub>2</sub> effects on C<sub>3</sub>–C<sub>4</sub> plant interactions and tissue nitrogen in a Chesapeake Bay tidal wetland. *Glob. Change Biol.* 13:202–15.
- Erwin RM, Brinker DF, et al. 2010. Islands at bay: rising seas, eroding islands, and waterbird habitat loss in Chesapeake Bay (USA). *J. Coast. Conserv.* 15:51–60.
- Erwin RM, Haramis GM, et al. 1993. Resource protection for waterbirds in Chesapeake Bay. *Env. Manage.* 17:613–69.
- Findlay S, Groffman P, Dye S. 2003. Effects of *Phragmites australis* on marsh nutrient cycling. *Wetl. Ecol. Manag.* 11:157–65.
- Flemer DA, Heinle DR, et al. 1978. Standing crops of marsh vegetation of two tributaries of Chesapeake Bay. *Estuaries* 1:157–63.
- Fredette TJ, Diaz RJ, et al. 1990. Secondary production within a seagrass bed (*Zostera marina* and *Ruppia maritima*) in lower Chesapeake Bay. *Estuaries* 13:431–40.
- Garbisch EW, Garbisch JL. 1994. Control of upland bank erosion through tidal marsh construction on restored shores: application in the Maryland portion of Chesapeake Bay. *Env. Manage.* 18:677–91.
- Greenberg R, Maldonado JE. 2006. Diversity and endemism in tidal-marsh vertebrates. In *Terrestrial vertebrates of tidal marshes: evolution, ecology, and conservation*, Greenberg R, Maldonado JE, et al., editors. Camarillo, CA: Cooper Ornithological Society, pp. 32–53.
- Hammerschlag RS, Baldwin AH, et al. 2006. Five years of monitoring reconstructed freshwater tidal wetlands in the urban Anacostia River (2000–2004). Laurel and College Park, MD: USGS Patuxent Wildlife Research Center and University of Maryland.
- Haramis GM, Jorde DG, et al. 2002. Breeding performance of Smith Island black ducks. In *Black ducks and their Chesapeake Bay habitats: proceedings of a symposium*, Perry MC, editor. Report USGS/BRD/ITR-2002-0005. Washington, DC: USGS, pp. 22–30.
- Haramis GM, Kearns GD. 2007. Herbivory by resident geese: the loss and recovery of wild rice along the tidal Patuxent River. *J. Wildl. Manag.* 71:788–94.
- Hardaway CS, Varnell LM, et al. 2002. An integrated habitat enhancement approach to shoreline stabilization for a Chesapeake Bay island community. *Wetl. Ecol. Manag.* 10:289–302.
- Harris HS Jr. 1975. Distributional survey (Amphibia/Reptilia): Maryland and the District of Columbia. *Bull. Maryland Herp. Soc.* 11:73–167.
- Harris VT. 1952. Muskrats on tidal marshes of Dorchester County. Publ. no. 91. Solomons Island, MD: Chesapeake Biological Laboratory.
- Havens KJ, Varnell LM, Watts BD. 2002. Maturation of a constructed tidal marsh relative to two natural reference tidal marshes over 12 years. *Ecol. Eng.* 18:305–15.
- Hayes MA. 1996a. Maryland and the District of Columbia wetland resources. In *National water summary on wetland resources* (Water-Supply paper 2425), Fretwell JD, Williams JS, Redman PJ, compilers. Reston, VA: USGS, pp. 219–24.
- Hayes MA. 1996b. Virginia wetland resources. In *National water summary on wetland resources* (Water-Supply paper 2425), Fretwell JD, Williams JS, Redman PJ, compilers. Reston, VA: USGS, pp. 387–92.
- Hicks SD. 1964. Tidal wave characteristics of Chesapeake Bay. *Chesap. Sci.* 5:103–13.
- Hindman LJ, Harvey WF. 2004. Status and management of mute swans in Maryland. In *Mute swans and their Chesapeake Bay habitats: proceedings of a symposium*, Perry MC, editor. USGS/BRD/ITR-2004-0005. Reston, VA: USGS, pp. 11–7.
- Hobbs CH III. 2004. Geological history of Chesapeake Bay, USA. In *Quat. Sci. Rev.* 23:641–61.
- Hobbs CH III, Halka JP, et al. 1992. Chesapeake Bay sediment budget. In *J. Coast. Res.* 8:292–300.
- Hopfensperger KN, Kaushal SS, et al. 2009. Influence of plant communities on denitrification in a tidal freshwater marsh of the Potomac River, United States. *J. Env. Qual.* 38:618–26.
- Hunter KL, Fox DA, et al. 2006. Responses of resident marsh fishes to stages of *Phragmites australis* invasion in three mid Atlantic estuaries. *Estuar. Coast.* 29:487–98.
- Jordan TE, Correll DL. 1991. Continuous automated sampling of tidal exchanges of nutrients by brackish marshes. *Estuar. Coast. Shelf Sci.* 35:527–45.
- Jordan TE, Correll DL, Whigham DF. 1983. Nutrient flux in the Rhode River: tidal exchange of nutrients by brackish marshes. *Estuar. Coast. Shelf Sci.* 17:651–67.
- Jordan TE, Pierce JW, Correll DL. 1986. Flux of particulate matter in the tidal marshes and subtidal shallows of the Rhode River estuary. *Estuaries* 9:310–19.
- Kassner SL. 2001. Soil development as a functional indicator of a reconstructed freshwater tidal marsh. MS thesis, University of Maryland, College Park.
- Kastler J, Wiberg PL. 1996. Sedimentation and boundary changes of Virginia salt marshes. *Estuar. Coast. Shelf Sci.* 42:683–700.
- Kearney MS, Grace RE, Stevenson JC. 1988. Marsh loss in the Nanticoke estuary, Chesapeake Bay. *Geogr. Rev.* 78:205–20.
- Keller JK, Weisenhorn PB, Megonigal JP. 2009. Humic acids as electron acceptors in wetland decomposition. *Soil Biol. Biochem.* 41:1518–22.
- Kemp WM, Batiuk R, et al. 2004. Habitat requirements for submersed aquatic vegetation in Chesapeake Bay: water quality, light regime, and physical-chemical factors. *Estuaries* 27:363–77.
- Kemp WM, Boynton WR, et al. 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Mar. Ecol. Prog. Ser.* 303:1–29.
- Kettenring KM, McCormick MK, et al. 2009. *Phragmites australis* (common reed) invasion in the Rhode River subestuary of the Chesapeake Bay: disentangling the effects of foliar nutrients, genetic diversity, patch size, and seed viability. *Estuar. Coast.* 33:118–26.
- Kettenring KM, McCormick MK, et al. 2011. Mechanisms of *Phragmites australis* invasion in the Chesapeake Bay: feedbacks among genetic diversity, nutrients, and sexual reproduction. *J. Appl. Ecol.* 48:1305–1313.
- Kettenring KM, Whigham DF. 2009. Seed viability and seed dormancy of non-native *Phragmites australis* in suburbanized and forested watersheds of the Chesapeake Bay, USA. *Aquat. Bot.* 91:199–204.
- Khan H, Brush GS. 1994. Nutrient and metal accumulation in a freshwater tidal marsh. *Estuaries* 17:345–60.
- King RS, Deluca WV, et al. 2007. Threshold effects of coastal urbanization on *Phragmites australis* (common reed) abundance and foliar nitrogen in Chesapeake Bay. *Estuar. Coast.* 30:1–13.
- Koch EM. 2001. Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24:1–17.
- Kroes DE, Hupp CR, Noe GB. 2007. Sediment, nutrient, and vegetation trends along the tidal, forested Pocomoke River, Maryland. In *Ecology of tidal freshwater forested wetlands of the southeastern United States*, Conner WH, Doyle TW, Krauss KW, editors. Dordrecht, The Netherlands: Springer, pp. 113–37.
- Langley JA, McKee KL, et al. 2009. Elevated CO<sub>2</sub> stimulates marsh elevation gain, counterbalancing sea-level rise. *PNAS* 106:6182–86.
- Langley JA, Megonigal JP. 2010. Ecosystem response to elevated CO<sub>2</sub> levels limited by nitrogen-induced plant species shift. *Nature* 466:96–99.

- Larsen C, Clark I, et al. 2004. The Blackwater NWR inundation model: rising sea level on a low-lying coast: land planning for wetlands. Open file report 04-1302. <http://pubs.usgs.gov/of/2004/1302/>. Reston, VA: USGS.
- Leck MA, Baldwin AH, et al. 2009. Plant communities of tidal freshwater wetlands of the continental USA and southeastern Canada. In *Tidal freshwater wetlands*, Barendregt A, Whigham DF, Baldwin AH, editors. Leiden, The Netherlands: Backhuys, pp. 41–58.
- Leonard LA. 1997. Controls of sediment transport and deposition in an incised mainland marsh basin, southeastern North Carolina. *Wetlands* 17:263–74.
- Li XY, Weller DE, et al. 2007. Effects of watershed and estuarine characteristics on the abundance of submersed aquatic vegetation in Chesapeake Bay subestuaries. *Estuar. Coast.* 30:840–54.
- Lippson AJ. 1973. *The Chesapeake Bay in Maryland: an atlas of natural resources*. Baltimore: Johns Hopkins University Press.
- Long CW, Burke RP. 2007. Habitat size, flora, and fauna: interactions in a tidal saltwater marsh. *J. Exp. Mar. Biol. Ecol.* 353:80–88.
- McCormick J, Somes HA Jr. 1982. *The coastal wetlands of Maryland*. Chevy Chase: MD DNR, Coastal Zone Management, Jack McCormick and Associates.
- McCormick MK, Kettenring KM, et al. 2010a. Extent and reproductive mechanisms of *Phragmites australis* spread in brackish wetlands in Chesapeake Bay, Maryland (USA). *Wetlands* 30:67–74.
- McCormick MK, Kettenring KM, et al. 2010b. Spread of invasive *Phragmites australis* in estuaries with differing degrees of development: genetic patterns, Allee effects and interpretation. *J. Ecol.* 98:1369–1378.
- Meanley B. 1965. Early-fall food and habitat of the sora in the Patuxent River Marsh, Maryland. *Chesap. Sci.* 6:235–37.
- Meanley B. 1978. *Blackwater*. Cambridge, MD: Tidewater.
- Megonigal JP, Neubauer SC. 2009. Biogeochemistry of tidal freshwater wetlands. In *Coastal wetlands: an integrated ecosystem approach*, Perillo GME, Wolanski E, et al. editors. The Netherlands: Elsevier, pp. 535–63.
- Mendelsohn IA, Batzer DP. 2006. Abiotic constraints for wetland plants and animals. In *Ecology of freshwater and estuarine wetlands*, Batzer DP, Sharitz RR, editors. Berkeley: University of California Press, pp. 82–114.
- Mendelsohn IA, Marcellus KL. 1976. Angiosperm production of three Virginia marshes in various salinity and soil nutrient regimes. *Chesap. Sci.* 17:15–23.
- Merrill JZ, Cornwell JC. 2000. The role of oligohaline marshes in estuarine nutrient cycling. In *Concepts and controversies in tidal marsh ecology*, Weinstein MP, Kreeger DA, editors. Dordrecht, The Netherlands: Kluwer, pp. 425–41.
- Meyer DL, Johnson JM, Gill JW. 2001. Comparison of nekton use of *Phragmites australis* and *Spartina alterniflora* marshes in the Chesapeake Bay, USA. *Mar. Ecol. Prog. Ser.* 209:71–84.
- Miller JK, Murphy D. 2002. 2001 Baseline wetland vegetation and monitoring for the Poplar Island restoration project. CBFO-FAO2-02. Annapolis, MD: USFWS.
- Mitchell JC. 1994. *The reptiles of Virginia*. Washington, DC: Smithsonian Institution Press.
- Mitchell LR, Gabrey S, et al. 2006. Impacts of marsh management on coastal-marsh bird habitats. In *Terrestrial vertebrates of tidal marshes: evolution, ecology, and conservation*, Greenberg R, Maldonado JE, et al., editors. Camarillo, CA: Cooper Ornithological Society, pp. 32–53.
- Mitsch WJ, Gosselink JG. 2000. *Wetlands*, 3rd edition. New York: Wiley.
- Moore KA. 2009. Submersed aquatic vegetation of the York River. *J. Coast. Res.* S157:50–58.
- Moore KA, Wilcox DJ, Orth RJ. 2000. Analysis of the abundance of submersed aquatic vegetation communities in the Chesapeake Bay. *Estuaries* 23:115–27.
- Morse JL, Megonigal JP, Walbridge MR. 2004. Sediment nutrient accumulation and nutrient availability in two tidal freshwater marshes along the Mattaponi River, Virginia, USA. *Biogeochem.* 69:165–206.
- Neckles HA, Wetzel RL, Orth RJ. 1993. Effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina* L.) dynamics. *Oecologia* 93:285–95.
- Neff KP, Rusello K, Baldwin AH. 2009. Rapid seed bank development in restored tidal freshwater wetlands. *Restor. Ecol.* 17:539–48.
- Neubauer SC, Anderson IC. 2003. Transport of dissolved inorganic carbon from a tidal freshwater marsh to the York River estuary. *Limnol. Oceanogr.* 48:299–307.
- Neubauer SC, Anderson IC, et al. 2002. Sediment deposition and accretion in a mid-Atlantic (U.S.A.) tidal freshwater marsh. *Estuar. Coast. Shelf Sci.* 54:713–27.
- Neubauer SC, Anderson IC, Neikirk BB. 2005. Nitrogen cycling and ecosystem exchanges in a Virginia tidal freshwater marsh. *Estuaries* 28:909–22.
- Neubauer SC, Craft CB. 2009. Global change and tidal freshwater wetlands: scenarios and impacts. In *Tidal freshwater wetlands*, Barendregt A, Whigham DF, Baldwin AH, editors. Leiden, The Netherlands: Backhuys, pp. 253–66.
- Neubauer SC, Givler K, et al. 2005. Seasonal patterns and plant-mediated controls of subsurface wetland biogeochemistry. *Ecology* 86:3334–44.
- Noe GB, Hupp CR. 2009. Retention of riverine sediment and nutrient loads by coastal plain floodplains. *Ecosystems* 12:728–46.
- Odum WE, Heywood MA. 1978. Decomposition of intertidal freshwater marsh plants. In *Freshwater wetlands: ecological processes and management potential*, Good RE, Whigham DF, Simpson RL, editors. New York: Academic Press, pp. 89–97.
- Odum WE, Smith TJ III, et al. 1984. The ecology of tidal freshwater marshes of the United States East Coast: a community profile. FWS/OBS-83/17. Washington, DC: USFWS.
- Orris PK. 1980. A revised species list and commentary on the macroalgae of the Chesapeake Bay in Maryland. *Estuaries* 3:200–06.
- Orth RJ. 1977. Effect of nutrient enrichment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. *Mar. Biol.* 44:187–94.
- Orth RJ. 1994. Chesapeake Bay submersed aquatic vegetation: water quality relationships. *Lake Reserv. Manage.* 10:49–52.
- Orth RJ, Moore KA. 1983. Chesapeake Bay: an unprecedented decline in submersed aquatic vegetation. *Science* 222:51–53.
- Orth RJ, Moore KA. 1984. Distribution and abundance of submersed aquatic vegetation in Chesapeake Bay: an historical perspective. *Estuaries* 7:531–40.
- Pasternack GB. 2009. Hydrogeomorphology and sedimentation in tidal freshwater wetlands. In *Tidal freshwater wetlands*, Barendregt A, Whigham D, Baldwin A, editors. Leiden, The Netherlands: Backhuys, pp. 31–40.
- Pasternack GB, Brush GS. 2001. Seasonal variations in sedimentation and organic content in five plant associations on a Chesapeake Bay tidal freshwater delta. *Estuar. Coast. Shelf Sci.* 53:93–106.
- Pasternack GB, Brush GS, Hilgartner WB. 2001. Impact of historic land-use change on sediment delivery to a Chesapeake Bay subestuarine delta. *Earth Surf. Process. Landf.* 26:409–27.
- Perry JE, Atkinson RB. 1997. Plant diversity along a salinity gradient of four marshes on the York and Pamunkey Rivers in Virginia. *Castanea* 62:112–18.
- Perry JE, Atkinson RB. 2009. York River tidal marshes. *J. Coast. Res.* S157:40–49.
- Perry JE, Bilcovic DM, et al. 2009. Tidal freshwater wetlands of the mid-Atlantic and southeastern United States. In *Tidal freshwater wetlands*, Barendregt A, Whigham DF, Baldwin AH, editors. Leiden, The Netherlands: Backhuys, pp. 157–66.
- Perry JE, Hershner CH. 1999. Temporal changes in the vegetation pattern in a tidal freshwater marsh. *Wetlands* 19:90–99.
- Perry MC. 1998. Wetland habitats for wildlife of the Chesapeake Bay. In *Ecology of wetlands and associated systems*, Majumdar SK, Miller EW, Brenner FJ, editors. Easton: Pennsylvania Academy of Science, pp. 332–49.
- Perry MC, Deller AS. 1995. Waterfowl population trends in the Chesapeake Bay area. In *Toward a sustainable watershed: the Chesapeake experiment* (Proceedings of the 1994 Chesapeake Research Conference, CRC Pub. 149), Hill P, Nelson S, editors. Edgewater, MD: Chesapeake Research Consortium, pp. 490–504.



- Peterson JE, Baldwin AH. 2004. Variation in wetland seed banks across a tidal freshwater landscape. *Am. J. Bot.* 91:1251–59.
- Petersen JE, Kennedy VS, et al., editors. 2009. *Enclosed experimental ecosystems and scale: tools for understanding and managing coastal ecosystems*. New York: Springer.
- Pinckney J, Zingmark RG. 1993. Biomass and production of benthic microalgal communities in estuarine habitats. *Estuaries* 16:887–97.
- Poffenbarger H, Needelman B, Megonigal JP. 2011. Salinity influence on methane emissions from tidal marshes. *Wetlands* 31:831–842.
- Posey MH, Alphin TD, et al. 2003. Benthic communities of common reed *Phragmites australis* and marsh cordgrass *Spartina alterniflora* marshes in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 261:51–61.
- Rheinhardt R. 1992. A multivariate analysis of vegetation patterns in tidal freshwater swamps of lower Chesapeake Bay, U.S.A. *Bull. Torrey Bot. Club* 119:192–207.
- Rizzo WM, Wetzel RL. 1985. Intertidal and shoal benthic community metabolism in a temperate estuary: studies of spatial and temporal scales of variability. *Estuaries* 8:342–51.
- Robbins CS. 1996. *Atlas of the breeding birds of Maryland and the District of Columbia*. Pittsburgh, PA: University of Pittsburgh Press.
- Roosenburg WM, Allman PE, Fruh BJ. 2003. Diamondback terrapin nesting on the Poplar Island environmental restoration project. In *Proceedings of the 13th Biennial Coastal Zone Conference*. Baltimore, MD: NOAA.
- Roosenburg WM, Green JP. 2000. Impact of a bycatch reduction device on diamondback terrapin and blue crab capture in crab pots. *Ecol. Appl.* 10:882–89.
- Roosenburg WM, Haley KL, McGuire S. 1999. Habitat selection and movements of diamondback terrapins, *Malaclemys terrapin*, in a Maryland estuary. *Chelonian Conserv. Biol.* 3:425–29.
- Rooth JE, Stevenson JC. 2000. Sediment deposition patterns in *Phragmites australis* communities: implications for coastal areas threatened by rising sea-level. *Wetl. Ecol. Manag.* 8:173–83.
- Ross KM, Hupp CR, Howard AD. 2004. Sedimentation in floodplains of selected tributaries of the Chesapeake Bay. In *Riparian vegetation and fluvial geomorphology*, Bennett SJ, Simon A, editors. Washington, DC: American Geophysical Union, pp. 187–214.
- Ruiz GM, Hines AH, Posey MH. 1993. Shallow water as a refuge habitat for fish and crustaceans in nonvegetated estuaries—an example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 99:1–16.
- Saltonstall K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *PNAS* 99:2445–49.
- Schenk ER, Hupp CR. 2009. Legacy effects of colonial millponds on floodplain sedimentation, bank erosion, and channel morphology, mid-Atlantic, USA. *J. Am. Water Resour. Assoc.* 45:597–606.
- Schmitz JP. 2000. Meso-scale community organization and response to burning in mesocosms and a field salt marsh. MS thesis, University of Maryland, College Park.
- Schubel JR. 1968. Turbidity maximum of the northern Chesapeake Bay. *Science* 161:1013–15.
- Schubel JR, Prichard DW. 1986. Responses of upper Chesapeake Bay to variations in discharge of the Susquehanna River. *Estuaries* 9:236–49.
- Sharpe PJ, Baldwin AH. 2009. Patterns of wetland plant species richness across estuarine gradients of Chesapeake Bay. *Wetlands* 29:225–35.
- Sherfy MH, Kirkpatrick RL. 2003. Invertebrate response to snow goose herbivory on moist-soil vegetation. *Wetlands* 23:236–49.
- Smith FR. 1938. Muskrat investigations in Dorchester County, MD, 1930–34. Circular no. 474. Washington, DC: USDA.
- Stewart RE. 1962. Waterfowl populations in the upper Chesapeake region. Special Scientific Report—Wildlife, no. 65. Washington, DC: USFWS.
- Stotts VD. 1986. A survey of breeding American black ducks in the Eastern Bay region of Maryland in 1986. Annapolis, MD: USFWS.
- Stotts VD, Davis DE. 1960. The black duck in Chesapeake Bay of Maryland: breeding behavior and biology. *Chesap. Sci.* 1:127–54.
- Stribling JM, Cornwell JC. 1997. Identification of important primary producers in a Chesapeake Bay tidal creek system using stable isotopes of carbon and sulfur. *Estuaries* 20:77–85.
- Swarth CW, Kiviat E. 2009. Animal communities in North American tidal freshwater wetlands. In *Tidal freshwater wetlands*, Barendregt A, Whigham DF, Baldwin AH, editors. Leiden, The Netherlands: Backhuys, pp. 71–88.
- Tatu KS, Anderson JT, et al. 2007. Mute swans' impact on submersed aquatic vegetation in Chesapeake Bay. *J. Wildl. Manag.* 71:1431–39.
- Tiner RE. 1985. Wetlands of the Chesapeake Bay watershed: an overview. In *Proceedings of the Conference—Wetlands of the Chesapeake*, Groman HA, Henderson TR, et al., editors. Washington, DC: Environmental Law Institute, pp. 16–29.
- Tiner RW, Bergquist HC, et al. 2001. Watershed-based wetland characterization for Delaware's Nanticoke River watershed: a preliminary assessment report. Newton Corner, MA: USFWS.
- Tiner RW, Burke DG. 1995. Wetlands of Maryland. Hadley, MA, and Annapolis, MD: USFWS and MD DNR.
- Tobias CR, Macko SA, et al. 2001. Tracking the fate of a high concentration groundwater nitrate plume through a fringing marsh: a combined groundwater tracer and in situ isotope enrichment study. *Limnol. Oceanogr.* 46:1977–89.
- Turner RE. 1976. Geographic variations in salt marsh macrophyte production: a review. *Contrib. Mar. Sci.* 20:47–68.
- Tzortziou M, Neale PJ, et al. 2008. Tidal marshes as a source of optically and chemically distinctive colored dissolved organic matter in the Chesapeake Bay. *Limnol. Oceanogr.* 53:148–59.
- US EPA. 1982. Chesapeake Bay: introduction to an ecosystem. Washington, DC.
- US EPA. 2004. Chesapeake Bay: introduction to an ecosystem. EPA 903-R-04-003. Washington, DC.
- Walter RC, Merritts DJ. 2008. Natural streams and the legacy of water-powered mills. *Science* 319:299–304.
- Wass ML, Wright TD. 1969. Coastal wetlands of Virginia. Special Report in Applied Marine Science and Ocean Engineering, no. 10. Gloucester Point: Virginia Institute of Marine Science.
- Weis JS, Weis P. 2003. Is the invasion of the common reed, *Phragmites australis*, into tidal marshes of the eastern US an ecological disaster? *Mar. Poll. Bull.* 46:816–20.
- Whigham DF. 2009. Primary production in tidal freshwater wetlands. In *Tidal freshwater wetlands*, Barendregt A, Whigham DF, Baldwin AH, editors. Leiden, The Netherlands: Backhuys, pp. 115–22.
- Whigham DF, Baldwin AH, Swarth CW. 2009. Conservation of tidal freshwater wetlands in North America. In *Tidal freshwater wetlands*, Barendregt A, Whigham DF, Baldwin AH, editors. Leiden, The Netherlands: Backhuys, pp. 233–40.
- White CP. 1989. *Chesapeake Bay: nature of the estuary: a field guide*. Centreville, MD: Tidewater.
- Wigand C, Stevenson JC, Cornwell JC. 1997. Effects of different submersed macrophytes on sediment biogeochemistry. *Aquat. Bot.* 56:233–44.
- Wood RJ, Boesch DF, Kennedy VS. 2002. Future consequences of climate change for the Chesapeake Bay ecosystem and its fisheries. *Am. Fish. Soc. Symp.* 32:171–84.
- Wray RD, Leatherman SP, Nicholls RJ. 1995. Historic and future land loss for upland and marsh islands in the Chesapeake Bay, Maryland, U.S.A. *J. Coast. Res.* 11:1195–203.
- Wulff BL, Webb KL. 1969. Intertidal zonation of marine algae at Gloucester Point, Virginia. *Chesap. Sci.* 10:29–35.
- Yozzo DJ, Smith DE. 1998. Composition and abundance of resident marsh-surface nekton: comparison between tidal freshwater and salt marshes in Virginia, USA. *Hydrobiologia* 362:9–19.

*This page intentionally left blank*