6 Wetlands in the Tidal Freshwater Zone

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6.1 Characteristics of Tidal Freshwater Wetlands

Tidal freshwater wetlands occur in the upstream reaches of many temperate estuaries. An estuary is “an inlet of the sea reaching into the river valley as far as the upstream limit of the tidal rise” (Fairbridge 1980). Within estuaries, tidal freshwater wetlands are restricted to the portion of the estuary where there is tidal action but little or no salinity. Depending on the magnitudes of tidal energy, river discharges and topography, freshwater tidal areas [practical salinity units (PSU) <0.5 parts per thousand (ppt), or <500 ppm] can be present between the highest point of tidal reach (i.e., the head of the estuary) and the oligohaline upper estuary, with PSU = 0.5–5.0 (McLusky 1993; Fig. 6.1). In some settings, tidal freshwater areas can be found as far as 150 km from the mouth of the estuary (Van Damme et al. 1999). The location of the tidal freshwater zone within the estuary depends on the balance between water volume and velocity of the incoming tide and the discharge of the out-flowing river. Towards the upstream tidal limit, the horizontal movement of tide becomes less important as the tidal wave attenuates and the vertical tide movement becomes zero partly due to the prevention of river discharge by the higher tide in the estuary. Further downstream, both the horizontal and vertical movement of the tide is important. Tidal characteristics are strongly dependent on river discharge: during high discharge, the tidal limit may be much further downstream than during low discharge. Symmetrical tides (i.e., tides with similar duration of flood and ebb) occur in the saline zone of estuaries, but in tidal freshwater zone they are not symmetrical. In the latter, there typically is a short period of intense incoming tide and a longer period of ebbing tide. Moreover, in the tidal freshwater zone, hydrologic conditions interact with the funnel-shape of the river channel to produce a tidal range that can be as high as 6 m.

In contrast to salinity, which changes in a unidirectional way, suspended matter concentrations often show a clear maximum near or in the freshwater
tidal zone, as illustrated in Fig. 6.2 (also in, e.g., Meade 1972; Grabemann et al. 1997; McManus 2005). Two processes are responsible for the high turbidity. First, saline water has a higher density; and it therefore remains at the bottom of the channel and forms a wedge as it moves upstream during a tidal cycle. During the change in tides, the upper freshwater flows downstream and the saline bottom-water flows upstream, facilitating the development of boundary conditions. At the tangent plane where the two flows meet, the velocity is zero, without physical disturbance, and the concentration of suspended matter is the highest (Officer 1981). Second, at the same location, physical–chemical conditions occur that result in the flocculation of suspended particles, increased by the input of particles from the brackish zone. This flocculation of suspended particles is stimulated by differences in electric charge in the particles, which is optimal at very low salinities (Eisma et al. 1994). As a result, the concentration of suspended particles is highest in the tidal freshwater zone just above the brackish zone (Meade 1972).

Tidal freshwater wetlands are thus unique ecosystems because of their physical location within river–estuarine systems. As will be described later, they have a high level of habitat and species diversity and, because they typically occur in upper parts of estuaries where human activities predominate, nutrient concentrations are also high (Mesnage et al. 2002). Accordingly, tidal freshwater wetlands are located in parts of estuaries that have had a long history of human intervention. Even though they are located in culturally important areas, they have not been studied as frequently or intensively as brackish and saline wetlands that occur nearer to the coast (Elliot and McLusky 2002). The lack of research focus on tidal freshwater wetlands has at least three explanations. First, marine ecologists have rarely investigated these systems, since the water is fresh and out of their scope. Second, river ecologists have rarely been interested in these systems because they are tidal. And third, these wetlands may be unattractive to some researchers since there are few species that are unique to freshwater tidal wetlands and, in
addition, the system is often rich in nutrients, very muddy, and not easily accessible.

Because there have been relatively few studies of tidal freshwater wetlands (for a bibliography, see Yozzo et al. 1994), their distribution has not been fully examined throughout much of the world. In western Europe, tidal freshwater wetlands occur in, at least, the estuaries of the rivers in northwest Europe from Elbe to the Gironde (Meire and Vincx 1993), including British and Irish estuaries. On the Atlantic coast in North America, tidal freshwater wetlands occur in all major river systems from the Gulf of St. Lawrence to Georgia (Odum et al. 1984). Tidal freshwater wetlands also occur on the Pacific coast of North America (Boule 1981; Tanner et al. 2002), including Alaska, but their distribution has not been adequately documented. Junk (1983) reported that tidal freshwater systems occur on the Atlantic Coast of South America; but he offered no details on where they occurred, nor their extent.

Another type of tidal freshwater wetland may also be abundant in the upstream portions of large river deltas, such as the delta of the Mississippi River in Louisiana, USA (Penfound and Hathaway 1938; Chabreck 1972; Gosselink 1984; Mitsch and Gosselink 2000). While much research has been conducted on the ecology of Louisiana delta plain wetlands, the freshwater wetlands in this area are rarely referred to as “tidal freshwater wetlands”. Many of the delta plain freshwater wetlands do have a tidal signature, but the range is small (<0.3 m). Also, there is no clear diurnal pattern of tidal flooding, but rather periodic flooding due to upstream runoff and wind effects, which can alter the water level by a meter or more. This pattern of tidal fluctuation is vastly different from those of tidal wetlands, where tides can fluctuate by sev-
eral meters twice daily. While the ecological and socioeconomic importance of delta plain wetlands is unquestioned, we choose to omit detailed discussion of their ecology in this review because their flat topography and microtidal environment make them a unique case compared with the wider distribution of tidal freshwater wetlands in non-deltaic environments.

In tropical regions, coastal wetland types are replaced by the mangrove forest (Mitsch and Gosselink 2000). One of the authors (D.W.) has observed tidal freshwater wetlands in the freshwater portions of several mangrove-dominated rivers in Okinawa (Japan), suggesting that they are probably more common on a global basis than has been recognized. The presence and abundance of tidal freshwater wetlands in river systems is controlled by several factors including:

- shape of the river mouth should result in estuarine conditions in which there is a tidal flow of saline water into the river.
- The river system should include enough of a lowland area for a relatively large tidal area to exist in the river system.
- There should be a constant discharge of freshwater from the river, so that the tidal freshwater portion of the estuary occurs throughout the entire year.
- The tidal impact should dominate near at least the mouth of the river (i.e., the freshwater flow does not reach the sea without being influenced by saline and brackish water).

Consequently, it is not likely that tidal freshwater wetlands occur in tropical areas where mountains reach the sea, areas where there are deltaic plains, and areas where river flows are so large (e.g., Amazon River) that fresh water flows directly into the sea without the important saline wedge.

The following review of tidal freshwater wetlands has several objectives. First, we want to combine the relevant literature from Europe and North America, a synthesis that has not been previously attempted. Second, we want to update and summarize the literature on tidal freshwater wetlands, since the publication of the few previous syntheses in the 1980s and 1990s (Simpson et al. 1983a; Odum 1988; Meire and Vincx 1993). The only other literature-update on American tidal freshwater wetlands has been provided by Mitsch and Gosselink (2000).
6.2 Human Activities

Since human activities have modified tidal freshwater wetlands in many ways, a short introduction to the historical changes in land use and water quality is given.

6.2.1 Historical Development

Tidal freshwater wetlands have been intimately linked to the development of human cultures, especially in parts of Europe. Archaeological research west of Rotterdam in The Netherlands suggests that humans associated with the “Vlaardingen culture” were present in tidal freshwater systems as far back as 2700 BC (De Ridder 1999). Basket-worked fish-traps have been found in former streams; and dams and dikes were constructed to change the flooding frequency. By 175 BC, people were using culverts made from tree trunks to drain tidal freshwater habitats. The culverts had a one-way valve at the outer side, preventing the inflow of water at high tide and thus allowing areas to drain. Analyses of pollen and plant remnants from that period suggest that the wetlands were dominated by grasses (probably Phragmites) and sedges, with other frequent species such as Typha, Atriplex, and Rumex. No species from brackish or saline conditions were represented. The most common woody plants in or near the wetlands were alder (Alnus), with some oaks (Quercus), pines (Pinus), and willows (Salix; Brinkkemper and De Ridder 2001). Paleological reconstruction suggests that, at that time, tidal freshwater systems were part of an open landscape at the edge of peatland with distinct tidal influences. There is also strong evidence that people had agricultural fields and kept cattle in the wetlands. Humans undoubtedly used tidal freshwater wetlands in North America but the impacts of humans in pre-colonial times have not been well documented (Kiviat 1991).

Due to sedimentation and erosion processes, enormous changes occurred over the centuries in the tidal freshwater zones in European rivers. From the Middle Ages to a century ago, maps of the tidal areas in western Belgium, southwestern Netherlands and northern Germany documented drastic changes. New estuaries were formed in the delta of the Rhine system and wetland areas were changed to land by diking to prevent flooding and for purposes of reclamation to agricultural lands. During the past 200 years, technology supported this change and the former large tidal areas are at present mostly restricted to the main stream-bed of the estuary, e.g., as illustrated by the river Seine (Avoine et al. 1981). Large port cities developed in the regions of rivers where tidal freshwater systems occurred and they were exploited by societies for their economic potential (Pinder and Witherick 1990; Preisinger 1991). Major cities and harbors in Europe and North America arose in this
way (e.g., Hamburg, Rotterdam, Antwerp, Dublin, London, Philadelphia, Richmond, Washington, D.C.). Odum et al. (1984, p. 88) state that “almost all of this habitat on the USA–Atlantic coast is in the 13 original colonies” and that diking, dredging and filling of these wetlands have occurred widely.

### 6.2.2 Water Quality Changes

In addition to physical changes and loss in area associated with agricultural and urban development, another important change was the enormous increase in the discharge of human and industrial wastewater into the rivers upstream of and within the tidal freshwater zone. As a result, the chemistry of the rivers changed in three ways. First, the discharge of sewage increased the nutrient load and the organic components, resulting in a high oxygen demand that led to a reduction of oxygen concentrations in the tidal freshwater zone (Riedel-Lorje and Gaument 1982; Marchand 1993; Van Damme et al. 1999). Second, the discharge of heavy metals and other contaminants resulted in the further degradation of tidal freshwater systems (Schuchardt et al. 1993; Khan and Brush 1994; Knight and Pasternack 2000; Middelkoop 2000; Ciszewski 2001; Walling et al. 2003). Third, the concentrations of organic micropollutants in river water increased. Due to severe sedimentation of the suspended matter including the pollutants, concentration of pollutants increased, resulting in toxicological problems in tidal freshwater systems (Heemken et al. 2000; Steen et al. 2002; Jonkers et al. 2003).

Many of these problems continue today, even though advanced wastewater treatment facilities are present and industries do a much better job of minimizing pollutant discharges. Pollution is especially problematic where sedimentation rates are very high. Consequently sediments contain high concentrations in heavy metals and organic micropollutants; sometimes the quantities are too large to be stabilized, transformed, or removed by natural processes (Ridgley and Rijsberman 1994). In The Netherlands, for example, harbor areas had to be dredged and the polluted sediments were often stored in newly created polders next to the river in the freshwater tidal areas.

### 6.3 Biological Variation Within the Freshwater Tidal Ecosystem

This section describes the zonation in vegetation, the temporal variation and seed dynamics in plant communities, and the presence of wildlife and other biota. The aim is to compare and contrast the biology and ecology of tidal freshwater wetlands on both sides of the Atlantic Ocean.
6.3.1 Vegetation Zonation

The primary ecological factors influencing the distribution of plant species are the impacts of tides and variations in surface elevations. The duration and frequency of flooding at any location depends on the elevation of the substrate relative to mean high tide and result in distinct zonation in vegetation (Zonneveld 1960; Simpson et al. 1983a; De Boois 1982; Preisinger 1991). North American and European tidal freshwater wetlands are comparable in processes and zonation; however, the species differ considerably. Table 6.1 summarizes the most important zones and their species. In general, the num-

<table>
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<tr>
<th>Vegetation Zone</th>
<th>Europe</th>
<th>North America</th>
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</thead>
<tbody>
<tr>
<td>Aquatic vegetation</td>
<td>Potamogeton spp, Nuphar lutea, Hydrilla verticillata, Myriophyllum spp, Po-</td>
<td>Ceratophyllum demersum, Elodea spp, Hydrilla verticillata, Myriophyllum spp,</td>
</tr>
<tr>
<td>Low marsh</td>
<td></td>
<td>Tamogotan spp, Vallisneria americana</td>
</tr>
<tr>
<td>High marsh</td>
<td>Scirpus spp, Phragmites australis, Caltha palustris</td>
<td>Nuphar advena, Peltandra virginica, Pontederia cordata, Sagittaria latifolia, Zizania aquatica</td>
</tr>
<tr>
<td>Forests/swamps</td>
<td>Willow species: Salix spp with, e.g., Anthriscus sylvestris, divided in subtypes: (1) with Callitriche stagnalis, (2) with Cardamine amara, (3) with Circe lutetiana</td>
<td>Trees: Acer rubrum, Chamaecyparis thyoides, Fraxinus pennsylvanica, Magnolia virginiana, Nyssa biflora, Carpinus carolinianaShrubs: Clethra alnifolia, Ilex verticillata, Itea virginica, Leucothoe racemosa, Rhododendron viscousum, Taxodium distichum, Vaccinium corymbosum, Viburnum spp.Vines: Parthenocissus quivefolia, Smilax spp, Toxicodendron radicansHerbs: many of the species listed under high and low marsh above; Cinna arundinacea, Viola cucullata, Osmunda spp, Thelypteris thelypteriodes, Woodwardia spp</td>
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ber of plant species in a zone increases with decreasing frequency and duration of flooding.

6.3.2 The Vegetation of European Tidal Freshwater Wetlands

In the tidal creeks, the current is usually too strong and turbidity too high for vascular plants to become established. Tidal creeks also have dynamic sand banks and areas of mud flats that just occur above low tide (Zonneveld 1960). Only in more isolated shallow pools are some aquatic plants present, such as *Potamogeton* spp, *Sagittaria sagittifolia*, and *Nuphar lutea*. Closer to high-tide level, vascular plants become common and four basic types of vegetation are present.

Below mean high tide, plant species are represented that can stand flooding and wave activity. In areas with wave energy, *Scirpus triqueter*, *S. maritimus*, and *S. lacustris* are most common. *Scirpus triqueter* is an endangered species (Deegan and Harrington 2004), being unable to persist in areas impacted by lack of wave energy (after human control). Just above mean high tide level, the vegetation dominated by *Scirpus* spp is replaced by a marsh vegetation that has many herbaceous plants, such as species in the genera *Lythrum*, *Phalaris*, *Epilobium*, *Typha*, *Sympyrum*, *Valeriana*, and *Sparganium*. As the marshes are eutrophic (Verhoeven et al. 2001), there is a dominance of *Urtica dioica* and *Calystegia sepium*. In habitats with a similar tidal regime but with a high concentration of organic material in the substrate, rare characteristic species are *Leucojum aestivum* and *Equisetum fluviatile*.

At other locations, reed (*Phragmites australis*) is the dominant plant but many other species, e.g., *Veronica anagallis-aquatica* also occur. Very characteristic at these locations is *Caltha palustris* var. *araneosa*, which produces special roots, at leaf nodes, that can be transported by the tides (Van Steenis 1971). However, the majority of locations in higher tidal zones are covered by willow (*Salix*) forests, either managed as plantations (osier beds) or as natural vegetation (Fig 6.3A, B). At present, three sub-types of this forest occur (Barendregt 2005). At or just below the mean high water line, where anaerobic conditions prevail and soil development is just starting, the conditions are still too wet for many terrestrial species; and *Callitriche stagnalis* and a species of *Vaucheria* occur. Just above high tide, *Cardamine amara* is abundant; and 50 cm above mean high water level *Circa luteitiana* occur. Within this wetland–upland transition zone, there is often evidence of succession (including species such as *Carex remota*) and soil genesis that results in the accumulation of organic matter. European freshwater tidal wetlands do not suffer for invasive species, although *Angelica archangelica* and *Impatiens noltitangere* might be represented in the vegetation.

Biomass varies across different zones within tidal freshwater wetlands and the general pattern is for biomass to increase with increasing elevation within
Fig. 6.3 A (top) Characteristic zonation in European tidal freshwater wetlands, with a tidal creek between the zones, close to the river a zone with low marsh (left side) dominated by bulrush (Scirpus lacustris), in the center a reed bed (Phragmites australis), and to the right side a willow forest (Salix spp). Photo from river Oude Maas, The Netherlands, by A. Barendregt. B (bottom) A tidal creek at low tide, entering the willow forest (both sides of the creek) and a small reed bed (center), illustrating the muddy soil in the creek. At high tide, the water table is up to the willow trees. Photo from the river Oude Maas, The Netherlands, by A. Barendregt
the tidal zone. This pattern is illustrated for a European tidal freshwater wetland (Fig. 6.4). At the lowest elevation within the tidal zone, the biomass of non-vascular plants (e.g., phyto-benthos) is low on both sandy and muddy substrates. At higher elevations, the biomass of vascular plants such as bulrushes (*Scirpus* spp) and reed (*Phragmites*) is intermediate and the highest biomass is associated with stands of willow (*Salix* spp) at the highest elevations within the intertidal zone.

### 6.3.3 The Vegetation of North American Tidal Freshwater Wetlands

In North America, tidal freshwater wetlands include swamps, which are dominated by trees and shrubs, and emergent wetlands dominated by herbaceous plants. Along the Atlantic Coast, tidal freshwater swamps may abut rivers or be separated from the river by a band of tidal freshwater marsh of varying width. Swamps often have a complex microtopography created by fallen logs that results in elevated “hummocks” interspersed with lower “hollows” (Rheinhardt 1992; Peterson and Baldwin 2004). The hummocks may extend 30 cm or more above the hollows, resulting in marked differences in species composition of herbaceous plants over short distances.

Tidal freshwater wetland habitats that are dominated by herbaceous species can be divided into two broad categories: high marsh and low marsh (Simpson et al. 1983a). The two habitats are distinguished by differences in hydro-period along an elevation gradient. In many locations, the pattern of zonation proceeding away from the river is low marsh–high marsh–swamp (Fig. 6.5A, B). Interestingly, the elevation of the high marsh may be above that of the swamp hollows due to a natural levee effect where river sediment
Fig. 6.5 A (top) Characteristic zonation in North American tidal freshwater wetlands. Visible on the right of the river at the lowest elevations is the low marsh, here dominated by *Nuphar advena*. At a slightly higher elevation is the high marsh, here visible as a line of lighter shade above the low marsh, with a diverse mixture of herbaceous annuals and perennials. Further to the right, but at a slightly lower elevation, lies the tidal freshwater swamp forest, with species-rich communities. Photo from the Nanticoke River, Maryland, by A. Baldwin. B (bottom) A tidal creek at low tide. In this late summer (August) scene, the dominant species are both annuals. Along the creek is *Polygonum punctatum* and the tall plant behind it is wild rice (*Zizania aquatica var. aquatica*). Photo from the Hamilton Marshes located near Trenton, New Jersey, by D.F. Whigham.
settles out primarily directly along the banks of the river during high tides or flooding events. Moreover, a latitudinal climate gradient results in large variation in species composition and distribution of types of tidal freshwater wetlands.

Tidal freshwater swamps are typically dominated by hardwood species, such as *Nyssa* spp, *Fraxinus pennsylvanica*, and *Acer rubrum*; they have a diverse shrub layer, containing species such as *Vaccinium corymbosum*, *Rhododendron viscosum*, *Viburnum* spp, and *Magnolia virginiana*. Herbaceous communities also occur in swamp habitats if the tree and shrub strata are sparse enough to allow adequate light penetration. Hummocks may be populated by species of *Carex* spp as well as grasses such as *Cinna arundinacea* and ferns such as *Osmunda cinnamomea*, *O. regalis*, and *Thelypteris palustris*. Other herbaceous species like *Viola cucullata* occur on hummocks. In low areas between hummocks (i.e., hollows) one finds species that also occur in the high marsh in full sunlight. Common species in hollows are *Peltandra virginica, Leersia oryzoides, Typha latifolia*, and *Zizania aquatica*.

High marsh vegetation is often more diverse than low marsh vegetation, containing mixtures of annual such as *Bidens* spp, *Impatiens capensis*, *Polygonum arifolium* and perennials like *Panicum virgatum*, *Peltandra virginica*, and *Leersia oryzoides*. Low marshes, in contrast, are dominated by perennials such as *Nuphar advena* and *Pontederia cordata*. The only annual species that is common to many low marsh habitats along the Atlantic Coast is *Zizania aquatica*.

Along the Atlantic Coast, only one species has been recognized as being rare, *Aeschynomene virginica* (Griffith and Forseth 2003); and it appears to be a fugitive species that persists by colonizing disturbance patches on the levee of tidal creeks. Invasive species have also received attention in tidal freshwater wetlands because of the potential impacts that they may have on native species and ecosystem processes (Findlay et al. 1990). Especially noteworthy is the increased abundance of European genotypes of *Phragmites australis* that invade and expand more readily than native North American genotypes (Saltonstall 2002). The expansion of *Phragmites* has been noted in several estuarine systems (Chambers et al. 1999; Meyerson et al. 2000), including freshwater areas (Rice et al. 2000), but the impact on native species remains undetermined and there are few efforts to eradicate or control it (Findlay and Groffman 2003; Teal and Peterson 2005). *Lythrum salicaria* and *Murdannia keisak* are two Eurasian species that occur in some tidal freshwater marshes in the United States (Baldwin and DeRico 1999; Baldwin and Pendleton 2003).
ied more than swamps. While species composition has been described in many systems, seed bank and vegetation dynamics have been studied primarily in high marsh habitats. One of the most dramatic features of plant communities of tidal freshwater wetlands is the tremendous variation in relative abundance of species throughout the growing season. Many of the species of tidal freshwater wetlands do not persist as dead culms or shoots above the soil surface over the winter; and so the wetland has a flat, barren appearance, with a layer of decomposing plant material that decreases in thickness during the winter months. Early in the spring (e.g., April in the mid-Atlantic), perennial species begin to send up shoots. Simultaneously, the high-light environment, increasing photoperiod, and warming temperatures stimulate germination of primarily obligate or facultative annual species that are part of soil seed bank, often yielding high densities of established seedlings (Leck 2003). The leaves and shoots of the emerging perennials (e.g., *Acorus calamus*, *Peltandra virginica*, *Leersia oryzoides*, *Hibiscus moscheutos*) typically grow more rapidly than the seedlings, reaching their maximum height and biomass and forming a canopy early in the summer (e.g., June in the mid-Atlantic; Odum 1988; Whigham and Simpson 1992). The marshes during this time of year have a deep green, lush appearance, perhaps broken by occasional splotches of flower color. The annuals continue to grow, experience thinning, and eventually overtop the perennials and reach their maximum biomass later in the season (e.g., September) as dominant perennials are senescing. Examples of annuals that dominate by late summer are *Polygonum arifolium*, *P. sagittatum*, and *Bidens laevis*. By the end of the season, the marshes have a red-brown appearance, enhanced by the yellow flowers of *Bidens*. However, this pattern does not hold for all species; some perennials also flower late in the season (e.g., *Symphyotrichum puniceum*, *Cicuta maculata*, *Helenium autumnale*).

In addition to seasonal changes in community structure, which are primarily a result of life history and phenology of the various species, vegetation of tidal freshwater wetlands changes in composition between years (Leck and Simpson 1995). Much of this variation may be due to changes in the abundance of annual species between years. Annual species are a major component of wetland vegetation, often comprising half or more of the species, number of individuals, and biomass (Parker and Leck 1985; Whigham and Simpson 1992). Because annuals must be recruited each year from the seed bank or recently dispersed seeds, conditions that inhibit germination and seedling establishment and growth (which occur early in the growing season) will result in lower abundance of those species throughout the growing season (Baldwin et al. 2001).
Seed–Vegetation Dynamics

Because of the abundance of annual species in tidal freshwater wetlands, seed banks, seed dispersal, and seed germination are important aspects of their plant community dynamics. Just as vegetation fluctuates between years in these systems, so does the relative abundance of species in the seed bank (Leck and Simpson 1995). However, the seed bank may not mirror the standing vegetation. While many species do occur in both seed bank and vegetation (e.g., Bidens spp. Impatiens capensis, Polygonum spp, Typha spp), some of the dominant vegetation species (e.g., Nuphar advena, Phragmites australis) are rarely found in the seed bank, while some common species (e.g., Juncus effusus, Cyperus erythrorhizos) in the seed bank occur rarely in undisturbed vegetation (Leck et al. 1988).

Differences between seed bank and vegetation have been noted in other ecosystems and are likely due to differences in evolved life history strategy. For example, seed banks provide a mechanism for species with persistent seeds to emerge following a disturbance such as ice scouring or fire that removes dominant canopy vegetation. The seed bank species in this case can be considered “fugitive species” that are recruited in patches following disturbances but are otherwise rare in matrix vegetation. Similarly, many perennial marsh species rely on clonal propagation as their primary mode of reproduction and may have lost their capacity to survive for long or even short periods as buried seeds due to genetic drift. Others may be incapable of sexual reproduction: Acorus calamus, a dominant perennial in many United States tidal freshwater wetlands, is sterile due to polyploidy, at least in Europe (Eckert 2002). Seeds also differ between species in how long they typically exist in the seed bank. Leck and Simpson (1987) identify three strategies for dominant seed banks species in mid-Atlantic tidal freshwater wetlands: (1) transient species that have seeds that overwinter but are completely depleted during spring germination (e.g., Impatiens capensis), (2) high turnover with some reserve of viable seeds (e.g., Bidens laevis), and (3) large long-term seed bank (e.g., Ranunculus sceleratus). Because species with different strategies are dependent to different degrees on annual renewal of the seed bank, variation in seed bank strategy contributes to interannual variation in species composition of vegetation. For example, if Impatiens capensis (a transient species) is not abundant in vegetation one year due to wetter-than-normal conditions, it contributes fewer seeds to the seed bank, and so it has less propagules available for establishment the following year. Species with persistent seed banks, in contrast, are less impacted by the prior year’s seed production.

Just as seed bank strategy varies between species, so do seed germination requirements (Leck 1996). Some species require light for germination (e.g., Bidens laevis), while others do not (e.g., Peltandra virginica). Others require the presence of oxygen (Impatiens capensis), while others germinate under anaerobic conditions (Pontederia cordata). Many species of temperate tidal
freshwater wetlands require cold stratification for two months or more before germination can occur; and germination percentage varies, depending on temperature regime. Flooding has been found to reduce richness and density of seedlings emerging from tidal freshwater marsh seed banks (Baldwin et al. 2001); and salinity was found to reduce seedling emergence from seed banks of oligohaline tidal marshes (PSU <5; Baldwin et al. 1996).

6.3.4 Wildlife

In Europe most mammals have been reduced in abundance and none of them seem to impact tidal freshwater wetlands in a significant way, with the exception of beaver (*Castor fiber*) which was reintroduced in one large area in the Netherlands (Biesbosch) about a decade ago. The beaver now has a stable population but its impacts are relatively restricted. In the United States two herbivores, the native muskrat (*Ondatra zibethicus*) and the introduced nutria (*Myocastor coypus*), are known to impact vegetation and nutrient cycling (Connors et al. 2000) in tidal freshwater wetlands, mostly by digging the rhizomes (Odum et al. 1984). Beaver are now also common and rapidly spreading in North America and they have become regular inhabitants of tidal freshwater wetlands (D.F. Whigham, personal observation).

The freshwater tidal region is important for birds, especially waterfowl such as ducks and waders, as resting and feeding places during migration (Ysebaert et al. 2000). Tidal freshwater habitats are especially important during freezing periods because the tidal influence causes open water areas to persist. These habitats are used by numerous migratory and resident species in the spring because they provide food resources early in the growing season (Odum et al. 1984). Tidal freshwater wetlands are also important breeding sites for a number of duck species and passerines (Hawkins and Leck 1977). In willow forests many passerine species breed, as well as species of herons and cormorants. In the Netherlands, for instance, there has been a sudden increase in the population of the endangered bluethroat (*Luscinia svecica*) in freshwater tidal wetlands, resulting in a stimulation of the whole national population (Meijer and van der Nat 1989).

6.3.5 Fish Species

Many fish species occur in estuaries, but no species are solely restricted to the freshwater tidal areas (Odum et al. 1984; Anderson and Schmidt 1989; Lobry et al. 2003). In contrast, most fish species occur only in the saline areas and brackish parts of the estuary and rarely move into tidal freshwater areas, except for the juvenile stage of some species (Thiel and Potter 2001; Lobry et al. 2003). In the freshwater tidal parts of estuaries, most of the common fish
species also occur in the non-tidal parts of the rivers. There are also anadromous fish species that pass through the tidal freshwater areas during movement from or to the sea (Pomfret et al. 1991). Because of river regulation (e.g., dams) and pollution, some anadromous species no longer occur in some European rivers that have tidal freshwater habitats. The salmon (*Salmo salar*) and the sturgeon (*Acipenser sturio*) disappeared from most European rivers more than 50 years ago (Verhey et al. 1961) and the allis shad (*Alosa alosa*) disappeared in 1920 from the river Rhine.

An important European fish species that requires freshwater tidal habitats is the Twaite shad (*Alosa fallax*). Their spawning grounds are at the upstream border of the tidal areas and the juveniles use the freshwater tidal areas as nursery grounds. Most of the populations of the Twaite shad have been affected by over-fishing and pollution, but damming of the estuary of the Rhine system in the 1970 also negatively impacted the species. However, in recent years the recovery of the Twaite shad has been reported from Germany and Belgium as a result of reduced water pollution (Gerkens and Thiel 2001). Along the Atlantic coast of North America, the American shad (*Alosa sapidissima*) and the alewife (*A. pseudoharengus*) occupy habitats similar to those of the Twaite shad and they have suffered many of the same consequences for the same reasons (Odum et al. 1984), indicating comparable ecology in the New World.

### 6.3.6 Other Biota

Just as elsewhere in the world, the biodiversity of other groups is high in tidal freshwater wetlands but most of them have not been studied in detail. In Europe and North America, the diversity and ecological importance of algal species (with special diatom species: Rehbehn et al. 1993; Muylaert and Sabbe 1996) has not been examined thoroughly (e.g., Kiviat and Barbour 1996; Muylaert et al. 1997). Animal-related publications for tidal freshwater wetlands in North America can be found in the bibliography published by Yozzo et al. (1994). Here we focus on two groups of animals: benthic species and terrestrial invertebrates that live on emergent herbaceous and woody vegetation.

Compared to brackish and saline zones in estuaries (Seys et al. 1999), the diversity of benthic species is less in tidal freshwater areas due to high turbidity of unconsolidated substrates (Van Damme et al. 1999, Wolff 1973). Only Oligochaeta (*Tubifex*) have been described as being abundant from The Netherlands by Heyligers (see: Verhey et al. 1961). In North America, studies of various animal groups in Tivoli Bay (Hudson River) and Chesapeake Bay have focussed on microbenthos (Simpson et al. 1984), meiofauna (Yozzo and Smith 1995), ostracods (Yozzo and Steineck 1994), and fish-microcrustacean interactions (Yozzo and Odum 1993).
In contrast to benthic animals, terrestrial invertebrates in tidal freshwater wetlands are highly diverse and include many taxonomic groups, such as spiders, beetles, woodlice, molluscs, millipedes, worms, and springtails (Barbour and Kiviat 1986). Only few investigators, however, have examined this group of animals in tidal freshwater wetlands. Heyligers (see: Verhey, 1961) reports the flooding frequency and the weakness of the soil as the principle variables controlling the diversity of terrestrial invertebrates. Desender and Mealfa (1999) and Hendrickx et al. (2001) suggested that the characteristics of the vegetation structure were also important. In the willow forests along the river Oude Maas, where nowadays the best freshwater tidal wetlands in The Netherlands occur, 65 pitfall traps at different locations have been used to examine ground-dwelling invertebrates (Barendregt 2005). For each species captured, Barendregt calculated their range according to mean high water table as an index of their response to flooding frequency. No species occurred over the entire range of locations and three types of distribution patterns were found (Fig. 6.6). A group of semi-aquatic species (low range) needs daily flooding and they are well represented only below mean high tide. A second group of species (high range) mostly occur above mean high tide, ranging from species that starting just 20 cm above mean high tide level (= occasionally flooded) to locations more than 60 cm above high tide (= rarely flooded). The lower the elevation, the more tolerant these species have to be to flooding. This second group consists of many common wetland or wet forest species. A third group of species (middle range) occurs around or just above mean high tide, in habitats that are flooded frequently; and this group avoids the higher range. This identification

Fig. 6.6 Cumulative relative preference in Dutch tidal freshwater wetlands of some ground-dwelling invertebrate species according to the elevation related to the level of mean high tide, indicated by three groups of species: (1) four species from the low range, (2) five species from the middle range, (3) six species from the high range
of three distinct groups of invertebrates supports the hypothesis that by stress
the competition from aquatic and terrestrial species is less prominent in this
intermediate zone and this facilitates the presence of another group of species
from the middle range, probably stimulated by this flooding stress. The evalu-
ation of all species from this system demonstrates that most rare or infrequent
species of the tidal freshwater systems of The Netherlands, such as representa-
tives from Mollusca, Coleoptera, Isopoda, and Araneae, are found in this inter-
mediate zone, supporting the explanation that characteristic tidal wetland
species are represented in this zone (Barendregt 2005).

In addition to the pattern in Fig. 6.6, another dimension of the biota in tidal
freshwater wetlands is given in the distribution of terrestrial invertebrates
within the wetland. In The Netherlands, willow forests are managed and are
cut, on average, every four years. Harvesting procedures result in significant
physical changes; areas of bare clay soils are exposed. Following harvesting
the habitat is characterized by high light intensity but after about two years of
vegetation recovery, light intensities in willow stands are much lower. When
areas are abandoned for a decade or more, the willow forest comes into the
next phase of succession and biomass plus litter fall within the system
increases. Some species of terrestrial invertebrates occur in all stages of vege-
tation development during the succession but about half of all invertebrate
species prefer the early or the late phase in succession.

6.4 Chemical and Physical Processes: the Wetland as a Filter

Estuaries are well known to act as filters that prevent compounds transported
by rivers from reaching the sea. Tidal action is not only the driving force
behind the existence of fringing wetlands in estuaries, but it also helps them
to play an important role in the estuarine filter function. As described in the
Introduction, tidal freshwater wetlands occur near the upper limit of tide in
the region of most rivers that is nutrient-rich. From a landscape perspective,
the salt, brackish, and fresh types of wetlands that occur in estuaries function
decidedly differently and the material presented in this section is mostly
based on comparisons between freshwater tidal wetlands and brackish or
saline wetlands.

A first obvious function that freshwater wetlands exert on the quality of
flooding water is physical aeration. As many estuaries are heterotrophic,
especially in their upstream stretches, wetlands provide a shallow distribu-
tion surface for oxygen poor water, enhancing oxygen influx from the atmos-
phere. As primary production in estuaries is often limited by turbidity, phys-
ical aeration often contributes more to the oxygen status of the water than
primary production (Soetaert and Herman 1995). Moreover, the oxygen lev-
els differ from neap to spring tides (Parker et al. 1994). The surplus in car-
bon input from the river does not reach the sea, since the majority of the organic input is broken down to CO₂ by bacteria and disappears from the system in the freshwater tidal zone. At the same time, the oxygen concentration is lowest in this zone, as a result of the metabolic activity of bacteria that interact with, for example, compounds with a high biological oxygen demand that result from human activities (Marchand 1993). Attempts to draw inferences about freshwater wetland – estuarine interactions were in the past predominantly performed by measuring nutrient concentrations of flooding and draining water over tidal cycles (classic exchange budgets; e.g., Simpson et al. 1983b). These results indicated that most of the nitrogen (N) and phosphorus (P) entering the wetland was transformed in its characteristics with nutrients mostly changed from particulate to dissolved forms. There is apparently only a relatively small net import or export of nutrients during a typical tide cycle (Fig. 6.7). Although these results may well be biased by errors in the hydrologic budget, concentration profiles show that the seepage water quality in creeks at low tide can clearly diverge from the river water quality.

Fig. 6.7 Concentration profiles of nutrients in the main creek of a freshwater marsh and in the adjacent river channel of the Scheldt estuary (Belgium), 29 April 1998. The seepage phase consisted of the outflow of water from the creek when the water level at the creek mouth was <30 cm deep. Time 0 is the moment of high tide in the river
In general, saline wetlands are considered to be carbon and nutrient sinks (e.g., Odum 1988; Mitsch and Gosselink 2000), brackish wetlands are either carbon sinks or sources depending on the flooding regime (e.g., Jordan and Correll 1991); and tidal freshwater wetlands have been shown to be nutrient sinks during the growing season and sources of carbon and nutrients in the non-growing season (Simpson et al. 1983a; Neubauer et al. 2000; Neubauer and Anderson 2003).

Seasonal patterns of nutrient uptake and release also differ among the three types of tidal wetlands, especially between freshwater tidal wetland and brackish and saline wetlands due to the influence of saline conditions in the latter two (Simpson et al. 1983a; Odum et al. 1984; Mitsch and Gosselink 2000). Patterns of nutrient uptake and release are also influenced by differences in patterns of sediment deposition. Brackish tidal wetlands and freshwater tidal wetlands occur in the maximum turbidity zone of tidal rivers where sediment deposition rates are high (Darke and Megonigal 2003). Sediment inputs and consequently the build-up of the height of the wetland surface is typically greater in freshwater tidal wetlands, which are closer than saline wetlands to upland sediment sources and the turbidity maximum zone (Pasternack et al. 2000; Neubauer et al. 2002). Sedimentation rates are, however, highly variable within freshwater tidal wetlands and both vegetation and location of the wetland relative to the turbidity maximum of the river are important factors in determining rates of sediment deposition (Uncles et al. 1998; Pasternack and Brush 2001; Darke and Megonigal 2003).


Patterns of nutrient cycling also differ even though all tidal wetlands are characterized by sediments that are mostly anaerobic. Anaerobic metabolism in tidal freshwater wetlands is dominated by methanogenesis compared to a dominance of sulfate reduction in saline wetlands (Odum 1988). All aspects of the nitrogen cycle (nitrification, denitrification, mineralization, fixation) are important in tidal freshwater wetlands and all components of the system play important roles in controlling the patterns and rates of N cycling (Bowden 1984b; Morris and Bowden 1986). Only the surface sediments are aerobic; and nitrate produced by mineralization is quickly assimilated (Bowden 1984a, 1986). The net transfer of N is to the sediments; and N appears to be used more efficiently than P (Bowden 1984b, 1986).

The bivalent aerobic–anaerobic characteristic of surface sediments in tidal freshwater wetlands triggers questions about which aspect dominates nutrient cycling: the aerobic surface sediments that are flooded with water that is
often oxygen-poor, or the anaerobic subsurface sediments into which and from which nutrient exchange is limited because of the waterlogged nature of the sediments and the presence of dense inorganic particles such as silts and clays. The relatively new technique of in situ stable isotope enrichment allows for the examination of N flow through multiple pools simultaneously while maintaining natural hydrologic and biogeochemical gradients and ecosystem functions. Some whole ecosystem $^{15}$N enrichments have been performed, showing unequivocally that nitrification is one of the most important transformation processes associated with eutrophic tidal freshwater marshes (Gribsholt et al., in preparation). Comparison of ecosystem-scale nitrification with pelagic nitrification demonstrated that the reactive surface area of the wetland is the key site for nitrification. Three key factors may potentially be important determinants of nitrification in wetland ecosystems: nitrifier biomass, oxygen dynamics, and ammonium availability for nitrifiers. The distribution, abundance, and activity of nitrifiers is known to be influenced by their attachment to particles; and the surfaces of the dense vegetation and plant litter in the marsh may provide an excellent substrate for microbial colonization.

Phosphorus cycling is mostly controlled by sediment input, phosphorus generation in anaerobic sediments through release, and interactions with iron. In freshwater tidal wetlands when FeO$_x$ is reduced in the anoxic sediments, the resulting Fe(II) diffuses upward into aerobic layers and is converted back to FeO$_x$ that binds PO$_4^{3-}$ that comes from external (e.g., tidal) or internal (mineralization) sources (Cornwell 1987, Chambers and Odum 1990), resulting in a net retention of phosphorus. In brackish wetlands, the efflux of dissolved PO$_4^{3-}$ from sediments is much faster and FeO$_x$ sequesters much less PO$_4^{3-}$ (Callender 1982, Callender and Hammond 1982, Hopkinson et al. 1999). The distribution of Fe(III) in the sediments of tidal wetland also varies along the salinity gradient, with higher abundance in freshwater sediments than in brackish sediments, and with a stronger tendency to be concentrated near the surface of the freshwater sediment (Phillips and Lovley 1987). Likewise, concentrations of FeO$_x$-bound PO$_4^{3-}$ in sediments decline from the freshwater reaches down the estuary into brackish waters.

Although silica (Si) plays a major role in coastal eutrophication events, the cycling of Si in freshwater tidal marshes has not received much scientific attention. The lithogenic fraction of Si in tidal marsh sediments is considered inert at biological timescales. However, tidal wetlands contain large amounts of biogenic Si (BSi) in vegetation and sediments (Norris and Hackney 1999). Dissolved Si (Dsi) taken up by wetland plants is stored in specific structures of various shapes, the phytoliths. Plant BSi can become available again to the estuarine ecosystem after the plants decay, through phytolith dissolution. However, phytoliths can be highly resistant to decomposition and a large part of plant BSi is buried in the sediments. Together with buried diatom BSi, buried phytoliths comprise the sediment BSi fraction. Due to the high BSi
amounts available for dissolution, DSi concentrations in marsh pore-water can be several times the DSi concentration in the main river channel, providing excellent conditions for benthic diatoms on the wetland surface and providing the energetic base for secondary production (Hackney et al. 2000). Moreover, floodwater containing lower DSi concentrations, compared to pore-water, is enriched with DSi when flowing through the sediments (Fig. 6.7). Thus, large amounts of DSi can be exported from tidal wetland sites to the main river channel between tidal inundations, especially in spring and summer, when DSi in the main river is depleted by diatom communities. Tidal freshwater wetlands could therefore play a major role in estuarine silica cycling, supporting secondary production through DSi recycling.

Heavy metals and trace metals can be retained in significant quantities in freshwater tidal wetlands, especially in areas with high sedimentation rates (e.g., Khan and Brush 1994). Vegetation plays a major role in removing heavy metals from tidal waters during the growing season and the metals are mostly transferred to the substrate for long-term sequestration via litter accumulation (Simpson et al. 1983b; Dubinski et al. 1986).

6.5 Restoration and Future Outlook

We have attempted to demonstrate that tidal freshwater wetlands are widespread and both ecologically and environmentally important, and they are thus worthy of both preservation and restoration. We also hope to convey the message that they are still threatened in many areas because of human intervention. The main problems that need to be considered now and into the future are issues related to water chemistry, the extent of tidal freshwater wetlands, and direct human impacts.

6.5.1 Europe

The pollution of European rivers that include tidal freshwater areas has improved drastically in the past couple of decades. Since the first positive changes in chemistry mentioned by Van Dijk et al. (1994), water quality has continued to improve during the past decade. The concentration in heavy metals and organic micropollutants has declined; but the concentration in nitrogen and the deficit in oxygen remain difficult problems due to diffuse pollution sources. Positive changes have, however, been reported in water quality for some systems (e.g., Gerkens and Thiel 2001; Soetaert et al. in press).

As a consequence of poor water quality, sediment quality in most tidal flats and wetlands has also deteriorated. Elevated concentrations of metals and
hydrocarbons can be found. In the Scheldt estuary, there are no signs that this has a negative impact on the vegetation (Van Regenmortel, personal communication) but spiders show a clear accumulation (Du Laing et al. 2002). Concentrations in the suspended sediments are however decreasing in parallel with the improving water quality, resulting in clear gradients: recent deposits have much lower concentrations than older ones. It remains unclear what the impact of improving oxygen conditions in the estuary will be on the mobilization of these pollutants. Also, polluted sediments can be brought into suspension by erosion.

The second issue that needs to be considered is the fact that many areas that once supported tidal freshwater wetlands have been destroyed or suffer from the absence of tidal influences (De Boois 1982). In many instances, the wetlands were reclaimed for other functions, such as agriculture or housing and industry (Preisinger 1991). The consequence of previous wetland losses is that there is a limited area available in tidal freshwater areas for ecosystem restoration. Restoration is an important element and it needs to be actively considered and pursued. At the same time, the closing of the tidal regions of rivers has caused serious problems in water quality. In the Netherlands, discussions have been held about the re-opening of the sluices of the estuary Haringvliet in order to restore tidal exchange between the former estuary and the sea. Changes in current hydrological management might result in a reduction of the enormous problems in blue-algal growth in some (former saline tidal) areas. This tidal flow can also restore the ecological conditions in the river and especially in the Biesbosch-region, the part of the system that historically had large areas of tidal freshwater wetlands.

At the same time, Europe fights the problem of excessive discharge of river water, heavier and more frequent storms, and a sea level rise which may occur due to climatic changes. Further heightening of dikes is possible but ultimately results in more risks. Indeed the height difference between the water levels during storms in the estuary and the adjacent polder areas becomes larger. In the case of a dike breach, the effects are then of course much more severe. In the Scheldt estuary in Belgium next to reinforcing dikes, controlled inundation areas are built to improve safety against storms. These areas are low-lying polders without human occupation. A high dike is build around the polder, and a lower one between the estuary and the polder. During storms the water overtops the lower dike and the polder is filled with water. Upstream water levels do not increase as most of the water flows into the polder. Through large sluices the polder is emptied during the next low tide and most of the storage capacity is restored before the next high-water event. These sluices can also be used to create a reduced tide in these polders, allowing the development of tidal wetlands, hence combining safety and restoring habitat (Meire et al. 2002; Van den Bergh et al. 2005). These new wetlands can also have a significant effect on the water quality. Modelling exercises show that they can substantially increase the oxygen content in the river and enhance
the primary productivity and nutrient removal. A first experimental site will become functional in 2005 and a larger area of about 300 ha is under construction. Next to combining safety and wetland development in controlled inundation areas, managed realignment by reshaping the river is an important option for restoration.

The third issue that impacts tidal freshwater areas of estuaries is direct human activity, such as modification of rivers for shipping. As the size of ships increases, there is increasing pressure to increase the depth of the shipping channels (Preisinger 1991). Dredging and increasing the depth of rivers increases the tidal range (e.g., up to 6 m in Elbe and Scheldt) and erosion of the shoreline by the stronger currents. This results in very steep gradients from the stream to the higher zones in the freshwater range, with the loss of mud flats and the bordering vegetation due to erosion. The only option is to reduce erosion in a structural way, such as widening of the river through managed realignment. Other activities that use stones or other structural materials to stabilize the eroding wetland edge only reduce the natural dynamics of the wetlands by preventing the development of low marsh or subtidal vegetation and hydrologic exchange between the river and adjacent wetlands.

The preservation of the remaining freshwater tidal areas in Europe might not be the problem, since most extensive areas are preserved as nature areas or reserves, mostly incorporated in the national ecological networks of reserves. For instance, the remaining 1000 ha in Belgium or the 1000 ha in the Netherlands are both protected by national regulations; the same is true for German or UK areas. In addition to national conservation programs, EU legislation known as the Bird and Habitat Directive is valid for many areas, including areas that have tidal freshwater wetlands, such as in the estuaries of the Elbe, Ems, Rhine, and Scheldt. However, only one animal and one plant species of tidal freshwater wetlands have been incorporated into the EU Bird and Habitat Directive. The Twaite shad (Alosa fallax) is restricted to these wetlands and is still seriously endangered, although it is recovering at some locations (Gerkens and Thiel 2001, Maes et al. 1998). Oenanthe conoides is the only endemic plant species in tidal freshwater wetlands that has been incorporated in the Bird and Habitat Directive. This plant is restricted to the Elbe catchments and preservation can only occur following the restoration of habitats in that estuary. More striking is the absence of the freshwater tidal systems as a priority ecosystem in the EU Bird and Habitat Directive, given the fact that these systems provide an important habitat for these two species.

6.5.2 United States

In the United States, federal, state, and local regulations protect coastal wetlands, and the rate of loss of estuarine areas has decreased by 82% between 1986 and 1997 (Dahl 2000) compared to the period from the mid-1970s to the
mid-1980s (Dahl and Johnson 1991). It is not possible, however, to determine the status and trends for tidal freshwater wetlands from the national assessment documents because they are not considered separately in the analysis of either estuarine or freshwater wetlands. In recent years, increased emphasis has been given to the restoration and conservation of tidal freshwater wetlands. Large freshwater tidal wetland restoration projects have been initiated in the Delaware estuary at the Hamilton Marshes (Leck 2003; Fig. 6.5B) and sites near the Philadelphia airport (D. Whigham, personal observation). In the Chesapeake Bay, restoration of tidal freshwater wetlands has been initiated in Washington (D.C.) in the Anacostia river, a tributary of the Potomac River (Baldwin 2004). Also in the Chesapeake Bay, governmental and non-profit conservation organizations have purchased and preserved tidal freshwater wetlands. The Nature Conservancy, for example, has preserved tidal freshwater wetlands on the Choptank and Nanticoke River in Maryland and the National Park Service created the Dyke Marsh Preserve near Washington, D.C. (Johnston 2000).

Several states on the Atlantic coast of North America (Maryland, Delaware, New York, Virginia) have included tidal freshwater systems as components of estuarine reserves that form the National Estuarine Reserve System (NEERS). New York NEERS sites include two tidal freshwater systems (Tivoli Bay, Stockport Flats). Three reserves in the Chesapeake Bay are freshwater tidal systems or include tidal freshwater wetland habitats. In Maryland, Jug Bay and Otter Creek represent two of the largest tidal freshwater wetland reserves in the country. In Virginia, the Virginia Coastal Reserve also includes tidal freshwater wetland habitats. The Delaware NEERS reserve system includes tidal freshwater wetlands at Blackbird Creek.

6.6 Conclusions

Tidal freshwater wetlands occur in the upper part of estuaries in Europe and North America (and likely elsewhere) and experience tides of up to several meters in amplitude twice a day. They occur at the interface between the brackish zone in the estuary and the river; and where brackish and fresh water mix is an area of maximum suspended matter (i.e., the maximum turbidity zone). The tidal freshwater zone within the estuary plays an important role in overall patterns of nutrient cycling for the whole estuary and the pattern appears to differ in the brackish and saline sections. Although tidal freshwater wetlands do not include many endemic or restricted species, they are characterized by high species and habitat diversity. There is distinct zonation in flora and fauna species, responding to the relationship between surface elevation and tidal amplitude. The dominant species are different between Europe and North America, but the structure of the system and the life strat-
egy of the species are fully comparable. The tidal freshwater wetlands in Europe and North America also have a common history of being highly influenced by human activities, resulting in altered hydrology, losses in wetland area, and high levels of sediment and nutrient input on both sides of the Atlantic Ocean. In recent years, restoration and preservation activities have also been initiated on both sides of the Atlantic and there is hope that tidal freshwater wetlands will increasingly become important elements of estuarine systems that provide many free ecological services to man and nature.

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