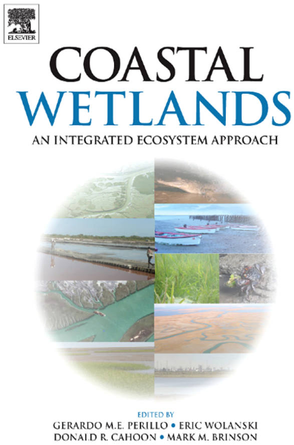

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CHAPTER 18

Tidal Freshwater Wetlands

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Contents

1. Introduction

Tidal freshwater wetlands (hereafter referred to as TFW) are the orphans of coastal wetland ecosystems. In many places, they are not recognized as a distinct type of coastal wetland and in most developed parts of the world they have been historically heavily impacted by human activities, resulting in their destruction or degradation. One consequence of their orphan status is that the literature on the distribution and ecology of TFW is relatively scant compared to the large number of publications on saline and brackish coastal wetlands. There are, however, current efforts to remedy this situation by compiling and summarizing the literature on TFW. First, Barendregt et al. (2006) recently summarized information on TFW in Europe and North America. In North America, many publications appeared in the 1980s, particularly from studies of TFW along the Atlantic coast (e.g., Odum, 1988; Odum et al., 1984 and references in Yozzo and Steineck, 1994). Another synthesis, relying heavily on the material compiled in Odum et al. (1984), for North American TFW appeared in Mitsch and Gosselink (2000). Prior to the Barendregt et al. (2006) summary, only one European review (Meire and Vincx, 1993) was available. The most recent effort to summarize the work on TFW will be an edited volume by Barendregt et al. (2009). The overview that we present in this chapter is based on the earlier reviews cited above, information summarized in Barendregt et al. (2006), and on selected materials from the forthcoming book. A recent book focuses on tidal swamps of the southeastern United States (Conner et al., 2007).

This chapter has five sections. We begin with an overview of the hydrogeomorphic settings in which TFW occur. We describe where TFW are known to occur, with the knowledge that a description of their global distribution is incomplete because a global inventory is lacking. In Section 3 we describe elements of biodiversity. TFW often have high plant species biodiversity and high community diversity, but few species are known to be restricted to TFW. Because of the importance of annual species, vegetation is also very often dynamic and we consider the relationship between the diversity of the seed bank and the diversity of extant vegetation in one well-studied TFW. Compared to plants, fewer studies have focused on animals in TFW. In this review, we focus on fish, birds, and mammals. Ecological processes are the theme of Section 4. Some of the highest levels of net annual primary production in temperate zone wetlands have been measured in TFW, but the level of productivity varies widely depending on geographic location and within-wetland habitat variation. TFW have also been shown to provide important water quality functions. In Section 5 we examine threats to TFW. Given their location near the upper limit of tide estuaries (i.e., also historically often the upper limit of navigation), TFW have been almost completely destroyed in some countries and the remaining areas are now viewed as being important and worthy of intervention to assure their survival or restoration. In other parts of the world, human impacts have been minimal and the major threats to TFW are increasing stresses associated with global environmental changes, such as sea-level rise and intrusion of brackish water into areas that are currently tidal freshwater habitats. In Section 5 we also consider approaches that have been and are being used to conserve and restore TFW, a topic treated in detail in Baldwin et al. (2009). We end with a prospectus.

2. Hydrogeomorphic Setting

TFW are almost always restricted to the upper limit of tide where coastal brackish water meets freshwater flow from nontidal rivers (Figure 1), resulting in a tidal freshwater zone where there is bidirectional flow of freshwater. These conditions primarily exist when there is sufficient freshwater flow from a river, where there is a relatively flat and long gradient from the ocean inland, and where there is a tidal range of 0.5 m or more (Odum et al., 1984; Mitsch and Gosselink, 2000; Barendregt et al., 2006). The tidal freshwater zone probably occurs in most rivers with an appropriate geomorphic setting but the extent of the zone would vary seasonally in response to annual rainfall patterns. For example, the tidal freshwater zone varies seasonally in estuarine systems in arid Mediterranean climates. During dry periods freshwater flows are so low that brackish or saline water extends to the upper limit of tide. In wet periods, freshwater flows are large enough to create a tidal freshwater zone with in the tidal portion of the river.

Patterns of sedimentation within tidal freshwater zones also influence the development and dynamics of TFW (Pasternack, 2009). Pasternack described two

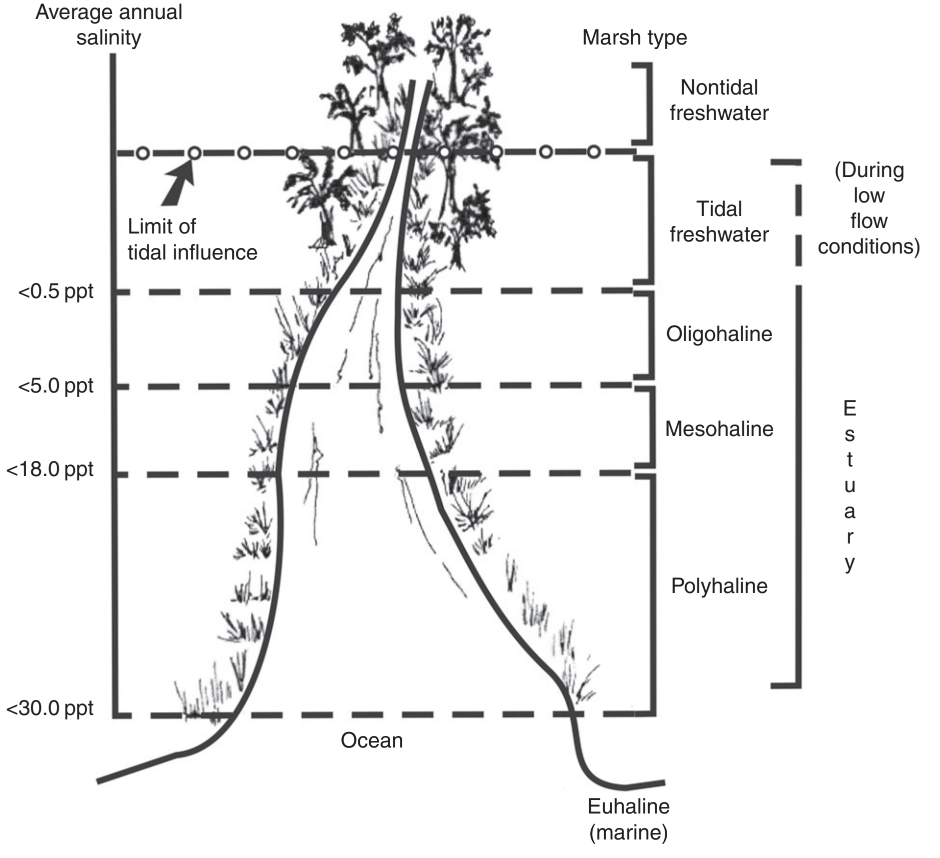

Figure 1 Distribution of wetlands along a salinity gradient from the open ocean to a nontidal river. Tidal freshwater wetlands occur in the tidal freshwater zone.
Source: Odum et al. (1984).

landscape positions in which TFW form, deltaic and fringe. TFW develop on dynamic deltaic deposits that form at the mouth of tidal basins where the sediment carrying capacity of river has been exceeded. Fringing TFW occur at any location in the tidal freshwater zone where the local supply of sediment is greater than the transport capacity of the water. Studies of sediment cores from TFW demonstrate that they are a recent landform, ranging in age from a little more than 100 years to almost 4,000 years (Pasternack, 2009). The influences that humans have had on sediment dynamics in the tidal freshwater zone have been especially important in recent history. Khan and Brush (1994) analyzed sediment cores from a TFW on the Patuxent River (Maryland, USA) and found that sedimentation rates between 630 and 1603 years AD ranged from 0.05 to 0.08 cm/year. Rates of sedimentation increased dramatically after European settlement; which signaled the onset of land clearing. The range of sedimentation rates for periods of time between 1690 and 1990 AD varied from 0.13 cm/year between 1686 and 1694 to a high of 0.77 cm/year in

1972–1973. In only one time period (1924–1927) did Khan and Brush measure sedimentation rates lower than 0.40 cm/year.

There has never been a global inventory of TFW and consequently there are no estimates of their worldwide extent. In North America, TFW are abundant along the mid-Atlantic Coast from southern New England to Florida (Odum et al., 1984). With the exception of the St. Lawrence Estuary (Glooschenko et al., 1993) TFW along the New England coast are fewer and smaller in extent because there are few geomorphic settings that are appropriate for their development (Leck and Crain, 2009). TFW occur along the Gulf Coast of the United States but they are hydrologically and geomorphically distinct from the definition for TFW given earlier. TFW on the Gulf Coast typically having a tidal amplitude that is less than 0.5 m, they occur far inland in areas where there is little slope to the land, and they are not associated with specific river systems (Sasser et al., 2009). Along the west coast of the United States, TFW are not abundant in areas where a Mediterranean climate dominates river hydrology (Leck et al., 2009). In Mediterranean climates, the tidal freshwater zone in rivers can be extensive during the rainy season but it disappears or is very narrow during the dry season. As a result, saline and brackish waters intrude far into river systems during the dry season and the wetlands are typically dominated by species that are associated with brackish tidal wetlands. TFW are more extensive along the larger rivers in the Pacific Northwest (e.g., Columbia) and British Columbia (Fraser), but there have been few detailed studies of TFW in those areas (Leck et al., 2009). The largest extent of tidal freshwater habitat in the United States occurs in Alaska (Hall, 2009) where acreage is probably greater than the estimate for all TFW in the lower 48 states. We assume that extensive TFW also exist in northeastern Russia where the landscape is very similar to Alaska, but we know of no assessment of TFW for Russia or any other part of eastern Asia. One of us (D.F.W.) has seen TFW dominated by herbaceous plant species on Hokkaido Island in northern Japan and forested TFW on Iriomote Island in southern (subtropical) Japan, but we are unaware of any assessments of either their extent or ecology in Japan.

TFW were historically common in northwestern Europe but many have been destroyed during centuries of human activities (Barendregt et al., 2006) and some of the remaining areas continue to be used for cultural activities (Figure 2). In The Netherlands, TFW were diked and drained in ancient times, using some of the first techniques to control water movement (Barendregt et al., 2006). Port development and diking eliminated most of the original TFW habitats in Germany, Belgium, and England. In The Netherlands, the massive Delta project resulted in the elimination or deterioration of most of the remaining TFW and they only remain in Belgium because the Scheldt estuary was not closed as part of the Delta project. Along the river Elbe remnants of many TFW still occur, although they suffer from the deepening of the channel for shipping (Garniel and Mierwald, 1996). The presence and abundance of TFW in other parts of the world are poorly documented. Junk (1983) briefly described the presence of TFW on the Atlantic Coast of South America, but he offered no details on their locations or extent. Characteristics of TFW in the Río de la Plata Estuary in Argentina have been described (Kandus and Malvárez, 2004; Pratolongo et al., 2007).

Figure 2 Tidal freshwater wetland on the Oude Maas (The Netherlands) in winter. On the right side of the tidal stream is a coppiced stand of osier (*Salix*). In historical and modern times, managed osier beds are sources of stems used for a variety of purposes (e.g., basketry, mats used in dike construction and maintenance).
Source: A. Barendregt.

3. Biodiversity

3.1. Plants

Plant diversity was often a topic for study by researchers of TFW on the Atlantic Coast of eastern North America. where factors associated with tides, such as increased soil aeration, combined with lack of salt water stress result in high species diversity and high primary production (the latter discussed in Section 4) (Odum et al., 1995). TFW almost always have a higher diversity of plants than brackish or saline tidal wetlands (Odum et al., 1984). TFW in Europe seem to have lower diversity than their counterparts in North America, most likely due to high rates of sedimentation and the highly eutrophic conditions in most European TFW, a condition that often results in dominance by fewer species (Barendregt et al., 2006).

While overall plant species diversity is high in TFW, diversity varies from one habitat to another and the variation can be explained by differences in the relationship between habitat setting and hydrology. A typical cross section through a TFW in the United States is shown in Figure 3 and similar zonation patterns occur in European TFW (Barendregt, 2005; Barendregt et al., 2006). Vegetation in the open water, low marsh, and high marsh habitats is dominated by herbaceous species with diversity increasing from the open water to high marsh habitats (Simpson et al, 1983a). At the upper extreme of tide, TFW are often dominated by woody species with areas being dominated by shrubs or by trees (Barendregt et al., 2006; Conner et al., 2007; Leck et al., 2009). Extensive lists of species for TFW vegetation can be found in Leck et al. (2009) and Odum et al. (1984). In general, subtidal habitats and low marsh areas that are exposed briefly at low tide (Figure 4) are dominated by species with relatively large leaves that are held above the water (e.g., *Nuphar lutea*

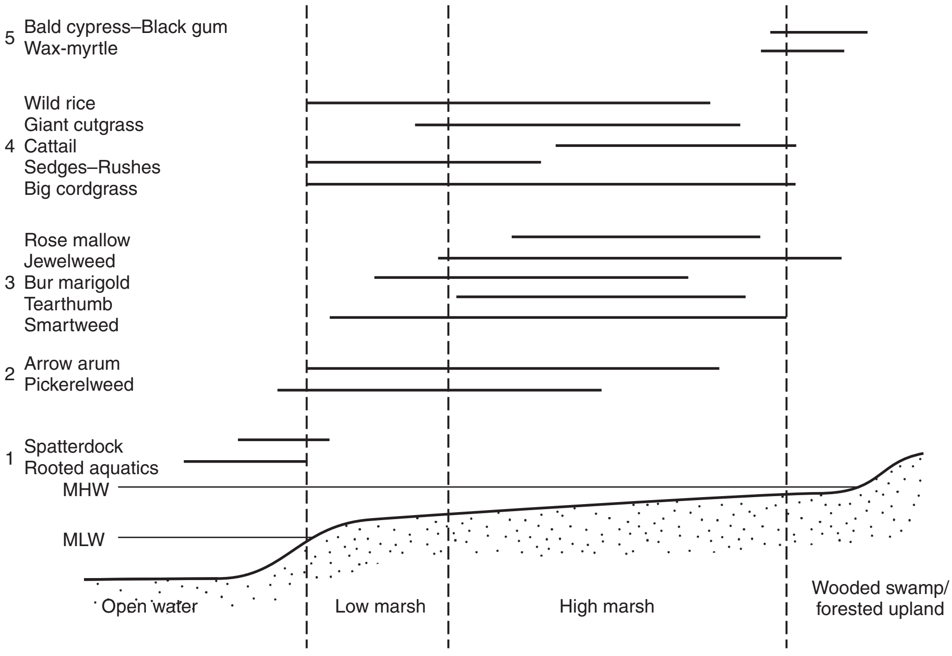

Figure 3 Cross section of a typical tidal freshwater wetland showing major habitats and distributions of species.
Source: Odum et al., (1984). Scientific names are as follows: bald cypress = *Taxodium distichum*, black gum = *Nyssa sylvatica*, wax myrtle = *Morella* (*Myrica*) *cerifera*, wild rice = *Zizania aquatica*, giant cutgrass = *Leersia oryzoides*, cattail = *Typha* spp., sedges−rushes = *Carex* spp. − *Juncus* spp., big cordgrass = *Spartina cynosuroides*, rose mallow = *Hibiscus moscheutos*, jewelweed = *Impatiens capensis*, bur marigold = *Bidens laevis*, tearthumb = *Polygonum arifolium* and *Polygonum sagittatum*, smartweed = *Polygonum punctatum*, arrow arum = *Peltandra virginica*, pickerelweed = *Pontederia cordata*, spatterdock = *Nuphar lutea*, rooted aquatics = for example, *Myriophyllum spicatum*, *Vallisneria americana*, MLW = Mean Low Water and MHW = Mean High Water.

(L.) Sm., *Peltandra virginica* (L.)Schott, and *Pontederia cordata* L. in North America). In northwestern Europe, most open water systems have no aquatic plants due to the high sedimentation rates and eutrophication. Low marshes in northwestern Europe with extensive mudflats that are flooded twice a day are dominated at the upper border by *Schoenoplectus triqueter* (L.), *Schoenoplectus lacustris* (L.) Palla, and *Bolboschoenus maritimus* (L.) Palla. The low marsh in the United States has many of the same species that occur in open water areas but it is also the habitat in which *Zizania aquatica* L. and *Polygonum punctatum* Elliott are often abundant. The creek bank associated with the low marsh commonly has several low-growing species (*Callitriche heterophylla* Pursh, *Gratiola neglecta* Torrey, *Lindernia dubia* (L.)Pennell, *Ludwigia palustris* (L.)Ell.) that form groundcovers. Figure 5 shows the transition zone between a low marsh and a high marsh habitat along the Nanticoke River (Maryland, USA). The high marsh habitat has the highest species diversity in both the United States and Europe. In the United States, high marsh habitats consist of a diversity of annual (e.g., *Ambrosia trifida* L., *Bidens laevis* (L.)BSP, *Impatiens capensis* Meerb., *Pilea pumila*

Figure 4 Mudflat with *Schoenoplectus lacustris* in the Elbe River (Germany).
Source: A. Barendregt.

(L.)A. Gray, *Polygonum arifolium* L., *Polygonum sagittatum* L.) and perennial (*Acorus calamus, Leersia oryzioides* (L), Swartz, *Peltandra virginica, Typha* spp.) species. The lowest diversity on the high marsh occurs when clonal perennials form dense patches in which few other species become established. Examples of patch-forming perennials are species of *Typha* and *Phragmites australis* (Cav.)Trin. ex Steudel. In Europe, perennials (e.g., *Lythrum, Phalaris, Epilobium, Typha, Symphytum, Valeriana, Sparganium*) dominate high marsh habitats (Barendregt et al., 2006).

Figure 5 Low marsh to high marsh transition on the Nanticoke River, Delaware (USA). The dominant species in the low marsh (left side of photograph) is *Nuphar lutea*. The dominant species in the high marsh (right side of photograph) is *Acorus calamus*. In the high marsh annual species become dominant toward the end of the growing season.
Source: A.H. Baldwin.

Figure 6 Forested tidal freshwater wetland on the Nanticoke River, Maryland (USA). Note relatively open forest canopy and diverse assemblage of herbaceous plants in the understory. *Source*: A.H. Baldwin.

TFW habitats dominated by shrubs and trees also can also have high species diversity (Peterson and Baldwin, 2004) because, in addition to trees and shrubs and a few herbs that rarely occur in more open habitats (e.g., *Osmunda regalis* var. *spectabilis* (Willd.) Gray), they contain many of the herbaceous species that occur on the high marsh. Examples of shrub and tree species (e.g., *Acer rubrum* L., *Viburnum dentatum* L., *Fraxinus pennsylvanica* Marsh) in the United States (Figure 6) and Europe can be found in Barendregt et al. (2006), Odum et al. (1984), Rheinhardt (1992), and Barendregt (2005). Living and fallen trees and shrubs are often the focal points for the development of mounds or hummocks that are the preferred habitat for a variety of herbs that are less tolerant of flooding, including species of *Carex*, grasses (*Cinna arundinacea* L.), ferns (*Osmunda cinnamomea* L., *O. regalis, Thelypteris palustris* Schott), and *Viola cucullata* Aiton (Rheinhardt, 1992; Leck et al., 2009).

Almost all plant species in TFW also occur in non-TFW. In the United States only one TFW plant species (*Aeschynomene virginica* (L.) BSP) has been listed as endangered (Griffith and Forseth, 2003). In Europe, almost all TFW plant species also occur in other types of freshwater wetlands and there are few species that have been identified as threatened or endangered. In TFW of the Elbe estuary close to Hamburg there are two endemic species, *Oenanthe conioides* Lange and *Deschampsia wibeliana* (Sond.) Parl (Burkart, 2001). Both species are listed in Germany and incorporated into the EU Habitats Directive to preserve the species. In TFW in The Netherlands and Belgium, a variety of *Caltha palustris* L. (var. *araneosa*), occurs that produces roots on the nodes below the flower that after the breaking of the stem can be transported by the tides permitting dispersal to almost all TFW in the region (van Steenis, 1971). An endangered European species that occurs in low marsh habitats that experience some erosion is *Schoenoplectus triqueter* (Deegan and Harrington, 2004). This species is distributed from the Elbe in Germany to the Gironde in the south of France.

There have been few studies of rarity in TFW. However, long-term studies in New Jersey (USA), based on monitoring of seed bank and vegetation in a created TFW in the Delaware River that is adjacent to a natural TFW, provide insights into the dynamics of TFW vegetation including rare species (Leck et al.,1988; Leck and Leck, 2005 and references cited therein). In 1988, 426 species were reported in the study area (Leck et al., 1988); by 2005 the number had increased to 875 with a number of rare (29) and endangered (8) species mostly from the created wetland (Leck and Leck, 2005). The increased number of taxa was the result of continued exploration of the study area, disturbances of the natural wetlands due to road construction, and inclusion of vegetation in upland habitats within the marsh complex. From a wetland perspective, one of the most interesting results was the number of rare species that appeared in the constructed wetlands attributed to the availability of new substrates for colonization. Over a 5-year period, 177 species emerged from soil seed bank samples from the constructed wetland, compared to 96 species from soils in the natural wetland over more than 15 years. Eighty-three of these species only occurred in soils in the constructed wetland, an indication of the potential for dispersion of rare species within the tidal freshwater zone of the river. In both the constructed and natural wetlands, the number of established plant species was much lower than the number of species that emerged as seedlings from the soil samples. Leck and Leck (2005) suggested that the differences were due, in part, to the absence of suitable field germination sites in both types of wetlands. The presence of a relatively high number of rare and endangered species at the constructed wetland, which was only one small portion of a larger tidal freshwater zone in the Delaware River, suggests the importance of maintaining a diversity of TFW habitats to assure the persistence of a diverse flora, especially species requiring open habitats with limited competition.

3.2. Animals

Animals associated with TFW have received less attention than flowering plants, as have other groups of plants (e.g., algae, bryophytes, ferns) as well as fungi and microorganisms. Much of the information on animals is adapted from Barendregt et al. (2006), Odum et al. (1984), Mitsch and Gosselink (2000), and Swarth and Kiviat (2009) and we focus on three groups of animals, fish, mammals, and birds. In general, benthic invertebrates may be less diverse in TFW compared to brackish and saline tidal wetlands, but the diversity of terrestrial invertebrates is higher (Barbour and Kiviat, 1986; Ysebaert et al., 1998, 2003; Barendregt et al., 2006).

Similar to plants, few animals are restricted to TFW, but beyond species identification, few animal groups have been examined in detail. Many animals that occur in TFW are wide ranging and also are common in brackish and saline wetlands or in non-TFW (Odum et al., 1984; Mitsch and Gosselink, 2000). Examples of wide-ranging fish, mammals, and birds in TFW in the United States are the yellow perch (*Perca flavescens* Mitchill), the predaceous river otter (*Lutra canadensis* Schreber), and herbivorous mammals such as the common muskrat (*Ondatra zibethicus* L.) and beaver (*Castor canadensis* Kuhl). Examples of widespread bird species are the great blue heron (*Ardea herodias* L.) and osprey (*Pandion haliaetus* L.).

Odum et al. (1984) listed 125 fish species for TFW, but only 59 were regular components of the fish community. The families with the greatest number of species were the Cyprinidae, Centrarchidae, and Ictaluridae. The fish fauna of TFW includes nonnative species such as the common carp (*Cyprinus carpio* L.). Cyprinid species of killifish (e.g., *Fundulus heteroclitus* L., *F. diaphanous* Lesueur) are examples of abundant forage fish (Lippson and Lippson, 1997).

Several fish species that are commercially important spawn in the tidal freshwater zone or as juveniles forage in that zone. Striped bass (*Morone saxitalis* Walbaum), yellow perch (*Perca flavescens* Mitchill), and American shad (*Alosa sapidissima* Wilson) are all abundant at one or more life history stages. Striped bass and American shad spawn in tidal freshwater zone. Yellow perch are potanadromous, migrating only within coastal rivers. They spawn in nontidal freshwater portions of rivers but larvae, juveniles, and adults forage in the tidal freshwater zone (Piavis, 1991).

The fish community has been described for many estuaries in Europe (Elliot and Dewailly, 1995), including the Minho, Lima, and Gironde (Lobry et al., 2003), Loire, Scheldt (Maes et al., 1998), Rhine, Meuse, and Elbe (Thiel and Potter, 2001), and Forth and Tyne (Pomfret et al., 1991). Similar to North America, some marine species that enter the estuary migrate through the tidal freshwater zone on a seasonal basis, either as adults or juveniles. Freshwater fish that occur in European TFW habitats also occur in nontidal freshwater habitats. Diadromous fish (anadromous and catadromous) that spend part of their life cycle at sea and part in nontidal portions of rivers use TFW habitats during migrations, and a few species, for example Allis shad (*Alosa alosa* L.) and Twait shad (*Alosa fallax* Lacépède), are protected at a European level, since they are listed in the EU Habitats Directive.

Odum et al. (1984) listed 10 mammals that are common in TFW. The most obvious mammals are the species that have visual impacts on the vegetation. The common muskrat builds lodges (up to 2 m high and 1–3 m wide) that are composed mostly of mounds of vegetation (Figure 7). They also construct feeding stations (Figure 7) that are not as large as lodges but are also distinct features within the vegetation mosaic. One consequence of lodge and feeding station construction is that muskrats apparently harvest more aboveground biomass than belowground biomass even though rhizomes of several species are preferred food (Lynch et al., 1947). Muskrats, however, appear to have little impact on plant diversity, but feeding activities alter soil nitrogen dynamics (Connors et al., 1999).

Beavers, eradicated throughout much of the Atlantic coast of the United States, have made a remarkable recovery in recent decades and are now common in TFW where they build lodges and consume large amounts of woody biomass. In some situations, beaver lodges occur on the high marsh, but they are most often found in areas where dams have been placed across shallow tidal areas, often located near food sources (Figure 8). In addition to the larger mammals, some smaller species (e.g., marsh rice rat (*Oryzomys palustris* Harlan)) can impact vegetation through their feeding activities. One of the authors (D.F.W.) has observed marsh rice rats consuming seedlings and juveniles of wild rice on numerous occasions, to the point where population size was reduced on a small scale.

Birds are also conspicuous components of TFW. Species may nest in TFW vegetation, forage on vegetation, or hunt animal prey. The most common birds that

Figure 7 Muskrat lodges at the Jug Bay National Estuarine Reserve on the Patuxent River, Maryland (USA). Several lodges can be seen in the photograph (dark mounds), as well as a lower feeding station to the left of the lodge in the foreground. Two people standing in the marsh provide scale.
Source: A.H. Baldwin.

Figure 8 Beaver dam across a tidal freshwater creek at the Jug Bay Wetlands Sanctuary on the Patuxent River in Maryland (USA). The dam can be seen running diagonally across the photograph from right to left in the foreground; the low marsh plant *Nuphar lutea* is visible in the background on the far side of the small pond created by the dam. In the foreground, to the right of the dam is a tidal creek and associated tidal freshwater wetland. To the left of the dam, the wetlands no longer experience any significant tidal influence.
Source: A.H. Baldwin.

nest in TFW vegetation on the Atlantic Coast are the least bittern (*Ixobrychus exilis* Gmelin), Canada goose (*Branta canadensis* L.), Virginia rail (*Rallus limicola* Vieillot), king rail (*Rallus elegans* Audubon), marsh wren (*Cistothorus palustris* Wilson), common yellowthroat (*Geothlypis trichas* L.), and red-winged blackbird (*Agelaius phoeniceus* L.).

In North America, the American black duck (*Anas rubripes* Brewster) is the most abundant waterfowl species, especially in the winter (Swarth and Burke, 2000) but many other species of waterfowl use TFW for resting and feeding during migration. Gulls are often abundant throughout the year. Large numbers of gulls. *Larus argentatus* (Pontoppidan, 1763, Denmark), *L. atricilla* (Linnaeus, 1758, Bahamas), *L. delawarensis* (Ord, 1815, Philadelphia) congregate in TFW at low tide (Wondolowski, 2001) and Chris Swarth (personal communication) has observed up to 12,000 *L. atricilla* resting in Maryland (USA) TFW prior to continuing on to summer breeding grounds.

TFW are used by a large number of wintering songbirds that roost individually or in small-to-large flocks and forage activity in all types of habitats. Red-winged blackbirds and common grackles (*Quiscalus quiscula* L.) are two species that congregate in enormous flocks, often roosting in tall emergent vegetation (Meanley, 1965). Red-winged blackbirds and bobolink (*Dolichonyx oryzivorus* L.) specialize on wild rice seeds (Figure 9) in the late summer (Meanley, 1993 as cited in Swarth and Kiviat, 2009).

Figure 9 The annual grass wild rice, *Zizania aquatica*, with inflorescences.
Source: A.H. Baldwin (shown in the picture).

The European TFW are rich in bird species, with nesting birds in the reedbeds, marshlands, and tidal forests during summer and additional migrating birds in the winter season (Ysebaert et al., 2000; Barendregt et al., 2006). Ducks and waders especially in the winter period are important. In some locations, their numbers are so great that TFW are of extreme conservation value, supporting 1% of the world population for many species.

4. Primary Production and Nutrient Cycling

TFW are one of the most productive types of wetlands in the temperate zone, but the level of biomass production varies among species and habitats, with a range of approximately 400–2500 g/m^2 for aboveground biomass (Whigham et al., 1978; Odum et al., 1984; Mitsch and Gosselink, 2000; Barendregt et al., 2006). Open water and low marsh habitats are also less productive because those sites are inundated for longer periods compared to high marsh and shrub- and tree-dominated habitats. The most productive habitat appears to be the high marsh (Neubauer et al., 2000) where annual net biomass production of more than 3,000 g/m^2 has been measured for individual species (e.g., Sickels and Simpson, 1985).

An interesting feature of many high marsh habitats is that there is less annual variation in aboveground production compared to brackish and saline tidal wetlands. Whigham and Simpson (1992) reported results from an 11-year study of a TFW in the Delaware River estuary. TFW had a lower coefficient of variation in annual production compared to brackish and saline tidal wetlands. They suggested that the low annual variation was due to the three factors. Plants in TFW are not stressed by salinity, nutrients levels are high in TFW because most of them are located near urban and suburban areas with high nutrient loading rates, and they have a high diversity of annual species. The high diversity of annual species allows for compensation among species resulting fairly constant levels of biomass production even though the abundance and growth of one or more species may vary considerably from year to year. This feature of TFW appears to be unique among tidal wetland ecosystems.

Most of the in situ organic matter produced by plants in TFW flows through the detritus food chain and leaves of most species have high decomposition rates (Odum and Heywood, 1978; Findlay et al., 1990). Internal cycling of nutrients seems to be sufficient to support the high rates of primary production (Morris and Lajtha, 1986; Bowden et al., 1991) and an experiment to test the hypothesis that production is nitrogen limited did not result in an increase in above ground biomass, an indication of the relatively high N status of many TFW (Chambers and Fourqurean, 1990; Bowden et al., 1991; Morse et al., 2004). Sediment deposition is also an important source of nutrients in TFW (Orson et al., 1990; Darke and Megonigal, 2003; Morse et al., 2004; Pasternack, 2009) and sediment inputs may enable surface elevations in TFW to keep pace with an accelerated rate of sea-level rise. Because they are accreting environments, TFW substrates also accumulate heavy metals (Khan and Brush, 1994), resulting in elevated concentrations in plant tissues (Simpson et al., 1983b).

High rates of primary production in many habitats and high rates of sedimentation both indicate that TFW would be net sinks for nutrients. The few nutrient-budget studies that have been conducted on TFW, suggest that there is a net accumulation of nutrients during the growing season and a net release of nutrients during the fall and winter months (Simpson et al., 1978, 1983b). Their primary contribution to coastal estuarine systems seems to be as sites for nutrient transformation, with particulate forms of nutrients dominating flood tides and dissolved nutrients dominating ebb tides (Odum et al., 1984; Bowden et al., 1991). Bowden et al. (1991) concluded that the nitrogen budget of a TFW in Massachusetts (USA) was "largely independent of the nitrogen budget of the river". In Europe, the TFW appeared to be the essential link between the rivers and the estuaries, where nutrients and suspended matter are transformed to detritus. The silica cycle appeared to be especially important in TFW (Barendregt et al., 2006).

5. Threats and Future Prospectus

Barendregt et al. (2006) described the fate of many TFW in northwest Europe and the Atlantic coast of the United States. The location of TFW near the upper limit of tide in major river systems resulted in their destruction, especially in European estuaries, as cities and associated port facilities developed. A small-scale example of the long-term effects of human activities in the United States can be observed in the Anacostia River, a tributary of the Potomac River within the city of Washington, DC. Most of the original 1,000 ha of TFW have been destroyed by dredging and filling and the sites that were not destroyed are now highly degraded (Baldwin, 2004). Ongoing efforts are currently directed toward protection and restoration of TFW on the Anacostia (Baldwin, 2004). An important component of the restoration activity is a watershed-level effort to improve water quality. The responses of existing TFW to improvements in water quality will be interesting to document because in recent history, TFW typically occur in areas that are rich in nutrients and sediments. Improvement in water quality will result in a decrease in nutrients and a reduction in sediment inputs. These changes are likely to result in shifts in species abundances within TFW habitats. Restoration of TFW is showing promise as a tool in reducing losses of TFW and restoring habitat and species diversity (see Baldwin et al., 2009).

In other parts of the United States, different activities were responsible for the historical losses of TFW. In New England, the placement of dams near the upper limit of tide was responsible for the losses of TFW (Leck and Crain, 2009). In South Carolina, large areas of TFW were diked and converted into rice fields and only recently have there been efforts to restore them to their original condition (Whigham et al., 2009). Diking and filling were also responsible for losses in the

Sacramento–San Joaquin river Delta (California, USA) and restoration efforts are underway to restore the important ecological functions associated with the TFWs (Jassby and Cloern, 2000; Hammersmark et al., 2005); however, loss of organic matter due to aeration has lowered substrate levels exacerbating flooding and negatively affecting restoration efforts.

In the United States, national and state regulations have resulted in the protection of most coastal wetlands and wetland losses in the costal zone have been reduced dramatically (Dahl, 2006), but degradation continues. Restoration of TFW in The Netherlands and Belgium, where there had been significant historical losses is currently under consideration (Barendregt et al., 2006). Technical procedures for restoration of TFW in Europe are well established and the ecosystems become well established within a few years when the conditions are optimal (e.g., Zonneveld, 1999). A range of restoration projects are planned or even in the implementation phase (Storm et al., 2005; Van den Bergh et al., 2005). However, in North America a suite of restoration techniques have been attempted, with varying degrees of success in establishing ecosystem structure and function comparable to undisturbed TFW (Baldwin et al., 2009).

On a global scale, as indicated in Section 2, there are undoubtedly large TFW areas that have not been heavily impacted by human activities. The extensive TFW that exist in Alaska, for example, do not face any immediate threat. Similar conditions probably prevail in other northern areas (e.g., Siberia) where human impacts have been minimal. In those areas the greatest threats are undoubtedly associated with the consequences of global climate change. In Alaska, increasing temperatures are causing glaciers to melt at a faster rate, resulting in increased sediment input to coastal estuaries. The long-term impacts of increased sediment loading are unknown and the consequences can be either positive or negative. Increased sediment input will enable TFW to increase their relative surface elevation and thus keep pace with rising sea levels. Too much sediment, however, can result in negative impacts of vegetation. In the Kenilworth Marsh in Washington, DC, for example, sediment was placed at a higher elevation in one of the cells that was constructed for restoration purposes. The cell became dominated by invasive species as a result of the higher surface elevation in the cell. Threats associated with global climate change may impact TFW in other ways (Neubauer and Craft, 2009). Increasing rates of sea-level rise may result in the intrusion of brackish water into tidal freshwater portions of rivers, resulting in the replacement of TFW by brackish wetlands. In situations where it is not possible for TFW to migrate upstream (e.g., near the upper end of tide in most rivers on the Atlantic coast of the United States, due to placement of dams, fault lines, and development), they will eventually be eliminated or their area will decrease significantly.

Ongoing efforts to protect and restore TFW present a paradox against the backdrop of the potential effects associated with global climate change. We strongly recommend that these efforts around the world be undertaken in the context of the dynamic location of TFW within the coastal zone. Effective conservation, restoration, and management will require vigilance and commitment by governmental and nongovernmental organizations.

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