BASIC CONCEPTS OF ESTUARINE ECOLOGY

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1 ESTUARINE SYSTEMS: THE LAND-OCEAN LINK

Estuaries are highly dynamic environments with their physical, chemical and biological structure characterized by high spatial and temporal variability. The temporal fluctuations and spatial gradients in these systems induce large variability in chemical and biological properties of the water and sediment. Estuaries are subject to continuous variations in wind, irradiance, rainfall, water level and freshwater runoff. Moreover, estuaries are very often heavily utilised and impacted by mankind, being used as (natural) harbours, for fish farming, recreation, as waste water recipient, etc. There are many ways to define what an estuary is. Probably the simplest definition is that an estuary is a partially enclosed coastal embayment where fresh water and sea water meet and mix. The estuary can have the simple morphology of a river entering the sea or a complex and lengthy one, like in fjords. Estuaries are among the most productive environments on earth and they are important ecotones, i.e., transition zones between different ecosystems. Ecotones are boundaries between resource patches in the landscape, regulating energy, nutrient and mineral sediment flow between adjacent patches (Naiman et al. 1995, Schiemer et al. 1995). Estuaries and their frequently associated fringes of tidal flats, salt marshes and mangrove forests are the transition zones between one environment and another - tidal flats, salt marshes and mangrove forests are the transition between land and sea, and estuaries the transition between fresh and sea water. Being the transitions between very different environments, all estuaries share significant physical, chemical and biological features. Thus, we can state that an estuary is a transition system governed by complex interacting elements which vary in space and time.

Usually, estuaries have more similarities with the marine than with the freshwater environment, but in all aquatic systems the throphodynamic structure and functions are very similar, with the exception of gelatinous plankton, which does not occur in freshwater systems. Nevertheless, in each and every aquatic system, the local mix of interactions between the abiotic and biotic environment results in different system behaviour and a different response to anthropogenic pressures, making it impossible to use simple rules of thumb to predict ecosystem responses to such pressures.

2 PHYSICAL AND CHEMICAL CHARACTERISTICS OF ESTUARIES

Estuaries and the adjacent coastal areas have a specific size, shape and bathymetry, a specific tidal influence, fresh water inflow, turbidity and residence times, sediment properties, carbon-to-nutrients ratios, water-column turbidity, etc. Together, all these characteristics, together with human-influenced environment make each estuary unique. Estuaries possess a unique combination of characteristics, frequently expressed in steep physical, chemical and biological gradients. Because it is where fresh and salt water meets, estuaries are influenced by processes affecting both these types of water, such as tides, coastal hydrodynamics, variations in the river, etc. These factors not only govern much of the physical and chemical characteristics of the estuaries but also its ecological dynamics. Extreme salinity and temperature fluctuations, muddy substrates, and other physical factors like light availability and residence time help make estuaries challenging ecosystems for aquatic organisms.

The shape of the estuary and its sediment, the wind, evaporation of water from the surface and river flow influences temperature and salinity in estuaries. The water temperature in estuaries varies markedly because of their shallow water and large surface area. Fjords are the exception because of their greater water depth. Water temperature affects the dynamics of a system because it regulates all biological rates. Therefore, a clear seasonality in biological activity is seen in estuaries at mid- to high latitudes. Generally, salinity decreases moving upstream but it fluctuates dramatically both from place to place and time to time. Salinity may also vary with depth in the estuary, as well as across the estuary due to the Coriolis effect.

2.1 Water circulation and stratification

Water circulation inside an estuary can change the conditions of the ecosystem over a much smaller temporal scale, when compared with neritic or oceanic areas. The hydrodynamics inside an estuary are driven by a complex interplay of mechanisms, all with a strong influence on biological processes. Water circulation is conditioned by tidal currents, river discharges, wind and local topography. The resulting circulation patterns may have a large effect on the abundance and production of the microbial community by controlling the supply of allochthonous organic matter, concentrating and retaining locally produced organic matter inside the system. They also produce conditions for long-term coupling of bacterial production and autochthons sources of organic matter. Because an estuary is not a closed system, tidal currents act as an oscillating conveyor belt with the coastal zone, moving plankton, organic and inorganic materials, and sediments back and forth, creating complex distribution patterns.

Estuaries can be classified according to their mean tidal range as microtidal (mean tidal range < 2m), mesotidal (mean tidal range between 2 and 4 m), macrotidal (mean tidal range between 4 and 6 m), and hypertidal (mean tidal range > 6m) (Dyer 1997). The difference in the tidal range confers distinct characteristics to the estuarine dynamics. As an example, macrotidal estuaries, which are characterized by high tidal energy, generally exhibit lower levels of chlorophyll a (Chla) than systems with lower tidal energy. They also exhibit a tolerance to high nutrient loadings from freshwater outflows (Monbet 1992). Estuaries are usually divided in two classes defined by their vertical density profile. When the currents of riverine fresh water inflow and tide are similar, turbulence is the major mixing agent. This process is induced by the periodicity of tidal action. In this case the vertical salinity profile is less variable because most of the energy dissipates in the vertical mixing, producing a rather complex set of layers and water masses. Under these conditions, estuaries are considered partially mixed or moderately stratified. In completely mixed and vertically homogeneous estuaries, however, the tidal action is strongly dominant and the water column is well mixed. Together with the shallowness in this type of estuaries, the balance between fresh and sea water, controlled daily by strong tidal currents and modulated seasonally by the river flow, contributes to the absence of a vertical stratification. Major salinity and temperature changes are more frequently observed horizontally rather than vertically and this spatial heterogeneity is thought to affect nearly every aspect of population dynamics, species interactions, and community structure.

2.2 Residence time

With the influence of tidal currents and river flow, the entire estuary experiences fluxes that interfere with the transport and expression of biological activities and with the distribution of biomass in the water column. The residence (or flushing) time of water depends strongly on tides, freshwater runoff and morphological size, especially length. Other processes can modify the residence time in an individual estuary, such as currents driven by a difference in density between fresh and salt water - this is particularly important in deep fjords, bays and semi-enclosed seas where the bottom waters can be nearly stagnant and where water quality can be degraded severely. Another key process is water storage and buffering by intertidal wetlands, mainly salt marsh or mangrove vegetation that flank the main estuary and results in drag to the flow and temporary storage of waters. The residence time reflects the rate at which dissolved and planktonic components in the water are flushed out to the sea. As such, it controls many of the elements that provide information on the health of the estuary. As such, the residence time of an estuary is an important parameter because it expresses its robustness and ability to cope with human-induced stress; Well-flushed estuaries are intrinsically more robust than poorly flushed systems. Environmental degradation is usually intensified during periods of reduced freshwater inflows, for example, during drought or when human activities in the catchment cause significant reductions in dissolved oxygen, for example through eutrophication. The residence time is usually more critical in areas where contaminant accumulation and increased turbidity from human influences are most likely to occur. This is usually the case in the upper reaches of the estuary and in confined areas in estuaries with intricate morphologies.

2.3 Nutrient availability

Nutrients can be present in two major forms: inorganic (or mineral) and organic (both living and detrital). Nitrogen and phosphorus are the most significant nutrients, and their main species include dissolved (nitrate, nitrite, ammonium, organic N, phosphate, organic P) and particulate (organic N, organic P) components. Particulate species tend to be dominant in the river loads reaching the estuaries, but nitrate and phosphate become more important in populous regions. The dynamics of nutrients depend on a number of physical, biological and chemical processes and their fate after entering the estuary varies as a function of turbidity, water flow and biota. Physical processes include mixing, flushing and sedimentation. Chemical processes include absorption and desorption. Biological processes include fixation of dissolved and particulate nutrients, primarily by bacteria and phytoplankton, and release of inorganic nutrients through mineralization, mostly by bacterioplankton (decomposers). Biological and chemical transformation processes increase in importance with increasing residence time because, when the residence time is large, there is more time for these processes to occur.

Systems with very long residence times can export much less of these nutrients to the coastal zone than systems with very short residence times. When the residence time is high the nutrients can end up being consumed while still in the estuary or lost by chemical processes like denitrification (i.e., loss of nitrogen to the atmosphere). There are no general rules to predict what nutrients limit estuarine primary producers, and when. Instead, the norm is that estuarine seasonal cycles depend on the temporal occurrence of deliveries of nutrients, the relative magnitudes of the sources of nutrients, and the biological demands. Each estuary may have its own combination of these three types of conditions, resulting in a seasonal cycle with reasonably well-understood control mechanisms (Valiela 1995). In some estuaries tidal mixing may be the major mechanism providing nutrients. In fjords for example, nutrients are regenerated by the benthos and the advection induced by tidal movements, together with turbulence, supplies phytoplankton with nutrients. River and estuarine waters are often enriched with phosphate from urban and industrial wastewater and from land runoff and they receive silicate from tributary river inflows via rock weathering and soil leaching. In pristine environments, the transport of nutrients from the drainage basin to its watercourses is dependent on the chemical and mechanical weathering of soil minerals, whereas in cultivated environments agriculture is considered to be the largest contributor to river nutrient loads (Tappin 2002).

2.4 Oxygen concentrations

In estuaries, salt marshes and mangrove forests, oxygen concentration is highly variable and often reaches extreme levels. Dissolved oxygen is an important chemical variable because of the metabolic requirement of aerobic organisms. Decomposition of the large quantities of organic matter produced in these environments or introduced as sewage or waste inputs may deplete dissolved oxygen to hypoxic and anoxic levels. Nitrogenous compounds may create a significant extra oxygen demand in estuaries through microbially mediated nitrogen transformations. Ammonia utilizes dissolved oxygen during nitrification to produce nitrate, via nitrite. Ammonia is usually a by-product of most biological processes and additional ammonia is input to estuaries via tributary rivers and wastewater discharges.

At the same time, high rates of photosynthesis may increase dissolved oxygen concentration to super-saturated levels. High nutrient inputs to estuaries and the associated eutrophication can lead to algal blooms and this, in turn, can result in the consumption of dissolved oxygen by decaying algae once the nutrients become depleted. Dead phytoplankton is further decomposed by bacteria, thus enhancing the oxygen demand. The residence time plays a major role in this process because it determines whether excessive nutrient inputs are likely to lead to algal blooms and oxygen sags. Low dissolved oxygen levels in estuarine waters are generally attributed to direct effluent discharges, sewage treatment plants and industrial pollution.

However, high oxygen demand and anoxia can also be associated with natural processes, especially with the increase of organic material in the estuary turbidity maximum. Considering the influence of varying residence times and other environmental factors, such as water temperature and wind intensity, there is usually no simple relationship between the oxygen demand of waste effluents and reductions in oxygen concentrations. The oxygen deficit depends on water flow, turbidity, and oxygen supply and demand, and this varies among and within estuaries (Owens et al. 1997).

2.5 Underwater light climate

Many estuaries are relatively shallow and one would expect an optimum underwater light climate for primary production, both in the water column and on the sediment. However, high concentrations of suspended sediment are common, which greatly reduces water clarity. This permits very little light to penetrate through the water column. The resuspension of fine sediments induced by tidal currents determines the underwater light climate. Tidally driven resuspension, and riverine sources of sediments influence suspended matter concentration, determining the photic depth in the water column. Mean annual chlorophyll a levels are significantly lower in strongly tidal than in weakly tidal estuaries with similar nutrient levels (Monbet 1992). Larger and more energetic tides ensure that accumulated sediment is systematically suspended, leading to high turbidity and low light levels with less potential for bloom conditions, regardless of nutrient levels. The result is that in many estuarine systems, light is a key limiting factor for pelagic primary production (Cloern 1999, 2001). Estuaries with marked tides generally exhibit a tolerance to eutrophication, being insensitive to some degree to the nutrient loading in their inflowing rivers.

3 TYPES OF ESTUARINE COMMUNITIES

Estuarine ecosystems include several distinct communities, each with their own characteristic assemblage of plants and animals. Some of these communities are permanent parts of the system, while others like plankton and nekton come in and leave with the tide. To better understand the role of the different estuarine communities, it is important to have a closer look at the main compartments of these systems.

3.1 Water column or pelagic communities

Typical features of oceanic pelagic systems are the dominance of locally-produced (autochthonous) organic material and the oligotrophic conditions with characteristically small phytoplankton cells. A rather different situation is found in estuarine ecosystems, where a high content of allochthonous material is present, as well as high levels of nutrients (indicating mesotrophic, eutrophic and even hypertrophic conditions), larger phytoplankton cells like centric diatoms, and intense bacterial activity. The type and density of plankton inhabiting estuaries varies immensely with the currents, salinity, and temperature. Most of the phytoplankton and zooplankton in small estuaries are marine species flushed in and out by the tides, while larger estuaries with longer residence times may also have their own, strictly estuarine species. The major distinction between estuaries and lakes, apart from salinity, is the tidal energy in estuaries, which ranges from small (the Baltic) to enormous (Bay of Fundy, Nova Scotia) in direct proportion to the local tidal range. The tide generates tidal currents, which in turn generate turbulent mixing, which leads to resuspension of sediments and hence to turbid water where the sunlight cannot penetrate very deeply, which reduces the thickness of the euphotic zone, strongly reducing the growth potential for phytoplankton. In a more general way the controlling mechanisms on the production of estuarine and coastal systems are usually summarized in five major conditions: ambient light, nutrient availability, temperature, grazing, and transport.

River inflow, reflecting climate variability, affects biomass through fluctuations in flushing, but also induces changes in the growth rates through fluctuations in total suspended solids. In well mixed estuaries, phytoplankton populations may have to adapt to continuously changing irradiance conditions ranging from complete darkness to saturating light. The result is that there may be several regulatory mechanisms acting at the same time or with particular spatial/temporal relevance. The specific mechanisms and timing by which light, nutrients, grazing and predation interact may differ, but the major variables are near-universal. Although estuaries may appear very distinctive environments at first sight, the seasonal cycle is determined by the same limiting factors that are prominent elsewhere in the sea, but modified to an extent by the seasonal input of fresh water (Valiela 1995).

The formation of blooms in the estuary is controlled by local conditions and transport-related mechanisms that govern biomass distributions (Lucas et al. 1999a, Lucas et al. 1999b). Local phytoplankton population growth rates may vary significantly in the horizontal due to variations in water column height, as well as differences in turbidity, nutrient availability, grazing pressure, and time scales for vertical transport through the water column. Biomass abundance at any particular place and time is a function of: (1) spatial variability of population dynamics, and (2) spatially variable transport of water. Several processes will determine if local high phytoplankton growth rates are the same as the bloom formation areas (biomass accumulation). The first control can be defined by the local combinations of both biotic and abiotic parameters responsible for the balance between production and loss (turbidity, nutrients, grazing pressure, etc.). Therefore, local conditions control net population growth at a particular location. The second major control - transport - determines biomass concentration and distribution, thus controlling if and where a bloom actually occurs (favorable conditions for patchiness vs. dispersion of mass through the domain, etc.). The transport inside the estuary determines the residence time of the water in different parts of the system, determining whether phytoplankton remain for the time necessary to generate a bloom, but also conditioning the exchanges between sediment and water column. Also with respect to bloom development, well-mixed shallow subtidal areas are much more dynamic environments than deep channel regions, exhibiting a broader range of effective growth rates over tidal time scales and potentially acting as a significant source and sink for phytoplankton biomass (Lucas et al. 1999a).

The relation between freshwater flow and accumulation of phytoplankton biomass in estuaries is complex. In estuaries where the processes of material transport are mostly tidally driven, tidal variability dominates seasonal effects. River discharges are particularly relevant in winter months characterized by high flow values. While high freshwater inputs can stimulate primary production by importing nutrients into the system, the development of blooms is only possible when the net rate of biomass accumulation exceeds the losses (either by biotic or abiotic means). Therefore, also low river inputs causing longer residence times may allow the accumulation of phytoplankton and may trigger a bloom.

3.2 Benthic communities in tidal flats

Sediment areas exposed at low tide are called tidal flats and, if they have a clay content of more than 10%, mud flats. Mud flats are particularly extensive in estuaries with a large tidal range. Estuaries with a high tidal range usually have large tidal flat areas, and sizable natural microphytobenthic communities, which play an important role in carbon fixation and nutrient removal in shallow waters (Gao and Mckinley 1994, Simas et al. 2001). Benthic primary productivity in shallow waters is strongly dependent on the regulation of underwater light climate by suspended particulate matter (Schild and Prochnow 2001). If an excess of nutrients exists, light availability will be the key limitation. In intertidal areas, the combination of shallow waters and strong tidal currents creates a complex pattern of SPM transport, deposition, and resuspension dynamics. Sub-tidal benthic primary production will probably be low due to natural turbidity.

In temperate climates the mudflats are often fringed by salt marshes that are inundated at spring tides or, in the tropics, by mangroves. These vegetated mudflats play a critical role in determining the robustness of the estuary, by trapping fine sediments, sequestering nutrients and pollutants, influencing the water residence time, and converting nutrients in the water column into plant biomass. Mudflats are home to a wide range of organisms that tolerate the changing conditions induced by the tidal movements. Almost always large numbers of benthic diatoms grow on the mud and frequently produce extensive blooms. Bacteria are also extremely abundant in the tidal flats where they decompose the organic matter brought in by rivers and tides.

3.3 Salt marshes

Salt marshes are buffer areas that link land and sea. Salt marshes generally start at the level of the average neap tide and extend upward to and beyond the height of the highest tides. They are one of the few examples of a community of higher plants that can tolerate saltwater and survive in the marine environment. In total there are about 500 species of plants belonging to 18 families of angiosperms found in salt marshes worldwide (e.g. *Spartina*). Many species are perennial grasses. The salt marshes are dominated by grasses such as *Spartina* spp., and by rushes, *Juncus* spp. The duration of exposure and inundation during the tidal cycle determines the species zonation. Even though salt marsh plants tolerate full strength seawater, they grow faster in low salinities because salts of seawater are an osmotic stress, with a metabolic cost imposed on plants.

Salt marshes occur in the alluvial plains associated with an estuary and generally include channels, called tidal creeks that fill and empty with the motion of the tides. These meandering creeks usually form an intricate network of drainage channels across a salt marsh. Besides having drainage creeks, salt marshes also have mud flat areas (called pans) and tidal flats. Salt pans are circular to elliptical depressions, which are flooded at high tide and remain filled with salt water at low tide. Salt marshes stabilize the sediments, thus promoting their own growth. The roots and stems tend to capture the suspended sediments carried by currents and waves. Few animals feed on the salt marsh directly, most of the energy captured by the marsh in photosynthesis being slowly released to the adjacent water and sediments as the vegetation decays. Terrestrial animals including insects, birds and mammals, account for about 50% of the fauna found in salt marshes. Marine animals, mostly invertebrates, include bivalves, gastropod snails and crabs. The salt marsh is a detrital system where grazing herbivores play a minor role. Most of the detrital material from *Spartina* of the low marsh is washed out by the tide; that of the high marsh is decomposed in place by bacteria.

3.3.1 Nutrient dynamics

The growth and development of salt marsh communities is influenced by the concentrations of nutrients and these, in turn, by groundwater flows. As such, salt marsh nutrient fluxes can be affected by the hydrological conditions, particularly the magnitude and status of groundwater flows (Sutula et al. 2001). The concentration of nutrients in salt marsh creeks depends on the balance between the supply (from inside and outside) and the rate of uptake by the growth of salt marsh vegetation. Where adequate levels of both phosphorus and nitrogen occur, other elements, such as silicon, can become limiting (Jacobsen et al. 1995). The importance of salt marshes as a nutrient source and sink for the estuary is an open question. The amount of nitrogen cycled depends on tidal input, physical and chemical exchanges with air and water, and biological fluxes. Salt marshes are characterized by their large nutrient storage capacities that under certain circumstances can become 'leaky' with subsequent nutrient releases (Turner 1993). The release of nitrogen and phosphorus from the salt marsh occurs generally during the process of the decomposition of organic matter, but direct losses by the leaching of nitrogen, phosphorus and also carbon, from live plant tissues can also take place. The flux of released nutrients can be high enough to account for significant increases in the activity of the estuarine phytoplankton community and, consequently, of potential significance for many other estuarine communities.

3.3.2 Fluxes of organic matter

Primary production and decomposition rates are high within the salt marsh, usually comparable to those of tropical rain forests. The behaviour of DOM and POM is essentially similar to suspended sediment and is based on the flux of the tidal water flow. The fate of excess carbon production within these systems is not well understood. Some salt marshes are dependent on tidal exchanges and import more than they export, whereas others export more than they import. Excess production may end up in the sediments, being transformed by microbes in water in the marsh and tidal creeks, or exported to the estuary physically as detritus, as bacteria, or as fish, crabs, and intertidal organisms in the food web. The possibilities for the export of organic matter to adjoining marine ecosystems have also been widely recognized. The basic model of salt-marsh estuaries as exporting systems usually referred to as the "Outwelling Hypothesis" (Dame et al. 1986), developed from the notion that marsh productivity may be "outwelled "as organisms rather than as organic matter and nutrients (Odum 2000).

3.4 Mangroves

Mangrove forests are important coastal ecosystems that provide a variety of ecological and societal services. At tropical and subtropical latitudes the herb-dominated salt marsh is replaced by mangrove forests. These are concentrated along low lying coasts with sandy shores and in estuaries. They stand as a transition between two environments (land and sea), usually in estuaries where they act as an interface between river and sea. Mangroves are associated with the terrestrial climates of the tropical rain forest, tropical dry forest, savanna and desert, due mainly to the sensitivity of mangrove to frost.

Mangroves are forests of trees and shrubs that are rooted in soft sediment in the upper intertidal zone where wave action is absent, sediments accumulate and the mud is anoxic. They extend landward to the spring tide high water line, where they are only rarely flooded. The term "mangrove" refers to a variety of trees and shrubs belonging to some 12 genera and up to 80 species of flowering terrestrial plants (angiosperms) found world-wide. Mangrove trees of different species are usually distributed relative to elevation within the intertidal zone. The most frequent are the Genus *Rhizophora* near the water (intertidal zone, inundation by average high tides), *Avicennia* (flooded by average spring tides) and Laguncularia (only reached by the highest tides). One of the most widely distributed is the red mangrove *Rhizophora*. The dominant genera (*Rhizophora*, *Avicennia*) share some common features: they are salt-tolerant and ecologically restricted to tidal swamps, and possess both aerial and shallow roots that interlink and spread widely over muddy substrate.

These forests are a unique marine system, having aerial storage of plant biomass, harboring both marine and terrestrial species. The forest comprises euryhaline plants, tolerant to a wide range of salinities, found in fully saline waters and well up into estuaries. Immersion of roots in seawater up to 1m in depth is common. The roots of mangroves are morphologically specialized for anchoring and nutrient transport. Mangroves and salt marshes have many similarities in physical and biological processes. These include their role in trapping sediment and pollution, converting nutrients to plant biomass and serving as a habitat for numerous organisms like fish and crustaceans.

Mangrove trees have special physiological adaptations that exclude salt from entering their tissue, or that allow the excretion of salt in excess. Many species are viviparous, producing seeds that germinate on the tree. Mangroves harbor a rich fauna where birds, monkeys, snakes, frogs and insects are common inhabitants. Barnacles, snails, fiddler crabs and land crabs are also found around mangroves.

3.4.1 Mangrove forest components and abiotic conditions

Ecologically, a mangrove community can be divided into: (1) Above-water forest. A study of Florida mangroves showed that about 5% of the total leaf production was consumed by terrestrial grazers, the rest entering the aquatic system as debris and becoming available for marine detritivores, either fish or invertebrates (Twilley et al. 1986); (2) Intertidal swamp. Leaf litter is a major source of nutrients and energy in the mangrove swamp, and many residents are detritivores; (3) Submerged subtidal habitat. High organic content in the fine-grained mud; burrowing animals (crabs, shrimps, worms, etc.) are common, and their burrows facilitate oxygen penetration into the mud and thus ameliorate anoxic conditions.

Mangrove systems occupy the full tidal range, and as a consequence, the organisms in these environments are exposed to highly variable light conditions, ranging from full sunlight at low tide to very little light at high tide. Penetration of light and water movement varies over short distances and in the course of a day. This physical variability is reflected in highly variable chemical conditions. Complex tidal currents flow in mangrove forests, where they are involved in ecological processes. In addition, these currents also fragment and transport the litter produced by mangrove vegetation. Temperature is also highly variable: because it is a shallow water system (particularly at low tide), water temperature varies with air temperature, seawater and river water temperature may be different inside the estuary, so temperature may change with each tidal cycle (shallow areas in these environments can heat up to 40 ℃). Oxygen concentration is highly variable and often reaches extreme levels. While decomposition of large quantities of organic matter can deplete dissolved oxygen, high rates of photosynthesis can increase its concentrations to super-saturated levels.

3.4.2 Production

Mangrove ecosystems rank amongst the most productive communities in the world, with their net primary production estimated at $1.1\,\mathrm{x}10^{15}\,\mathrm{g\,yr^{-1}}$ worldwide (Duarte and Cebrián 1996). Most of the plant material is not eaten directly, but decays and enriches the adjacent waters through detritus food chains. Mangrove forests export a considerable portion of their production to the surrounding waters, largely as leaf fall and other detrital material. Concentration of dissolved inorganic P in mangroves is generally low. A close microbe-nutrient plant connection may serve as a path to conserve scarce nutrients necessary for the existence of these forests (Alongi et al. 1993). Numerous studies have shown that the influence of mangrove forests on the adjacent lagoonal and near-coastal ecosystems is variable in terms of matter transfer balances. Whether mangroves act as a source or sink of organic matter depends on factors such as topography, forest types, and tidal regime.

Tidal inundation generates a nutrient exchange between sediment and estuarine waters. Water exchange transports nutrients into mangrove areas, and exports organic material out. But mangroves are rich in recycled nutrients because the roots trap detritus which are mineralised in the sediments. The recycled nutrients then become available for uptake by the roots of the mangroves. As such, the mangroves are not solely dependent on dissolved nutrients in the surrounding (oligotrophic) seawater. Other typical features of mangrove sediments are relatively low concentrations of dissolved inorganic nutrients, for example, nitrate, ammonium and phosphate in porewater, and the presence of tannins derived from leaching and decomposing roots and litter. Ammonium is the main form of inorganic N in mangrove sediments because nitrification is prevented due to the lack of oxygen in the sediment.

3.4.3 Interaction with sediments

Mangrove forests tend to accumulate sediment by creating conditions for the fine particles trapped in the root system to become permanently deposited. This sediment trapping capacity of mangroves is essential for the ecosystem. Mangroves form protective barriers against wind damage and erosion in regions that are subjected to severe tropical storms. In some areas they may facilitate the conversion of intertidal regions into semi-terrestrial habitats by trapping and accumulating sediment. The intertwined roots further reduce water velocities, trapping suspended sediments and organic material (particularly leaves).

3.5 Sea Grass Meadows

Other communities that thrive in the shallow and well lighted areas in some estuaries, coastal lagoons and coastal areas are the sea grass meadows. These are among the few higher plants that are totally adapted to the marine environment, with about 50 species that can live totally submerged in seawater. In temperate waters, the most common genus is *Zostera* (eelgrass), while in tropical waters it is *Thalassia* (turtle grass). These plants absorb nutrients directly from the water across the leaf surface and from the sediment by their roots. Sea grass meadows are rich biological communities with high rates of primary production. Few animals eat sea grass directly: manatee, green turtles, parrot fish and surgeon fish are the principal vertebrate herbivores in the tropics. Sea urchins are the only invertebrates feeding on these plants. Sea grass meadows serve as host to epiphytes including micro- and macroalgae such as benthic diatoms and filamentous red algae. Between 25-30% of total photosynthesis may be due to epiphytic algae. Invertebrate species feeding within the sea grass meadows on epiphytic algae include gastropods, nudibranchs, isopods, amphipods and shrimp. A considerable fraction of the leaves are sloughed off and may float considerable distances, breaking down, sinking and becoming part of the sediment, eventually entering the detritus food chain. During this breakdown process, the leaves become floating bacterial cultures. These in turn are used as a food source by filter and deposit feeders. Sea grass meadows stabilize the sediments in which they grow because the leaves deflect and reduce the water movements from waves and currents. Suspended material tends to settle in the quiet waters in the meadow and is bound by the network of rhizomes and roots.

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