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ECOSYSTEMS

The Function of Marine Critical Transition Zones and the Importance of Sediment Biodiversity

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ABSTRACT

Estuaries and coastal wetlands are critical transition zones (CTZs) that link land, freshwater habitats, and the sea. CTZs provide essential ecological functions, including decomposition, nutrient cycling, and nutrient production, as well as regulation of fluxes of nutrients, water, particles, and organisms to and from land, rivers, and the ocean. Sediment-associated biota are integral to these functions. Functional groups considered essential to CTZ processes include heterotrophic bacteria and fungi, as well as many benthic invertebrates. Key invertebrate functions include shredding, which breaks down and recycles organic matter; suspension feeding, which collects and transports sediments across the sediment–water interface; and bioturbating, which moves sediment into or out of the seabed. In addition, macrophytes regulate many aspects of nutrient, particle, and organism dynamics above- and belowground. Animals moving within or through CTZs are vectors that transport nutrients and organic matter across terrestrial, freshwater, and marine interfaces. Significant threats to biodiversity within CTZs are posed by anthropogenic influences; eutrophication, nonnutrient pollutants, species invasions, overfishing, habitat alteration, and climate change affect species richness or composition in many coastal environments. Because biotic diversity in marine CTZ sediments is inherently low whereas their functional significance is great, shifts in diversity are likely to be particularly important. Species introductions (from invasion) or loss (from overfishing or habitat alteration) provide evidence that single-species changes can have overt, sweeping effects on CTZ structure and function. Certain species may be critically important to the maintenance of ecosystem functions in CTZs even though at present there is limited empirical evidence that the *number* of species in CTZ sediments is critical. We hypothesized that diversity is indeed important to ecosystem function in marine CTZs because high diversity maintains positive interactions among species (facilitation and mutualism), promoting stability and resistance to invasion or other forms of disturbance. The complexity of interactions among species and feedbacks with ecosystem functions suggests that comparative (mensurative) and ma-

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nipulative approaches will be required to elucidate the role of diversity in sustaining CTZ functions.

Key Words: climate change; diversity; ecosystem function; estuaries; eutrophication; functional group; habitat alteration; mangrove; overfishing; salt marsh; species invasion; wetlands.

INTRODUCTION

Estuaries and coastal wetlands, both vegetated (mangroves, salt marshes, and seagrass beds) and unvegetated (mudflats and sand beaches), are critical transition zones (CTZs) between land, freshwater habitats, and the sea. These zones provide essential ecosystem services, including shoreline protection, water quality improvement, fisheries resources, and habitat and food for migratory and resident animals. They also have aesthetic appeal and offer recreational opportunities for human populations. Extreme fluctuations often occur in salinity, temperature, water level, and dissolved oxygen within any single locale, restricting the number of species in these environments. Consequently, essential ecosystem functions performed by species in CTZs are associated with a relatively low biodiversity.

In this paper, we examine the role of biodiversity (both species composition and species richness) in ecological functions of marine CTZs. We first discuss processes inherent to the ecological integrity of marine CTZs, including pathway functions that connect and transfer water, material, and organisms among land, fresh water, and the ocean. We then describe functional groups of organisms that are key to maintaining these processes, identify threats to biodiversity in marine CTZs, and consider the potential consequences of diversity change for ecosystem function. Our goal is to promote the recognition of CTZs as important features within the landscape and to stimulate thinking about whether changes in the biodiversity of CTZs will have far-reaching ecological significance.

We will consider primarily marine sediments and sediment-dwelling or sediment-associated organisms, rather than the water column or other CTZ components. Sediments are a pivotal component of aquatic ecosystems where important transformations and exchange processes take place (Snelgrove and others 1997; Snelgrove 1999; 2000). We will focus on local (alpha rather than beta or gamma) diversity in CTZ sediments, considering not only the numbers of species in a given area but also their specific identities and relative dominance.

CTZ FUNCTIONS

The basic functions of decomposition, nutrient cycling, and production, together with the fluxes of nutrients, water, particles, pollutants, and organisms, are inherent to the ecological integrity of CTZs. Materials are mixed, deposited, fed upon, introduced, or otherwise processed as they pass through wetlands or estuaries; most of these materials interact with CTZ sediments during this journey (Snelgrove and others 1997; 2000).

CTZ sediments are complex environments with extensive feedbacks involving the water, air, and biota. Long periods of exposure to air or inundation by standing water can change oxygen levels, reduce the diversity of animals, alter the available forms of nutrients, and influence the formation of toxic compounds such as hydrogen sulfide and trace gases such as methane, carbon monoxide, nitrous oxide, and hydrogen (Fenchel and Finlay 1995; Nealson 1997; Nealson and Stahl 1997). Flow rates and water depth affect vascular plants and their role in bringing food particles to animals, removing wastes, and enhancing oxygenation (Denny 1988). Sediment-dwelling benthic animals in turn can increase the percolation of water and oxygen levels through solute pumping or by the bioturbation associated with deposit-feeding or burrowing (Aller 1982; Rhoads and Boyer 1982). Vegetation has a similar effect by transporting oxygen to roots, where it enters the rhizosphere (Armstrong 1964; Moorhead and Reddy 1988). In addition, vegetation moderates rates of water flow, affecting animal movement, nutrient dynamics, and particle deposition (Jumars and Nowell 1984). We will first discuss these processes, and then consider the functional groups of organisms whose diversity may be most intimately tied to them (Table 1).

Ecosystem Processes in the Coastal Transition Zone

Decomposition and nutrient recycling. CTZs are hotspots of organic matter input, decomposition, and nutrient cycling that are responsible for global contributions proportionally much greater than might be expected from their small areal coverage (Meybeck 1982; Alongi 1998). Salt marshes, seagrass beds, and mangrove forests produce large amounts of dead plant material (litter), much of which enters the system as relatively large detrital particles. Allochthonous detritus, entering from rivers and the coastal ocean, typically occurs in smaller fractions and later stages of conditioning. In all marine CTZs, the organic matter is rapidly incorporated into a complex decomposer food web (for example, see

Table 1. Key Ecosystem Functions within Marine Coastal Transition Zones and Organism Functional Groups Hypothesized to be Most Involved in Performing those Functions

	Estuaries	Coastal Wetlands	
Process	Functional Group (Redundancy)*	Functional Group (Redundancy)*	Threats to Diversity
Decomposition	Heterotrophic bacteria (H), Deposit feeders (H), Sulphate reducers (H), Filter/ suspension feeders (L), Shredders, Detritivores (H), Bioturbators (M), Saprophytic fungi (H)	Tramplers (H) Detritovores (H) Suspension feeders (L) Sulphate reducers (H) Shredders (M) Deposit feeders (H) Bacteria (H) Saprophytic fungi (H) Bioturbators (M)	Organic loading (rate and amt.) Nutrient loading (rate and amt.) Turbidity Invasive species Changes in water flow (flushing) Heavy metals Fishing Anoxia Dewatering
Nutrient Cycling/trace gas production	Heterotrophic bacteria (H), Deposit feeders (H), Sulphate red. bacteria (H), Filter/ suspension feeders (L), Shredders, Detritivores (H), Bioturbators (M), Saprophytic fungi (H), Denitrifying bacteria (H), Macrophytes as oxygenators (L)	Tramplers (H), Detritivores (H), Sulphate reducers (H), Shredders (M), Deposit feeders (H), Bacteria (H), Saprophytic fungi (H), Bioturbators (M), Nitrogen fixers (cyanobacteria) (H), Macrophytes as oxygenators (L)	Turbidity Invasive species Changes in water flow (flushing from ocean) Heavy metals, salinity change Fishing Nutrient loading, Anoxia Dewatering Agricultural runoff Atmospheric inputs (N/S) Changes in sea level, temperature
Primary Production	Microalgae (H), Macroalgae (L), Submerged macrophytes (L)	Microalgae (H), Macro algae (L), Chemosynthesis (H) Macrophytes (L), Epiphytes (H), Chemosynthesizing bacteria (H), Chemosynthesizing metazoans (L)	Turbidity, Nutrient loading Invasive species Heavy metals, Salinity change Changes in water flow (flushing from ocean) Anoxia Agricultural runoff, Dewatering Changes in sea level, temperature Atmospheric inputs (N/S)
Secondary Production	Annelids (H) Crustaceans (M) Bivalves (L) Fishes (L)	Annelids (H) Crustaceans (M) Fishes (M)	Areal loss, Fragmentation Invasive species Overfishing Changes in sea level, temperature Nutrient loading, Anoxia
Pollution Transport, Transformation, Metabolism	Bioturbators/ solute irrigators (L), Dehalogenating bacteria (H), Bioaccumulators (L), Adsorbers (H) (diatoms/bacteria)	Bioturbators/solute irrigators (L), Dehalogenating bacteria (H), Bioaccumulators (L), Adsorbers (H) (diatoms/bacteria), Macrophytes (L)	Circulation, Flushing changes, Turbidity Nutrient loading, Anoxia Invasive species Heavy metals, Salinity change Fishing Dewatering, Agricultural runoff Atmospheric inputs (N/S) Changes in sea level, water temperature

Table 1. (Continued)

Process	Estuaries	Coastal Wetlands	
	Functional Group (Redundancy)*	Functional Group (Redundancy)*	Threats to Diversity
Sediment Movement	Filter feeders (L), Deposit feeders (H), Bioturbators (L), Mucous-producing biota (H), Microalgae (H), Macroalgae (M), Biogenic structurers (L)	Filter feeders (L), Deposit feeders (H), Bioturbators (L), Mucous-producing biota (H), Microalgae (H), Macroalgae (M), Macrophytes (L), Biogenic structurers (L) Sediment stabilizers (L)	Dredging, Turbidity Sediment loading Overfishing Invasive Species
Food Web Modification	Filter feeders (L), Pivotal species (L), Predators (L), Parasites (L)	Filter feeders (L), Deposit feeders (H), Bioturbators (L), Mucous-producing biota (H), Microalgae (H), Macroalgae (L), Macrophytes (L), Biogenic structurers (L), Sediment stabilizers (L)	Area loss, Fragmentation Invasive species Overfishing Nutrient Loading, Anoxia
Critical Habitat	Submerged macrophytes (L), Macroalgae (M)	Filter feeders (L), Pivotal species (L), Predators (L), Parasites (L), Macrophytes (L)	Area loss, Fragmentation Invasive species Overfishing Turbidity
Physical Buffering/Erosion Control	Submerged macrophytes (L), Tube, reef, and mat builders (M), Micro- and macroalgae	Macrophytes (L)	Area loss, fragmentation Invasive species Overfishing of shellfish Turbidity

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**Loss of diversity in groups with lowest redundancy (L), in which there are few species, is predicted to produce the largest consequences for ecosystem functioning. Species loss in highly redundant groups (H), where many species perform a similar function, is predicted to have limited effects. (M) = moderate redundancy.*

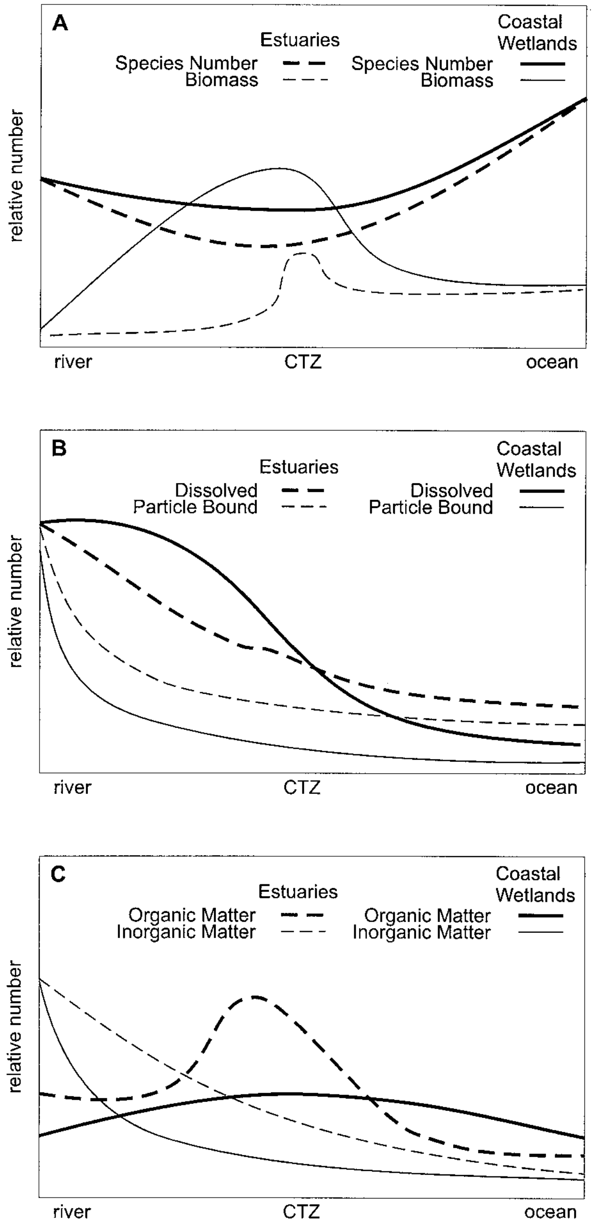


Figure 1. Schematic representation of (**A**) species number and biomass, (**B**) pollutant concentrations, and (**C**) suspended organic and inorganic (sediment) matter concentrations across the marine critical transition zone.

Newell 1993; Chong and others 2000) or buried in the sediments. High rates of decomposition are critical to the sustained functioning of coastal ecosystems. The release of nutrients and dissolved organic matter (DOM) from CTZ sediments supports phytoplankton and bacterial production in overlying waters (Hopkinson and others 1998).

The benthic and epibenthic biota of CTZs are crucial for decomposition and nutrient recycling. Microbial communities, including bacteria and fungi, directly remineralize organic matter (Fenchel and Blackburn 1979; Newell 1996). Sediment protozoans and metazoans enhance microbial metabolism and thus increase the rate of decomposition by grazing on microbes attached to the plant detritus (Lopez and others 1977). Metazoan omnivores, which feed on both plants and the decomposer communities, provide important direct links to higher trophic levels (Kneib and others 1997; Graça and others 2000). Animal activities facilitate the mechanical breakdown of detritus (Newell and Berlocher 1993; Lillebo and others 1999), and enhance the transfer of nutrients from the sediments to the overlying water column through burrowing and bioturbation (Montague 1980; Robertson 1986).

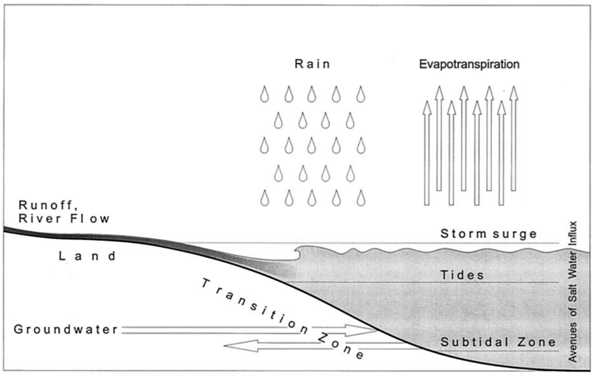


Figure 2. Avenues of water flux (freshwater and seawater) into and out of the marine critical transition zone.

Primary and secondary production. Coastal wetlands and estuaries are among the most productive natural systems in the world and support higher plant and animal biomass than the adjacent seaward or landward ecosystems (Mitsch and Gosselink 2000; Alongi 1998). However, this high productivity is accompanied by low species richness (Figure 1A), a relationship common in many marine, terrestrial, and aquatic systems (Rosenzweig and Abramsky 1993; Waide and others 1999). CTZs have high secondary production, standing stock, and turnover rates because of the rich supply of organic material from both detritus and algae (Covi and Kneib 1995; Alongi 1998). Sediment-dwelling invertebrates, including nematodes, copepods, annelids, molluscs, and peracarid crustaceans, are the food base for many species of fish and larger invertebrates (Sarda and others 1998). Because CTZs provide abundant infaunal prey and a habitat that is structurally complex with abundant refugia in the form of macrophyte beds, they serve as nursery grounds not only for many commercially important species (for example, shrimp, crabs, lobsters, menhaden, halibut, weakfish, spot, and croaker) but also for large populations of resident shellfish and fishes that play key roles in production transfers across estuarine ecoscapes (Kneib 1994, 1997, 2000). Although mangroves, marshes, and estuaries may be net exporters of nutrients, organic matter, and organisms (Alongi 1998), their contribution to detrital food chains differs among habitat types (Robertson 1988). Loss of sediment biota and/or benthic autotrophs could—either directly or indirectly—diminish the overall secondary production and the value of these areas as nursery grounds.

Estuaries and Wetlands as Pathways between Land and Ocean

Mixing of water and salt. Mixing of salt water and fresh water within marine CTZs is spatially and temporally complex, occurring both on and beneath the sediment surface. The major sources of fresh water to the CTZ are river inflow, groundwater inflow, direct precipitation, and runoff (Figure 2) (Mitsch and Gosselink 2000). Salt water enters the system driven by tides, wave surge, and wind, as well as through percolation into groundwater. Both fresh water and salt water are altered by evaporation and aerosol transport, which increase salinity in coastal wetlands and adjacent terrestrial systems. Airborne salt deposits accumulated during dry periods can be transported horizontally or moved down into sediment or groundwater. Mixing occurs where rivers and streams meet the ocean, where storm water drains enter coastal habitats, and groundwater penetrates coastal sediments. The mixing of fresh water and salt water in unvegetated areas often creates strong vertical gradients (stratification) and a well-developed frontal zone (for example, turbidity maximum). In vegetated systems, mixing is much more complex and involves greater vertical homogeneity.

CTZs are particularly sensitive to hydrologic modifications (Nichols and others 1986). Relatively small changes in freshwater input or saltwater flushing can cause large changes in the vascular plant species that dominate coastal wetlands (Zedler and others 1980; Zedler 1983). In mangrove forests, plant species diversity is a function of salinity; higher diversity is associated with waters of moderate salinity (Ball 1998). Salinity-induced changes in plant species and vigor will alter root structure, leaf litter, and decomposition products, which could in turn influence the diversity of benthic sediment communities. In salt marshes of the Pacific coast, loss of regular ocean flushing leads to the elimination of Pacific cordgrass (*Spartina foliosa*), a species that supports the endangered light-footed clapper rail (Zembal and Fancher 1988). Pickleweed (*Salicornia* spp.), which replaces Pacific cordgrass in poorly flushed lagoons, supports a different infaunal assemblage (Talley and Levin 1999) and another endangered bird species, the Belding's Savannah sparrow (Powell 1996). Changes in seagrass composition have been linked to ichthyoplankton community composition (Tolan and others 1997) and may therefore influence the recruitment of fishes that rely on seagrass habitat.

Nutrient transfer and transformation. Ultimately, water on land reaches the sea by passing through a CTZ. Among the major nutrients associated with these freshwater inflows are dissolved forms of nitrogen (N) and relatively small concentrations of phosphorus (P), both of which are rapidly taken up by vascular plants and algae in the CTZ. Large amounts of nutrients also enter the ocean on inorganic and organic particles. N delivery to estuaries has been steadily increasing in many regions of the world through loading in surface waters, groundwater, and the atmosphere (Peierls and others 1991; Howarth and others 1996; Vitousek and others 1997). Although we tend to think that inputs are transferred largely from upland drainages to the ocean, nutrients and pollutants may be exchanged across the coastal zone in both directions. Upwelled nutrients or toxic algal blooms (red tides) move into wetlands, spilled oil or fish kills are deposited in the estuary, and algal and seagrass mats are stranded on the beach. For several decades, the outwelling hypothesis has emphasized that multidirectional movements of organic matter are important to the tightly coupled ecosystems associated with CTZs and include several mechanisms that influence directional transfers (Lefeuvre and others 1999). Intertidal production can subsidize terrestrial taxa that move into CTZs to feed (for example, raccoons, coyotes, lizards). These subsidies can be especially important in arid environments where terrestrial primary productivity is low or in other areas during dry years (Rose and Polis 1998; Anderson and Polis 1998, 1999).

Vascular plants in coastal wetlands slow water flow and enhance the deposition of fine particles and organic material (Leonard and Luther 1995; Fonseca 1996). As a result, coastal wetlands play a key role in removing and storing both nutrients and pollutants, with vegetated habitats removing considerably more nutrients, sediments, and pollutants than unvegetated CTZs (Figure 1B and C).

Denitrification in estuarine sediments is particularly important for removing nitrate from the water. Denitrification converts nitrate to dinitrogen gas through anaerobic microbial processes that utilize nitrogen as an electron acceptor. Especially high rates of denitrification occur in estuarine tidal mudflats and salt marshes (Seitzinger 1988, 1994; Alongi 1998).

On a global scale, nutrient input to estuaries has a strong latitudinal pattern (Gross and others 1988). Nutrient-poor oligotrophic river waters mix with higher-nutrient ocean waters in high-latitude estuaries. In the tropics, the pattern reverses, with low-nutrient ocean water mixing with higher-nutrient river waters. Historically, the nutrient resources driving production in estuaries were mainly marine-derived in high-latitude regions and freshwater-derived in low-latitude regions. The predominance of anadromy in high latitudes and catadromy in low latitudes for fish populations using both marine and freshwater ecosystems is driven by these gradients in productivity between marine and fresh waters (Gross and others 1988).

Particle flows and pollutant transport. In general, estuaries and coastal wetlands are net depositional environments (Reineck and Singh 1980; Lisitzyn 1999), with particles entering the system via riverine flow and runoff from land or by tidal and wind transport from the ocean (Figures 1C and 2). Geomorphic and hydrologic factors determine the patterns of deposition within the CTZ (Davis 1978). Low-gradient estuarine environments with high sediment loads produce complex deltaic deposits at the interface. Estuaries with higher gradients and high sediment inputs transport greater amounts of sediment to the ocean. Sediment-poor rivers lack the extensive tidal mudflats and fine-grained sediment habitats of systems that receive large quantities of land-derived sediments. During storms, huge amounts of sediment and wrack can be transported into coastal wetlands from the land and ocean (Cahoon and others 1996; Leithold and Hope 1999). Such events can lead to the death of vegetation, the burial of animals, and in some cases the complete loss of the habitat. Heavy sediment deposition can also alter the elevation of coastal wetlands, causing changes in the distribution and species composition of vascular plants (Callaway and Zedler 1998) and almost certainly of animals as well. Overall, the quantity of particulate and organic matter inputs and the distribution of these inputs are crucial factors in the structuring of the sediment communities of estuaries.

Marine CTZs play important roles in trapping and transforming synthetic organic chemicals and trace metals released from land (Figure 1B and C). Because these chemicals are often highly particle-reactive, estuaries, river deltas, and shelf environments serve as effective traps for pollutants moving through CTZs. Organisms can determine the fate of particle-bound contaminants through biodeposition, biochemical modification, alteration of the geochemical environment where sediments are deposited, the mixing and ventilation of sediments, and the bioaccumulation of hydrophobic compounds. Biological stabilization of sediments (Grant and Gust 1987) also may help retain contaminants.

Organism movements. A wide variety of animals move into, out of, or across marine CTZs during one or more life stages (Dame and Allen 1996; Kneib 2000). They have different life-history patterns and use these habitats in different ways (Figure 3). CTZs may provide invertebrates and vertebrates with spawning habitat, nesting sites, nursery grounds, refugia, adult habitat, or feeding grounds, or they may simply serve as dispersal corridors. Some CTZ species spend their entire life within the estuary (for example, the killifish *Fundulus* spp. or the mud crab *Rhithropanopeus harrisii*), whereas others (for example, blue crabs *Callinectes sapidus*) release larvae that develop in the open ocean and return to settle in the CTZ for the juvenile and adult stages (Williams 1984). Other species (for instance, menhaden *Brevoortia patronus*) migrate from the estuary to the ocean to spawn, develop offshore as larvae, and then return to the CTZ as juveniles to feed and grow (Shaw and others 1985; Deegan 1993). Some freshwater shrimp and terrestrial crabs migrate to the CTZ to release larvae; in other cases, the larvae are transported passively downstream to develop in the CTZ or ocean before migrating back as postlarvae or juveniles (Anger 1995; March and others 1998). Some insects (for example, certain species of damselflies and dragonflies) develop as larvae in rivers and streams and migrate to coastal wetlands to feed and mate as adults (Thorp and Covich 2001). Other insects (for instance, certain species of midges and mosquitoes) have larvae that feed in CTZs and spend their adult stages on land or in wetlands (Foster and Treherne 1976; Naiman and Decamps 1997). Additional migrators include planktonic species that have resting stages in sediments (Marcus and Boero 1998). Sediments may provide a refuge for pathogenic species, such as the toxic dinoflagellate *Pfiesteria piscicida*. After remaining dormant for long periods in coastal sediments, this species can emerge and cause massive fish kills within and adjacent to estuarine areas (Burkholder and Glasgow 1997), with strong consequences for biodiversity (Smith and others 2000).

Some migrating organisms cover extremely long distances, passing through the CTZ to complete their life cycles (Figure 3). Examples include

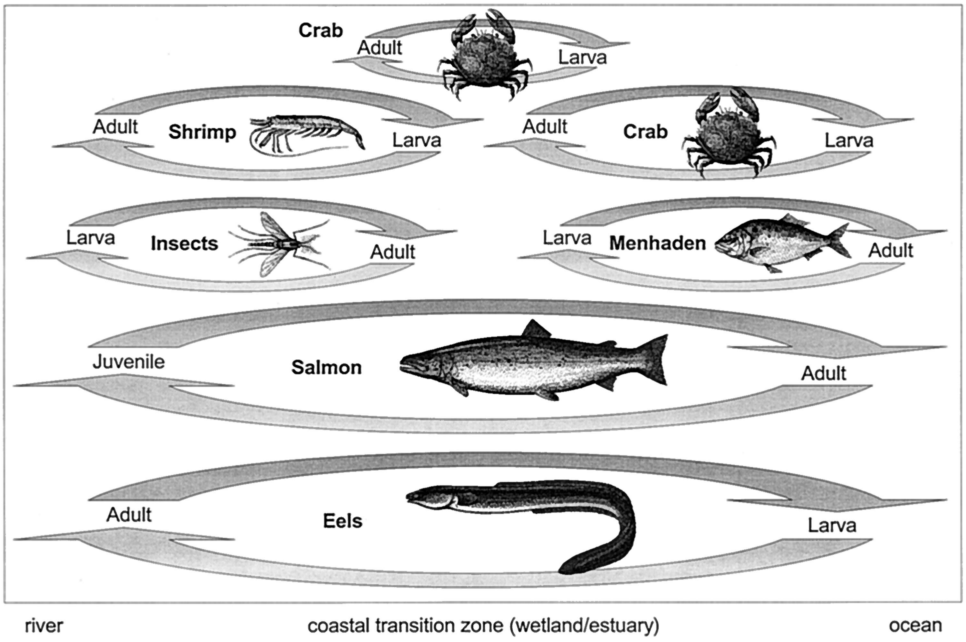


Figure 3. Life-history movement patterns of organisms migrating into, out of, through, or within CTZ (estuary and coastal wetland) habitat.

salmon and the rare gulf sturgeon, which spawn in rivers, migrate through and often feed extensively in estuaries, and develop further as adults in the ocean. Catadramous fishes, such as eels, reproduce and develop as larvae in the ocean and spend their adult stages in estuaries or fresh water, using CTZs as feeding grounds (Haedrich 1983). Thus, estuaries can be conduits of carbon (C) and nutrients traveling in different directions. Pacific salmon migrate upstream to spawn and then die, providing a transfer of nutrients from the ocean to inland ecosystems. Atlantic salmon migrate upstream, spawn and feed, and return to the ocean, transporting nutrients in both directions. Terrestrial mammals, reptiles, and birds feed directly on animals in the CTZ (Rose and Polis 1998) or prey on migratory species that export nutrients from the CTZ (Hilderbrand and others 1999).

For many migrating species, CTZs serve as a feeding or breeding ground; indeed, most of the commercially harvested species in coastal US Atlantic and Gulf waters rely on CTZs as nursery habitat (McHugh 1967; Weinstein 1979). Estuaries—and especially the wetlands within them—provide to juvenile fish and shellfish (a) a complex mosaic of physical structure that affords them refugia from predators, and (b) higher food availability than in the adjacent freshwater or saltwater environments. Because estuaries serve as spawning or nursery areas for many species, invertebrate, fish, and mammal predators also feed in estuaries (for example, crabs, sharks, dolphins). Many more transient fish and shellfish species use US Atlantic Coast wetlands as nursery or feeding grounds than US Pacific Coast wetlands, perhaps because of the greater aerial cover and continuity of wetlands on the Atlantic Coast. Foraging activities of mobile epibenthic predators can have complicated direct and indirect effects on the structure of benthic assemblages in CTZs (for example, see Kneib 1985, 1991). The functional consequences of top-down effects in CTZs (for instance, addition or removal of epibenthic predators) are not well known and may provide fertile ground for future research.

ORGANISMS AND RELATIONSHIPS CRITICAL TO CTZ FUNCTION

Key Functional Groups

Many of the habitat functions that we have described for CTZs rely heavily on sediment-dwelling organisms that perform specific activities (Table 1). Groups of organisms that play similar roles in ecosystem processes are termed “functional groups”. Key functional groups within CTZ sediments include heterotrophic bacteria, deposit feeders, suspension feeders, shredders, and bioturbators among the invertebrates, as well as macrophyte and algal primary producers. Those groups with the fewest numbers of species performing the same functions are considered to have the lowest redundancy; those with many species performing the same function have high redundancy. Within estuaries and coastal wetlands, key animal activities necessary for decomposition and nutrient cycling include suspension feeding (also called "filter feeding"), bioturbation, and shredding (Table 1).

Suspension feeders are particularly characteristic of marine CTZs. They capture particulate organic material from the water column and introduce it to the benthic system. If this organic matter originates within the CTZ, the effect is to retain production; if it was produced elsewhere (for example, by coastal plankton or in the adjacent upland), it becomes a significant new import to the system. The dominant suspension feeders within CTZs are often bivalve molluscs, such as mussels, oysters, scallops, and clams. Bivalve feeding activities can increase water clarity and light levels; they also reduce pollutant and suspended loads within estuarine waters (Alpine and Cloern 1992; Strayer and others 1999). Other common suspension feeders within CTZs, including polychaetes, crustaceans, cnidarians, bryozoans, ascidians, and sponges, have similar but often lesser effects.

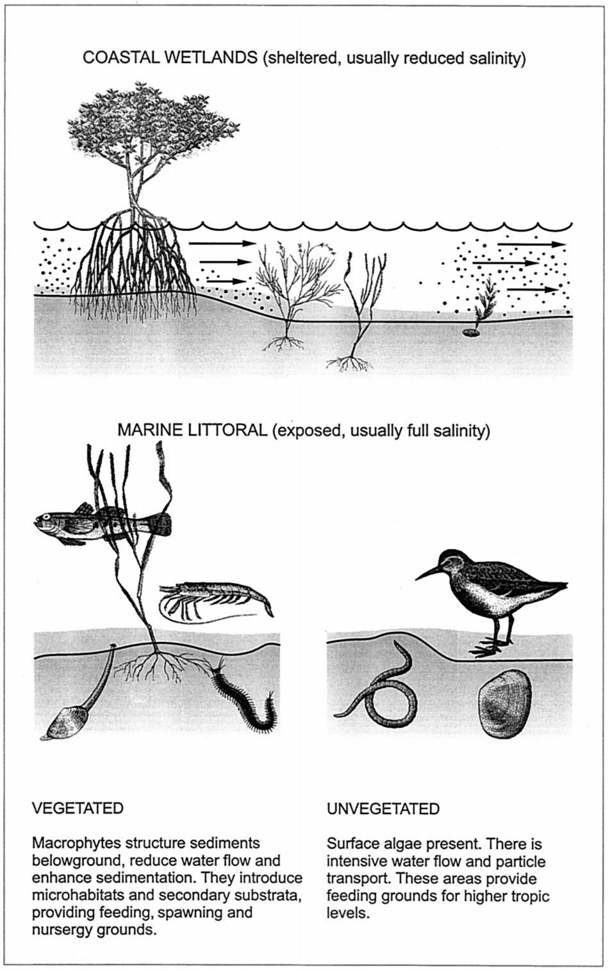
Once particulate organic material reaches the bottom, bioturbators may bury it or remobilize it by bringing sediments upward to the surface. This translocation may affect the rate at which organic matter is decomposed and whether anaerobic or aerobic decomposition occurs. Bioturbators within CTZ sediments can form large, deep burrows, as is characteristic of many kinds of crabs and shrimp, or small burrows, such as those of annelids (oligochaetes and polychaetes), a group that is extremely abundant in estuarine and wetland sediments (Levin and Talley 2000).

Shredders are animals that break up large pieces of organic matter (such as leaves) into small pieces, thereby mediating the rate at which the refractory tissues of vascular plants are made available to microbial decomposers. The gastropod *Littoraria irrorata* (marsh periwinkle), one of the most conspicuous shredders in the salt marshes of the southern US, frequently scrapes microbial and epiphytic material from the senescent and dead leaves of the marsh grass *Spartina alterniflora* (Newell and Berlocher 1993). The resulting rain of fecal material and organic particles hastens the return of nutrients to the sediment. Some common species of marsh insects, such as the grasshopper *Orchelium fidicinium*, consume portions of living *S. alterniflora* leaves (Smalley 1960; Pfeiffer and Wiegert 1981), often leaving behind unconsumed fragments hanging in shreds at the distal ends of the leaf blades (R. Kneib personal communication). As a consequence, these fragments die prematurely; thus, insects may accelerate the rate at which plant production enters the decomposition process and becomes available to the benthos of intertidal CTZs. Grazing sea turtles perform a similar function in seagrass beds (Bjorndal 1980). This activity amplifies the internal cycling of organic matter. Like shredders, fungi play a key role in the remineralization of the vascular plant material from tidal wetlands (Newell 1993) and are among the few organisms capable of penetrating the tough structural elements of senescent and dead intertidal macrophytes. However, they are less likely to be dominant decomposers in permanently saturated estuarine sediments.

Macrophytes contribute both structure and function in tidal freshwater habitats, tidal estuarine wetlands, and shallow subtidal habitats. Emergent vascular plants (for example, reeds, marsh grasses and succulents, seagrasses, and mangroves) are usually represented by a few dominant, very productive species. In deeper, subtidal estuarine habitats, much of the primary production either occurs in the water column or is imported from adjacent systems; macroalgae may also be important local primary producers.

About 90% of particulate organic matter entering the coastal zone is transferred to the sediments due to chemical flocculation, adsorption, and physical deposition that occur where fresh and salt water meet (Lisitzyn 1999). Vascular plants are key to the nutrient and particulate flux functions of CTZs because they slow the flow, enhancing deposition and nutrient uptake (Figure 4). Different species of marsh grasses (Leonard and Luther 1995) and seagrasses (Fonseca 1996) have different flow-retarding properties. The retention of deposited material in vegetated wetlands is enhanced by sediment stabilization derived from roots and rhizomes as well as from retarded flow (Figure 4). Animal tubes or tube mats, shells or shell reefs, byssus threads, cocoons, and mucous from macroalgae, bacteria, and invertebrates also stabilize sediments in CTZs. Changes in species composition of vascular plants, algae, or animals may affect the erodability of substrates as well (Grant and others 1986; Grant and Gust 1987). The composition of the community is especially important during storms, when vegetated CTZs often buffer inland development from the full force of wind and waves.

In addition to the functional groups described above, the fate of dissolved and particulate pollutants may be influenced by (a) microbial sulfate reducers, which produce sulfide that binds trace metals in sediments; (b) dehalogenating bacteria, which are capable of cleaving chlorine radicals from chlorinated organics; and (c) bioaccumulators (for example, bivalves), which can build up high concentrations of organics and metals in their tissues.



Macrophytes structure sediments belowground, reduce water flow and enhance sedimentation. They introduce microhabitats and secondary substrata, providing feeding, spawning and nursergy grounds.

Surface algae present. There is intensive water flow and particle transport. These areas provide feeding grounds for higher tropic levels.

Figure 4. Schematic diagram showing effects of vegetation on biotic and abiotic processes for coastal wetlands and subtidal estuaries.

The consumption of bioaccumulators by predators may move contaminants into and out of CTZs.

Positive Species Interactions

As the number of species in a community increases, the possibility for mutualistic and facilitative interactions among those species also increases, along with the possibility for functional redundancy. Positive interactions may be key features of many intertidal CTZ environments (Bertness and Leonard 1997; Chong and others 2000) and are likely—either directly or indirectly—to enhance key CTZ functions such as nutrient cycling, nutrient production, and the support of migratory species. For example, at mid-tide levels in salt marshes, the reed *Juncus* reduces abiotic stress, enhancing the diversity of vascular plants (Hacker and Bertness 1999). Mutualistic interactions between *Spartina alterniflora* and burrowing crabs (Bertness 1985) or mussels (Bertness 1984) enhance the growth of both plants and animals. Within tidal flat sediments, burrowers, such as the lugworm *Arenicola marina* or the ghost shrimp *Callianassa*, act to create oxygenated microhabitats (burrow linings) and depositional sinks for numerous meiofaunal and macrofaunal species (Reise 1985; DePatra and Levin 1989). Positive feedbacks among deposit feeders on food resources are probably common (Bianchi and others 1989). Animals that subduct organic matter, such as maldanid and arenicolid polychaetes, are likely to have keystone biogeochemical functions and may enhance rates of organic matter cycling and diagenesis (Levin and others 1997).

Invertebrate assemblages that inhabit wetland sediments rich in root, rhizome, and leaf detritus may be responsible for mutually enhancing consumption and digestion of bacteria. Assemblages of tubificid oligochaetes typically occur in organic-rich sediments associated with mangroves (in particular, species in the subfamilies Limnodriloidinae and Rhyacodrilinae) (Diaz and Erséus 1994; Erséus 1997, 1999). Co-occurrence of these species may be based on either the use of similar resources or resource enhancement from multispecies processing chains, as has been demonstrated in fresh water (Brinkhurst and others 1971; Milbrink 1993, 1995; Heard 1995).

THREATS TO BIODIVERSITY AND THEIR POTENTIAL IMPACT ON ECOSYSTEM PROCESSES

Potential threats to biodiversity that can influence critical ecosystem processes within CTZs include eutrophication, nonnutrient pollutants, species invasions, overfishing, habitat alteration, and global climate shifts (Table 1). Although the ecological consequences of these threats have been treated generally in other reviews (Smith and others 2000), we focus here on the potential consequences that threats pose for CTZ diversity and subsequently for the maintenance of ecological structure and function of CTZs. As the recent spate of papers on the relationship between biodiversity and ecosystem function has emphasized, which species are present may be as important or even more important than the number of species (Naeem and others 2000; Wardle and others 2000). Thus, many of our examples focus on the important role of individual species or groups of species.

Eutrophication

Human activity is bringing about major changes in the amount of nutrients delivered to estuaries through surface waters, groundwater, and precipitation (Kennish 1992). Nitrate loading of estuarine waters, in particular, appears to be increasing over the long term (Kennish 1992; Turner and Rabalais 1994; Rabalais and others 1996). Atmospheric inputs of ammonia and nitrate are also increasing (Schlesinger 1991). Therefore, CTZs become a critical zone for N processing.

In many estuaries, heavy nutrient loading stimulates phytoplankton and algal production and ultimately increases organic input to the seabed, while reducing oxygen availability. In warm temperate and tropical estuaries, such events might cause a shift from a diverse bottom assemblage, including many crustaceans, to one dominated by deposit-feeding annelids (Sarda and others 1996). Under these conditions, a shift in nekton community structure is probable, from dominance by crustaceans such as penaeid shrimps to species such as juvenile mojarra with feeding preferences that include smaller deposit-feeding polychaetes (Ley and others 1994; R. Kneib personal communication).

In Scotland, following eutrophication, seagrass was replaced by green algae, changing the system from a crustacean-dominated assemblage supporting wading birds to a benthos-poor algal mat without wading birds (Raffaelli 1999). In a number of places in the Baltic, a similar process occurred, leading to the loss of more than 40 species of macrophytes (Zmudzinski 1997; Jansson and Dahlberg 1999). These plants were replaced by a single brown filamentous alga, and there was a consequent drop in the number of associated infaunal invertebrate species. Fish (perch and pike) spawning ground was lost as plants disappeared; fish prey were lost as invertebrates disappeared. An overall result of eutrophication was the reduced efficiency of trophic transfer between benthic infauna and bottom-feeding fish (Narkko and Bonsdorff 1996; Jansson and Dahlberg 1999).

A dramatic, large-scale example of nutrient effects is the case of hypoxia in the Gulf of Mexico. Although water flow through the Mississippi Basin has long been altered by land conversion, drainage, impoundment, and channelization, the last half of the 20th century produced a dramatic increase in the flux of nitrogen, particularly nitrate, down the river. This nutrient enrichment has contributed to large-scale oxygen depletion (hypoxia) of bottom waters of the inner continental shelf off Louisiana and Texas during summer, as phytoplankton blooms sink to the bottom and decompose (Turner and Rabalais 1994). Intense midsummer hypoxia, which can cover up to 15,000 km^2, greatly reduces the diversity of animals living in or on the sediments (Boesch and Rabalais 1991; Harper and others 1991). The effects of this reduction of diversity on local populations and the ecosystem services provided by the benthos, including waste processing through sediment reworking and support of fisheries, are as yet unquantified. However, the scale of the annual cycle of stress and local extinction suggests that the consequences must be substantial. Although the Gulf of Mexico is not technically a CTZ, the system responses to hypoxia in marine CTZs are expected to be similar.

A variety of biological processes can influence nitrogen recycling within the CTZ. For example, studies in the Chesapeake Bay (Boynton and others 1995) and elsewhere demonstrate that as bottom sediments become anaerobic, nitrifying bacteria are unable to convert to nitrate the ammonium generated by the decomposition of organic matter. Consequently, denitrifying bacteria become nitrate-limited, resulting in the flux of more ammonium back into overlying waters (where it may fuel more phytoplankton production) and less denitrification (which generates dinitrogen) to remove the nitrogen from the marine system. This reduction in the diversity of sediment biological processes by oxygen stress thus constitutes a positive feedback to the eutrophication process.

One effect of severe eutrophication may be to reduce system diversity to a few tolerant species. When prey species are limited in number, prey are less likely to be interchangeable in nutritional value. For example, a gastropod (*Hydrobia*) replaced a bivalve (*Macoma*) as the primary food item in the diet of a sand flat goby in the northern Baltic Sea. Up to 90% of the gastropods passed through the goby alive compared to complete digestion of *Macoma*, implicating limited food value of the gastropod (Aarnio and Bonsdorff 1997). Shifts in food web structure may alter the well-being of predators in CTZs, where there is already low species diversity of prey.

Problems associated with eutrophication may be exacerbated by the loss of suspension feeders, which have the capacity to filter suspended particles including phytoplankton, or bioturbators, which influence burial and remineralization rates. These activities often determine whether organic matter is deposited, retained, and decomposed within the transition zone or exported to adjacent ecosystems. Without key suspension feeding and bioturbating species within the estuary, export to the shelf would be expected to increase along with potential for eutrophication.

Several related hypotheses emerge from these examples. (a) Nutrient-driven shifts in plant diversity and composition may reduce the complexity of food webs and even the number of trophic levels. (b) Simplification of food webs and shifts in potential food resources toward deposit feeders reduce habitat use and availability of resources for migrant marine species in CTZs. At the same time, an increase in abundance of estuarine resident species within these CTZs is predicted, due to reduction in abundances of larger predators and competitors.

Nonnutrient Pollutants

Particle inputs to estuaries worldwide are increasing as populations grow in coastal regions and along major waterways. Anthropogenic effects on the amount and composition of particles in an estuary can alter the composition and biodiversity of sediment-dwelling estuarine organisms, many of which rely on particulate organic matter for food. Human activities affecting particle inputs and movements are especially likely to impact filter feeders and bioturbators in estuarine ecosystems.

The functional diversity of sediment biota may play a significant role in pollutant transformation and transport (Palmer and others 2000), but this may vary across the salinity gradient. Low-salinity zones are generally characterized by high sediment deposition rates (but also often by high resuspension rates) and low diversity both among and within functional groups. Here contaminant transport processes may be dominated by physical processes. Mesohaline conditions are characterized by more diverse microbial processes, including sulfate reduction important in regulating metal binding and degradation of complex organics. Such zones exhibit higher densities of bioturbators but a lower diversity of such forms than under full-salinity conditions.

Contaminants may alter species diversity through direct toxicity or sublethal effects that influence fitness (for example, see, Levin and others 1996). Alternatively, they may lead to the loss of species through effects elsewhere in the ecosystem—for example, through reductions in prey, primary producers, or structure-providing organisms. Contaminant-induced species loss may initiate a series of feedbacks that further influence contaminant fates. The loss of biodiversity associated with reduced bioturbation and oxygenation of sediments could decrease the mobilization, biodegradation, and transport of pollutants and effectively increase long-term sequestration of these contaminants in anaerobic sediments (Palmer and others 2000). The strong effects of bioturbators on sediment pollutants are exemplified by the appearance and disappearance of the deeply burrowing echiuran *Listriolobus pelodes* on the southern California shelf. When it is present, the burrowing, respiratory, and feeding activities of this species reduce sulfide and contaminant levels and promote the establishment of a diverse infaunal community (Stull and others 1986). Interactions between burrower diversity and decomposition functions may be complex, as burrowers produce geochemical gradients and microenvironments in sediments that diversify the microbial assemblage (Dobbs and Guckert 1988).

Human effects sometimes interact with natural events to produce unpredictable and catastrophic occurrences. Flooding associated with Hurricane Floyd (1999) carried sediment, fertilizers, hog waste, and other pollutants from throughout North Carolina into the Pamlico-Ablemarle estuary, one of the nation's most productive CTZs, creating widespread anoxia and the potential for tremendous ecological and economic damage (Dixon 1999). Generally, large-scale disturbance within CTZs due to contamination, flooding, sediment burial, or other catastrophic events creates a low-diversity, early successional system that is vulnerable to colonization by fast-growing, opportunistic, or invasive species.

Invasive Species

Estuaries that are used heavily for shipping—such as San Francisco Bay (Cohen and Carlton 1998), Chesapeake Bay (Ruiz and others 1999), and the Hudson River (Mills and others 1996; Strayer forthcoming)—now contain hundreds of exotic species and are currently subject to invasion rates of approximately one new species per year. These high invasion rates probably result chiefly from high propagule pressure; many estuaries have received enormous numbers of potential colonists from ballast water, solid ballast, ship fouling, and aquaculture releases (Carlton 1992; Carlton and Geller 1993; Mills and others 1996; NRC 1996). In addition, the low species richness and high disturbance rates in many estuaries may contribute to successful establishment by new invaders.

As in other ecosystems, some species invasions have changed the functioning of CTZs, with profound consequences (Pimentel and others 2000). Introductions and invasions of vascular plants in CTZs include *Phragmites australis* in the northeastern US (Fell and others 1998), *Hydrilla verticillata* in the upper reaches of Chesapeake Bay (Posey and others 1993), and *Spartina alterniflora* on the West Coast of the US (Callaway and Jocelyn 1992). Typically, the diversity of macrophytes is low in most estuaries and coastal wetlands. The loss or addition of even one species, accompanied by the above- and below-ground structure it provides, can have a significant impact on productivity, nutrient cycling, sediment trapping, erosion control, habitat structure, and food quality (see for example, Wainright and others 2000).

Plant invasions of unvegetated tidal flats—for example, *Spartina alterniflora* in Willapa and San Francisco bays, *Zostera japonica* in Oregon, *Spartina anglica* in England, and mangroves in Hawaii (Allen 1998)—have resulted in the loss of open foraging area for birds or fish, flow reductions, higher sediment accretion, changes in incident light, and the potential loss of algal production (Posey 1988; Zipperer 1996). Modified habitats may be considered less desirable within a particular region—for example, because they are less suitable for migratory shorebirds or other species that rely on open space. In the salt marshes of San Francisco Bay, the invasive Atlantic Cordgrass (*S. alterniflora*) is not only covering mudflats at low tidal levels and replacing native grasses and succulents at the upper end of its range, it has also hybridized extensively with the native Pacific Cordgrass (*S. foliosa*) (Antilla and others 1998). Hybridization can pose a serious threat to biodiversity and ecosystem function when it endangers the existence of the native species and changes plant functions (Ayers and others 1999).

In wetlands of the US Atlantic Coast, the freshwater reed *Phragmites australis* has spread widely into salt marsh habitat, perhaps as a result of anthropogenically altered salinity regimes. Hybridization of a subspecies from Europe with an American form may have produced the invasive morph, which is tolerant of oligohaline waters (Besitka 1996). Whereas nekton may use the new *Phragmites* marshes as a source of habitat and food to some degree (Fell and others 1998; Wainright and others 2000), such a large, invasive macrophyte changes the structural features of the intertidal landscape in ways that may reduce or block intertidal access (Weinstein and Balletto 1999). Studies of below-ground processes in Connecticut salt marshes indicate that litter and fine organic-matter accumulation as well as infaunal community structure, all differ in *Phragmites* marshes relative to native salt hay (*S. patens*) meadows (Talley and Levin forthcoming). The ecosystem-level consequences of habitat modifications such as those for *S. alterniflora* and *P. australis* and for invasive mangroves (Cox and Allen 1999) are only beginning to be explored, while wetland managers struggle for effective techniques to control invasive species.

Invasions also reveal the powerful habitat-modifying effects of single-species changes in animal communities, particularly those involving suspension-feeding bivalves. The rapid population explosion of the invasive Asian clam, *Potamocorbula amurensis*, in San Francisco Bay following a long drought led to reductions in phytoplankton and to shifts in planktonic food webs and benthic communities (Nichols and others 1990; Alpine and Cloern 1992). The Asian mussel, *Musculista senhousia*, an invader of tidal wetlands along much of the US Pacific Coast, has modified sediments through cocoon construction and mat formation in ways that both enhance (on small scales) and reduce (on large scales) the diversity of the native sediment fauna (Crooks 1998a, b; Crooks and Khim 1999). Another habitat modifier, the invasive isopod, *Sphaeroma quoyanum*, burrows heavily into salt marsh edge and channel bank habitat, weakening sediments and hastening bank collapse, causing considerable loss of marsh surface in San Diego and San Francisco Bays (Talley and others 2001). As species loss or invasions occur, comparative studies can test hypotheses regarding unique functions of single species or guilds. Changes in species that are habitat modifiers are predicted to have especially significant consequences.

To what extent have invasions originating in marine CTZs spread to and affected the function of adjoining ecosystems? Several examples show that CTZs can be important gateways for species invasions. The spread of the zebra mussel (*Dreissena polymorpha*) across western Europe in the 19th century began in estuaries such as the Rhine, the Elbe, the Thames, and the Frisches Haff (Oderbrecht 1957), which were centers for the shipping activities that carried zebra mussels. The species then moved into fresh waters, where it has been shown to affect many aspects of ecosystem function (See for example, MacIsaac 1996; Strayer and others 1999). Likewise, the Rio de la Plata estuary was the site of the initial introduction to South American rivers of the invasive bivalves *Corbicula fluminea* and *Limnoperna fortunei* (Morton 1997; Amestoy and others 1998). These species, which are capable of strong effects on freshwater ecosystems (Morton 1997; Darrigran and others 1998; Ricciardi 1998; Strayer 1999; Hakenkamp and Palmer 1999), are beginning to spread further into the continent. The Chinese mitten crab (*Eriocheir sinensis*) burrows into muddy marsh banks, destabilizing drainage channels in wetlands. Mitten crabs are highly migratory, and their life cycle may take them into fresh waters thousands of kilometers from the sea. Mitten crabs have been introduced to Europe and San Francisco Bay (Cohen and Carlton 1997) and probably will eventually spread along both coasts of North America.

These compelling examples notwithstanding, it appears that most invasions of estuaries do not spread to adjoining fresh or marine waters. For example, Ruiz and others (1997) noted that although San Francisco Bay contains 212 exotic species, fewer than 10 are known from the nearby open coast. Similarly, of the 113 exotic species known from the freshwater part of the Hudson River basin, only semi-aquatic plants that were brought into the basin with solid ballast are thought to have originated from the coastal CTZ. Presumably, important environmental differences between estuaries and fresh or marine waters—especially salinity—prevent most successful estuarine invaders from spreading into other habitats. It is possible that species changes may occur more readily and have a more pronounced effect on ecosystem functioning in the low-diversity CTZ habitats than in adjacent, more diverse systems.

Overfishing

Fishing removes large numbers of secondary producers, and the effects of overfishing reverberate through the food web and the abiotic environment. The removal of oysters from Chesapeake Bay by overfishing, habitat loss, and disease has reduced the productivity of that system and contributed to low water quality (Newell 1988; Ulanowicz and Tuttle 1992; Dame and Allen 1996). No other filter feeder has filled the function of the oyster in Chesapeake Bay, suggesting that low functional redundancy is related to significant change in usable production for humans.

Many species that derive their food from coastal wetlands (for example, shrimp and fishes) can have an impact on the structure and function of CTZs, while their abundance may be affected by fishing activities in another habitat (Houde and Rutherford 1993). The use of fishing gear (for instance, benthic trawls) often causes considerable sediment disturbance, which may result in large-scale changes to the structure of the benthic community (Dayton and others 1995; Thrush and others 1998). The high structural complexity of vegetated coastal wetlands can restrict the use of trawls and many other types of fishing gear, but fishing gear can damage vegetation. In addition, fishing impacts on adjacent estuarine waters can affect wetland ecosystems. Improved understanding of the effects of overfishing on biodiversity and ecosystem function may be acquired by restricting fishing access in certain areas; US National Estuarine Research Reserves would be logical choices to receive such protection.

Alteration of Habitat

CTZ environments are subject to constant change due to both natural processes and anthropogenic activities. Areal loss and physical and chemical alterations of marine CTZ habitats have occurred following dredging; the construction of ditches, channels, bulkheads, impoundments, roads, and railways; and large-scale changes in watershed land use. These activities can substantially modify the depth, direction, and velocity of water flows, as well as altering the transport and redistribution of sediment and other materials. These types of changes are most likely to affect the biodiversity of species that rely heavily on water flow (and salinity) or drainage to maintain suitable habitats. Vascular plants such as those discussed earlier (for example, mangroves, Pacific Cordgrass [*S. foliosa*], or the reed *P. australis*) and filter-feeding species are most likely to be affected directly, but numerous indirect effects are likely to reverberate throughout the ecosystem.

Habitat loss, degradation, fragmentation, and reduced connectivity to upland or ocean settings will reduce biodiversity. California salt marshes currently support several endangered bird species and one endangered plant species; their endangered status is directly attributable to loss of marsh area and fragmentation of existing patches (Fink and Zedler 1990; Powell 1993, 1996; Zembal and Fancher 1988). To date, four extinctions of coastal species have been documented (Carlton 1992). These include the salt marsh gastropod *Cerithidea fuscata*, the eelgrass limpet *Lottia alveus*, a Chinese periwinkle *Littoraria flammea*, and the limpet *Collisella edmitchelli*. If the destruction of marine CTZ habitat continues, many more local and global extinctions can be expected, leading to a gradual decline in CTZ biodiversity.

Climate Change

Marine CTZs in most parts of the world have for some time experienced a rising sea level, not only as a result of the 1.5 mm yr^{-1} increase in the level of the world's oceans witnessed over the last century but also due to regional subsidence of coastal landforms (Hatton and others 1983; Gornitz 1995). A few CTZs in areas of regional uplift of landforms have actually experienced a fall in relative sea level (Redfield 1965), but the overall rate of sea level rise is projected to accelerate due to thermal expansion of the ocean volume and the melting of some continental glaciers such that globally the level of the sea will be approximately 0.7 m higher by the end of the 21st century (Warrick and others 1995). Although sea level rise is a complex phenomenon and coastal ecosystem responses will be affected by material supply (peat and mineral sediments) for aggrading soils, shoreline erosion, and retreat over uplands, it is generally expected that tidal wetlands will decrease in extent and that the intertidal gradients within wetlands will narrow (Warrick and others 1995). We predict that biological diversity in tidal wetlands will decline as a result of compression of the wetland gradients, resulting in less effective trapping of sediments and nutrients.

Changes in temperature and precipitation regimes strongly influence the structure of sediment communities. Large fluctuations in these parameters occur during El Niño–La Niña regime shifts along the eastern Pacific (Quinn and others 1987), but other drought cycles occur as well. For intertidal wetlands, increased seasonal temperature, stress, and desiccation may reduce biodiversity (Nordby and Zedler 1991). Some warm-water CTZ taxa may expand their range poleward, whereas cold-water species may become locally extinct; in both cases, resulting shifts in community composition may have cascading effects. The lack of suitable habitat may preclude poleward shifts in some instances, resulting in complete loss of the CTZ habitat in that region. Regionally, warming could increase community metabolism and the cycling of nutrients within sediments; but this effect may be countered by changes in bioturbation, ventilation, disease, and disturbance by predators. Regional changes in salinity accompany altered precipitation regimes. In Laguna Madre, Texas, salinity shifts have altered seagrass composition and led to reductions in the quality of nursery habitat for fishes (Tolan and others 1997).

As the atmosphere of Earth warms, evaporation, and consequently precipitation, will also increase. Models that consider both precipitation and evapotranspiration suggest that significant changes in the amount and timing of river runoff into estuaries or onto continental shelves may occur during the 21st century as a result of global climate change. However, uncertainty is high even with regard to the direction of the change. Increases in freshwater runoff and in extreme runoff events will deliver more nutrients and sediments to the coast and lower salinity. However, the regional extraction of fresh water to support growing human populations may ameliorate or even reverse the expected shifts. Importantly, changes in nutrient flux, sedimentation, and salinity in either direction could reduce the biodiversity of estuarine sediments and diminish the role of sediment communities in regulating sediment transport and nutrient cycling.

Global climate change also may alter coastal currents causing, for example, the kind of regime shifts seen as a result of shorter-term climatic variations related to the El Nino Southern Oscillation or the North Atlantic Oscillation and increases in the intensity or frequency of tropical and other storms (McGowan and others 1998; Henderson-Sellers and others 1998). These major physical changes also have obvious consequences for the diversity and structure of biological communities (McGowan and others 1998; Smith and Kauffman 1999), although the effects on marine CTZs have yet to be fully determined.

CONSEQUENCES OF SPECIES LOSS FOR MARINE CTZs

Declines in biodiversity may establish feedback loops that ultimately accelerate diversity loss. For example, there often appears to be a positive relationship between species diversity and resistance to invasion in some other ecosystems (Elton 1958; Usher 1988; McGrady-Steed and others 1997; Tilman 1996; Naeem and others 2000). Experiments with estuarine epifauna suggest that reductions in diversity can increase assemblage susceptibility to invasion by exotic species, in this instance by increasing the availability of free space (Stachowicz and others 1999). Subsequent invasions by exotics are likely to cause further loss of diversity. Similar experiments have yet to be conducted for CTZ sediments. However, a common explanation for the high invasibility of Pacific estuaries is their relative youth and low diversity of native species (Carlton 1979). We hypothesize that, as with invasions, the loss of diversity makes CTZ ecosystems more susceptible to the long-term, destabilizing effects of eutrophication, nonnutrient pollutants, overfishing, climate change, and other forms of habitat alteration. Facilitative or mutualistic interactions—which appear to be particularly important in physiologically stressful settings such as CTZs—may collapse due to the loss of one or more component species, causing further reductions in diversity. Finally, primary production may decrease with species losses because species diversity can often promote more efficient resource utilization and thus higher rates of primary production (Tilman and others 1997; Loreau 2000).

We predict that major shifts in marine CTZ ecosystem functions will occur when species losses lead to the following conditions:

Table 2. Hypotheses Addressing Diversity Influence on Ecosystem Function of Marine Coastal Transition Zones

- Where redundancy is low but importance of function is great, biodiversity plays a particularly important role in ecosystem function.
- Species change, either loss or addition, will have a more profound effect in low-diversity than high-diversity systems.
- Where disturbance is great, in the form of frequent or unpredictable catastrophic events (either physical or biotic), diversity has a key stabilizing role, affecting resilience, resistance to invasion, and the importance of mutualistic interactions.
- Anthropogenic threats to diversity create an array of large-scale experiments to test the following hypotheses:
  Nutrient-driven shifts in biodiversity affect food web complexity and ecosystem stability.
  Eutrophication- or contaminant-induced shifts in sediment functional groups (toward deposit feeders) alter habitat use and production by migrant CTZ species.
  Overfishing changes community structure in ways that alter key ecosystem functions.
  Species invasions occur more readily in low-diversity systems and themselves exacerbate diversity loss.
  Climate change alters CTZ diversity in ways that affect transport functions for nutrients, sediments, water and contaminants.
- Changes in vascular plant, suspension feeder, and large-bioturbator diversity are most likely to affect key CTZ functions (production, decomposition, nutrient cycling, and transfer processes).
- Facilitative interactions, which are prevalent in the physiologically stressful CTZ, will collapse with loss of diversity, further disrupting ecosystem function.

1. A reduction in the number of types of food items such that the nutritional needs of CTZ species are no longer met (see, for example, Snelgrove and others 2000), or obligate food resources are lost
2. A removal of large bioturbators that rework sediments and enhance decomposition and regenerate nutrients
3. A loss of suspension-feeding bivalves that regulate particle removal from the water column and flux to the bottom
4. A change in above ground plant, reef, or mat structure such that flow, nutrient, and sediment dynamics are altered
5. A collapse of facilitative or mutualistic interactions in marine CTZs

Any of these changes will almost certainly affect the fates of CTZ nutrients, sediments, organisms, and pollutants.

RESEARCH DIRECTIONS

The current state of our understanding of the role of biodiversity in CTZ ecosystem function is still in its infancy. There are important gaps in our knowledge of organisms and their functions within sediment ecosystems, particularly as concern fungi, protists, and some meiofauna (Snelgrove and others 1997, 2000; Palmer and others 1997, 2000; Wall and others 1997). For example, we do not know if rates of organic matter decomposition and nutrient recycling within CTZs depend on the species diversity of microbes. Although more is known about larger taxa, even for these species many questions remain concerning links between biodiversity and function.

Despite the many gaps in our knowledge, there is sufficient information to generate testable hypotheses that can guide future research on the roles and functioning of marine CTZs (Table 2). Where redundancy is low but importance of the function is great (see Table 1), biodiversity may play a key role in ecosystem function. Because the topic of biodiversity and ecosystem function has proven so controversial, in part because it is difficult to study empirically, relatively simple systems may be ideal for future work. The relatively low species richness in marine CTZs provides a model system for testing hypotheses about the role of species richness and specific species in ecosystem function. Species change, through either loss or addition, is predicted to have a more profound effect in very-low-diversity systems than in high-diversity systems. As species changes occur regionally, comparative studies can test hypotheses regarding functional redundancy and the uniqueness of single species. Similarly, where disturbance is great, in the form of frequent or unpredictable catastrophic events (either physical or biotic), diversity may have a key stabilizing role. Theoretical work has suggested that the relation between species diversity and ecosystem function may vary with disturbance regime (Cardinale and others 2000). Within CTZs, a range of disturbance regimes (flood, drought, storms, species range shifts, invasions, mass mortality) allows comparative tests of the effects of diversity on resilience, resistance to invasion, and the importance of mutualistic interactions.

Anthropogenic threats to diversity could be viewed as large-scale experiments allowing tests of whether (a) nutrient-driven shifts in biodiversity affect food web complexity and ecosystem stability, (b) eutrophication–or contaminant-induced shifts in sediment functional groups (toward deposit feeders) alter habitat use and production by migrant CTZ species, (c) overfishing changes community structure in ways that alter key ecosystem functions, (d) species invasions occur more readily in low-diversity systems, and themselves exacerbate diversity loss, and (e) climate change alters CTZ diversity in ways that affect transport functions for nutrients, sediments, water, and contaminants.

There are linkages among factors threatening biodiversity (Table 1), and these factors influence suites of species, which themselves have complex interactions. Watershed-level changes in adjacent or even distant ecosystems affect the transfers of energy, water, and particles, with consequences for CTZ diversity and function. A combination of mensurative and manipulative approaches, including those that take advantage of ongoing natural and anthropogenic change, will be required to unravel the complex relationships between diversity and function within marine CTZs. Created or restored habitats in CTZ systems may be particularly suitable for the manipulation of diversity (Ewel and others 2001).

Much can be gained by addressing similar questions and using comparable methods to facilitate comparisons across geographic areas and across different types of critical transition zones. Many of the issues identified here are relevant to CTZs in riparian or groundwater settings (Bardgett and others 2001). Several programs have shown how the cooperation of freshwater, terrestrial, and marine scientists can enhance our understanding of transition-zone transfers of material and energy. An investigation in the South Pacific contrasts landscapes from mountains to coral reefs on islands across a gradient of increasing distance to the mainland (Mueller-Dombois 1998, 1999). The trans-European LITUS study of exposed sandy beaches will evaluate the biodiversity of infauna and show how it is affected by human use and the consequent effects on ecosystem function. Continued cross-disciplinary collaboration among ecologists, ocean and atmospheric scientists, and social scientists is needed to further characterize the linkages among species diversity, ecosystem function, and human activities.

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