



*Suffolk County Vector Control & Wetlands
Management Long Term Plan & Environmental
Impact Statement*

DRAFT

TASK 3: LITERATURE SEARCH

*BOOK 9, PART 2: SALT MARSH FUNCTION
AND VALUE*

Prepared for:

**Suffolk County Department of Public Works
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**SUFFOLK COUNTY VECTOR CONTROL AND WETLANDS MANAGEMENT
LONG - TERM PLAN AND ENVIRONMENTAL IMPACT STATEMENT**

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EXECUTIVE SUMMARY

Salt marshes are often said to fill certain ecological and physical functions and thereby provide certain environmental values. This report describes current understandings regarding functions provided by salt marshes, and thereby provides context for the description of the values that may be ascribed to these systems.

Early studies of salt marshes often ascribed ecological functions to salt marshes on the basis of little to no data. Much more research has been conducted on salt marshes since the 1960s, but the accumulation of information has not necessarily resolved all issues associated with the functions provided by salt marshes.

Ecological functions include high productivity, energy transfer, and nursery and other habitat values. The productivity of marsh grasses is high, and is augmented by algal production. Because grasses are highly refractory, algal production is receiving attention as the primary means for trophic transfer of energy. The transfer of energy from the marsh is perceived of as occurring primarily through transient nekton, as opposed to the earlier hypothesis that transfer of plant matter directly linked marshes and estuary. Trophic transfer is less efficient than the direct export of the results of photosynthesis, and so the quantitative importance of marsh production for estuarine food web dynamics has been reduced. Nonetheless, because estuaries have been quantified as consuming more than they produce, salt marsh exports are clearly essential to the health of associated estuaries. Besides providing foraging opportunities for many adult finfish, and refuges from predators for juvenile species, marshes also serve as necessary habitat for certain bird species, and important feeding grounds for many others.

In addition, in settings where human effects have stressed and/or damaged natural estuarine systems (particularly the linkage among sea grasses, benthic infauna, and plankton abundances), marsh systems may serve important surrogate roles because marsh plants cannot be shaded by phytoplankton blooms and so remain as refugia for early life stages for many organisms, and filter feeders populations are not as extensively harvested so that they remain to crop down phytoplankton populations.

Marshes can serve as important coastline buffers. The vegetation found on the marsh means that they often accrete sediment during storm events whereas sandier coasts erode under the same

stresses. It is possible that the vegetated nature of the marshes also ameliorates coastal flooding, although this notion is less well supported by rigorous studies.

In addition, it is thought by some that marshes may improve coastal water quality. Data to support this is mixed, and appears to be site dependent. One important water quality aspect of salt marsh functioning may be short term nutrient buffering. This is more important given the human-derived nutrient enrichment of coastal waters. Salt marshes have been characterized as being sinks for nutrients when surrounding coastal waters are enriched, and sources of nutrients when concentrations decrease. This may serve to limit eutrophication impacts associated with pulsed nutrient inputs.

These functions of the salt marsh help determine the value of marshes to society. The recognition of the importance of the environmental features associated with the coastal zone is growing among the general population, and has led to political decisions to emphasize coastal zone planning. The positive aesthetics of salt marshes, little valued at one time, have also experienced a resurgence. The rise of environmental economics, whereby explicit valuations are created for ecosystem processes (largely by determining the costs to replace these functions with man-made alternatives), has the potential to further quantify and define the benefits provided to society by these natural systems

1 INTRODUCTION

Salt marshes represent an important coastal ecosystem by serving as a transition area between land and sea. In particular they play a vital role in helping maintain healthy estuaries and their adjoining marine systems. This role was not fully recognized until the middle of the 20th century, and thus early management practices of salt marshes were not well informed (Dale and Hulsman, 1990). However, extensive research since this time has revealed many initial misperceptions in the mechanisms of marsh functioning, and even today many contributions remain poorly quantified (Childers et al., 2000; Kennish, 2001; Rapport et al., 1998). Nevertheless, the estimation of salt marsh value remains high among both the public and research communities (Costanza et al., 1997). This is easily reflected in the myriad functions and values that salt marshes have come to embody in the literature, including everything from support of biological systems to physical shoreline protection to an array of recreational uses (Farber and Costanza, 1987). These functions are discussed in detail in the following sections, with the goal of explaining their

- Mechanisms and processes
- Relative significance to coastal ecosystems
- Broader societal and environmental value

In historical times our perception of salt marsh value and function has shifted with changes in demographics and land-use patterns. Historically, Native Americans recognized the abundant finfish and shellfish resources associated with salt marshes, and regularly established settlements near them (Rozsa, 1995). Following European settlement positive regard for salt marshes continued, with colonists extensively utilizing high marsh grasses for livestock fodder and bedding. This practice continued well into the 20th century and gave rise to the English name for *Spartina patens* – salt marsh hay. However, with improved transportation and increasing middle-class wages of the early 1900's, significant populations shifted toward U.S. shorelines both permanently and for seasonal recreation. The demographic change gave the wealthier middle and upper classes its first widespread exposure to prodigious populations of salt marsh mosquitoes and their related vector-borne diseases. Thus ensued the now long-standing approach of grid ditching salt marshes to mitigate this problem, and as a consequence an increasingly negative view of salt marshes and their role in 'modern' society. With diminished

value through this time, and the continued pressure of rapid coastal development, salt marshes were extensively dredged and filled in the 1950s and 1960s.

Concurrent with the widespread destruction of marsh lands, researchers were completing the first ecosystem-scale investigations of these systems (e.g., Odum, 1961; Teal, 1962). Seminal publications generated from these efforts, including popular books like John and Mildred Teal's *Life and Death of the Salt Marsh* (1969), contributed significantly to the 1960s environmental movement and a renewed appreciation for coastal wetlands. In large part, these early works comprise the basis for today's perception of marsh value and function. Following major amendments to the Clean Water Act in 1972, newly legislated protection of coastal wetlands, mainly against dredging and filling, once again placed humans in a stewardship role and spawned the modern era of wetlands research and management. Despite their protected status, though, pressures on coastal wetlands remain high with 70 percent of the world's population living within a day's travel of the coast (Dale and Hulsman, 1990). In addition, more than 37 percent of the human population is concentrated in coastal areas, and two-thirds of the world's largest cities are found in coastal areas (Crooks and Turner, 1999; Small and Nicholls, 2003). These statistics show the tremendous reliance people place on coastal systems and the inevitable stress imparted upon them. It is therefore important to understand, from a scientific perspective, exactly how salt marshes function in order that their diverse functions are properly protected and preserved.

It remains widely accepted by the scientific community, as well as by much of the general public, that salt marshes are highly valued ecosystems (e.g., Costanza et al., 1997). However, much of the early work upon which these perceptions are based have proven to be only partially correct at best. For example, a review article by Scott Nixon (1980) begins with a quote from one of John Teal's early publications that continues to be widely cited,

... the tides remove 45% of the production before the marsh consumers have a chance to use it and in so doing permit the estuaries to support an abundance of animals.

This statement suggests that large amounts of organic matter being exported from salt marshes is what makes the high level of secondary production of estuaries possible. Nixon (1980) says of this quote that at the time it was written it was unsupported by any direct measurements and today provides an incorrect assessment of a salt marsh's role in estuarine processes. It has been

since shown that much of the marsh production ‘exported’ to an estuary is not from the physical transport of detritus, but rather from

- a) previously underestimated diatom production on marsh and creek surfaces
- b) by in-situ secondary production via fungal and microbial activity

(Kreeger and Newell, 2000; Sullivan and Moncreiff, 1990)

Thus, the significance of Teal’s original estimation remains largely valid, yet the mechanisms are entirely different. In reviewing other literature, many less specific, but similarly unqualified, terms continue to be used in describing salt marsh functions. For example, Turner et al. (1999) describe direct uses of estuarine systems to include fish, recreation, transport and navigation, and the indirect values to include flood control, storm protection, nutrient cycling, waste assimilation, sedimentation, habitat loss reduction, and groundwater protection. Similar lists are widely reported, yet all of these contributions remain largely unquantified and poorly understood. One final example comes directly from the US Environmental Protection Agency report on *Wetlands and West Nile Virus*, which states that the function of wetlands is

to provide a home for natural mosquito predators, water purification, floodwater retention, wildlife habitat, recreational space, and educational opportunities.

This report further explores the various functions of salt marshes by taking an organizational approach much like that of Dale and Hulsman in their 1990 review article. These publications organize the functioning of salt marshes into the categories of biological functions, physical functions, and cultural values. Similarly, this literature survey has been organized into the same structure of these publications. In each of these reports on the role of salt marshes, the answer to two fundamental questions are sought:

- 1) Why are salt marshes important?
- 2) How should they be functioning?

The separation of these simple questions is important and highlights a distinction that needs to be made in the perception of marsh systems – notably that ‘value’ and ‘function’ are discrete entities and should be considered as such. Value is a human-oriented concept involving politics, economics, emotion, and aesthetics, whereas function is a mechanistic concept rooted in natural

processes and understood through the scientific method (Costanza, 2000; Costanza, 2003). The importance in distinguishing these terms is several fold:

- 1) our understanding of marsh function remains far from complete, so there is a potential pitfall in linking value with our changing views of how a marsh functions;
- 2) similarly, the function of individual marshes itself varies as the marsh evolves and land use, water quality, and other related forcings change.

In reality, salt marsh value and function are likely to remain interrelated, but this report attempts to make distinctions between the two where appropriate.

2 ECOLOGICAL FUNCTIONS

The primary ecological functions provided by salt marshes are recognized as high productivity, food-web dynamics (energy transfer), and protective habitat. Primary production by salt marsh grasses has long been known to be among the highest of any floral community in the world (Mitsch and Gosselink, 2000). In addition, it is now recognized that algal and phytoplankton production in salt marshes contribute significantly to overall rates of carbon fixation (Childers et al., 2000). Secondary production through fungal and microbial activity is another important process with regard to marsh/estuarine food-web dynamics (Newell, 2001a; Newell, 2003). This complex trophic transfer is recognized as another important ecological contribution of salt marshes, particularly when considered with nutrient cycling and hydrological exchange in a wetland. Salt marshes also provide protective habitat for many species of birds, fish, and invertebrates. In particular salt marshes are recognized as essential habitat for migratory shorebird and waterfowl species, as well as nursery grounds for finfish and shellfish which eventually make their home in the estuary (Mitsch and Gosselink, 2000). Owing to significant physical alterations to marshes and adjacent habitats, there is concern with respect to the declining ability of these systems to provide essential habitat for species.

2.1 Salt Marsh Productivity

Salt marshes are highly productive ecosystems with rates of 2000 to 8000 g/m²/yr that are comparable with those of subsidized agriculture (Mitsch and Gosselink, 2000). Although they occupy only 0.4 percent of the world's area, salt marshes are responsible for 2.3 percent of its net productivity (Dale and Hulsman, 1990). Traditionally, focus has been placed on vascular plant production – the seasonal regrowth of marsh grasses. With above-ground production rates of 400 to 1000 g C/m²/yr typical for Atlantic coast marshes, the grasses dominate total biomass production. However, about 75 percent of this biomass comprises refractory cellulose that is indigestible for most marsh grazers, and thus not directly available to higher trophic levels. There are also significant limitations on availability for the remaining 25% of vascular plant production, because this labile fraction is highly soluble (Wilson et al., 1986). As a result, this nutritious component of grass production is rapidly lost to the environment following the autumn dieback. Consequently, direct grazing of marsh grasses is not an especially viable life strategy for consumers, because readily digestible material is only available during the growing season, and even then consumption is an inefficient process owing marsh grass's high cellulose content.

Therefore, the mechanism by which abundant salt marsh grass production fuels higher trophic levels is through the secondary production of fungi and bacteria (Newell and Porter, 2000). In addition, edaphic (benthic) algae growing at or near the marsh surface are now recognized to contribute significantly to marsh primary productivity, at rates of 25 to 140 percent that of their vascular plant counterparts (Sullivan and Moncreiff, 1990). This algal biomass is highly nutritious and thus directly available for grazing, rather than needing to involve microbially-mediated secondary production as for the grass biomass.

2.1.1 Vascular plants – the marsh grasses

Although primary production by marsh grasses is generally high, it varies greatly with such environmental factors as latitude, tidal amplitude, salinity, and nutrient inputs. Latitude controls length of the growing season and number of daylight hours, which within the mid-Atlantic/New England region is not tremendously different. However, the latter factors vary considerably at both regional (10^4 - 10^5 m) and local (10^1 - 10^3 m) scales, resulting in strongly heterogeneous patterns of production. Although spatially complex, some generalizations can be drawn. For example, it is widely reported that rates of productivity are lower in low tidal amplitude and low salinity settings, as compared with their higher tidal and salinity counterparts (Odum, 2000). On Long Island, this phenomenon is observable when comparing the tall-form *S. alterniflora* that dominates mesotidal settings in Jamaica Bay and North Shore bays versus the short-form *S. alterniflora* that typifies microtidal settings in Great South Bay and Peconic Bay. Originally suggested by EP Odum (1980), this tidal subsidy hypothesis states that higher tidal amplitudes favor

- 1) increased sediment flux into the marsh
- 2) flushing and oxygenation of porewaters
- 3) enhanced nutrient flux

By contrast, reduced energy and flushing in microtidal salt marshes can limit nutrient delivery and favor the build-up of pore water sulfides toxic to plants. A comparative study of *S. alterniflora* along New England coasts confirmed that indeed peak biomass varied linearly with tidal range, increasing from less than 600 g/m²/yr for tidal amplitudes less than one m to production over 1200 g/m²/yr in settings where tides exceeded two m (Steever et al., 1976).

Observations of above-ground productivity reveal only half the story, although, as marsh plants place a considerable portion of their biomass below ground. Below-ground production is exceedingly difficult to measure, largely because of challenges in separating individual plants and the living from dead biomass in dense marsh peats. Available estimates range an order of magnitude but are centered about reported values for above-ground production, suggesting that rates for above- and below-ground production are comparable. Once again, despite difficulty in quantifying production, general observations can be made regarding how above- and below-ground biomass are partitioned. Specifically, plants tend to put more of their energy into below-ground production when subject to unfavorable soil conditions, resulting in a high root to shoot ratio (Mitsch and Gosselink, 2000). This explains in part why short-form *S. alterniflora* is not reported a priori to be less productive than its seemingly more vibrant tall-form alternate. Also, it is also notable that estimated rates of primary production among the dominant grass species are all comparable, with most studies unable to resolve significant differences between *Distichlis spicata*, *Spartina alterniflora*, *Spartina patens*, and *Juncus roemerianus* (de la Cruz, 1974; White et al., 1978). This report contains few absolute values for primary production, because several authors note that various methods of calculating production yield results five to six-fold different from one another (Linthurst and Reimold, 1978; Shew et al., 1981). Actual rates remain difficult to quantify, and Dale and Hulsman (1990) specifically suggest that there are “major knowledge deficits in the area of measurement and comparison between marshes” with respect to productivity. Nevertheless, the relative trends and patterns described above are generally still considered to be valid, if not very well constrained.

2.1.2 Microphytes – the benthic algae

Among the major discoveries to emerge following the early ecological models of Teal (1962), Odum (1961), and others, one of the most significant is that benthic (edaphic) algae contribute to salt marsh primary production at rates 10 to 140 percent of their vascular plant counterparts (e.g., Sullivan and Moncreiff, 1990; Zedler, 1980). Thus, the availability of labile organic matter for marsh grazers is greatly augmented by algal production, and so by extension it provides energy that fuels higher trophic levels and overall ecosystem vigor. In the mid-Atlantic-New England region, the ratio of benthic algal production to above-ground vascular production is typically 25 to 33 percent (Sullivan and Currin, 2000). However, because most (75 to 90 percent) production by marsh grasses comprises refractory, indigestible material, then the contribution of highly

nutritious benthic algae to metazoan grazing easily matches or exceeds that from the grasses. In fact, the emerging role of benthic algae in salt marsh trophic dynamics has led researchers (e.g., Kreeger and Newell, 2000) to question the long-standing paradigm that salt marshes support detritus-based food webs (i.e., Teal, 1962; Odum, 1961). These algal trophic contributions are discussed in more detail in the following section, but here it is emphasized that despite a lack of a significant visual presence on the salt marsh, microalgae comprise a major, perhaps even dominant, component of salt marsh productivity.

Within these so-called secret gardens of the marsh, the dominant algal groups are diatoms and cyanobacteria, with the former typifying Atlantic coast marshes (MacIntyre et al., 1996; Miller et al., 1996a). The diatoms are dominated by pennate forms that colonize the thin marsh surface layer and adjacent creek banks, as well as wetted surfaces of the marsh grasses. Studies of the microalgal communities reveal numerous genera and colony types, typically distributed along gradients of elevation, wetness, ammonium, and canopy height (Sullivan, 1975; Sullivan, 1977; Sullivan, 1978). Most species were tolerant of wide salinity ranges, and this is not primary control on algal production patterns.

2.1.3 Secondary production – fungi and bacteria

The notion that marshes represent detritus-based ecosystems stems from the estimated 90 percent of vascular plant production that enters the fungal and microbial-mediated detrital loop rather than supporting direct grazers. In Teal's (1962) original energy-flow model, bacterial decomposition was the almost singular pathway for energy transfer to marsh fauna, with as much as 45 percent of organic production being exported to adjacent coastal ecosystems. This view has changed significantly, and what has emerged from subsequent research is

- 1) that fungi are major decomposers in the marsh, dominating the breakdown of standing grass stems and
- 2) that a significant component of faunal biomass (25 to 75 percent) is supported not by the detrital loop, but rather by direct grazing of benthic algae and, secondarily, of estuarine phytoplankton from the creek systems

(Allen et al., 1995; Litvin and Weinstein, 2003; Wainright et al., 2000)

Regarding marsh-grass decomposition, the processes of secondary production are now known to occur in the following sequence:

- 1) the highly soluble and labile component of marsh grasses (up to 25 percent of production) is rapidly lost (leaked) from dying plant stems during the annual fall dieback, and much is presumably exported as dissolved organic matter to the adjacent estuarine system via tidal exchange;
- 2) the remaining component of refractory, cellulose-rich organic matter is subsequently decomposed by ascomycetous fungi, as it is present in standing grass stems and wrack deposits;
- 3) further decomposition occurs via aerobic bacteria at the soil surface microlayer, where its biomass is highest on grass fragments that have been shredded by metazoan grazers;
- 4) and finally anaerobic bacteria continue detrital respiration in the subsurface soils, though at a greatly slower rates, which are reflected in the typically high preservation of organic matter in subsurface peats.

For the fungi, standing biomass varies seasonally but reaches a maximum in winter. At that time it may equal 25 percent of live *Spartina alterniflora* biomass, reflecting the major contribution fungi plays in marsh productivity (Newell et al., 2000). This role is further enhanced by its high trophic efficiency, with up to 50 percent of ingested grass being converted to new fungal biomass, as compared with more typical efficiencies of 10 percent (Newell, 2001b). In the summer months, the fungi are least active and productivity may decline to only one tenth the winter rate. This high winter activity of the fungi is opposite to that of the bacterial decomposers, which are most active under the warmer temperatures of summers. Bacterial decomposition rates may be twice those of fungi at that time, but decline significantly to only one-tenth fungal production rates in winter (Wilson and Stevenson, 1980). In this way, the cycle of decomposition begins with the fall die-back as fungi begin degrading the previous season's grass production, then continues the following summer with bacterial degradation of the old grass stems that have been shredded and fallen to the marsh surface. The shredding process is a consequence of gastropods and amphipods that graze on dead grass stems that host the fungi (Mitsch and Gosselink, 2000). Overall these decompositional pathways provide the base for salt

marsh food webs by efficiently converting low-nutrition, cellulose-rich biomass produced by the grasses to a nutritional food source available to a variety of grazers.

2.2 Salt Marsh Trophic Dynamics

That salt marshes are highly productive ecosystems is not disputed – their rates of primary production are among the highest in the world, as are the abundant fauna associated with marsh ecosystems. What is complex and only recently becoming understood are the pathways by which production is passed to higher trophic levels, particularly within the aquatic food web (e.g., Smith et al., 2000). Implicit in this question is the degree to which marsh production supports the broader estuarine and coastal food webs, which is an oft-cited function of salt marsh systems and presumed value to society (e.g., Cicchetti and Diaz, 2000; Deegan et al., 2000). The varied mechanisms of primary and secondary production discussed in the previous section support a similarly diverse grazing community, including largely separate aerial and aquatic food webs.

2.2.1 Aerial Food Web

On the aerial side insects are the dominant grazers, and unlike the detritus-based aquatic food web, insects are direct consumers of the marsh grasses. They mainly crop living and newly dead biomass. The insect grazing community includes a diversity of grasshoppers (*Orchelimum* spp.), plant hoppers (*Prokelisia* spp.), weevils (*Lissorhoptrus* spp.), and other insect groups that can collectively exceed 80 species in Atlantic coast marshes (Pfeiffer and Wiegert, 1981). Although they consume only a small percentage of total grass production (less than 10 percent), their abundance is high and supports a short, but vibrant, food chain. In this chain, the numerous grazing insects are prey for a significant population of marsh-dwelling spiders. In turn, these spiders, together with their insect prey, serve as primary food sources for passerine birds, including marsh-obligate species of wrens (*Cistothorus* spp.) and sparrows (*Ammodramus* spp.), as well as facultative users like red-winged blackbirds (*Agelaius phoeniceus*) and several swallow species (*Hirundo rustica*, *Tachycineta bicolor*, and *Stelgidopteryx serripennis*). The insects and spiders may also contribute to the diets of wading and shore-bird communities, particularly the marsh-obligate capper rail (*Rallus longirostris*). Beyond these major interactions, the only other linkage of this insect-bird-dominated food chain with the marsh community is through egg predation by rodents and raccoons (Urban, 1970 Mitsch and Gosselink, 2000).

Two other groups of herbivores associated with salt marsh grazing are the waterfowl and several species of rodents. For waterfowl, their use of wetland habitats can be intense but also highly seasonal and spatially discontinuous. In general, waterfowl grazing in Atlantic salt marshes is concentrated during Spring, when large migrant flocks exploit tender and relatively more nutritious grass shoots and tubers. Some studies have shown that repeated and intense herbivory of this type can lead to plant dieback and marsh loss; however, this effect is not well quantified beyond very local settings (Evers et al., 1998; Miller et al., 1996b; Smith, 1983). For the rodents, primary grazers are the muskrat (*Ondatra zibethicus*) and nutria (*Myocastor coypus*). Unlike most waterfowl, these rodents are permanent marsh residents and can maintain grazing pressure throughout the year on a specific marsh site (Bellrose, 1950). In southern Atlantic and Gulf Coast marshes, this has led to widespread eat outs similar to those created by intense waterfowl herbivory (Carter et al., 1999). However, only the muskrat is present in New England marshes, where it is typically not found at such high densities that marsh habitats become degraded (Simpson and Boutin, 1993). In terms of food-web dynamics, both waterfowl and rodents play important roles in salt marsh herbivory, but neither support any significant predator population.

In summary, the trophic pathways of aerial marsh habitats are short, direct, and based on direct herbivory of marsh grasses. This is in strong contrast with the aquatic food web, which is large, complex, and based mainly on algal growth and secondary fungal and bacterial production. In addition, there is relatively little trophic exchange between the aerial and aquatic food webs. The only major pathway of exchange is through bird predation of aquatic organisms, including the consumption of finfish, crustaceans, mollusks, and other macroinvertebrates by waders (*Ardeidae* and others), shorebirds (*Charadriidae* and others), and gulls and terns (*Laridae*).

2.2.2 Aquatic Food Web

The aquatic food web is much more complex than the aerial ecosystem. The aquatic food web begins with a diverse suite of meiofaunal and macrofaunal grazers. Encompassing several taxonomic orders, the aquatic grazing community feeds on a rich marsh-surface broth that comprises variable proportions of edaphic algae and the fungal and bacterial biomasses associated with decomposing grasses. The meiofaunal grazers are dominated by nematodes but also include significant proportions of protozoa, copepods, annelids, rotifers, and larval-stage

macroinvertebrates (Fleeger, 1978; Yozzo and Smith, 1995). This meiofaunal community has not been well studied, and relatively little is known of the abundances, distributions, and total biomass of the various species (Bell, 1979). In contrast, the macrofaunal grazers are a better known group and include most aquatic invertebrates and vertebrates under about 20 cm in size. The invertebrates dominate this groups in terms of numbers and biomass, including generally abundant organisms such as surface-gleaning gastropods (e.g., *Littorina* spp., *Melampus* spp., and *Ilyanassa obsoleta*), filter-feeding bivalves (e.g., *Geukensia demissus* and *Crassostrea virginica*), and polychaete worms of the low marsh and creek banks (Mitsch and Gosselink, 2000). Other important grazers include a variety of crabs (eg., *Uca* spp., *Sesarma* spp., and *Callinectes sapidus*), fish (e.g., *Fundulus* spp., *Cyprinodon* spp., and *Menidia* spp.), and shrimp (*Palaemonetes* spp.).

Among the macrofaunal grazers, most are not true herbivores but are rather omnivorous and prey readily on the meiofaunal community described above. This is not surprising with regard to many crabs and finfish, but even passive filter feeders such as ribbed mussels (*Geukensia demissus*) have been shown to consume 35 to 80 percent heterotrophic organisms in their diet (Kreeger and Newell, 2000; Kreeger and Newell, 2001). Other unexpected consumers of the meiofauna include several surface-gleaning gastropods and the polychaete worms of low-marsh and creek soils (Kikuchi and Wada, 1996; Kurata et al., 2001). The point that food sources other than detritus (e.g., algae and heterotrophs) comprise a major portion of grazer diets is an important one and challenges the long-held notion that marshes are detritus-based ecosystems (Montague and Weigert, 1990; Pfeiffer and Wiegert, 1981). This line of research has largely been pursued using stable carbon and sulfur isotopes, which are fractionated differently in the unique photosynthetic pathways of marsh primary producers (Haines, 1976). These signals are preserved in the organic matter that is subsequently consumed by grazers, thereby recording relative contribution to their food uptake. Most research results are complicated and reflect the complexity of marsh food-webs, but in general studies have shown that *Spartina*-based food sources comprise less than 50 percent (commonly much less) of the diet of marsh-obligate aquatic grazers (Stribling and Cornwell, 1997). Rather, benthic algae and phytoplankton most frequently comprise the dominant component of their diets (Kreeger and Newell, 2000).

At the top of the aquatic food web, there are actually few true carnivores. The carnivores are probably limited to the diamondback terrapin (*Malaclemys terrapin*) and stickleback fish (*Gasterosteus* spp.), among the marsh obligate species (Whitelaw and Zajac, 2002). Most top predators in the salt marsh are transient and more associated with adjacent aerial and marine food webs (e.g., birds and marine fishes and crabs, respectively) (Bildstein et al., 1982; Fitz and Wiegert, 1991; Weinstein et al., 2000). Without many organisms at the higher trophic levels, the aquatic food web is in some ways relatively simple, primarily consisting of producers, meiofaunal grazers, and macrofaunal omnivores. However, great complexity is introduced in the aquatic food web because each trophic level is taxonomically and physiologically diverse. These levels include:

- 1) vascular and algal primary producers, and bacterial and fungal secondary producers
- 2) metazoan, protozoan, and larval meiofaunal grazers
- 3) crustacean, molluscan, and annelid invertebrates and fish vertebrates.

Thus, the basic aquatic food-web pathways are:

- 1) During Fall die-back of marsh grasses, up to 25 percent of the season's primary production is quickly released to the environment as dissolved organic matter. The fate of this material is not well known, but it most likely goes to bacterial secondary production as almost no other organisms could utilize dissolved food sources. In a well-flushed marsh system, much of this dissolved organic matter presumably enters the adjacent estuary and is consumed by bacterioplankton.
- 2) Edaphic algae, now known to be a major component of marsh primary production, have also been shown to comprise 12 to 17 percent of the food consumed by the ribbed mussel. Furthermore, stable isotope studies show that the diet of most marsh grazers is not dominated by *Spartina*-based production, but rather by edaphic algae and phytoplankton.
- 3) Diverse meiofauna are the dominant grazers of the marsh surface 'broth', which comprises admixtures of algal, fungal, bacterial, and vascular plant biomass. The meiofauna, include nematodes, protozoans, and the larvae of macroinvertebrates. Among the macrofaunal grazers, both invertebrates (crustaceans, mollusks) and vertebrates

(finfish) are well represented. Most of these animals are also omnivorous and prey directly and indirectly on the abundant meiofaunal community.

- 4) Among marsh-obligate organisms, there are few exclusively predatory species that can be considered to top the food web. The closest to being top-carnivores among marsh specialists are the diamondback terrapin and stickleback fishes. More typically the top salt marsh predators are transient consumers that spend relatively brief periods on the marsh and are more characteristic of either the aerial or marine ecosystems.

3 ECOSYSTEM FUNCTIONS

Salt marshes play a critical role in estuarine food webs and in the pathways of nutrients to and through estuaries. Habitat structure affects the pathways and efficiency of transfer to higher level consumers in the food web (Hobbie, 2000). The source and amount of organic matter at the base of estuarine food webs is determined by a diversity of processes. For example, marshes can be used as an index of fish and wildlife production, in particular for addressing nursery habitats of economically important fish and shellfish. From an ecological perspective there can be a strong connection between protozoans and fish, because the fish ultimately depend on the food-web pathway that is initiated by the lower trophic level of the protozoa (Hobbie, 2000). Continued study of marsh ecosystems and their relationship with adjacent habitats confirm a prominent role in trophic energy transfers and ontogenetic contributions, but also increasingly reveal complexity and temporal variability in these linkages.

3.1 Benthic-Pelagic Coupling in Estuaries

Estuaries, particularly the broad shallow systems of the Atlantic coast, are among the world's most productive ecosystems in terms of shellfish and finfish yields (Crooks and Turner, 1999). There are many reasons involved in this unique productivity of estuarine systems, and salt marshes play a notable role. First, however, it is useful to understand one of the primary differences between estuarine ecosystems and those of the open ocean. In the open ocean, seabed habitats are largely decoupled from the photic zone because light does not penetrate to the seafloor and water-column stratification limits physical mixing between the surface and deep waters. Therefore, benthic communities in the open ocean cannot graze directly on surface productivity and are relegated to being detritivores, an ecological role that supports comparatively little biomass. In contrast, light in coastal estuaries typically penetrates to the seabed and the water column is often fully mixed by physical processes (Malone, 1992). A twofold consequence is:

- 1) vascular plants (seagrasses) can colonize the seabed because of ample light penetration (Dawes, 1998);
- 2) benthic infauna can graze directly on phytoplankton that are advected to the seabed by water-column mixing, thus sustaining high biomass with this nutritious food source (Nixon, 1981).

A third characteristic of estuaries that contributes significantly to their ecological productivity is an abundant land-derived nutrient supply that helps maintain large stocks of phytoplankton for macrofaunal grazers (Malone, 1992).

Over time, this coupled benthic-pelagic ecosystem is sustainable because filter-feeding benthos limit phytoplankton abundance, which in turn preserves water clarity and light penetration necessary for seagrass proliferation. All of these of these characteristics bear on the higher trophic levels (e.g., fishes), whereby seagrasses provide refuge for juvenile fish and the abundant benthic and pelagic grazing fauna provide valuable food resources for predators (Nixon, 1993; Wolfe, 1986).

Within these vibrant estuarine ecosystems, salt marshes can play a role similar to that of the seagrass communities and contribute significantly to benthic-pelagic coupling. As with their subtidal counterparts, salt marshes are characterized by high vascular-plant production that is further augmented by an substantial component of algal production. With these food resources and sufficient physical mixing (in this case, lateral mixing by tidal exchange), the salt marshes support large populations of filter-feeding benthos like oysters (*Crassostrea* spp.) and the ribbed mussel (*Geukensia demissus*) (Mitsch and Gosselink, 2000). Therefore, salt marshes may contribute to ecosystem health in ways similar to estuarine seabed communities, including:

- providing physically complex grass habitats that serve as refugia for early-life and juvenile finfish;
- support major benthic communities that feed on estuarine phytoplankton and help maintain grazing pressure on these organisms.

The former of these, that salt marshes are an important nursery habitat, has long been recognized and is among the frequently cited benefits (e.g., Targett and Wester, 1985; Weinstein, 1979). However, the latter point of marsh benthos grazing on estuarine phytoplankton has only recently become recognized. One of the best estimates for marsh fauna grazing on estuarine phytoplankton is from a detailed food budget for the ribbed mussel, which revealed that estuarine phytoplankton delivered to the marsh during tidal exchange comprise about one-third of its diet (Kreeger and Newell, 2000). The abundance of such organisms in salt marshes suggests that they can play a large role in filtering estuarine phytoplankton and maintaining water clarity necessary for subtidal seagrass beds.

The characteristics and interactions described above largely refer to healthy marsh-estuarine ecosystems. In reality, most estuaries have experienced major environmental degradation over the past century. Many reasons for this decline are cited, but without doubt myriad anthropogenic pressures have been placed on them in this time (McClelland and Valiela, 1998; Nixon, 1993). Notable among these pressures have been:

- overharvesting of finfish and shellfish (Prins et al., 1997);
- increased nutrient inputs and widespread eutrophication (Pinckney et al., 2001);
- dredging and filling of salt marshes; and spread of diseases, parasites, and exotic species.

Overharvesting of macrofaunal grazers has reduced grazing pressure on phytoplankton at the same time that eutrophication has greatly enhanced primary productivity (Cerrato et al., 2004). In many cases this increased water-column productivity has led to reduced light penetration, enhanced biofouling, and a consequential loss of seagrasses (Short and Wyllie-Echeverria, 1996). Under such conditions the coupling of benthic and pelagic communities breaks down. Typically these changes lead to a shift toward greater bacterial dominance, in both primary and secondary production source estuarine food webs. In contrast to larger phytoplankton such as diatoms, pelagic communities dominated by tiny bacterioplankton introduce more trophic levels into the food web (e.g., microfauna), and therefore less energy is transferred to higher trophic levels (e.g., commercially harvestable macrofauna) (Sommer et al., 2002).

In this modern reality of degraded coastal and estuarine ecosystems, salt marshes play a critical role by providing services similar to those of lost seagrass communities, including protective habitat and water-column filtering. Although they do not fill the same ecological niche, salt marshes are not subject to light limitation (as with subtidal seagrasses), and thus are not as susceptible to losses under common estuarine stresses. It is probable that this stability of salt marshes even under degraded estuarine water quality, make them key to coastal sustainability and restoration. Thus, in such modified settings, salt marshes remain a critical link in the coupled benthic-pelagic communities that typify healthy and productive estuarine ecosystems.

3.2 Outwelling Hypothesis

A longstanding, although widely debated, paradigm of salt marshes has been the outwelling hypothesis that emerged from early salt marsh energy budgets (Teal, 1962; Odum, 1968). This

early work noted that primary and secondary production in salt marshes greatly exceeds respiration demands, leading to the notion that excess nutrients and organics were transported out of the marsh and fueled adjacent estuarine and coastal ecosystems. Original estimates suggested that export was as high as 45 percent of primary production. Such high numbers have major implications regarding the contribution of salt marshes to economically valuable coastal fisheries. Consequently, the hypothesis has been tested often by researchers with widely varying results (see reviews by Nixon, 1980, and Childers, 2000). What emerges after 40 years of investigation is that the general concept of salt marsh outwelling remains largely well supported; however, the mechanisms, rates, patterns, and sources of outwelling have been completely revised and bear little resemblance to the original model.

Two major advances in the outwelling hypothesis have been the identification of

- a) multiple sources of organic production (e.g., Kreeger and Newell, 2001); and
- b) the pathways by which they are exported (e.g., Smith et al., 1984).

As originally conceived, marsh outwelling was believed to comprise the largely passive export of vascular plant detritus to the adjacent coastal system. It is now known that edaphic algae comprise a major component of marsh primary production (Sullivan and Moncreiff, 1990). Further, these edaphic algae have been found to comprise up to 25 percent of suspended estuarine algae (i.e., phytoplankton), indicating that marsh algae can be readily transported off the marsh surface during tidal exchange (MacIntyre and Cullen, 1995). A second source of marsh export to adjacent is that of the ‘soluble organics’ in vascular marsh plants (Alberts et al., 1988). During Fall die-back of marsh grasses, up to 25 percent of the season’s primary production is quickly released to the environment as dissolved organic matter. The fate of this material is not well known, but it most likely goes to bacterial secondary production as almost no other organisms could utilize dissolved food sources. In a well-flushed marsh system, much of this dissolved organic matter presumably enters the adjacent estuary and is consumed by bacterioplankton (Cai et al., 2003).

In terms of export pathways, it was traditionally believed that most energy transfer from marsh to adjacent ecosystems occurred by the direct export of organic matter. However, there is a growing body of evidence that energy transfer via non-permanent fish populations is a major pathway. Numerous pathways may be involved, including:

- 1) emigration of juvenile nursery fish after reaching maturity
- 2) seasonal marsh use by migratory estuarine fish
- 3) predation of marsh nekton by transient predatory fish

Larval and juvenile fish that inhabit salt marshes for sanctuary from predators and an abundant food supply commonly move to more openwater habitats as they mature (e.g., croaker – *Micropogonias undulates*; spot – *Leiostomus xanthurus*), thereby transferring a significant biomass from marsh to estuarine and coastal ecosystems (Smith et al., 2000). Other fish move into marsh habitats in large numbers during seasonal onshore-offshore migrations (e.g., menhaden – *Brevoortia tyrannus*), which similarly accommodates large energy transfer through consumption of marsh meiofauna and algae (Cicchetti and Diaz, 2000). Finally, bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), and other coastal marine predators often hunt along marsh edges to take local nekton, thereby providing a trophic relay from local marsh communities to open marine ecosystems (Deegan et al., 2000). More recently, numerous stable isotope studies have furthered evidence for marsh energy export via fish, showing that many coastal fishes bear the isotopically light carbon signature of a *Spartina*-based food web (Melville and Connolly, 2003; Weinstein et al., 2000).

The actual contribution of marsh outwelling to coastal ecosystems remains poorly quantified, but recent studies clearly show that earlier estimates up to 45 percent are too high. This in large part because this process involves multiple sources of organic matter and multiple transfer steps from marsh to creek, estuarine, and finally coastal environments. Childers et al. (2000) specifically notes that many studies have been conducted at different spatial scales, from marsh creeks to the coastal ocean, making results difficult to compare. Furthermore, each of these factors vary significantly depending on a marsh's tidal regime and coastal physiography (Childers et al., 2000; Odum et al., 1979). Despite the complexities involved, most studies continue to suggest that the coastal ocean benefits from productivity leaked from salt marshes. For example, simple water column respiration studies in the coastal ocean have shown that these marine areas are often heterotrophic, meaning that the respiration of organic matters exceeds local primary production (Hopkinson, 1985). This requires an exogenous input of organic matter, for which salt marshes are a logical source. As E.P. Odum (2000) notes,

Material and energy usually flow from concentrated hot spots to lower concentration areas. Salt marshes are hot spots of production, so it is logical to expect an outwelling of production and food energy (paraphrased by Mitsch and Gosselink, 2000).

Many fisheries studies also support linkages between marsh production and coastal harvests. Turner (1977) found that the regional yield of estuarine and coastal shrimp harvests were closely correlated with the area of coastal marsh, and similarly Teal and Howes (2000) found that fish catches in Long Island Sound since 1880 tracked the declining length of marsh-bordered coastline. Although neither of these studies provides any causative linkages, they echo a consistent body of literature supporting the model of salt marsh contributions to estuarine and coastal ecosystem.

3.3 Habitat and Natural Resources

Salt marshes and adjacent flats are widely cited as providing essential nursery habitat and shelter for commercial fish and shellfish species, and thus play an important role in the productivity of adjacent waters (Feierabend and Zelazny, 1987). In 1994, the output of the United States fisheries industry was valued at 19.8 billion dollars, with 93 percent of commercial fisheries species being dependent at some point in their life cycle on coastal wetlands (Crooks and Turner, 1999). The extent of this higher trophic level production largely defines our socioeconomic and cultural dependence on estuarine systems, of which salt marshes are an integral part (Farber and Costanza, 1987; Farber et al., 2002).

3.3.1 Nekton

Salt marshes are important habitats for both resident and transient finfish. Kneib (1997) wrote an excellent review article on the importance of tidal marshes to estuarine nekton. These nekton are typically less than 150 mm in length, and are comprised mostly of finfish, although crustaceans can be found in abundance. The killifish comprise the dominant fish family in every intertidal marsh habitat, under all salinity conditions. The frequency and duration of tidal flooding, along with salinity, ultimately control potential habitat of estuarine nekton. A combination of creeks, ditches, pannes and aquatic microhabitats become important homes for any number of nekton. In particular, aquatic microhabitats (only a few millimeters deep and centimeters across) are often overlooked despite their importance as intertidal low tide refuge for larvae and juveniles of marsh resident nekton (such as killifish and grass shrimp). Subtidal habitats are generally

composed of a subset of the nekton species found in the adjacent estuary or bay, and many of these species are transient. In contrast, resident species are dominant in the vegetated part of the salt marsh. High marsh pools contain mostly killifishes and sticklebacks, as these species seem to be physiological tolerant to the extreme changes in salinity, temperature, and concentration of oxygen and sulfide associated with these pools.

A review of the literature by Minello et al. (2003) examined the role salt marshes play as nurseries for transient nekton. Density data from 32 studies conducted throughout the world (including eight Atlantic Coast sites) were analyzed in order to determine what type of habitat makes the most desirable nursery. The results ranked seven marsh habitats from most desirable to least desirable:

- 1) Seagrass
- 2) vegetated marsh edge
- 3) non-vegetated marsh
- 4) open water
- 5) macroalgae
- 6) oyster reefs
- 7) vegetated inner marsh.

In addition, the analysis found that the growth of decapod crustaceans was higher in vegetated marsh than in non-vegetated marsh and that nekton had a higher survival rate in salt marsh than in open water. Such studies are useful in identifying how and where various species are utilizing marsh sites, but salt marsh-nursery value is ultimately dependent on geographic location, salinity regime, and tidal amplitude. Furthermore, rankings of habitat desirability – particularly when focused on a single issue, such as nursery habitat – also need to be considered in a broader context. Notably, this report emphasizes that vegetated inner marsh – categorized in the Minello et al. study as the least desirable habitat – is arguably the keystone habitat among those listed. This is because vegetated inner marsh provides many other critical services, each of which contribute positively to more desirable habitats, such as improved water quality that benefits seagrass communities (and perhaps also oyster reefs) and physical habitat stability for marsh

edge and non-vegetated marsh, which are otherwise susceptible to erosion without baffling of wave and tide energy.

3.3.2 Birds

Coastal ecosystems also provide essential habitat for both resident and migratory bird species. Each of the major estuarine habitats – mud flats, tidal ponds, as well as salt marsh – is used by a variety of bird species, although most birds utilize more than one type of coastal habitat, moving between them seasonally and on tidal cycles (Reinert and Mello, 1995). Many species of birds breed on salt marshes and several species, such as the clapper rail (*Rallus longirostris*) and the seaside sparrow (*Ammodramus maritimus*), are obligate marsh-nesting species, and thus have no alternative breeding grounds (Kozicky and Schmidt, 1949; Marshall and Reinert, 1990). To a similar extent, this is true of willets (*Catoptrophorus semipalmatus*) and laughing gulls (*Larus atricilla*) (Burger and Shisler, 1978; Montevecchi, 1977). During the winter months, the American black duck (*Anas rubripes*) depends almost entirely upon estuarine habitats for its survival. In addition, many migratory bird species depend upon salt marshes as resting and feeding sites; these migratory bird species include gulls, terns, shorebirds and wading birds (Burger, 1991). Specifically, the study done by Reinert and Mello (1995) looked at the habitat use of 126,566 birds observed in a 158 ha tidal pond and salt marsh system in Massachusetts over a five year period. Birds were most abundant in the fall and winter seasons, but that species richness was higher in the summer (26 species) compared to the winter (15 species). In addition, waterfowl, shorebirds, and gulls used ponds and mud flats more than marsh habitats, but use of the salt marsh by each of these groups increased with tidal stage. Wading birds were more abundant in salt marsh habitat than in pond habitats, and songbirds only used salt marsh. Tidal stage played an important role on the activity patterns of coastal birds due to pond substrate exposure (which bears the food) as a result of tidally driven changes in water depths. Shorebirds, waterfowl, and gulls used the estuary during the low tidal stages when sand flats were exposed or only shallow water covered the pond substrate. In respect to pond versus marsh habitat, one-third of all birds in the estuary used marsh habitat: marshes are particularly important to wading bird and songbird species. As was the case with fish and nekton species, it is difficult to quantify the function of salt marsh in terms of bird productivity.

4 PHYSICAL FUNCTIONS

In addition to their biological roles, salt marshes display a variety of important physical functions. These functions include coastline protection, as well hydrological and geochemical roles (Mitsch and Gosselink, 2000).

4.1 Coastline Protection and Land Accretion

Salt marshes can act as physical buffers that limit coastal erosion, and, to a certain degree, provide protection from flooding. First, daily tides are one of the main processes controlling sediment transport in coastal settings, and are especially significant for salt marsh accretion (Allen, 2000). On Long Island, tidal cycles are semi-diurnal (occurring twice daily). This frequency of exposure to tidal currents, leads to the seabed being in a quasi-steady-state equilibrium with tidal stresses (Wright, 1995). Thus, on any given tidal cycle, relatively little sediment is transported, as is observed by generally clear coastal waters. This phenomenon is largely a consequence of shear-stress hardening of the seabed, whereby daily stresses placed on seafloor sediments leads to compaction and strengthening of these sediments. In addition to shear-stress hardening, tidal flows are relatively ineffective at eroding the seabed because their flows are almost exclusively horizontal. With largely horizontal flow, the velocity of tidal currents decreases exponentially near the seabed in a zone called the boundary layer (Wright, 1995). This decreasing flow near the seabed means that tidal currents, on average, are unable to move a significant amount of sediment.

In contrast to the largely horizontal motion of tides, wave motion is orbital (circular) in nature. A major component of orbital wave motion is in the vertical direction (i.e., up and down). This up and down pressure that waves impart on the seabed causes sediment grains to lose their contact with one another (liquefy), thereby allowing them to be moved much more easily. Thus, wave action is extremely effective at resuspending sediments off the seabed, even when the seabed is relatively resistant to erosion under ambient conditions (Wright, 1995). However, waves are actually ineffective at transporting sediments significant distances. Once again this is a consequence of a wave's circular motion, such that sediments resuspended from the seafloor have little or no horizontal movement.

Taken together, it is well recognized that periods of combined strong wave action and currents (tidal or storm-driven) dominate the redistribution of sediment in the coastal zone (Friedrichs et

al., 2000). Such conditions are most commonly realized during severe weather events, when wind stresses generate steep, short-period waves that resuspend much sediment from the seafloor and allow tidal and storm-driven currents to move this material significant distances.

What role do salt marshes play in this process? First, marsh grass canopies have been shown to be extremely efficient in baffling wave energy, such that wave-orbital velocity decreases ten-fold as far as 50 cm above the marsh surface (Leonard and Luther, 1995). Attributes of the grass canopy contributing to this baffling are:

- 1) generally high stem densities that block flow;
- 2) complex interfingering of stems and leaves that generate energy-dispersive eddies;
- 3) stiff but flexible stems that suppress orbital wave motion.

In addition, marsh deposits are further strengthened by their extensive root-rhizome matrix, which physically binds together muds and other dissociated organic matter. This substrate stability, in conjunction with grass-canopy baffling, means that waves are unable to significantly erode most vegetated marsh surfaces (Leonard et al., 2002). In fact, these properties often allow sediment to actually be trapped during storms and other high-energy conditions (Goodbred and Hine, 1995; Reed, 1989).

It is also worth noting that even sparsely vegetated marshes can withstand high-energy events because of physical and chemical properties of the fine sediments that typically comprise them. For sediments finer than 50 μm or so (i.e., silts and clays), individual mineral grains have a high surface to volume ratio, which means that the binding of these sediments by surface-water tension is relatively strong compared with the drag (stress) that is placed on them by currents (Nalluri and Alvarez, 1992). Thus, muddy surfaces are comparatively smooth and thus difficult to erode, in contrast to sandy sediments that have a high drag coefficient and tend to generate near-bed turbulence capable of initiating sediment movement. In addition to this physical cohesion, clay particles also have a highly charged mineral surface that allows them to physicochemically bond with organic material and other particles thereby forming a cohesive deposit, although only under brackish and marine conditions (Stolzenbach et al., 1992). Thus, even where plant baffling is limited (e.g., marsh edge), sediment binding by surface tension and physicochemical bond result in relatively erosion-resistant deposit.

Taken together, these properties of marsh systems explain their resilience against, and often benefit from, many high-energy weather events. This reaction to storms contrasts starkly with that of sandy shorelines, which tend to be significantly reworked under similar conditions, often resulting in land loss and damage to coastal infrastructure.

4.2 Flood Mitigation

Flood control is another function that has been ascribed to salt marshes because of their effective attenuation of wave energy (e.g., Crooks and Turner 1999). However, Dale and Hulsman (1990) point out that there is little direct quantitative evidence to support this aspect of the physical functioning of salt marshes. Nevertheless, the idea of flood control by marshes is consistent with known causes of storm-surge flooding. Storm surges are generated by two main processes:

- lowered atmospheric pressure
- wind-driven surface currents.

Marshes will have no impact on flooding caused by low atmospheric pressure, which accounts for about 1.5 cm of sea-level rise for every one mm drop in a mercury barometer. For the most severe storms, this process may result in 0.5 to 1.0 m of surge elevation. For the same storm, however, wind-driven surface currents can easily contribute another 3.0 m or more of surge, making it the dominant component of coastal flooding.

Thus, by absorbing wave energy and limiting wave development, the salt marsh grass canopy can be effective in limiting the height of storm surges. This specifically occurs because:

- 1) water ripples and waves provide the surface roughness that is needed for the efficient transfer of wind energy into the surface ocean;
- 2) wind energy absorbed by the surface ocean is mainly translated into water flow (i.e., surge waters) by the breaking of small waves, which is commonly indicated by white caps.

As noted by Dale and Hulsman (1990) note, the extent of protection that any given marsh can provide will depend on its fetch, width, and the composition of its vegetation. Without detailed quantification, it is safe to say that the absence of marshes where they formerly existed can only serve to exacerbate coastal flooding.

4.3 Coastal Water Quality

Perhaps the most studied aspect of salt marsh functions, and arguably the most controversial, is the role that these systems play in geochemical cycling and water quality. In general, estuarine wetlands are thought to contribute to the maintenance of water quality because accreting intertidal deposits are sinks for sediment and the metal and organic pollutants bound to them (Crooks and Turner 1999). In addition, early marsh studies (e.g., Teal, 1962) suggested that marshes were sinks for nutrients and sources for organic production. The export component of this idea has since been significantly revised, with most scientists agreeing that marshes do export some energy, but less than previously suggested and through much more diverse and complex trophic pathways (see Section 3.2). The nutrient uptake aspect remains unresolved, in large part reflecting the temporal and spatial diversity of marsh system processes. Nevertheless, it is accepted that there is a tremendous cycling of nutrients through marsh systems, which is an important process regardless of the net flux (Nixon, 1980). Taking an even broader perspective, Crooks and Turner (1999) suggested a public-health benefit resulting from marshes limiting pathogen levels in coastal waters. In this case, tidally inundated marshes provide a venue for increased ultraviolet radiation, water oxygenation, soil-water interactions, and predation by protozoa, each of which could serve to lower many common pathogen populations. Although not well studied, this is a potentially important social benefit given the rapidly increasing number of beach closings because of high *E. coli* levels. However, it needs to be noted that avian populations can serve as source of coliform, and so marshes that support waterfowl can increase pathogen indicator levels.

Before discussing these various roles, it is worth noting the general attributes of marshes that are considered relevant to water quality (Mitsch and Gosselink, 2000):

- 1) high rates of primary production that can rapidly uptake available nutrients;
- 2) high rates of organic burial that can sequester nutrients for long periods;
- 3) geochemically active mineral substrates that can bind particle-reactive contaminants;
- 4) trapping and retention of suspended sediments and organic particulates;
- 5) frequent tidal inundation that exposes a large water volume to marsh biogeochemical processes.

This last aspect of tidal inundation and general marsh hydrology are ultimately the precursor for processes that will occur within the system (Dale and Hulsman 1990). Thus hydrology is a first order control on the magnitude and efficiency of marsh exchange with land, river, and coastal ecosystems, regardless of whether the marsh functions as a filter, source, or sink. In general, marshes with higher tidal ranges will exchange more mass as particulate load compared with low tidal range settings where exchange to involve dissolved matter (Allen, 2000). For high tidal ranges, frequent flushing of porewater limits the development of strong soil redox gradients, which is where a significant amount of geochemical cycling occurs (Lord and Church, 1983). The strong flow velocities associated with large tidal ranges are also capable of mobilizing and transporting particulate matter, especially low density organics. In low tidal range settings, particulate matter is largely trapped on the marsh surface and porewater exchange is much slower, facilitating microbial and redox-sensitive reactions (Howes and Goehringer, 1994; Rocha and Cabral, 1998). The complexity of the factors involve mean few generalizations can be drawn regarding marsh biogeochemistry, except that marshes are indeed sites of major chemical transformations, which are linked to surrounding ecosystems largely through their hydrological regime.

4.3.1 Metals

Metals are a major class of environmental pollutants, many of which bind directly to particle surfaces or precipitate in new mineral phases. Marsh deposits, with their matrix of saturated organic and fine-grained mineral sediments, provide an abundance of surface binding sites for such particle reactive elements. As such, marsh sediments are known to act as sinks for several trace metals, including lead, copper, zinc, iron, and manganese (DeLaune et al., 1981; Giblin et al., 1983). Cochran et al. (1998) studied this behavior specifically in Long Island marshes and found that these metals and cadmium were retained in marsh sediments. These findings agreed with the notion that marsh sediments are sinks for metals, but the accreting concentrations could be largely explained by atmospheric deposition alone, with only moderate marine or terrestrial input. Thus, these marshes did not act to specifically concentrate metals but merely to retain those introduced to the system, a pattern also recognized in some Connecticut marshes (Rozan and Benoit, 2001).

Such patterns can be significantly affected by the hydrological and physical setting. For example, marsh deposits near point sources of metals have much higher concentrations, indicating that marshes indeed have a high capacity for metal retention where exposed to high levels (Leendertse et al., 1996). Ultimately, any generalizations regarding the cycling and fate of metals in salt marshes are futile, or misleading at best. This is clearly illustrated in a review paper by Williams et al. (1994) on metal accumulation within salt marsh environments. There, the complexities involved in salt marsh geochemistry are aptly described:

It is evident that the salt marsh environment cannot be treated as a simple system. There are a number of interlinked chemical and physical factors that can affect the mobilization and availability of both major and minor metals. Even small changes to the surrounding environment can significantly affect the overall cycling of the metal species. Cycling of metals within the sediments is dictated by the effects of tidal inundation which control a variety of physical and chemical factors such as redox potential, pH, temperature, salinity levels, particle size and distribution, vegetation zonation, soil organic content as well as influencing physical disturbance of the sediments and alkylation via bacterial action. The diversity of factors dictating metal interactions within a salt marsh environment cause a great deal of spatial and temporal variability in metal loadings, which is compounded by differences in the type and degree of anthropogenic fluvial, marine and atmospheric metal inputs, surface-microlayer interactions (both deposition and adsorption mechanisms) together with biological uptake and release by marsh plants and detrital associations.

Based on a large body of literature, as well as related review articles (e.g., Gambrell, 1994), it is possible to conclude that metals are taken up by salt marsh plants and sediments, but their ultimate fate is not readily predicted.

4.3.2 Nutrients

An ongoing debate revolves around the issue of marshes being a source or a sink for nutrients. This is extremely complicated, and involves not only the biological pathways discussed previously, but also a myriad of climatic, hydrological, and geochemical processes. After critically reviewing a number of studies on marsh biogeochemical cycling, Nixon (1980) found that there was a general consensus that tidal marshes export dissolved and particulate organic carbon, dissolved organic nitrogen, and dissolved phosphorus. However, marshes take up nitrate

and nitrite. However, this source and sink behavior may change in response to a variety of factors, including sediment type and accretion rate. This continued uncertainty regarding positive or negative nutrient fluxes reveals that marsh systems are neither an overwhelming source nor sink, but rather are comparatively balanced in their exchange of total nitrogen, phosphorous, and carbon. Thus, without detailed local studies, it is not possible to ascribe source or sink status to a particular marsh system. These arguments parallel those made regarding the cycling of metals through salt marsh systems.

What this general view overlooks, however, is the potential for marshes to buffer nutrients and organic production. Specifically, high rates of primary production allow marshes to take up nutrients much faster than they are released, thereby sequestering nutrients on a timescale of months to years. Crooks and Turner (1999) specifically note this buffering capacity with regard to agricultural runoff, which is often delivered to coastal settings in pulses that contribute to environmentally-degrading plankton blooms. This boom-bust cycle of estuarine production can be mitigated when an overabundance of nutrients is taken up by marsh grasses and stored in their relatively refractory biomass. Subsequent biodegradation of the grasses may release nutrients back to the estuary, but at a much slower rate that avoids major plankton blooms (Hamersley and Howes, 2003; Taylor and Allanson, 1995).

Furthermore, the standing mass of organic matter and nutrients in marshes is comparable to that of adjacent coastal waters, despite marshes covering a much smaller area. This is a consequence of the high rates of primary production and storage of this material as subsurface marsh peats (Mitsch and Gosselink, 2000). The total biomass stored in marshes has led some scientists to speculate that, when the adjoining estuary is depleted in nutrients, marshes release nutrient reserves, thus fortifying the estuarine system (e.g., Childers et al., 1993; Spurrier and Kjerfve, 1988; Taylor, 1992). Conversely, when marine nutrient levels are high, marshes have the capability to store these nutrients. This view is consistent with observed high rates of nutrient uptake and more more persistent but slower rates of respiration and nutrient remineralization in marsh systems.

5 SALT MARSH VALUE

Not every marsh has equal share in the above functions, and the value of the system to a manager may depend on the importance of the functions to some desired endpoint. In addition, other factors can impact the valuation of a marsh. Growing environmental awareness in the 1960s helped cultivate broad public interest in the beauty of natural systems, including salt marshes. What emerged was the first national-scale valuation of ecosystems based on aesthetic appeal, rather than solely the hard-currency of harvestable resources. Nixon (1980) notes:

[Salt marshes] are important to me and to many other people who enjoy looking across the sweep and green openness of them, who like to walk out across them and observe their patterns of life and form. And these are not trivial reasons for maintaining that the marshes are important.

But aesthetic appeal is difficult to quantify, especially as expressed in the popular proverb that “beauty is in the eye of the beholder.” In response to the continual demand for justifying environmental protection and stewardship, or more specifically the costs thereof, researchers frequently attempt to provide approaches or justifications in their publications. As an example, one such suggestion for salt marshes has been to assign higher value to those systems nearest to their natural state and to decrease the value of those that are degraded (i.e., farther from pristine) (Crooks and Turner 1999). Degradation in itself is a subjective notion, and given the incomplete understanding of marsh functions, somewhat suspect as a characterization of an ecosystem. Context may be extremely important; one could argue that any functions of a degraded marsh are of considerable value in an ecologically/environmentally stressed setting.

While salt marshes can be appreciated and valued for their beauty, or as to how they do or do not correspond to untouched natural settings, it remains to determine whether this is sufficient justification for the high cost of protection, preservation, and management of marsh ecosystems. Data, scientific evidence, and scholarly research clearly cannot sufficiently assess value to be relevant to legislative and budgetary decisions.

An emerging approach is that function, as defined by research, must be combined with aesthetics, economics, and social perspectives to generate values. This is the field of interest for ecological economics, with its focus on determining the ecological and economic services provided by natural systems. This provides justifications for natural systems in terms of

particular functions, and compares them to the artificial systems that would be required to replace them (if that were possible) (Balmford et al., 2002; Foley et al., 2005). Others try to extend the argument further, arguing that value is merely a product of a complex value system and valuation process (Dailey et al., 2000). Value can thus be the result of an overriding framework in which people assign importance and necessity to their beliefs and actions – that is to say, human culture, where the collective perception of a community often differs from that of individuals because of social sensibilities. Exactly how these subjective and malleable concepts can be quantified is quite controversial, although some are not shy to attempt the deed (Costanza, 2000; Costanza, 2003).

At all civic levels, this is a time when people are increasingly aware of the ecological and economic importance of coastal zone resources, including those from salt marshes (Crooks and Turner 1999). Integrated coastal-zone management practices must encompass all stages of progress, from planning and design to financing and implementation. However, Turner et al. (1999) stress that historical, socio-economic, and cultural context will be required for sustainable coastal resources management to be effective. This will necessarily draw from the fields of ecology, geology, marine biology, economics, engineering, political science and law (Turner et al. 1999), but must also be amplified by a public community that holds some positive social valuation for natural coastal resources, including, necessarily, salt marshes.

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