Salt marshes: biological controls of food webs in a diminishing environment

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This essay is dedicated to John M. Teal, a leader in basic and applied studies of salt marsh ecosystems, now retired from the Woods Hole Oceanographic Institution, but still remarkably and admirably active in salt marsh restoration efforts

Abstract

This essay reviews two important topics in coastal ecology: the work on the relative role of bottom–up and top–down controls in natural communities and the loss of wetlands worldwide. In salt marshes and other coastal wetlands, bottom–up and top–down mechanisms of control on natural communities are pervasive. Bottom–up effects through nutrient supply may propagate to upper trophic levels via better food quality, or indirectly by altering water and sediment quality. Top–down control by consumers alters lower trophic levels through consumption of primary producers, and indirectly by trophic cascades in which higher predators feed on grazers. The combined forcing of bottom–up and top–down controls govern assemblages of species in natural communities, mediated by physical and biogeochemical factors. Although there is much information about biological controls of coastal food webs, more information is needed. Even more important is that large losses of wetland are occurring along coastlines worldwide due to a variety of economic and social activities including filling, wetland reclamation, and sediment interception. Such losses are of concern because these wetlands provide important functions, including export of energy-rich material to deeper waters, nursery and stock habitats, shoreline stabilization, and intercept land-derived nutrients and contaminants. These important functions justify conservation and restoration efforts; barring such efforts, we will find it increasingly difficult to find coastal wetlands where we can continue to gain further understanding of ecology and biogeochemistry and lack the aesthetic pleasure these wetlands provide to so many of us.

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1. Introduction

Research done in salt marshes has made many contributions to environmental science, and has generated a number of lively controversies. Experimental as well as comparative and correlational approaches have all been used in salt marshes, each contributing to advances in the field. A comprehensive text, now in a second edition (Mitsch and Gosselink, 2000), as well as publication of reviews reported in a major conference on recent issues and advances (Weinstein and Kreeger, 2000) make it less pressing to revisit the many topics illuminated by work in salt marsh research during the time that JEMBE has been in existence, many of which have been explored in its pages.

As in all disciplines, there is an overwhelming plethora of recent publications on salt marshes, a seemingly reasonably narrow and specialized topic: a search in just one search engine (Aquatic Sciences and Fisheries Abstracts) yielded 991 references that appeared just in the decade 1993–2003. Below we include just a few of the many worthy references that could have been cited. Drastic curtailing of bibliographic citations seems an increasingly unavoidable feature of future reviews of any but the narrowest of scientific topics. Fortunately, the availability of the timely Weinstein and Kreeger (2000) and Mitsch and Gosselink (2000) compendia makes it somewhat easier for us to more narrowly focus this contribution.

The first part of this essay reviews work in salt marsh environments on the relative role of top–down and bottom–up controls in natural communities. This is a topic in which differing views have flared in the recent ecological literature, but was not a central theme in Weinstein and Kreeger (2000) or Mitsch and Gosselink (2000). There should be more than a little interest on this topic, since in fact, human beings are conducting worldwide experiments as we fertilize the world's natural waters and over-fish many top predators. Progress in knowledge of the relative primacy of control by consumer activity cascading down food webs, or by nutrients forcing up through food webs, or how these controls may interact in specific environments, seem high priorities for ecological research.

Second, it would be remiss here not to re-emphasize a truly major conservation issue, the widespread loss of coastal wetlands around the world. Wetland loss has been rightly highlighted by many authors in many settings, but given that continuing loss of wetlands remains a global issue, it merits revisiting in a tribute to a major international journal whose content has from the beginning supported environmental conservation.

2. Bottom–up and top–down controls of food webs

There is a venerable history of thought on the search for generalities about how natural communities are controlled, from Elton (1927), through the critical and profound dialogues between Solomon (1949) and Andrewartha and Birch (1954) and others, to the still-seminal "etude" by Hairston et al. (1960).

Perhaps out of the need to search for broad conclusions, in many recent papers, there seems to be a tendency to highlight one or the other mechanism of control.

Estuarine researchers, in particular, have written many papers in which distributions, composition, and abundance of producers, are, to their satisfaction, explained on the basis of nutrient supply alone (Boynton et al., 1982; Nixon et al., 1986; Iverson, 1990; Sand-Jensen and Borum, 1991; Paerl et al., 1999; Valiela et al., 2000; Pinckney et al., 2001). Some of these papers add the complicating feature that physical factors—such as flushing time—may mediate bottom–up controls of abundance at different trophic levels (Nixon, 1988; Pace et al., 1992; Valiela et al., 2000).

In contrast, many authors emphasize the dominant role of top–down controls of food webs, arguing that predators are particularly effective in controlling the composition of lower trophic positions in a wide variety of coastal systems. For example, Hughes (1994) and Hughes et al. (1999) aver that macroalgal blooms in Jamaican coral reefs were controlled by human harvest of herbivorous fish, and storm and disease-related declines in abundance of a herbivorous sea urchin.

In an earlier paper (Foreman et al., 1995), we compiled a few selected passages that, although fragmentary and quoted out of context, do convey a sense of the range of views. Here, we add a few more:

Predation serves as the chief source of density-dependent regulation in many animal associations (Mills et al., 1987).

...predators...have the potential to interact strongly with certain prey and to mould community structure... (Paine, 1980).

...fishes could reverse the overgrowth of coral by macroalgae... (Jackson et al., 2001).

...the...weak coupling of N loading and phytoplankton productivity with higher trophic levels...implies that anthropogenic nutrient loading to coastal waters is unlikely to result in increased fish biomass... (Micheli, 1999).

There may be many ways to produce large numbers of fish, but all must ultimately require an adequate supply of...nutrients... (Nixon, 2003).

...the removal of higher trophic levels leaves lower levels intact (if perhaps greatly modified), whereas the removal of...producers leaves no system at all (Hunter and Price, 1992).

Plants have obvious primacy in food webs; in particular, their primary productivity is a fundamental control of higher trophic levels (Power, 1992).

...virtually all present explanations for the high productivity of estuaries and coastal marine areas involve nutrient inputs or nutrient regeneration (Nixon et al., 1986).

...carnivorous fish production is controlled by the amount of new N annually incorporated into phytoplankton biomass and transferred through food webs (Iverson, 1990).

...nutrient supply is related in a fundamental way to the abundance and production of animals in marine ecosystems (Nixon and Buckley, 2002).

Such papers have highlighted the dominance of one control over others, while many authors have, instead, dwelled on the complementary action of various biological controls operating on populations making up food webs. Fretwell (1977), Oksanen et al. (1981), Carpenter et al. (1985), Menge (1992), Worm et al. (2000), and others (many listed in Foreman et al., 1995) have set out modified notions about how biologically mediated processes that cascade up and down food webs might control the composition of natural communities.

Therefore, there is an apparent, broad gap in our understanding about the workings of major potential controls in food webs. The discrepancies may derive from differences in approach, interpretation of results, or to actual differences among the environments studied. In part, the gap in understanding made evident by the quotes cited above may also be a product of the differences in the criteria used to measure responses to treatments. For example, Rosemond et al. (2001) experimentally changed the supply of phosphorus and the abundance of macroconsumers in a freshwater stream in Costa Rica. If the response criterion was rate of loss of leaf litter, the effect of more consumers was larger than that of more phosphorus. On the other hand, if abundance of insects that grazed on the litter was used as the response criterion, phosphorus supply had larger effects than fewer consumers. Conclusions about the relative effects of the two treatments, therefore, artifactually depended on the criterion used to measure responses.

We are unable here to tease apart all the reasons underlying the gap in understanding identified above. Instead, below we go on to give a few examples that, to us, provide convincing evidence that bottom–up and top–down controls in various environments and in coastal wetlands exert meaningful influences, and then move on to consider studies designed to examine the relative impress of these controls, particularly in wetlands.

2.1. Bottom–up effects in food webs

Rate of growth of phytoplankton in near-shore waters is associated to supply of nutrients, particularly nitrogen (Downing et al., 1999; Howarth et al., 2000). These bottom–up effects can be seen higher up food webs, for example as increased abundances of secondary consumers (Nixon et al., 1986). In addition, phytoplankton growth responses may be affected by flushing times of the marsh-estuary, other hydrodynamic features (Nixon et al., 1986; Pace et al., 1992), and local particulars, so that the undoubted relationship of phytoplankton to nutrients is often one with substantial scatter (Micheli, 1999). Most of the relatively weak relationships were developed by correlational studies; Nixon and Buckley (2002) review more experimental studies in which increased nutrient supplies can be more causally linked to producers and consumers.

There are significant effects of nutrients on macroalgae and coastal vascular plants (Duarte, 1995; Valiela et al., 2000). Many examples exist in various environments.

Nitrogen supply limited biomass and distribution of Australian seagrasses (Udy et al., 1999). Hauxwell et al. (2001) showed that increases in the limiting nitrogen loads thoroughly reshuffle the composition of producers in shallow estuaries, fostering epiphytes, benthic macroalgae, and phytoplankton, and, consequently, impairing seagrass meadows. In mangrove forests, nutrient supply seems responsible for variation in mangrove growth rates in Florida (Onuf et al., 1977) and Southeast Asia (Duarte et al., 1998). Similarly, experimentally increased nitrogen supply to salt marshes restructured competitive relationships, and altered plant community composition, morphology, biomass, and production (Valiela et al., 1985; Levine et al., 1998; Rogers et al., 1998).

Bottom–up effects through nutrient supply may propagate up coastal food webs beyond the producer level. Nixon and Buckley (2002) concluded that greater nutrient (particularly nitrogen) loads not only elevated phytoplankton production, but increased consumer production in many coastal systems. A good example of nutrient–consumer linkages is the collapse of the crustacean and fish harvest from the nutrient-depauperate Eastern Mediterranean after the High Aswan Dam began operation, and reduced the transport of nutrients through the Nile Delta. Further corroboration of the dependency on nutrients is the recent recovery of the fishery there after delivery of nutrients was unwittingly "restored" by the release of nutrient-containing wastewater through the Delta (Nixon, 2003).

Nutrient supply also strongly affects macrophyte-dominated systems. Nutrient-stimulated macroalgal canopies may, for example, determine success of predaceous shrimp feeding on infaunal amphipods and bivalves (Norkko, 1998), of shorebirds seeking prey on marsh mudflats, and many other upwardly cascading effects (Raffaeli et al., 1998). In Nova Scotia, a collapse of seagrass meadows was followed by sharp reduction of populations of Canada geese (Seymour et al., 2002).

Similar bottom–up effects have been repeatedly reported in food webs of salt marshes and mangroves. Nitrogen-enriched salt marsh-fringed estuaries held higher concentrations of food particles that were of higher nutritive quality and stimulated growth rate of ribbed mussels (Evgenidou and Valiela, 2002). In New England salt marshes, experimental addition of nitrogen increased density of grazers by up to 4-fold, with responses of different grazer species differing substantially (Vince et al., 1981), and raised the rate of growth of aphid populations by about 20% (Levine et al., 1998). In a Florida mangrove, increased nutrients led to faster growth of leaves, flowers, and stems, and more herbivores on mangroves (Onuf et al., 1977). Consumers in marshes and mangroves therefore do depend on food quantity.

There is substantial evidence that bottom–up effects might depend even more on nutritive quality of food (Pedersen and Borum, 1996; Hemmi and Jormailanen, 2002). Different types of macrophytes have evolved quite distinct chemical make-ups, and consumers have specific feeding and assimilation responses to the different food types. There are quite variable and diverse bottom–up effects that pervade food webs of salt marshes and other macrophyte-dominated environments. In the examples of the New England salt marsh (Vince et al., 1981) and Florida mangrove forest (Onuf et al., 1977), the larger number of herbivores was closely tied to greater nitrogen content of the plants. In both cases, more herbivores, of course, fostered grazing: in the mangrove

example, the greater nitrogen supply led to a 3-fold increase in loss of leaf production to herbivores (Onuf et al., 1977). Experimental additions of nitrogen about doubled the number of a herbivorous leafhoppers in plots in a Florida marsh (Bowdish and Stilling, 1998); the bottom–up effects, however, weakened further up the food web, since the abundance of a wasp parasitic on the leafhopper was not affected.

Bottom–up effects can also materialize through mechanisms other than trophic links. For example, nutrient-stimulated macroalgal canopies foster more frequent hypoxic conditions, which, in turn, lowers abundance of grazers (Hauxwell et al., 1998). This indirect effect counters the positive effects of more food available for consumers, and impairs the ability of grazers to control macrophyte blooms. Similarly, for fish, hypoxia may counter the positive effect of more food made available by enrichment, by impairing survival and growth, as well as altering foraging behavior and distribution of coastal fish (Breitburg, 2002; Deegan, 2002). There may also be non-trophic "ecological engineering" effects, such as burrowing and bioturbation. For example, Chasmagnathus granulata, an unusually abundant Patagonian crab, altered sediment character enough to change suitability for foraging by shorebirds on mudflats and marsh areas (Botto et al., 2000). The effects on sediments by activity of two similar Patagonian crab species, however, differed, with one stabilizing, and the other making sediment more erodable (Botto and Iribarne, 2000). Thus, much as in the case of macrophyte nutrient content, species-specific differences prevent ready generalizing about "environmental engineering" effects.

In general, then, bottom–up effects have a chain of well-established consequences: more nutrients create blooms of producers, and these blooms in turn, through their abundance as well as their composition, variously affect upper trophic levels, by providing more and better or worse quality food, or by altering water and sediment quality, and hence shifting conditions for consumers. Consumers may or may not physically alter the environment in ways that further affect upper levels of food webs. In addition, all these bottom–up effects can be further constrained by physical processes.

2.2. Top–down effects of consumers on estuarine food webs

Consumption of phytoplankton by consumers in salt marshes can be quantitatively significant. Ribbed mussels, for instance can filter the entire volume of tidal water entering a Massachusetts salt marsh twice daily (Jordan and Valiela, 1982); this would suggest the potential for major control of the water column flora. Microzooplankton grazing rates might be equivalent to 73% of the growth rate of estuarine phytoplankton, and in certain places, grazing might partly relieve nutrient limitation of phytoplankton growth (Gallegos and Jordan, 1997). Grazing by bivalves is a major control on phytoplankton in Danish fjords (Kaas and Møhlenberg, 1996), and where alien bivalves have become numerous, such as in San Francisco Bay (Cloern, 2001). There are, however, exceptions where grazers have a lesser influence: filtration by the abundant oyster Crassostrea virginica in a South Carolina salt marsh estuary, however, did not affect composition and abundance of the microbial community in the water, except for a modest depletion of nanoflagellates (Wetz et al., 2002).

Some papers report intense top–down control of macrophyte production and biomass. Reductions of biomass and cover in certain seagrass meadows and salt marshes have been clearly attributed to grazer pressure (Srivastava and Jefferies, 1996; Valentine and Heck, 1999; Handa et al., 2002). Silliman and Bertness (2002) experimentally manipulated density of periwinkle snails (600 and 1200 adult snails m^{-2}) in a Georgia salt marsh, and in these treatments the snails extirpated the grass canopy in a matter of months. Earlier studies in the same site reported densities of adult snails between 100 and 200 m^{-2} (Odum and Smalley, 1959), that energy use by the snails was about an order of magnitude lower than grass production (Odum and Smalley, 1959), and that adult snails "grew very slowly" (Teal, 1962). Estimates of ambient periwinkle densities in other marshes in Florida, Louisiana, and Georgia ranged between 0 and 88 snails m^{-2} (Subrahmanyam et al., 1976). Salt marsh herbivores such as the snails therefore do have the potential to control the plants they indeed feed upon (Haines and Montague, 1979), but ambient densities may or may not reach densities that would exert the potential control. Establishing such density thresholds would be of interest.

The relative ability of certain grazers to consume specific macrophytes (and the degree of top–down control) may depend on the presence of chemical defenses in the producers, and susceptibility of the grazers to the deterrents (Buchsbaum et al., 1984; Buchsbaum and Valiela, 1987; Valiela, 1995). Macrophytes, for example, may contain defensive phenolic compounds that deter grazing by amphipods and snails (Geiselman, 1980; Lubchenco, 1980; Valiela and Rietsma, 1984), but snow geese may be able to thoroughly overgraze marsh grass stands (Cargill and Jefferies, 1984). Chemical feeding deterrents and susceptibility are so species-specific as to make it difficult to generalize, except that higher plants are more likely to possess grazer deterrent than algae, and invertebrate grazers may be more affected than vertebrates.

There is ample evidence that top–down effects of one consumer on another are common in coastal food webs, but that the effects are quite varied. Exclusion of fish, crabs, and shrimp from benthic plots in a South Carolina marsh increased density of benthic meiofauna by a factor of less than 2 (Bell, 1980). Larger order-of-magnitude increases in meiofauna resulted from similar experiments in a Rhode Island salt marsh (Hoffman et al., 1984). Experimental exclusions of shorebirds—important predators of salt marsh and tidal flat benthos—showed that the responses of abundance of a variety of benthic invertebrate species to predation could be significant but were inconsistent from one area to another, and varied too much from site to site to be able to generalize broadly (Botto et al., 1998; Botto and Iribarne, 1999). Predation by fish and crabs potentially controlled population abundance and size classes of snails and amphipods in a New England salt marsh, but the relative impact of the top–down control was strongly constrained by the complexity of the plant canopy (Vince et al., 1976). Predators were most effective where the canopy was sparse, and ineffective in dense canopies. The architecture of the environment thus mediated the degree of top–down influence by predators. Different effects of habitat structure were also found in Panamanian mangroves, where mangrove seedlings had better survival in forest gaps away from the mangrove canopy, where scolytid beetles more frequently attacked seedlings (Sousa et al., 2003).

Too little is known about the role of predatory birds and mammals in salt marshes and mangroves. Egrets, herons, rails, raptors, and many other large vertebrates are common in wetlands. Whether these top predators exert pressure on their target foods or simply respond to the relative supply of their preferred foods can only be conjectured at present. Research on these predators will be of interest, particularly if based on experimentation.

Top–down "ecological engineering" effects have also been suggested. For example, fiddler crabs, through their burrowing, alter irrigation rate and surface area of salt marsh sediments exposed to oxic water, and thus can change biogeochemical conditions of the marsh sediments, potentially affecting the growth rates of marsh grasses on the sediments altered by the crabs. Such alterations are in competition with those of other agents of change; for instance, Gribsholt et al. (2003) found that the oxidizing impact of crab burrows on sediment biogeochemistry was smaller than that of grass roots and rhizomes.

Experience in study of wetland systems, plus evidence such as just reviewed above, suggest that controlling effects of both nutrient supply and of consumers are incontrovertibly evident in coastal wetlands, just as they are in other types of environments. It therefore does not take much imagination to suspect that in any one environment what we see as the assemblage of species is likely governed by combined forcing by both top–down and bottom–up controls (with additional constraints provided by the physical and biogeochemical environment, some consideration to historical contingencies as to species that might have been present, and architecture of the environment). It is therefore of interest to turn now to efforts made to assess the relative synchronous effects of nutrient supply and consumers within a variety of aquatic environments.

2.3. Studies of simultaneous consumer and nutrient effects

Verity and Smetacek (1996), Cloern (2001), and others reviewed many sources of information, and concluded that assemblages of species in planktonic environments are likely controlled by a mix of top–down and bottom–up forces, mediated by external physical constraints. In freshwater lakes, experiments with grazers and fertilization showed that the interplay was complicated. Grazers, indeed, exerted a powerful influence on phytoplankton, but the degree of control depended on rate of supply of the limiting nutrient, and on the composition of the phytoplankton (less-palatable blue-green taxa proliferated under high nutrients) (Carpenter et al., 1985). Similarly, Menge (2000), reviewing information on rocky shore environments, concluded that "...top–down and bottom–up processes can be important joint determinants of community structure...", and the interaction may depend, in turn, on the physical setting.

Similar conclusions have been reached after study of many macrophyte-dominated systems. Lapointe (1999) reviewed several lines of experimental and sampling evidence that pointed to increases in nutrient (N and P) supply, in addition to decreased herbivore abundance (caused by overfishing, storms, and disease, as argued by Hughes, 1994), as joint controls on increasing development of macroagal blooms in reefs of Jamaica and southeastern Florida. A review of much research on coral reefs (Szmant, 2002), however, concluded that it was difficult to generalize because of local complexities, but that nutrient enrichment may play a secondary role (relative to the impact of

sedimentation, overfishing, and global warming), perhaps because reefs occur largely in sites of very high hydrodynamic activity, which, by flushing, mixing, and dilution may diminish potential impact of a given supply of nutrients. Perhaps the same can be said of rocky intertidal shores or kelp forests, habitats that have produced the core information that generated the viewpoint of top–down dominated control.

Nielsen (2003) set out to manipulate nutrient supply and grazer pressure on biomass of algae in pools within the rocky intertidal of the west coast of the U.S. There were no evident responses to attempts to either increase nutrient supply or reduce grazers by algal groups that made up about 75% of the cover on the rocks. There was, however, a group of fleshy algae that were rare in treatments with higher herbivore abundance, and were much more abundant where herbivores were in lower abundance. Apparently, the fleshy macroalgae were far more palatable to grazers, as reported quite some time ago (Geiselman, 1980; Lubchenco, 1980). Biomass of fleshy algae increased by about 5× where higher nutrient supply was provided. These results suggest that only a fraction of the algal assemblage (the fast-growing, fleshy, palatable species) was sensitive to the two sorts of controls, and that grazers, if sufficiently abundant, could suppress the response of these algae to increased nutrient supply. In addition, algae in sites more exposed to wave action were unaffected by the apparent treatments; where there was exposure to waves, hydrodynamic constraints appeared to overwhelm biological controls in an undefined fashion. The overwhelming dominance of hydrodynamic forces in this exposed site may have prevented the majority of the algae from responding to the treatments.

Worm et al. (2000) ran experiments in which nutrient supply was set at four different levels (and achieved a variable 6–98% increase in nutrient concentration), and also used cages to include and exclude grazers. They then measured the responses of four types of macroalgae and benthic diatoms across the seasons. The responses were species- and season-specific. Percent cover by *Fucus vesiculosus* seemed to depend largely on seasonal cues, with a minor decrease where there were no grazers and where nitrogen supply was highest (probably shaded by other faster-growing algae). Cover of *Pilayella littoralis* was significantly lowered by the presence of grazers, but also evidenced strong unexplained cage and seasonal effects. Cover of *Ulvopsis grevillei* was low and unresponsive to all factors. Cover of *Enteromorpha* spp. was highest during warmer months, and responded to both grazing and nitrogen supply (Table 1). Although the supply of dissolved inorganic nitrogen varied seasonally, and the experimental concentrations were not always higher

Table 1
Percent cover of *Enteromorpha* spp. during the warmer months of the year, within treatment combinations where nutrient supply was not altered, increased to three different levels, and grazers were excluded by use of cages

Nutrient treatments	No grazers (closed cages)	Grazers (open cages)	Grazers (no cages)
Ambient	18.5	4	0
Low additions	44	3.5	1
Intermediate additions	34	8.3	4.8
Higher additions	58	15	9.8

Cage effects were evaluated by open cages, or no cages were deployed.
Data summarized from Worm et al. (2000).

than ambient, the addition of nutrients managed to increase cover of *Enteromorpha* by more than 3-fold. The increases in cover seen in the absence of grazers were more than 9-fold at the lowest (ambient) nutrient supply, and were more than 4-fold at the highest nutrient supply. These rough comparisons suggested that both nutrient supply and grazing were important controls of cover of *Enteromorpha* spp., and that the influence of grazers was relatively more pronounced at lower nutrient supplies.

Studies of the top–down/bottom–up question have also been carried out in estuaries of New England. Hauxwell et al. (1998) compared the growth rates of the dominant macroalgae to the rates of consumption of the dominant grazers (amphipods and isopods) in three different estuaries within the Waquoit Bay estuarine complex in Massachusetts, U.S. (Fig. 1). The three estuaries were subject to demonstrably different rates of land-derived nitrogen loading, and hence provided settings in which the nutrient forcing differed significantly. In the estuary with the lowest nitrogen loading rate, the relative rates of macroalgal growth and grazing were approximately similar: there, grazers could have been expected to exert some degree of control of the resulting macroalgal crop. In estuaries subjected to higher nitrogen loads, the macroalgal growth rates exceeded the potential consumption by grazers. The result in the more enriched estuaries was accumulation of greater biomass of macroalgal canopies (Valiela et al., 1992, 1997, 2000). The bottom–up effect in this case came about through two
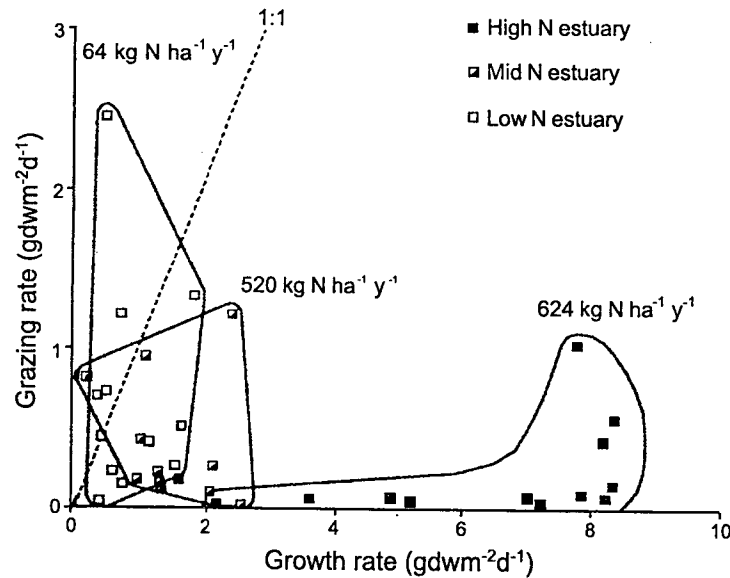

Fig. 1. Comparison of the rate at which grazers (amphipods and isopods) could remove biomass of the macroalga *Cladophora vagabunda* (*y*-axis) relative to the growth rate of the same macroalga (*x*-axis), in three different estuaries within the Waquoit Bay estuarine system. The three estuaries received different nitrogen loads from land (numbers above each of the three loops). From Hauxwell et al. (1998).

mechanisms. First, more nitrogen in the water accelerated rates of macroalgal growth, particularly those more opportunistic species (Peckol et al., 1994; Valiela et al., 1997). In addition, as already noted above, enriched estuaries were exposed to more frequent incidence of hypoxic and even anoxic episodes (D'Avanzo and Kremer, 1994), which in turn led to lower densities of benthic grazers (Hauxwell et al., 1998). The inability of grazers to keep up with increasing nutrient forcing was also suspected for lake phytoplankton, as discussed above (Carpenter et al., 1985).
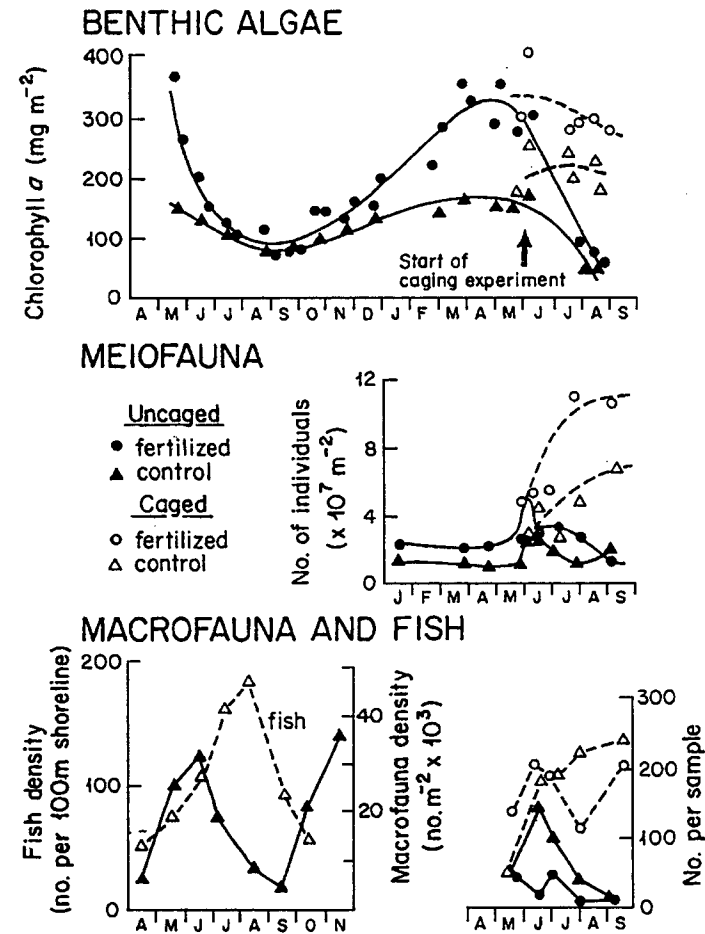

Fig. 2. Interactions among and responses to fertilization and caging by benthic microalgae (top), meiofauna (middle), and benthic macrofauna and fish (bottom). From Foreman et al. (1995) (top and middle) and Wiltse et al. (1984) (bottom).

In work on New England salt marshes, Foreman (1989) studied the responses of benthic microalgae and meiofauna in plots subject to fertilization and predator exclosures (Fig. 2). Chlorophyll in benthic microalgae varied seasonally, but abundance was clearly higher in fertilized sediments (Fig. 2, top panel). After the start of caging treatments in late spring, however, chlorophyll remained high. This suggested that activity of macroconsumers checked the abundance of microalgae. A very similar pattern was evident for meiofauna (Fig. 2, middle panel). These results are quite clear evidence of the joint influence of top–down and bottom–up effects in this salt marsh system.

In the same salt marsh ecosystem, Sardá et al. (1996, 1998) found that after 15 years of nutrient enrichment, the macrofauna of fertilized salt marsh creeks was significantly more abundant and productive than in control creeks during most of the year, and the response was mainly owing to proliferation of two oligochaete species. During summer, the bottom–up effect of fertilization disappeared, and top–down control by predators (fish, crabs, shrimp) controlled macroinvertebrate abundance. There were close linkages between the benthic macrofauna and the fish that fed on them (Foreman et al., 1995). As predators consumed invertebrates during the active summer season, invertebrate abundance diminished (Fig. 2, bottom left), and diet of the fish became more dependent on algae and detritus (Werme, 1981; Foreman et al., 1995; Sardá et al., 1998). Unlike the effects on meiofauna, macrofauna in fertilized plots then became less abundant than in control plots (Fig. 2, bottom right). Perhaps these differences arose because of more desirable or available prey species in the fertilized plots. Growth rates of fish decreased as summer wore on and prey became less available, since the alternate foods were of lesser nutritional quality (Foreman et al., 1995). These various linkages across several trophic steps occurred in all experimental treatments, and were mediated, not always in similar direction, by the interplay of nutrient supply and activity of consumers in the experimental plots.

The salt marsh studies discussed above highlight the importance of the contingent occurrence of specific taxa in specific ecological settings. A different assemblage of species, even in the same setting might create a rather different outcome, which could easily be interpreted as demonstrating the primacy of one or another control process. If the species that were favored by more nutrients were to inherently be not palatable, rather than palatable, we might conclude that bottom up features were dominant, for instance.

In recent years, there have been many studies dealing with specific details of salt marsh community ecology that should have some bearing on the issues of top–down and bottom–up controls. Perusal of the many papers, unfortunately, reveals that the notion of the primacy of top–down or bottom–up controls—simple in concept at first thought—turns out to be far more nuanced and ill-defined than we might have suspected. The attractive initial conceptual simplicity dissolves into a multifaceted series of direct and indirect relationships, often species- and locale-specific. The many types of producers (species of phytoplankton, benthic microalgae, macroalgae, vascular plants) may have species-specific responses to top–down and bottom–up forcings. The same might be said about consumers, and in addition, consumers may influence lower trophic links by "cascading effects" based on consumption across more than one trophic step, as well as through other more indirect mechanisms, such as altered water and sediment quality, and what has been described as "ecological engineering." Just as problematic is that conclusions may be pre-determined by the response measured, and by the choice of habitat being studied.

We began this section by a brief recounting of the search for general theories about the biological process that may control food webs, began as early as the 1920s, and extending to the present. Now we can ask whether we can generalize to any extent, or are ecological assemblages simply particularistic arrays, depending on contingencies of species composition by chance and history, and from which the effect of nutrients and consumers are another intensely local result? That seems a trivial result, since we could make only the most limited predictions.

The foregoing paragraphs reviewed just a few of the many examples available. Even these selected examples give perhaps a bewildering variety of results, many quite particular to species and sites. It is difficult to generalize, but we might speculate that, first, in most environments, both bottom–up and top–down controls will be active, but their relative importance will likely depend on local conditions, and composition of biota. Second, effects of biological controls will be constrained or mediated by physical features (flushing times, wave action, storms, and so on). Third, top–down controls are more likely to play important roles where nutrient supplies are relatively low, and might be overwhelmed by bottom–up controls as nutrient loads increase to high levels. Fourth, top–down controls are more likely to be important where producers are most palatable or susceptible to grazing, but increased nitrogen content may increase the susceptibility of macrophytes to grazers.

From the fourth point above, we might speculate that consumers might be more prominent as governors in coastal systems dominated by palatable phytoplankton and green macroalgae, less so in systems dominated by less palatable, chemically defended vascular plants. If this is so, we might conjecture that top–down control by consumers might be less influential in salt marshes and mangroves than in other coastal systems, since marsh grasses and mangroves have strong anti-herbivore defenses. All these suppositions need support from further studies; repeating experimental manipulations of nutrients and consumers in a variety of different ecological settings might be a fruitful way to synthesize the differences seen in diverse habitats.

3. Losses of coastal wetland habitats

The current discussions, and many papers in JEMBE and other journals about the relative primacy of different mechanisms that might control food webs in general are

Table 2
Condition of estuarine marsh areas in Chesapeake and Delaware bays, based on 1993 satellite imagery

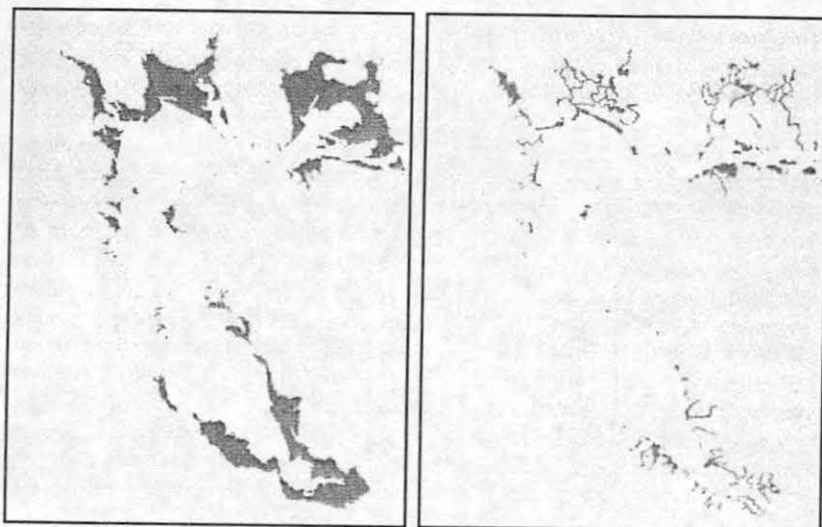| Sites		Condition (as % of the area of wetland)		
		Non-degraded	Slightly to moderately degraded	Severely to completely degraded
Chesapeake Bay	Upper and middle bay	31	50	19
	Lower bay	28	52	20
Delaware Bay	North shore (NJ)	38	43	19
	South shore (DE)	55	35	10

Data from Kearney et al. (2002).

Fig. 3. Past and present area of tidal marsh (represented by green) on San Francisco Bay. A version of this figure appeared in Goals Project (1999), files for this version by courtesy of Robin Grossinger of the San Francisco Bay Institute.

doubtless an indication of widespread interest in basic understanding of ecological assemblages. While the papers published in journals such as JEMBE have appropriately addressed such issues of basic research, many of the environments in which the work was and is being done are disappearing or being severely altered. This is particularly true for coastal wetlands worldwide.

Table 3

Conversion of coastal wetland habitats in San Francisco Bay, across nearly two centuries, from natural system to human-dominated land covers

	Area (acres)		
	Ca. 1800	Ca. 1988	% Change
Native aquatic habitats			
Open bay water	273,911	254,228	− 7
Tidal flats	50,469	29,212	− 42
Tidal marsh	189,931	40,191	− 79
Human-dominated aquatic habitats			
Lagoons	84	3620	4209
Salt ponds	1594	34,455[a]	2062
Other altered areas	266	155,021	58,179
Native coastal land habitats	89,357	23,286	− 74

Data from Goals Project (1999).

[a] Now being restored to marshland under Federal and State support and management (L. Valiela, U.S. Environmental Protection Agency, personal communication, and http://www.southbayrestoration.org/Project_description.html).

Table 4

Losses of coastal wetlands in the United States (excluding Alaska and Hawaii), and in Louisiana, 1920s–1990s

Years	ha × 10³	ha × 10³ year⁻¹	% Loss	% year⁻¹
Coastal U.S.				
1922–1954	260	8.1	6.5	0.2
1950s–1970s	146	7.3[a]	–	–
1970s–1980s	29	2.9	1.7	0.15
1975–1985	24	2.4	1.1	0.11
1982–1987	0.4	0.06	1.1	0.18
Coastal Louisiana				
1958–1974		10.8		0.86
1983–1990		6.6		–

From data compiled by Mitsch and Gosselink (2000), Brady and Flather (1994), and Dahl and Johnson (1991).

[a] Another value for this period of losses of 19 ha × 10³ per year for the period 1954–1974 seems too high and was not included in this table.

A few examples from North America convey the dimensions of the problem. In Chesapeake and Delaware Bays, only 28–55% of the estuarine marshes remained non-degraded by 1993 (Table 2). Orson et al. (1998) estimated that by the year 2000 in the state of Connecticut, U.S., 45% of the salt marsh area was gone, an estimated 41% was in the course of destruction, and 14% was likely to remain in conservation. In San Francisco Bay, conversion of natural to human-dominated habitats resulted in losses of 79% of the tidal marsh habitats (Fig. 3), plus losses in the actual area of the Bay, tidal flats, as well as adjoining coastal land covers (Table 3); the percentage increase in human-dominated environments is startling. Similar large losses of wetlands in Louisiana have been recorded (Table 4). In general, the loss of coastal wetland area in the U.S. diminished across the 20th century, but that is only because the area of wetlands have diminished in magnitude: the percentual rate of loss remained similar toward the end of the century (Table 4). One hopes that more recently, awareness of the losses have lowered the rate of disappearance.

Table 5

Current mangrove swamp areas, % loss, annual loss rate, and % of original area lost per year, for the mangroves of the continents and the world

	Current mangrove area (km²)	% Loss of mangrove forest area	Annual rate of loss (km² year⁻¹)[a]	% Original area lost per year
Asia	77,169	36	628	1.52
Africa	36,529	32	274	1.25
Australia	10,287	14	231	1.99
Americas	43,161	38	2251	3.62
World	166,876	35	2.834	2.07

From data in Valiela et al. (2001a).

[a] Annual loss rates calculated from the mean number of years between earliest and latest information available for the countries within each continent. For the World, for example, the data average out to span the period 1980–1997.

Table 6
Uses of mangrove swamp area leading to loss of habitat

	World total (10^3 km^2)	% of total
Shrimp culture	14	38
Forestry uses	9.5	26
Fish culture	4.9	14
Diversion of freshwater	4.1	11
Land reclamation	1.9	5
Herbicides	1	3
Agriculture	0.8	1
Salt ponds	0.05	–
Coastal development	0.05	–

The data used in this table cover 66% of the world's mangrove swamp area; data were not readily available for the remainder area.
Data from Valiela et al. (2001a), compiled from many sources.

Losses of coastal wetlands are not just a North American problem. For example, losses of mangrove forests across the tropics have reached alarming proportions (Table 5). Appropriate data are difficult to find, but best estimates are that, on a worldwide basis, perhaps 2% of the mangrove forest area has been lost per year since 1980 (Table 5). These losses have amounted to an estimated loss of 35% of the area of mangroves present worldwide in 1980. More detailed regional studies (for example, Blasco et al., 2001) confirm the worldwide losses.

Losses of coastal wetland areas come about from a variety of human activities, largely filling and wetland "reclamation" for marshes as was the case, for instance in San Francisco Bay (Table 2), or interception of river-borne sediment by levees and other earth works, as in the case of losses of Louisiana salt marshes (Reed and De Luca, 1997; Day et al., 2001). A number of other mechanisms lead to losses in area of mangrove forests (Table 6). As in all cases of environmental damage, there are good economic and social reasons for the losses. Aquaculturists who raise shrimp and fish in ponds dug out of erstwhile mangrove forest areas (Table 6) do so because of imperative economic pressures. Economic pressures have historically been more

Table 7
Percentage of salt marshes ($n = 19$) that exported materials out to deeper waters

Materials	Percentage of salt marshes studied that exported materials to deeper waters
Ammonium	64
Nitrate	36
Dissolved organic nitrogen	100
Particulate organic nitrogen	67
Total nitrogen	100
Dissolved organic carbon	91
Particulate organic carbon	59
Total carbon	82

Data from Valiela et al. (2001b), compiled from many sources.

powerful than arguments for conservation of wetlands. The reason we have lost wetlands is that we have repeatedly made the economic decision that other land covers are more profitable and desirable.

If we believe it is worthwhile to maintain coastal wetlands as natural systems, we will have to redouble efforts to help the public and political sectors of society better reconcile the balance between economic imperatives and the less-apparent benefits provided by coastal wetlands. It therefore seems useful to once again review the benefits provided by wetlands.

3.1. Export of energy-rich materials important to food webs of deeper waters

Eugene Odum's and John Teal's hypothesis that salt marshes exported materials to deeper waters, has, on the whole, been supported by many studies. A compilation of data collected on exchanges of materials between marshes and adjoining deeper waters
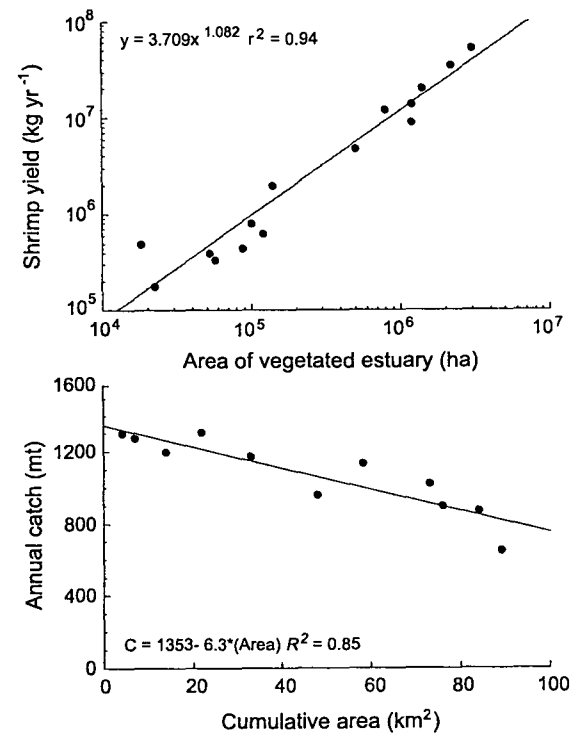

Fig. 4. Harvest by the shrimp fishery off Louisiana in relation to the area of adjoining coastal wetland (top). Metric tons of shrimp caught annually off Louisiana in relation the cumulative loss of adjoining coastal wetland (bottom). From Valiela et al. (2001b), data compiled by Turner (1992).

shows that the large majority of salt marsh ecosystems exported energy-rich substances (reduced nitrogen compounds, dissolved and particulate organic matter) to deeper waters (Table 7). These exports are a quantitatively important subsidy supporting ecosystem metabolism in the receiving ecosystems. For example, measured exports of organic matter from Georgia salt marshes were large enough to furnish the energy needed to support the high rates of metabolism in the near-shore Georgia Bight ecosystem (Turner et al., 1979; Kinsey, 1981; Hopkinson, 1985). Recognition of the role that salt marshes play by providing energetic subsidies that support populations in deeper waters has become a leading argument for conservation of salt marshes, at least in the west coast of the Atlantic.

3.2. Nurseries to many species, including commercially important fisheries stocks

Many species of commercial and ecological importance use coastal wetlands as nurseries (Robertson and Duke, 1987; van der Velde et al., 1992; Nagelkerken et al., 2000; Mumby et al., 2004). An example of the importance of coastal wetlands to coastal stocks was given by Turner (1992), who reported that shrimp yields along the coast of the Gulf of Mexico were proportional to the area of coastal marsh landward of the harvest area (Fig. 4, top). During the 20th century the shrimp harvest fell, and the reduction in catch was correlated to the cumulative loss of marshland in the Louisiana area (Fig. 4, bottom). These relationships could follow from the nursery role played by the marshes for juvenile shrimp, and also from the energy-rich materials exported from these marshes to deeper waters off-shore.

Many commercially important species use salt marshes as foraging areas during their early life stages. These include fish such as menhaden, a species that contributes the largest biomass to the North American fish harvest, bluefish, and striped bass, among many others. A study by Werme (1981) provided evidence as to why fish from deeper

Table 8
Comparisons between species of fish resident in Great Sippewissett Marsh and species of fish whose adults live in deeper water, but whose young invade salt marsh estuaries

	Resident species[a]	Invader species[b]	Paired t-test
Mean length of fish in marsh	41 ± 4	59 ± 9	n.s.
Mean length of adults	106 ± 19	422 ± 121	*
% Full guts	26 ± 4	59 ± 9	**
% Carnivory in diet	48 ± 13	78 ± 16[c]	**
Mouth gape	1.9 ± 0.3	4 ± 0.6	**
No. fish/100 m of shoreline	57 ± 31	0.8 ± 0.3	**
% growth/month	18 ± 4	127 ± 27	**

Results of paired t-test are non-significant (n.s.), significant at 0.05 (*), or highly significant (**).
From Valiela et al. (2001b), data from Werme (1981).

[a] Resident species include *Menidia menidia, Apeltes quadracus, Fundulus heteroclitus, Fundulus majalis,* and *Cyprinodon variegatus.*

[b] Invader species included *Alosa pseudoharengus, Brevoortia tyrannus, Gasterosteus aculeatus, Tautoga onitis, Centropristes striatus,* and *Pseudopleuronectes americanus.*

[c] >90% if *Brevoortia tyrannus* was excluded.

waters might use wetlands as nursery areas (Table 8). Within the salt marsh estuary, the size of fish that resided year-round in the estuary did not differ from that of the juveniles of species whose adults live in deeper waters ("invaders" in Table 8): there are disadvantages to having a larger size in these systems, because larger fish are easily stranded in shallow pools at low tide, and are readily eaten by the many top predators (herons, egrets, terns, and many other birds) often common in salt marshes. Juveniles from deeper-water species had fuller guts, and were far more carnivorous than resident fish (Table 8). The invaders achieved these feats by their larger gape (Table 8), which arise from the allometry of vertebrates: the young have relatively larger heads than adults, and, as it turns out, invaders are all juveniles. Invader species, on average, therefore had access to larger food items than the resident species (Fig. 5). Feeding on larger prey places stringent bounds on abundance of invaders, because, as is well known, larger prey are much less abundant than small prey. Invaders trade off the much lower densities than those of resident species, but achieve growth rates an order of magnitude larger than resident species (Table 8). Thus, though obligatorily less numerous, juvenile invaders from the adjoining deeper-water environment achieved fast growth rates in salt marsh estuaries. This faster growth, based, at least in part, on
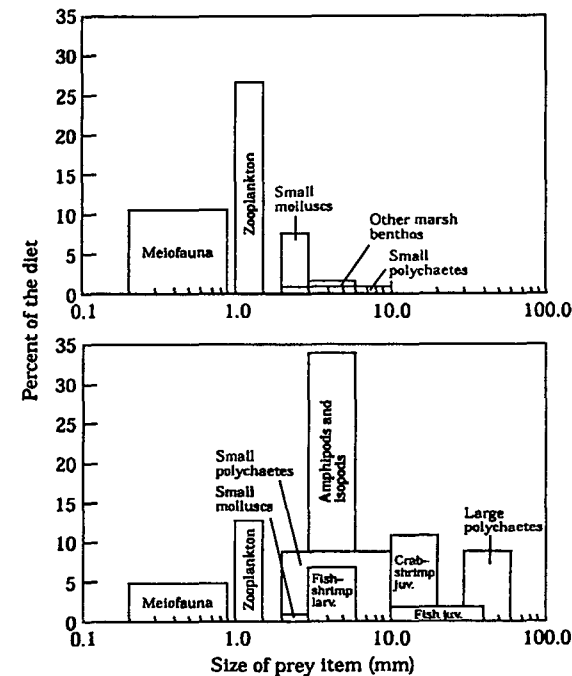

Fig. 5. Percent diet of resident (top) and invading (bottom) fishes consisting of animals ranked by increasing size. The addition of percentages of different prey items is the percent carnivory in their diets and is plotted in the inset of both graphs. Note that the x-axis is on a log scale. From Sardá et al. (1998).

higher relative abundance of larger food items, accounts for the nursery function of salt marshes for juveniles of species from deeper waters. An additional, if minor, consequence of the nursery role of wetlands is that the movement of the erstwhile juveniles to deeper waters add up to a measurable, but modest, export of larger, marsh-grown units of high-quality organic matter to coastal waters (Deegan, 1993).

3.3. Habitat for shellfish and finfish stocks

The shallow, protected bays, inlets and lagoons that are fringed by wetlands are rich in phytoplankton and other particles that are prime food for suspension feeders, and support reasonably dense faunas of other consumers. Wetland-fringed environments are almost inevitably areas where humans harvest a variety of stocks. For example, oysters, quahogs, scallops, soft-shell clams, blue crabs, winter flounder are among the many valuable crops taken from such environments in temperate latitudes of Eastern North America. In warmer waters fringed with mangroves, there is often artesanal harvest of mullet, shrimp, mangrove oysters, and mangrove cockles from Mexico to Peru (Mackenzie, 2001). Values of crops from Eastern North American marsh-fringed environments are typically an order of magnitude larger, on a per-unit area basis, than those obtained from grains in terrestrial agriculture (Mackenzie, 1989).

3.4. Sites for aquaculture

The food-rich shallow waters fringed by wetlands are potentially useful sites for mariculture efforts. For example, artesanal culture of mangrove oysters in Cuba provide reasonable yields in less than a year. Shrimp farms have proliferated in many mangrove areas (Valiela et al., 2001a), in part to make use of rich waters. Incidentally, feeding of cultured shrimp is supplemented by fish meal mostly manufactured from marsh-dependent species such as adult menhaden, harvested from deeper waters. Ideally, stocks of shellfish could be grown in high densities in wetland-fringed estuaries, and their suspension feeding could be a tool to improve or restore water transparency, as has been argued in attempts to restore oyster banks in Chesapeake Bay (Cloern, 1982; Ulanowicz and Tuttle, 1992). A concern with this management option is the simultaneous production of fecal material by shellfish, a process that adds organic matter to sediments and depletes near-bottom oxygen (Roman and Tenore, 1984).

3.5. Intercept contaminants

To a certain extent, salt marsh sediments retain contaminants of many kinds, including heavy metals (Teal, 1986; Giblin et al., 1986), chlorinated hydrocarbons, and petroleum hydrocarbons (Reddy et al., 2002). Mangrove sediments also retain metals (Tam and Wong, 1999). In general, contaminants such as heavy metals have few discernible effects on wetland macrophytes or marsh fauna (Valiela et al., 1976). To the degree to which any contaminant from land is buried in marsh or mangrove sediments, these wetlands are preventing more widespread contamination of coastal waters.

3.6. Stabilize shorelines

The roots and rhizomes of marsh plants add coherence to sediments, as do the dense roots of mangrove trees (Savage, 1972). By their very presence these macrophytes therefore consolidate otherwise loose sediments, and hence lower erosion of vegetated sediments. Storms often fail to disturb marsh sediments that are covered by grasses (Valiela et al., 1996).

3.7. Sources of forage and hay

Marshes have long been used as grazing lands; one can see remnants of such practices all over the world, where salt marshes are still used as pastures. For example, visitors to most Scottish marshes will see grazing sheep on them. Cattle in coastal areas of Argentina can frequently be seen feeding on salt marsh hay, assimilating the forage as well as obtaining essential salts. Historically, use of salt marshes for grazing was also the case in Eastern North America; many colonial-era property deeds included a parcel of marshland for pasture purposes. Marshland was highly desirable because no worksome logging and uprooting were needed to create pastures. During more recent centuries in the east coast of North America, marsh grass was cut, dried over photogenic staddles (Fig. 6), and the dry matter used as marsh hay to feed livestock, and as horticultural mulch. Currently, there is a small market in developed countries for salt marsh hay, valuable because it does not sprout weeds when used as garden mulch.
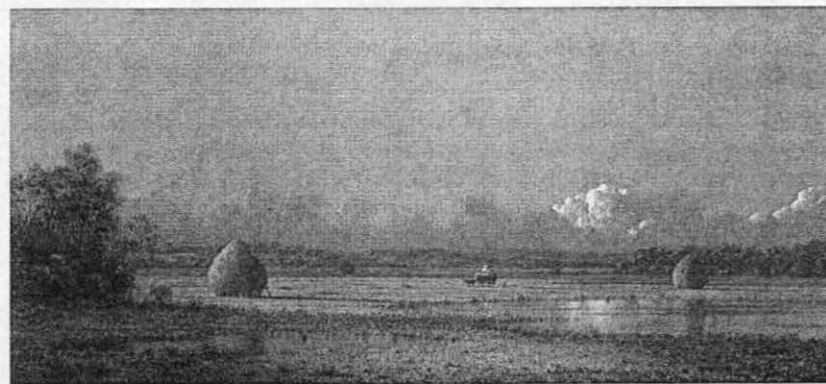

Fig. 6. 19th-century use of salt marsh grasses from the coast of Massachusetts. The *Spartina* and *Distichlis* grasses were cut, and piled on cedar supports—*staddles*—that held the hay above the high tide marks, and allowed the hay to dry before being used as winter feed for livestock. Uses of marsh grass as livestock feed began as soon after the initial European colonization of North America. The illustration is "Hayfields: a clear day," painted about 1871–1880 by Martin Johnson Heade. Reproduced from Stebbins (1999).

3.8. Waterfowl refuges and migratory stop-over sites

A large and diverse set of migratory birds depend on having adequate wetland areas as stop-over sites during migration and as wintering sites. Most of the population of European storks passes through or winters in the threatened Coto Doñana wetland in Southern Spain, plus what is left of the Nile Delta wetlands. Preservation of these wetland habitats is therefore essential for this charismatic species, but there are many other waders, shorebirds, birds of prey, herons, egrets, and so on, that, though less well known to the public, also depend on such wetlands during migration for refueling and rest.
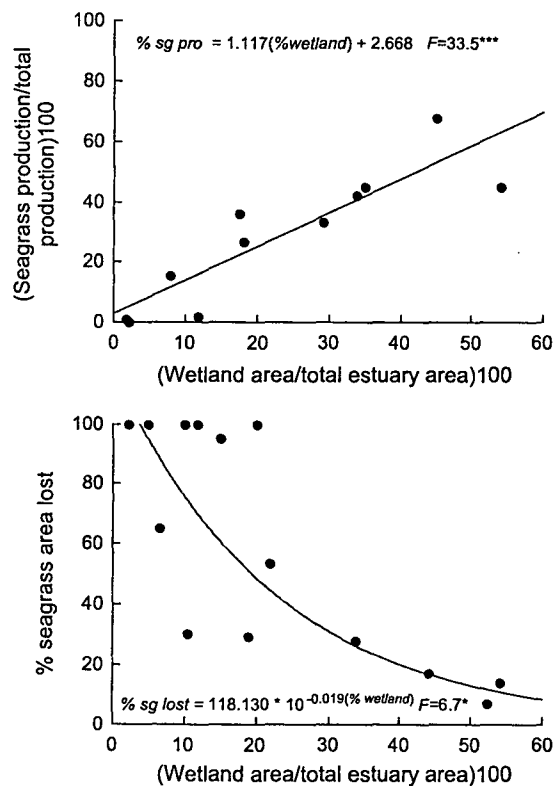

Fig. 7. Seagrass production expressed as % of total production in many estuaries, plotted versus the area of fringing wetland expressed as % of total estuary area (top). Percent of area of seagrass habitat lost (over the last 10–30 years) plotted versus the % of area of the estuary made up by fringing wetland (bottom). From Valiela and Cole (2002).

3.9. Intercept land-derived nutrients

Wetlands intercept certain material transported from land and moving toward the sea. Note, for example, in Table 7 that nitrate is exported by a minority of coastal marshes: marshes tend to intercept rather than export nitrate, a major form of the nitrogen that limits growth of most coastal algae and plants in most coastal environments. Salt marshes may provide substantial interception of land-derived nitrogen because of their position between land and estuary, as well as because of their high rates of denitrification and burial of nitrogen (Valiela, 1983). One example of the potential importance of nitrate interception is given in Valiela and Cole (2002), who showed that the larger the area of salt marsh, or of mangrove swamp, the greater the production by seagrasses in adjoining meadows (Fig. 7, top), and the smaller the loss of seagrass meadows that occurred as nitrogen loads increased (Fig. 7, bottom). Seagrass meadows are highly sensitive to increased nitrogen loads: interception of land-derived nitrogen in coastal wetlands can be interpreted as an important protective ecological "subsidy" furnished by salt marshes (and mangrove swamps) to adjoining coastal environments such as seagrass meadows.

The items listed above are reasons we can muster to point out that human interests in coastal wetlands might include many important natural subsidies, rather than just cash crops or building sites. In some quarters it has become fashionable to develop valuations of ecological features, seeking equivalencies of natural services with currency. Two problems with this approach are, first, that in many cases, it is simply not realistic to make such conversions; in almost all cases, the methodology used in valuation does not withstand critical scrutiny, although space precludes an exegesis of the procedures here. Second, and far more important, is that any time a price is placed on anything, *it is for sale*, and the highest bidder is unlikely to share our priorities about conservation of wetlands in their natural state.

There are some encouraging signs. Salt marsh restoration efforts of some magnitude are under way in a number of places in the U.S., including the Delaware River estuary, North Carolina, the Pacific Northwest, southern New England, Louisiana, and California (several chapters in Weinstein and Kreeger, 2000 and Craft et al., 2003), and there are plans to restore the extensive areas of salt flats and lagoons in South San Francisco Bay to their original salt marsh status (L. Valiela, U.S. Environmental Protection Agency, personal communication, and http://www.southbayrestoration.org/ Project_Description.html). These are local efforts, but do portray a rising and perhaps widespread awareness on the part of public and political sectors about the need to at least slow the loss of coastal wetlands.

In discussions about coastal wetland conservation, there is a certain hesitation to mention that many of us simply take great pleasure in wetlands and the organisms and settings they provide. One cannot—we are tempted to say ought not—put a price tag on this, but the aesthetic appreciation of wetlands by many people is a powerful force that should be harnessed. Arguments highlighting the aesthetic worth of wetlands, as well as the list of natural subsidies furnished by wetlands, need to be mustered, and repeated, in reaching out to the public and politicians. Success in raising awareness of wetland losses might ensure that we can continue to delight in wetlands, and that our

students and their students might have enough wetlands in which to continue doing exciting research, such as adding to our incomplete knowledge about how wetland food webs are controlled, and lead to new directions by which salt marshes might further add to environmental science in general.

Acknowledgments

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