

Top-Down Control and Human Intensification of Consumer Pressure in Southern U.S. Salt Marshes

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Salt marsh ecosystems in the western Atlantic are widely considered to be controlled exclusively by bottom-up forces (e.g., salinity, redox, nutrients). However, mounting experimental evidence challenges this established theory and shows that top-down control of marsh grass growth by consumers (i.e., plant-grazing snails and their predators) has been greatly underestimated and that human disturbance is currently triggering intensified consumer control. In the southeastern United States, unambiguous experimental evidence has revealed that marsh snail populations, likely released from predator regulation and stimulated to overgraze marsh grass by drought-induced soil stress, have formed massive grazer fronts and are contributing to large-scale salt marsh die-offs by denuding marsh substrate and leaving exposed mudflats in their wake. Unfortunately, such runaway consumption is likely to increase in the near-future concomitant with predicted increases in drought stress and human harvest of key marine predators (e.g., blue crabs) that facilitate marsh grass via a trophic cascade. Combined, these experimental results call for a complete realignment of the current marsh paradigm and for marsh scientists to incorporate experiments into future investigations of salt marsh productivity and die-off to properly account for consumer impacts. Reliance on field and lab correlation studies, which has led to dangerous theory dependency in salt marsh conservation and ecology, can no longer be the default scientific methods of choice. The lack of recognition of the importance of consumers in this system may have grave repercussions for coastal ecosystem management and conservation, since government agencies and nongovernmental organizations are managing marsh die-offs only considering bottom-up forces as causal agents.

TOP-DOWN AND BOTTOM-UP CONTROL OF PLANT COMMUNITY STRUCTURE

Prevailing ecological theory has long held that climate ultimately controls the distribution and primary productivity of ecosystems. Of these

ecosystems, those dominated by plants (e.g., tundra, deciduous and coniferous forest, rain forest, grasslands, kelp forest, seagrass beds, mangroves, salt marshes) are typically green in appearance, and consumer control in these communities was considered insignificant

or subtle—for example, potentially affecting species composition, productivity, and some ecosystem properties, but not capable of regulating the long-term persistence and distribution of these systems.

In 1960, Hairston, Smith, and Slobodkin proposed an opposing view that suggested the consumers play a much more important role in structuring plant-dominated ecosystems. They argued that the world is green because higher trophic levels control herbivore abundance. In essence, they suggested that grazers must not be food limited given the abundance of green material on Earth and that, therefore, what keeps herbivore populations and their negative impacts on plants in check is top-down control by predators. Thus, the world is kept green by a tritrophic interaction, where predators control grazers that would otherwise overgraze and denude substrate. In response, other scientists pointed out that what is green is not necessarily edible or of sufficient quality to allow increases in herbivore populations. This chemically mediated, bottom-up view purports that most plants have “won” the predator–prey arms race and are heavily defended and free from significant enemy attack. This debate is ongoing, but the dominant view remains that consumers can impact many aspects of plant ecology, but that they are not key drivers of plant productivity over entire ecosystems.

In recent decades, however, examples of conspicuous grazer control of entire plant ecosystems have emerged. These studies show that runaway herbivory can replace more subtle community effects with obvious overgrazing, converting potentially green ecosystems to barrens. In several cases, foundation plant species (*sensu* Dayton 1972) are grazed and replaced with unvegetated substratum or small inconspicuous species. In terrestrial systems, both invertebrates (e.g., native or introduced beetles and moths) and vertebrates (e.g., introduced possums) can denude entire forest canopies (Hard, Holsten, and Werner 1983; McManus et al. 1992; Holsten, Werner, and DeVelice 1995; Norton 2000), insects can defoliate mangrove

stands (Anderson and Lee 1995; Feller 2002), and ungulates and elephants can convert savannas to sandy deserts. Similar examples exist from marine systems, where urchins can convert kelp forests and seagrass beds to barren rock bed and sandflats, respectively (Camp, Cobb, and van Breedveld 1973; Ogden, Brown, and Selesky 1973; Estes and Palmisano 1974; Lawrence 1975; Estes et al. 1998; Rose et al. 1999). These examples of runaway consumption are considered undesirable from a conservation and management perspective, because overgrazed systems tend to have lowered biodiversity and productivity, and less economic and aesthetic human value. From an ecological perspective, these examples warn that whole-ecosystem regulation by consumers may be much more prevalent than currently recognized.

TROPHIC CASCADES: CONSUMER CONTROL TRICKLES UP THE LADDER

Since the world is generally green, runaway grazer effects have been considered exceptions and viewed as relatively unimportant. Over the past fifty years, however, it has become clear that consumers can be important drivers of ecosystems even when they are overwhelmingly green. This has happened by focusing on the predators of grazers. When ecosystems are green, predators are often holding grazers in check, while when they are overgrazed, predator loss or removal is often responsible for elevated grazer densities and plant loss. This tritrophic interaction, where predators facilitate plants by controlling grazer populations, is known as a *trophic cascade*. Hairston et al. (1960) first hypothesized that the world is green because predators control grazers, and Carpenter and colleagues further developed the trophic cascade concept with experimental studies in lakes, demonstrating that fish can control zooplankton that, in turn, control phytoplankton (Carpenter, Kitchell, and Hodgson 1985; Carpenter and Kitchell 1988). Since these seminal studies, manipulative experiments have demonstrated trophic cascades in many other communities,

and rules of thumb have emerged predicting where and when trophic cascades occur. In general, trophic cascades tend to be more important in aquatic versus terrestrial systems, in simple versus complex food webs, in homogeneous versus heterogeneous systems, in communities dominated by nonvascular plants (i.e., algae), and in systems where impalatable plants don't replace those that have been overgrazed (Strong 1992; Pace 1999; Shurin et al. 2005). With the widespread occurrence of ecosystem shaping trophic cascades, ecologists and conservation biologists must now consider the relative importance of top-down effects in controlling plant ecosystems and must not end their scientific inquiry at the second trophic level, as they have in the past. Predators and their indirect effects need to be incorporated into ecological models and conservation strategies of plant communities.

Importantly, ecologists differentiate between population- and community-level trophic cascades. In population-level cascades, predator removal leads to overgrazing and local extinction of a plant species. However, the overgrazed plant is then replaced with an impalatable plant species so that the ecosystem remains green and intact. In contrast, in a community-level cascade, predator removal leads to overgrazing of the entire plant community with the concomitant loss of associated ecosystem services. Both types of cascades occur in coastal salt marshes, with community-level cascades having the potential to destroy marshes and the services they provide (see chaps. 5 and 7, this volume). To identify management strategies needed to help preserve coastal plant communities, conservation practitioners and researchers need to use field experiments to test for the presence and impacts of both types of trophic cascades.

THE BOTTOM-UP-ONLY MARSH PARADIGM AND ITS REACH

For nearly fifty years, ecologists have recognized and promoted salt marshes as the quintessential model ecosystem controlled by physical

forces, where primary production was controlled by bottom-up factors, such as soil nutrient concentrations, pH, salinity, redox, air temperature, sea level, and precipitation (Teal 1962; Odum and De La Cruz 1967; Adam 1990; Mendelssohn and Morris 2001). This paradigm grew from classic work by Eugene Odum, John Teal, and others on Sapelo Island, Georgia, in the 1950s and 1960s stressing the dominant role of physical factors in regulating ecosystem productivity and structure. The importance of consumers, while not rigorously tested with experiments that removed grazers, was largely disregarded, and the dogma that herbivores were unimportant became deeply entrenched in coastal wetland ecology. Since marshes provide crucial ecological and societal services, this paradigm also became the bedrock of coastal conservation. The Odum model of physically controlled ecosystems gained such wide acceptance that it was exported to other ecosystems dominated by lush vascular plant production, including mangrove forests, seagrass meadows, and temperate and tropical forests. This conceptual exportation to other systems, however, did not question its basic, untested assumption that consumers were irrelevant. Thus, theory dependency and demonstration, rather than falsifying science, led to the widespread application of the salt marsh bottom-up theory throughout coastal conservation and ecology.

THE OVERTURNING OF THE BOTTOM-UP ONLY PARADIGM

Salt marshes are relatively homogeneous, low-diversity ecosystems characterized by simple food webs. Despite the early work of Odum and colleagues suggesting that consumers were irrelevant to marsh plant community dynamics, these community and food web characteristics of salt marshes theoretically makes them ideal candidates for top-down control via trophic cascades (see earlier discussion; Strong 1992). Indeed, in clear contrast to the still-persisting and widely invoked bottom-up paradigm of salt marsh ecology, large-scale, top-down control of plant growth was demonstrated experimentally

in arctic salt marshes by Robert Jefferies and coworkers over two decades ago (e.g., Bazely and Jefferies 1986; Jefferies 1988; Kotanen and Jefferies 1997; Jefferies and Rockwell 2002; Jefferies, Jano, and Abraham 2006).

Jefferies studied these systems in the early 1970s, initially focusing on the positive effects of geese grazing on primary production through soil disturbance and nitrogen cycling. But by the 1980s, the snow geese that annually migrated to Hudson Bay switched from feeding in temperate zone wetlands to agricultural fields and golf courses, which were receiving nitrogen fertilizer subsidies. Consequently, snow geese populations nearly tripled during the 1980s, leading to runaway consumption and the denuding of extensive areas of Arctic marshes (currently more than thirty-seven thousand hectares in southern Hudson Bay alone). This collapse was driven by birds grubbing roots and rhizomes that then led to low plant cover and hypersaline and anoxic soil conditions. This grazer-generated soil stress created a negative feedback loop where the remaining vegetation died, soil salinity increased even further, and plants that recruited into the newly denuded areas died rapidly from osmotic stress, preventing ecosystem recolonization. Essentially, at high densities, geese foraging turned off habitat-ameliorating, positive feedbacks that had historically allowed plants to establish and support arctic marsh ecosystems. Jefferies and colleagues attributed this ecosystem collapse to a trophic cascade, where geese populations increased due to human activities of declining hunting pressure and expansion of agricultural fields and golf courses that subsidized geese with plant nitrogen.

Most recently, the marsh bottom-up paradigm has been challenged on Sapelo Island, Georgia, where salt marsh ecosystem ecology started. On this island and in marshes in Virginia, South Carolina, and Louisiana, Silliman and colleagues employed consumer removal and addition experiments to demonstrate that salt marsh primary production

throughout the region is largely regulated and suppressed by the most common and widespread (from Maryland to Texas) grazer in the system, the marsh periwinkle, *Littoraria irrorata* (Silliman and Zieman 2001; Silliman and Bertness 2002; Silliman and Bortolus 2003; Silliman and Newell 2003; Silliman et al. 2005). Removal of these snails at commonly occurring field densities (fifty to five hundred snails per square meter) increased production of the dominant salt marsh plant in the southeastern United States, the smooth cordgrass *Spartina alterniflora*, by 30 to 80 percent (fig. 6.1).

These results clearly challenged the bottom-up paradigm, but they were widely disregarded by established marsh ecologists who claimed results were largely generated from experimental artifacts of caging. These scientists also dismissed the work because in numerous past studies, *Littoraria* had been shown to eat only *dead* marshgrass and associated fungi (Marples 1966; Alexander 1979; Kemp, Newell, and Hopkinson 1990; Currin, Newell, and Paerl 1995). Unfortunately, as was the case in past studies that investigated the importance of marsh grazers (Teal 1962; Odum and De La Cruz 1967), studies of *Littoraria* feeding ecology did not use experiments. Instead, they relied solely on correlation studies (i.e., gut content and isotopic analyses) and concluded that snails preferred fungi and dead grass, did not graze live grass, and were the most important detritivores in the marsh system. However, when Silliman employed manipulative experiments to examine snail feeding in the field, he noticed periwinkles grazed not only on dead but also live marshgrass (Silliman and Zieman 2001). When grazing on live *Spartina*, *Littoraria* used its radula to create longitudinal wounds one to twenty centimeters long and one to three millimeters wide (see fig. 6.2; Silliman and Zieman 2001; Silliman and Bortolus 2003). Those grazer-generated wounds subsequently became infected with fungi (fig. 6.2), and snails then concentrated their grazing activity on those



FIGURE 6.1 Effects of periwinkle grazing on *Spartina* standing crop and canopy structure in the tall zone after eight months: (A) low-density plot and (B) high-density plot. After twenty months, cordgrass in all medium-density plots was reduced wholesale and the marsh substrate completely denuded (B). From Silliman and Bertness 2002.

wounds to consume the facilitated fungal crop (Silliman and Newell 2003).

Thus, even though Silliman's results concurred with past marsh researchers', that snails preferred fungi for food, the data disagreed with how periwinkles procured fungus. Instead of waiting for grass to die and be colonized by fungi, snails grazed live grass and exhibited low-level, fungal-farming behavior that utilized live leaves as a substrate for fungal crop growth (Silliman and Newell 2003). Further experiments in the same marshes that crossed fungicide application with snail presence showed that



FIGURE 6.2 Periwinkle snails and the radulations (i.e., grazing scars) they generate.

the end result of this farming activity for the plant host, *Spartina*, was growth suppression or death due to grazer facilitation of fungal infection (Silliman and Newell 2003). Thus, even though snails did not consume much live plant tissue, they severely suppressed grass growth through facilitation of microbial invasion, giving these grazers the ability to exert strong, top-down control that is greatly disproportional to the amount of live grass consumed.

Caging experiments further showed that at naturally occurring high densities (1,200 snails per square meter) the top-down effect of fungal-farming snails is even more dramatic, and *Littoraria* can completely denude marsh substrate and reduce standing crop by as much as 3,500 g dry wt C m⁻² to 0 g dry wt C m⁻² (Silliman and Bertness 2002). When snail presence was crossed with nutrient additions (a bottom-up force) and across naturally occurring nutrient gradients (from the short to the tall *Spartina* zone), snail impacts were greatly amplified. Increased bottom-up resources for plants and resultant higher nitrogen content in their tissue tripled grazing intensity and resulted in snails denuding the substrate in less than eight

months (Silliman and Zieman 2001; Silliman and Bertness 2002). Combined, these caging studies demonstrate that if snail populations are left unchecked by regulatory forces, these systems have the potential to be overwhelmed and destroyed by runaway grazing.

Simultaneous food web experiments examining the role of predators in controlling snail distribution and abundance across the marsh surface in Georgia salt marshes showed that marine predators such as blue crabs and terrapins largely control snail distribution (Silliman and Bertness 2002; fig. 6.3). Tethering and caging experiments demonstrated that predators completely exclude snails from the highly productive tall *S. alterniflora* zone, where they both recruit and grow better, and strongly suppress their densities in the short *S. alterniflora* zone. These results, combined with caging experiments showing snails, at naturally occurring densities, can completely kill a tall *Spartina* zone in eight months, reveal that the growth and success of southern U.S. marshes is controlled by a trophic cascade, where crabs, fish, and terrapins suppress densities of potent plant-grazing snails that would otherwise increase in density and destroy salt marsh plants (fig. 6.3). These experimental findings clearly overturn the long-held paradigm that grazers and their predators are unimportant players in salt marsh ecosystems. Thus, the new marsh paradigm must now reflect the fact that both bottom-up and top-down forces are important in controlling salt marsh structure and function. In addition, this paradigm realignment compels marsh scientists and conservation biologists to use field experiments to test for the relative importance of top-down impacts when investigating physical controls on marsh grass growth and success.

Given that blue crabs have declined dramatically in recent decades in many southeastern estuaries (Jordan 1998 and references therein), partly due to overharvesting and partly to disease and drought, it is possible that the newly

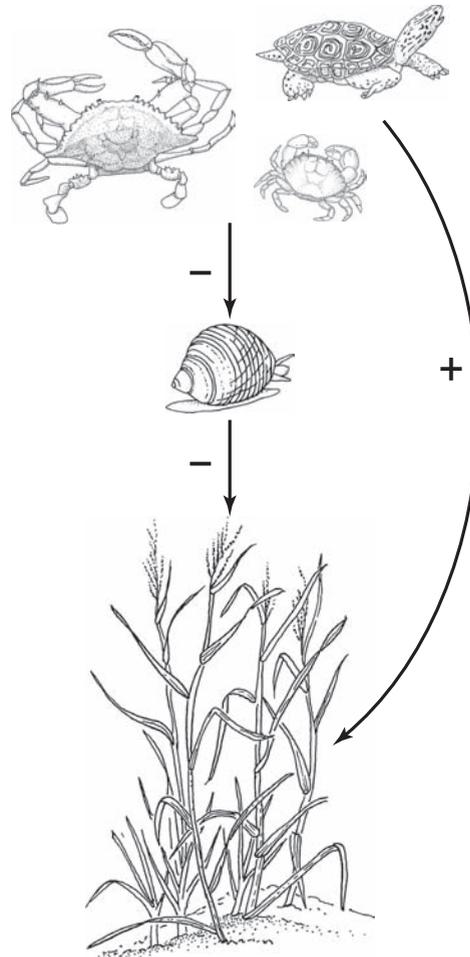


FIGURE 6.3 The marsh trophic cascade. From Silliman and Bertness 2002.

revealed marsh trophic cascade has been partially unleashed, thereby increasing top-down control by snails and the likelihood of runaway consumption events. Because the new interaction network of controls on cordgrass growth now includes top-down forces (fig. 6.3) in the form of snails and their blue crab predators, humans must also be included as apex predators. Humans, by suppressing and stressing blue crab populations via fishery take, could be indirectly intensifying top-down control on *Spartina* grass by releasing fungal-farming snails from predator regulation. As in the case

of Jefferies's research in subarctic marshes, humans thus have the potential to unleash a powerful and devastating trophic cascade in intertidal grasslands.

MASSIVE DIE-OFF OF SOUTHEASTERN SALT MARSHES: COULD TOP-DOWN FORCES BE INVOLVED?

Over the past decade, massive marsh die-offs have occurred on the southeastern and Gulf coasts of the United States. These die offs have been extensive, impacting over 250,000 hectares, and have received considerable media and scientific attention in South Carolina, North Carolina, Georgia, Florida, Texas, and Louisiana (McKee, Mendelssohn, and Materne 2004). Until recently, however, these die-offs had been attributed solely to harsh physical conditions killing marsh plants, an interpretation consistent with the Odum model and interannual correlations between drought stress and the occurrence of die-offs. Experimental work over the past five years, however, has shown that increasing consumer control of marsh plants is an important contributing factor driving these die-offs. As was the case in past studies challenging the bottom-up marsh paradigm, these experimental results are in direct contrast to those found by marsh ecologists employing correlation studies.

Observational studies have concluded that top-down effects are not playing a direct role in the recent dieback events (Carlson et al. 2001; McKee et al. 2004; L. Blum, personal communication). Upon examination of die-back plants at particular Louisiana sites, McKee et al. (2004) reported no visible evidence of grazing on live *S. alterniflora* tissue. At other sites where snail grazing was observed, grazing activity appeared to occur post-plant mortality (McKee et al. 2004). These assertions, however, were based on observations of plant condition and not on experimental study or data gathering on snail-grazing intensity (McKee et al. 2004). When

experiments were used at many of these same sites in Louisiana to test for snail-grazing effects, extensive snail fronts (twenty to one hundred meters long, one to two meters wide, with five hundred to two thousand snails per square meter) were discovered on the edges of dieback areas (fig. 6.4). After six to twelve months of exclusion, marsh plants in control plots exposed to snail grazing were completely killed and exposed mudflats remained, while those in caged areas protected from snails were robust and growing healthily (Silliman et al. 2005). Importantly, reconstruction of snail densities prior to Louisiana die-off events clearly showed that snails could not have initiated these die-off events. Instead, Silliman et al. (2005) concurred with McKee et al. (2004) that climate-induced stress(es) (e.g., soil acidity or salinity) likely caused initial grass mortality and/or extreme sublethal stress. This physical stress then likely intensified snail grazing, as stressed plants are more susceptible to snail grazing (Silliman et al. 2005), resulting in increased grazer impacts and potential to kill off marsh grasses. These experimental results demonstrate that grazers played a significant contributory role in Louisiana marsh die-off events (i.e., they increased original die-off area by at least 15 percent) and challenge the observational conclusion of McKee et al. (2004) that grazers were unimportant in Louisiana die-off.

Carlson et al. (2001) also observed heavy grazing on dead *S. alterniflora* shoots at dieback sites along the Florida panhandle. No data were taken on this observation or whether snails were actively grazing remaining live marsh grass. The authors concluded that grazing was a secondary event and not the primary cause of that dieback event. Again, in the absence of direct experimental evidence or even data collection, it is scientifically difficult, if not impossible, to accurately assess the relative effects of grazing or its role in plant mortality. Manipulative studies should therefore be conducted wherever possible and will be necessary



FIGURE 6.4 Snail front exclosures (wrapped in hardware cloth) installed on die-off border at one site in Louisiana.

before the relative role of consumers (top-down forces) and bottom-up forces in driving marsh dieback can be fully elucidated.

Experimental and survey evidence from several other dieback sites in Georgia and South Carolina also support the finding that snail grazing played a key but overlooked, contributory role in dieback of southern salt marshes (fig. 6.5). Silliman et al. (2005) reported elevated

density of the marsh periwinkles on the edges of dieback areas (*Littorina irrorata*) at eleven of twelve sites surveyed across 1,200 kilometers of shoreline in Louisiana, Georgia, and South Carolina. The highest densities of snails were located at the boundary between dieback areas and healthy marsh where snail density ranged from ~400 to 2,200 individuals per square meter (fig. 6.6). Exclusion experiments in Georgia, as



FIGURE 6.5 Effect of snail exclusion cage on *Spartina alterniflora* biomass on die-off border at the Light House marsh on Sapelo Island, Georgia. Plants protected from snails in cages are healthy and robust, while those exposed to snails in uncaged control areas, and those in uncaged, wrack removal areas (with many stakes) where completely killed and exposed mudflat was left in their wake.



FIGURE 6.6 Representative extreme snail densities found in snail fronts in Georgia.

in Louisiana (discussed earlier), resulted in a more than 400 percent increase in *S. alterniflora* biomass over three months; after six months, plants in control areas still exposed to snail grazing were completely grazed down, and exposed mudflats remained. These snail fronts maintained their integrity for six to twelve months and continued moving through healthy areas of *S. alterniflora*, resulting in expansion of original dieback areas by as much as 185 percent in what was described as a runaway grazing event (Silliman et al. 2005).

As mentioned, coincident with initial marsh die-off events in the southern United States were record droughts throughout the Gulf and southeastern Atlantic coasts from 1999 to 2001 (McKee et al. 2004; Silliman et al. 2005). Researchers investigating the dieback throughout the region suspected that the drought had played an important role as an antecedent condition (trigger event) for marsh dieback. One set of proposed mechanisms operating at the Louisiana dieback sites (episodic acidification and elevated metal toxicity) was investigated in the lab experimentally (McKee et al. 2004). To test for the potential interactive effects of grazing and sublethal, drought-induced physical stress (in this case, elevated soil salinities, which were observed in both Louisiana and Georgia), Silliman et al. (2005) experimentally elevated salts in the presence (controls) and absence (exclusion cages) of snails in a healthy Georgia marsh. Experimental results revealed that exposure to sublethal salinities, combined

with grazing, resulted in nearly doubling the reduction in *S. alterniflora* biomass, as compared to single-stressor treatments, and caused severe plant mortality and small-scale, localized marsh die-off. Combined, the outcome of this stress-enhanced field experiment, grazer exclusion experiments at the edges of die-off areas in both Louisiana and Georgia, and model analyses of snail front movement and formation (Silliman et al. 2005), suggests that drought-induced soil stress and grazers acted synergistically and, to varying degrees, to cause initial plant death (if snails were not present at sites, then there could not be a synergism, and just drought-induced effects are implicated). Following these localized disturbances, if snails were present, snail fronts formed on die-off edges and subsequently propagated through healthy marsh, leading to cascading vegetation loss. Whether or not declines in densities of one of the snails' major predators, the blue crab, *Callinectes sapidus*, over the past ten years in southeast estuaries (Silliman et al. 2005) contributed indirectly to marsh die-off by leading to elevated snail salinities and thus greater potential for overgrazing, remains to be investigated. Importantly, though, the potential for the marsh trophic cascade to act as a significant contributing factor to marsh health deterioration can no longer be ignored or dismissed.

The recent, catastrophic die-off of salt marshes that seemingly fit the Odum physical control model on the southeastern and Gulf coasts of North America is increasingly being controlled by consumers, whose influence is likely greatly exaggerated and intensified due to human-generated diffuse disturbance (i.e., intensification of drought events via climate change and overharvesting of predators—terrapins and blue crabs—of potent snail grazers). This potentially catastrophic development—one that is completely opposite of the current marsh paradigm and of what is currently being promoted in conservation circles as the detrimental effects of human impacts on marine food webs (i.e., humans dampen top-down control)—may be an early sign of global shifts in the processes controlling salt marshes and coastal ecosystem

services. The indirect role of humans in generating and unleashing intensified top-down control in salt marshes that can reduce biomass of plant foundation species wholesale and leave exposed mudflats in its wake can clearly no longer be ignored or dismissed.

FUTURE RESEARCH AND RECOMMENDATIONS TO MARSH MANAGERS

Future experimental research investigating the importance of top-down control in southeastern U.S. marsh systems should focus on (1) the species-specific role of marsh predators in regulating historical and present-day grazer densities and distributions, (2) the relative role of recruitment and predation in controlling grazer populations across marsh landscapes, (3) how variation in physical soil stressors and climate change impact grazer distribution and grazing intensity, and (4) the relative role of consumers in regulating marsh grass recovery from die-off events. Marsh ecologists and managers in systems throughout the world should also strive to use experiments to test for the presence of powerful, but cryptic, top-down impacts in their local systems (e.g., Chile, South Africa, China).

To mitigate top-down impacts on marshes, managers should look to maintain healthy populations of predators that suppress densities of commonly occurring marsh grazers through regulation and marine reserves. Management must also begin to monitor both marsh grazer (e.g., snails in the Southeast and sesarmid crabs and insects in the Northeast; see chap. 8, this volume) and predator densities along with soil salinities, redox, and acidity levels in healthy marshes, so that the magnitude of marsh grass stressors can be measured before, during, and after dieback events and the relative importance of top-down and bottom-up forces properly assessed. In addition to reexamining current regulations in tidal marshes, managers should consider actions such as freshwater releases on managed rivers to coincide with drought and

tighter regulation of populations of marsh predators (e.g., blue crabs).

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