Consumer Control of Salt Marshes Driven by Human Disturbance

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Abstract: *Salt marsh ecosystems are widely considered to be controlled exclusively by bottom-up forces, but there is mounting evidence that human disturbances are triggering consumer control in western Atlantic salt marshes, often with catastrophic consequences. In other marine ecosystems, human disturbances routinely dampen (e.g., coral reefs, sea grass beds) and strengthen (e.g., kelps) consumer control, but current marsh theory predicts little potential interaction between humans and marsh consumers. Thus, human modification of top-down control in salt marshes was not anticipated and was even discounted in current marsh theory, despite loud warnings about the potential for cascading human impacts from work in other marine ecosystems. In spite of recent experiments that have challenged established marsh dogma and demonstrated consumer-driven die-off of salt marsh ecosystems, government agencies and nongovernmental organizations continue to manage marsh die-offs under the old theoretical framework and only consider bottom-up forces as causal agents. This intellectual dependency of many coastal ecologists and managers on system-specific theory (i.e., marsh bottom-up theory) has the potential to have grave repercussions for coastal ecosystem management and conservation in the face of increasing human threats. We stress that marine vascular plant communities (salt marshes, sea grass beds, mangroves) are likely more vulnerable to runaway grazing and consumer-driven collapse than is currently recognized by theory, particularly in low-diversity ecosystems like Atlantic salt marshes.*

Keywords: consumer control, human impacts, salt marsh conservation, trophic cascades

Control por Consumidores en Marismas Conducido por Perturbación Humana

Resumen: *Se ha considerado extensamente que los ecosistemas de marismas son controlados exclusivamente por dinámicas abajo-arriba, pero se ha acumulado evidencia de que las perturbaciones humanas están provocando el control por consumidores en marismas del Atlántico occidental, a menudo con consecuencias catastróficas. En otros ecosistemas marinos, las perturbaciones humanas rutinariamente disminuyen (e.g., arrecifes de coral, pastos marinos) y refuerzan (e.g., varec) el control por consumidores, pero la teoría de marismas actual predice una leve interacción potencial entre humanos y consumidores en las marismas. Por lo tanto, las modificaciones humanas al control arriba-abajo en las marismas no estaba anticipada y aun era descontada en la teoría de marismas actual, a pesar de advertencias sobre el potencial de impactos humanos en cascada en trabajos en otros ecosistemas marinos. No obstante los experimentos recientes que han desafiado el dogma de marismas establecido y que han demostrado la desaparición gradual de marismas conducida por consumidores, las agencias gubernamentales y las organizaciones no gubernamentales continúan manejando la disminución de marismas en el marco de la teoría vieja y sólo consideran como agentes causales a factores abajo-arriba. Esta dependencia intelectual en la teoría sistema-específico (i.e., teoría de marismas abajo-arriba) de muchos ecólogos y manejadores costeros tiene el potencial de tener repercusiones graves para el manejo y conservación de ecosistemas costeros frente a las crecientes amenazas humanas. Enfatizamos que las comunidades plantas vasculares marinas (marismas, pastos marinos, manglares) son potencialmente*

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más vulnerables al pastoreo descontrolado y al colapso conducido por consumidores que lo que reconoce la teoría actualmente, particularmente en ecosistemas con baja diversidad como las marismas del Atlántico.

Palabras Clave: control de consumidor, impactos humanos, conservación de pantano de sal, cascadas de trophic

Introduction

Over the past decade the pervasive impact of overharvesting marine ecosystems has become clear. Overharvesting top marine consumers has led to the collapse of shallow-water marine ecosystems around the globe (Jackson et al. 2001; Duffy 2002), including coral reefs (Hughes et al. 2003), sea grass beds (Jackson 1997), and kelp forests (Estes et al. 1998). These shallow-water marine ecosystems protect shorelines from erosion, chemically process terrestrial runoff and act as nursery grounds for commercial species, and the loss of the ecological services historically provided by these ecosystems has become an urgent scientific and conservation priority. Although the impact of overfishing on coastal systems has finally been recognized by coastal managers and conservation organizations, more recently shallow-water salt marsh ecosystems—long thought to be the gold standard of habitat-generated marine ecological services and relatively impervious to these consumer impacts—have been found to be on the verge of succumbing to entirely different anthropogenic forces that, in turn, generate a complex suite of destructive food-web forces.

In salt marshes human activities, such as nitrogen subsides and climate change, are triggering, instead of dampening, consumer control. This is happening in marsh systems that historically have been thought to be controlled by bottom–up forces entirely. The resultant consequences are potentially catastrophic and completely unanticipated by environmental scientists and resource managers and pose management dilemmas that challenge our scientific understanding of coastal systems. Theory dependency (i.e., subconscious favoring of identifying and/or examining natural phenomena that tend to confirm rather than refute the current paradigm of a study system [Kuhn 1962]) and demonstration, rather than falsifying science, have, more than any other factors, been the leading culprits in this ecological and management oversight.

For nearly 50 years ecologists have recognized and promoted salt marshes as the quintessential model ecosystem controlled by bottom–up forces. This paradigm grew from classic work by Eugene Odum (1971), John Teal (1962), and others on Sapelo Island, Georgia, (U.S.A.) in the 1950s and 1960s. This work stressed the dominant role of physical factors in regulating ecosystem productivity and structure. The importance of consumers, although not rigorously tested with experiments, was largely disregarded, and the dogma that herbivores were unimportant became deeply entrenched in the conceptual understanding, management, and conservation of coastal wetlands. Because marshes provide crucial ecological and societal services, this paradigm became the bedrock of coastal conservation. The Odum model of physically controlled ecosystems gained wide acceptance and was exported to other ecosystems dominated by lush vascular plant production, including mangrove forests, sea grass meadows, and temperate and tropical forests. This conceptual exportation to other systems, however, did not question its basic assumption that consumers were irrelevant in spite of its implications for conservation and management.

The first serious challenge to the Odum model came from sub-Arctic marshes (Jefferies 1997). Robert Jefferies studied these systems in the early 1970s, initially focusing on positive effects of geese grazing on marsh primary production mediated through soil disturbance and nitrogen cycling. But by the 1980s the Snow Geese (*Anser caerulescens*) that annually migrate to Hudson Bay switched from feeding in temperate-zone wetlands, which were being lost to human activity, to agricultural fields and golf courses, which were receiving nitrogen fertilizer subsides. Consequently, populations of Snow Geese nearly tripled during the 1980s, leading to runaway consumption and the denuding of extensive areas of Arctic marshes (currently > 37,000 ha in southern Hudson Bay alone) that serve as their summer breeding and feeding grounds (Fig. 1). This collapse was driven by intensive goose grubbing of plant roots and rhizomes, which then led directly to low plant cover, quickly followed by hypersaline and anoxic soil conditions. This grazer-generated soil stress created an unstoppable feedback loop in which the remaining, adjacent vegetation died, soil salinity increased even further, and plants that recruited into the newly denuded areas died almost immediately from osmotic stress, preventing ecosystem reestablishment. Essentially, at high densities, geese foraging turned off habitat ameliorating positive feedbacks that had historically allowed plants to establish, dominate, and support arctic marsh ecosystems. These precipitated and cascading events that led to wholesale system collapse were begun almost entirely by the luxuriant use of artificial nitrogen fertilizer in the temperate zone. Unfortunately, this scenario of seemingly unrelated human activities indirectly triggering top–down forces is not restricted to arctic marshes.

Eerily similar marsh die-offs have been occurring for nearly two decades on the southeastern and Gulf Coasts

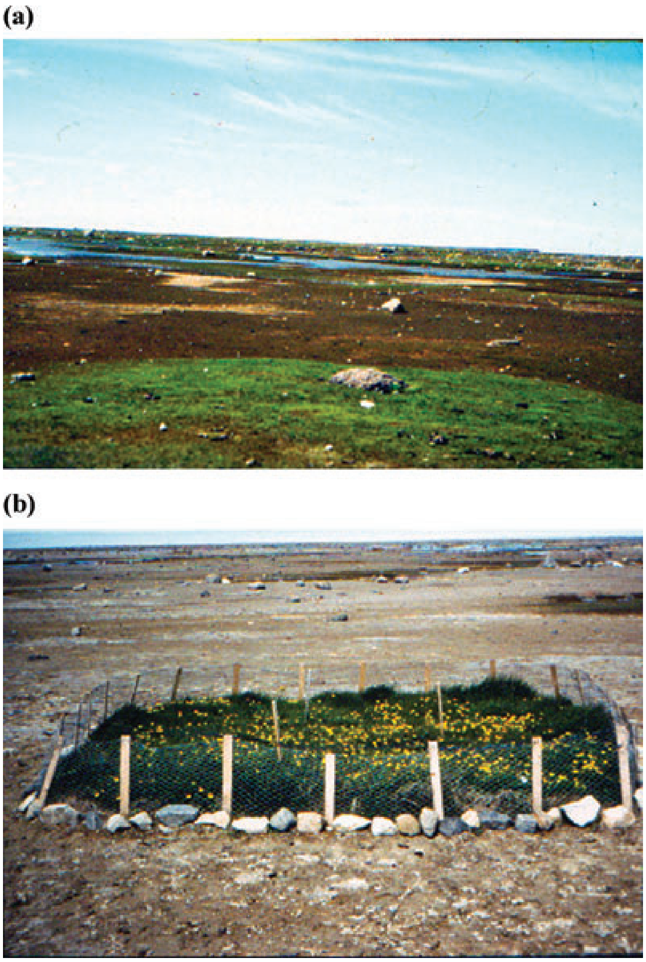

Figure 1. Snow Geese damage to Canadian subarctic salt marshes: (a) Jefferies' (1997) study sites in 1974 and (b) the same site in 1999 with a goose exclosure.

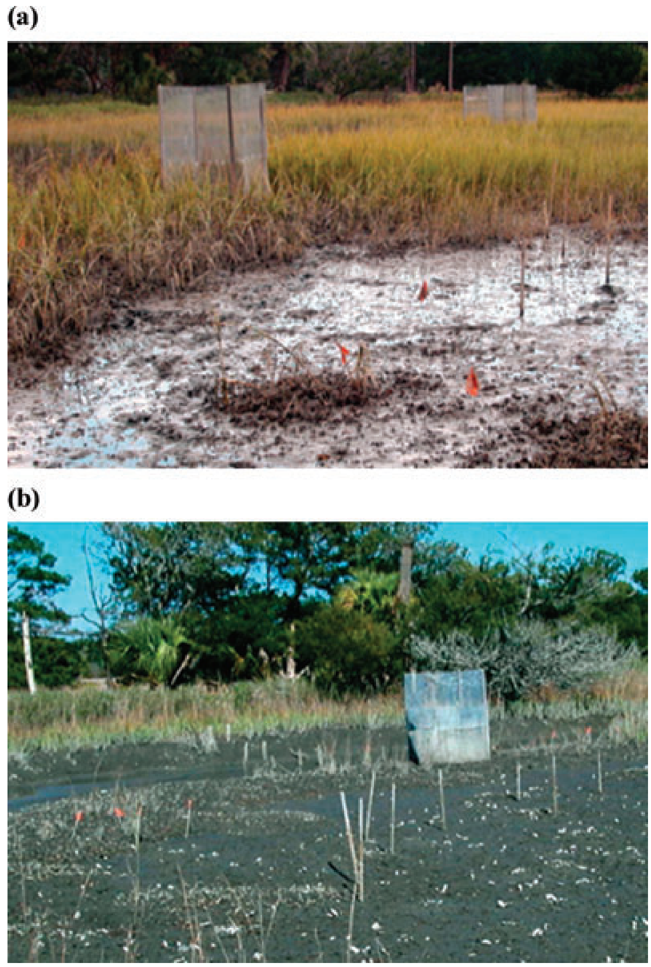

Figure 2. (a) Snail exclusion cage at the edge of a die-off area in a high marsh in May 2003 and (b) the same area 3 months later after snail grazing had expanded the size of the die-off area.

of the United States. These die-offs have been extensive, affecting more than 250,000 ha and have received considerable media and scientific attention in South Carolina, North Carolina, Georgia, Florida, Texas, and Louisiana. 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.

Results of experimental work over the past 5 years (Fig. 2), however, show that increasing consumer control of marsh plants is an important contributing factor driving these die-offs. Simple field experiments have revealed that commonly occurring high densities of the marsh snail, *Littoraria irrorata*, can entirely denude stands of marsh cordgrass (>2.5 m tall) in less than a growing season by facilitating lethal fungal infection in vertical grazing scars on leaf surfaces (Silliman & Newell 2003). Historically, snail densities were controlled primarily by predators, such as blue crabs (*Callinectes sapidus*) and terrapins (*Malaclemys terrapin*), which have been overharvested and now suffer from diseases and other maladies of small populations. This release of top–down pressure on snail densities may have led to increased snail densities (Silliman & Bertness 2002), although the release is not enough alone to generate a quintessential trophic cascade.

Compounding potentially increased and naturally occurring high consumer densities, intense drought stress, ostensibly a product of human-driven climate change that can increase climatic extremes, has elevated soil salinities and acidity throughout southeastern marshes and increased the vulnerability of cordgrass to consumer control by snails and catastrophic die-off (Silliman et al. 2005). When sublethal drought and sublethal grazer densities occur simultaneously in a marsh, the result is often lethal for the foundation-species marsh grasses and the services they provide. Per capita rates

Figure 3. Example of a low marsh die-off area on Cape Cod Massachusetts, August 2007.

of grazing by snails double and sometimes triple on salt- or acid-stress-weakened plants. After these physical and biological stressors act synergistically to kill marsh grasses, exposed mudflats emerge in localized areas, and a cascading vegetation loss propelled by consumer snail waves can occur if threshold concentrations of both drought-generated salt stress and grazer densities are present.

Thus, the catastrophic die-offs of salt marshes that seemingly fit the Odum physical control model in the Canadian sub-Arctic and on the southeastern and Gulf coasts of North America are increasingly being controlled by consumers whose influence is greatly exaggerated and intensified due to human-generated diffuse disturbance (i.e., intensification of drought events via climate change). This potentially catastrophic development, and one that is completely opposite of what is currently being promoted in conservation circles as the detrimental effects of human impacts on marsh ecosystems (i.e., increased bottom–up forcing through elevated nutrient loading and rising sea levels), may be an early sign of global shifts in the processes controlling salt marshes and coastal system services. Indeed, in both Argentine and New England salt marshes, there are early signs that similarly strong, human-generated runaway consumer effects may be at work in large marsh die-offs and community collapse.

In Argentina salt marshes are dominated by extraordinarily high densities of the burrowing shore crab (*Chasmagnathus granulata*, up to 60 individuals/m^2 with burrows covering up to 40% of the substrate surface; Botto & Irbarne 1999). This large (up to 7 cm wide) crab excavates and maintains burrows up to 1 m deep and is a voracious herbivore of emerging marsh grass. Like many marshes on the southeastern and Gulf coast of North America, Argentinean and Brazilian salt marshes are often characterized by unvegetated substrate. These unvegetated areas can represent half of the marsh habitat and potential primary production and are characterized by high densities of crab burrows. Recent crab-removal experiments have revealed that these bare areas are created and maintained by crab herbivory (Fig. 3) because marsh grasses rapidly colonize these areas when crabs are excluded (Alberti et al. 2007). We suspect that these unprecedented (in comparison with other natural communities) high densities of such a large crab in this system are in part due to the overfishing of top predators, analogous to sea urchin densities in the Caribbean half a century ago driven by overfishing of turtles and predatory fish.

In New England salt marshes current research is also revealing human disturbances triggering consumer control in marshes, suggesting that this scenario may be ubiquitous in the western Atlantic. In Narragansett Bay the primary production of pristine marshes is controlled by nitrogen availability, but nitrogen additions trigger insect herbivores that suppress primary production by nearly 60%. Moreover, insect herbivores are already suppressing the primary production of human disturbed salt marshes by nearly 40%, whereas marshes without human shoreline development are exclusively under bottom–up control (Bertness et al. 2008). Thus, even in intensively studied systems where ecologists are confident that consumers are not important, human activities are shifting salt marshes from the Odum model of bottom–up control to top–down consumer control.

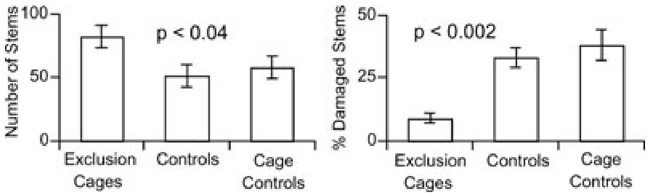

Figure 4. Results of caging experiment at Wellfleet Marsh on Cape Cod from August 2006, where the herbivorous crab Sesarma cinereum *was excluded from the edges of die-off areas. All data are means and SE.*

Most disturbing are recent reports of the extensive die-off of New England salt marshes on Cape Cod that have been compared with die-offs that have decimated salt marshes in the southeastern United States over the past decade. These New England marsh die-offs have received considerable media attention from the *Boston Globe*, *New York Times*, and National Public Radio, but rigorous research has not addressed the cause. Although following the Odum model, physical processes are the suspected cause, results of preliminary studies suggest that herbivory by a common, but nocturnal and largely unrecognized crab (*Sesarma reticulatum*) is playing a leading role in generating these die-offs (Fig. 4). When we excluded crabs on the borders of Cape Cod die-off areas in August 2006 for less than a month, herbivore damage was reduced 4-fold and cordgrass density was increased by one-third in comparison with cordgrass exposed to crabs. These results warn that consumer pressure, potentially triggered by a historical depletion of marine predators (Myers & Worm 2003), or the dramatic acceleration in the use of artificial nitrogen fertilizers over the past few decades and weakening of plant defenses by climate-induced soil stress (Vitousek et al. 1997; Howarth et al. 2000), could be triggering runaway consumption and system collapse of New England salt marshes.

Invasive consumers have also contributed to increased consumer control in Western Atlantic salt marshes. On the southeastern and Gulf Coasts of the United States, the introduced rodent nutria (*Myocastor coypus*) has led to consumer control of marsh vegetation (Gough & Grace 1998), whereas feral horses originally kept on the sea islands off the coasts of Virginia, Maryland, and the Carolinas by European settlers have entirely denuded salt marsh habitats and destroyed most of the ecosystem services naturally provided by salt marshes (Levin et al. 2002).

Together, these examples warn that although historically western Atlantic salt marshes may have been under bottom–up control consistent with the Odum model, human disturbances ranging from the use of nitrogen fertilizers, overharvesting of top predators, climate-change–induced drought, and to exotic consumer invasions are triggering consumer control in western Atlantic salt marshes, sometimes with catastrophic results.

Because salt marshes are arguably the most critical remaining ecosystem in the western Atlantic in terms of the ecological and ecosystem services they provide, the consequences of human activities triggering consumer control and potential collapse of coastal marsh systems could be dire. Salt marshes provide storm buffering, erosion control, biochemical processing of runoff, and nursery grounds for many marine species, making conserving and managing the remaining salt marshes an urgent priority for the health of coastal systems.

In spite of mounting evidence that salt marshes are becoming increasingly vulnerable to runaway consumer control throughout the western Atlantic, virtually all salt marsh management, conservation, and restoration efforts are determined on the basis of the Odum model of bottom–up control. The reality is that both bottom–up and top–down forces are interacting to cause these die-offs over large spatial scales. Consequently, one of the largest threats to salt marsh ecosystems and the ecological services they provide are being entirely overlooked. Sacred, deeply entrenched dogma is preventing ecologists and conservation biologists from recognizing the most serious immediate threats to coastal systems with potentially devastating consequences to coastal systems and human populations.

Given this evidence from salt marshes, coastal scientists and practioners in other vegetated marine communities, where the Odum model was actively imported, must also reevaluate the dominance of bottom–up theory in the intellectual understanding and conservation of their systems. In many of these communities, including sea grass (Zimmerman et al. 1996) and mangrove systems, there have been numerous examples of local overgrazing of rooted mangroves (Smith et al. 1989, mangroves) and top–down control of seedling establishment and success (Zimmerman 1996, sea grasses; Heck & Valentine 2007). Understanding whether these top–down forces operate over similarly large spatial scales as bottom–up forces do in these systems, and as we have shown occurs in salt marshes, will be essential to establishing whether or not the Odum model has been applied inaccurately to the ecology and conservation of these systems as well. Certainly, the results of studies that show local, strong top–down control in mangroves and sea grasses warn that this could be the case.

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