Consumer impacts on ecosystem functions in coastal wetlands: The data gap

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Abstract. Over the last 30 yr, our understanding of the factors that control the structure and function of coastal wetlands has shifted from a narrative that focused on bottom-up control to one that explicitly includes top-down factors. However, the emphasis of this transition has been on how consumers influence wetland vegetation; comparatively, few studies evaluate how consumers influence broader ecosystem properties and functions such as nutrient cycling and decomposition while fewer still investigate how trophic interactions affect these relationships. Here, we review the literature on consumer impacts on coastal wetland ecosystems and highlight areas where additional studies are sorely needed. It is our hope that identifying the current gaps in our knowledge will provide additional impetus for the study of community and ecosystem ecology within these globally important ecosystems.

Key words: coastal wetlands; consumers; ecosystem functions; trophic interactions.

INTRODUCTION

The historical paradigm of coastal wetland ecosystem ecology emphasized bottom-up control of wetland functions via plant–soil interactions and abiotic factors (Odum and Smalley 1959, Smalley 1960, Teal 1962, Sala et al. 2008). Seminal studies by Smalley (1960) and Teal (1962) found that within southern United States salt marshes, the tides are responsible for the high amount of smooth cordgrass (Spartina alterniflora) production by supplying nutrient subsidies and limiting consumer access. Within these systems, common consumers such as grasshoppers only ingest about 2% of the net production. Similarly, early work in Florida mangroves utilized the foundations established by Odum (1980) and his contemporaries and found that the production of organic detritus was little affected by top-down biotic processes and was instead largely regulated by tidal action (Twilley 1985, Twilley et al. 1986). These and other studies concluded that the structural aspects of coastal wetlands, including species richness, plant distribution patterns, and overall productivity, were maintained principally by abiotic processes acting from the bottom-up (Cannicci et al. 2008). The frequency and duration of tidal flooding, salinity, and sediment characteristics were thus considered the primary drivers of coastal wetland structure and function (Odum 1971, Odum and Heald 1972, Smith 1994).

However, research over the last 30 yr has provided evidence that is contributing to a
paradigm shift in which consumers that rely on plant productivity are becoming increasingly recognized for the role they play in regulating wetland ecosystem properties and functioning (He and Silliman 2016). Early research suggested that burrowing sesarmid (Grapsidae) and fiddler crabs (Ocypodidae), often the most common macroinvertebrates in coastal wetland habitats, can significantly alter energy flow and the export of organic material through herbivory and ecosystem engineering effects (Beever et al. 1979, Bertness 1985, Robertson 1986, Smith 1987). Experimentation in New England salt marshes found that the presence of fiddler crabs (Uca pugnax) is strongly associated with a shift in S. alterniflora morphology and growth and that these effects are mediated by crab burrowing behavior (Bertness 1985). Further, crabs found in mangrove swamps change sub-surface and near-surface redox conditions as well as increase microbial heterogeneity with significant implications for decomposition activity and vegetation growth (Emmerson and McGwynn 1992, Micheli 1993, Botto and Iribarne 2000, Kristensen 2008).

Though this initial work was heavily focused on macroinvertebrates, recent studies indicate that both smaller and larger consumers can also regulate wetland properties (Dahdouh-Guebas et al. 2006, Cannicci et al. 2008, Elschot et al. 2015). From ants to hippopotami, consumers have become increasingly recognized as important drivers of large-scale ecosystem properties and functions in wetlands. However, though it is now largely accepted that wetlands are influenced by the interplay between bottom-up and top-down factors, our understanding of the latter has focused predominantly on the role that consumers play in driving vegetation (Silliman and Zieman 2001, Smith et al. 2009, Bertness et al. 2014b, etc.). Yet, ecosystems are defined by properties and processes beyond primary production; they also include resource capture, nutrient content and cycling, and decomposition. How consumers fit into our understanding of the controls of these additional features is less clear.

Further, studies that evaluate consumer effects often only consider one trophic level (He and Silliman 2016), yet emerging evidence suggests that predator–prey dynamics can have both consumptive and nonconsumptive effects on coastal wetland vegetation growth (Coverdale et al. 2013, Vu and Pennings 2018). Experimentation in salt marshes of the southern United States has shown that predators alter the feeding behavior of the herbivorous purple marsh crab (Sesarma reticulatum) with implications for S. reticulatum fitness and S. alterniflora productivity (Vu and Pennings 2018). In the absence of predators, S. reticulatum reduced aboveground biomass by 66–81% and belowground biomass by 35–67%. However, when predators were present, there was a threefold increase in aboveground biomass due to predator avoidance behavior and a decrease in S. reticulatum functional density (Vu and Pennings 2018). Studies such as these highlight the importance of considering trophic interactions in the maintenance of wetland ecosystem properties and functions, but such evaluations are currently few and far between.

Though our understanding of the factors that influence the maintenance and functioning of coastal wetlands has improved significantly over the last 30 yr, identifying the multifaceted roles that consumers play in regulating these features is important not only for general ecological knowledge, but also for the protection and restoration of these vulnerable and valuable ecosystems. Here, we summarize how consumer studies have been deployed in coastal wetlands and what we currently know about consumer effects as a result, outline the current status of studies evaluating consumer impacts on wetland properties other than primary production, and end by commenting on the unique importance of considering trophic interactions.

**WHAT WE KNOW: CONSUMERS ARE COMMON DRIVERS OF COASTAL WETLAND VEGETATION**

Observational and manipulation studies of consumer effects in coastal wetlands have increased significantly since the early 1990s, shedding new light on the ways consumers shape wetland structure and function (He and Silliman 2016). Seminal observational studies evaluated ecosystem properties under conditions of varying consumer densities and found that wetland functions and stability were significantly affected (Jefferies 1988, 1997, etc.). Manipulation studies built upon these early findings by
explicitly testing for consumer effects through in situ caging experiments (Fig. 1). Often, the presence or absence of common herbivores is manipulated to evaluate their direct effect on ecosystem properties (Silliman and Zieman 2001, Silliman and Bertness 2002). As the number of studies testing for consumer effects in wetlands has increased over the last three decades, so too has our understanding of the scale at which they impact these ecosystems.

A recent summary of these studies has made it clear that consumers are important drivers of wetland vegetation. He and Silliman (2016) synthesized consumer control studies in coastal salt marshes and mangroves to provide a global perspective on consumer control of coastal wetland vegetation. Utilizing observational and experimental studies with consumer present and absent treatments, they evaluated impacts on plant demographic, growth, chemical, and diversity responses. Across both ecosystem types, herbivorous consumers ranging in size from insects to livestock negatively affected nearly all of the observed response variables. Though the data available were less robust, He and Silliman (2016) also noted that in salt marshes, trophic cascade effects, whereby changes in predator-level dynamics alter those at the primary producer-level via herbivory suppression, were also noteworthy. Omnivores, on the other hand, had no significant effect on plant growth.

These findings challenge decades of accepted thought on coastal wetland functioning, showing that consumers of various taxonomic groups significantly impact wetland vegetation growth, survival, and reproduction. This work advances a more complete understanding of the controls of coastal wetland properties, but also highlights clear limitations. Studies of bottom-up control in wetlands outnumber those of top-down control nearly 3:1 (He and Silliman 2016). Among existing top-down control studies, few consider the role of consumers in regulating wetland properties other than primary production (however, see Davidson et al. 2017) and even fewer evaluate more than one trophic level. Therefore, what follows here is an expansion of these critiques for the purpose of identifying areas where additional studies are needed to fill the gaps.

**WHAT IS LESS CLEAR: THE ROLE OF CONSUMERS IN MAINTAINING OTHER COASTAL WETLAND FEATURES**

As the historical ecological paradigm in wetlands has shifted over the last several decades, this newfound understanding of how consumers influence wetland vegetation prompts the question: How might consumers influence additional wetland ecosystem properties and functions? To date, there is not a comprehensive evaluation of consumer effects on soil-based ecosystem properties and processes in coastal wetland ecosystems. Therefore, we aim to address this gap in the literature by outlining the current status of studies evaluating consumer impacts on wetland properties and functions other than primary production.

To compile a list of publications on consumer control in coastal wetlands, we searched Web of Science in December 2018 using the following query: TS = (top-down* OR herbivor* OR grazing* OR predat* OR consumer* OR trophic cascade*) AND TS = (salt marsh* OR mangrove* OR coastal wetland* OR coastal marsh*) AND TS = (soil* OR nitrogen* OR carbon* OR phosphorus* OR mineralization* OR nutrient* OR ecosystem process* OR ecosystem function* OR organic matter* OR decomposition*). This resulted in 1,272 publications. Employing filtering methods similar to He and Silliman (2016), we examined each study and retained those that (1) examined the effects of detritivores, herbivores, omnivores, or predators on soil features in observational studies and field or laboratory experiments; (2) measured effects of consumers on ecosystem properties (excluding primary production); and (3) reported mean values of the
data in both consumer present and absent treatments. After excluding all publications that did not meet these criteria, 57 experiments and observations reported in 28 studies were retained (Data S1).

For each experiment and observation, we extracted data on various soil properties in consumer present and absent treatments from texts, tables, and figures. The response variables included decomposition, ammonium and nitrate mineralization, total soil nitrogen, total soil carbon, soil bulk density, organic matter content, redox potential, salinity, and accretion rate. In addition to these response variables, we also extracted information on study duration, location, and habitat type. These data were then summarized to highlight the current status of studies evaluating consumer effects on soil-based ecosystem properties (Table 1). Variables that produced enough replicates using the same metrics were statistically analyzed using a one-way ANOVA to test for differences between consumer presence and absence treatments. All statistical analyses were conducted in RStudio (v. 1.1.456).

Four key takeaways are observed: (1) The number of studies that meet the aforementioned criteria for inclusion is very small; (2) there is little overlap in the response variables measured among studies; (3) there is a bias toward evaluating macroinvertebrates and livestock vertebrates; and (4) experiments and observations in salt marshes far outnumber those in mangroves or seagrass beds.

Within the 57 experiments and observations, soil organic matter content and bulk density were measured most often, with 27 and 24 entries, respectively (Table 1). Vegetated coastal habitats bury carbon significantly faster than tropical forests and contribute 50% of the total carbon buried in ocean sediments (Atwood et al. 2015); therefore, measurements that quantify these services predominate in the literature. Of the studies that contained entries using the same metrics to evaluate bulk density (20 entries) and soil organic matter content (8 entries), consumer presence and absence treatments did not significantly impact their change ($P > 0.1$ and $P > 0.4$, respectively, Fig. 2). However, it is worth noting that despite these results, bulk density was often observed to be higher in the presence of a consumer while there was often less organic matter content when the consumer was present. These observations suggest that consumer functional roles and behaviors (including direct consumption of organic matter/vegetation and burrowing behavior) may moderate changes in these large-scale ecosystem properties.

Among the included studies, decomposition and mineralization were measured the least, with 5 and 3 entries, respectively (Table 1). The rate at which wetlands decompose organic matter and mineralize nutrients has major implications for primary production at the local scale and climate regulation at the global scale (Coverdale et al. 2014, Atwood et al. 2015). Therefore, studies that aim to evaluate consumer control of wetland soil dynamics should include standardized measures of decomposition and mineralization, thereby providing a more holistic framework within which consumer effects can be understood.

The bias in taxonomic groups evaluated is likely due to the associated bias in habitat type.

| Summary Variable              | Number of Entries |
|-------------------------------|-------------------|
| Habitat Type                  |                   |
| Salt Marsh                    | 53                |
| Mangrove                      | 4                 |
| Seagrass Bed                  | 0                 |
| Consumer Type 1               |                   |
| Predator                      | 0                 |
| Herbivore                     | 45                |
| Omnivore                      | 0                 |
| Detritivore                   | 12                |
| Consumer Type 2               |                   |
| Vertebrate                     | 26                |
| Invertebrate                  | 31                |
| Response Variables            |                   |
| Decomposition (2)             | 5                 |
| Ammonium Mineralization (2)   | 3                 |
| Nitrate Mineralization (2)    | 3                 |
| Total Soil Nitrogen (3)       | 9                 |
| Total Soil Carbon (2)         | 7                 |
| Bulk Density (1)              | 24                |
| Organic Matter Content (3)    | 27                |
| Redox Potential (1)           | 11                |
| Salinity (5)                  | 20                |
| Accretion Rate (1)            | 4                 |

Note: Values in parentheses indicate the number of unique metrics used.
Macroinvertebrates are among the most common organisms found in salt marshes; their abundance is indicative of their ecological importance while their size makes them tractable to study. Furthermore, salt marshes are frequently used for livestock grazing, which provides a convenient means through which consumer effects can be evaluated (Yu and Chmura 2010, Di Bella et al. 2015). These biases, however, limit our ability to generalize and understand the role that consumers play in regulating coastal wetland processes at a global scale. In particular, mangroves and seagrass beds harbor a diverse array of consumers ranging from crabs and molluscs to large-bodied vertebrates such as crocodiles and water buffalo (Duffy 2006, Cannicci et al. 2008). Studies of these species in the context of coastal wetland ecosystem properties and functions are extremely limited.

Individual studies show that consumers have the potential to significantly influence coastal wetland properties and processes, but the evidence is inconsistent and haphazard at best. Furthermore, even for studies with overlapping experimental approaches, the same response variable is often measured using incompatible metrics, and therefore, study outcomes cannot be easily compared. For instance, the studies included here measured soil nitrogen content in units of grams per square meter, parts per million, and percentage. These differences preclude the development of generalizable conclusions for any given ecosystem property. Hence, standardization is sorely needed to provide a more comprehensive understanding of how consumer dynamics shape ecosystem properties and functions.

**THE DATA GAP: WHAT ABOUT TROPHIC INTERACTIONS?**

Across all of the world’s major biomes, terrestrial, freshwater, and marine systems, the importance of predators has been well documented (Estes et al. 2011). Trophic cascades and top-down forcing have landscape-level effects, often driving changes in species abundance and composition, potentially leading to regime shifts and alternative stable states of ecosystems (Estes et al. 2011). Coastal wetlands are important habitats for numerous predatory species, yet none of the studies presented here evaluate the effects of predator presence/absence on their prey and the concomitant ways this may influence ecosystem properties. Observation and experimental studies in New England have shown that predator removal due to intense recreational fishing has led to the proliferation of herbivorous crabs, resulting in runaway consumption of marsh vegetation and loss of wetland extent (Altieri et al. 2012, Bertness et al. 2014a,b). These findings clearly identify trophic interactions as important regulators of ecosystem properties. Though data on the role that consumers play in regulating coastal wetland dynamics are sparse, the near complete absence of data on predators and trophic interactions is the most significant data gap.

The historical notion that bottom-up factors drive coastal wetland structure and function has

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**Fig. 2.** Average response of bulk density (A) and soil organic matter (B) to consumer presence and absence treatments. Error bars indicate standard error.
limited our ability to fully understand the dynamics of these ecosystems. Thus, concerted efforts to evaluate top-down control and trophic cascades through large-scale observations and exclusion/inclusion experiments are imperative. This need is particularly true for vulnerable regions, such as seagrass ecosystems off the coast of Western Australia and tidal salt marshes of the northeastern USA, where the loss of large-bodied consumers and commercially important species is widespread. In a landscape of prevalent trophic downgrading, generating strong predictive power from comprehensive studies of how these losses may impact ecosystem health and stability is crucial.

**Conclusions**

Community ecology and species functional roles are integral components for the understanding of ecological systems. Emerging evidence indicates that ecosystem properties and functions are affected by the nature and strength of interactions between the species that comprise coastal wetland food webs. However, at present, our understanding of how species identity and community composition influence ecosystem properties in coastal wetlands is limited to the study of primary production. Worldwide, coastal wetlands are crucial not only for their productivity, but also as ecosystems that serve as habitat and refuge for a diversity of species, provide coastal storm protection, filter pollutants and toxins, regulate the global carbon cycle, and more. In order to have an holistic understanding of the role that consumers play in the maintenance and health of coastal wetland ecosystems, it is imperative that future studies address the following: (1) expand into less well-studied coastal wetland systems, including mangrove and seagrass beds, and evaluate the impact of the associated dominant consumers found therein; (2) incorporate trophic interactions; (3) evaluate consumer impacts on not only primary productivity, but other large ecosystem properties and processes, including soil nutrient content and cycling, mineralization, and decomposition; and (4) use metrics already present in the literature to allow for quantitative comparisons of results. Only by filling in these data gaps will we be able to develop a shared understanding of how the health and functioning of these globally important ecosystems are maintained.

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SUPPORTING INFORMATION

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