Impacts of a large-bodied, apex predator (*Alligator mississippiensis* Daudin 1801) on salt marsh food webs

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**Abstract**

Large-bodied apex predators (e.g., sharks, wolves, crocodilians) are believed to regulate food web structure and drive ecosystem processes, but there remains relatively little experimental evidence. Here we use field surveys and a mesocosm experiment to evaluate the cascading effects of an apex predator (American alligator) on a salt marsh food web. Consistent with previous studies (*n* = 10), field surveys revealed blue crabs (*Callinectes sapidus* Rathbun 1896), an important marsh mesopredator, were a frequent component of estuarine-occurring alligator’s diet (mean ± SD, 47 ± 20%, *n* = 1384). In mesocosms, we examined potential consequences of this interaction in a simplified salt marsh community. We experimentally isolated alligator effects on the abundance (consumptive effect) and behavior (non-consumptive effect) of blue crabs and on blue crab consumption of plant-grazing snails and ribbed mussels. Alligators reduced blue crab abundance by ~40% over 3 days and induced behavioral changes, resulting in decreased foraging activity and increased refuge use by blue crabs. The combined effects of reduced crab abundance and altered behavior translated into increased survival of both a keystone grazer (snails) and a mutualist (mussels) within the salt marsh food web. Our findings experimentally demonstrate that a large-bodied, apex predator has the potential to 1) generate a trophic cascade, 2) elicit behavioral changes (i.e., non-consumptive effects) in mesopredator prey, and 3) indirectly affect the potential for both grazing and mutualism to occur in this food chain. Our results generate testable hypotheses regarding the broad-scale effects of alligator presence and top-down forcing in salt marsh ecosystems.

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1. Introduction

Across diverse ecosystems, predators drive community structure and ecosystem function (Estes et al., 2011; Hairston et al., 1960; Schmitz et al., 2010). Over the past 50 years, a myriad of experimental studies have manipulated small and medium bodied predators and demonstrated that they can exert strong trophic feedbacks in food webs (Menge and Sutherland, 1976; Paine, 1980; Power and Matthews, 1985, Power et al., 1989; Schmitz et al., 2000) which, at times, can cascade down three or even four trophic levels (Letourneau and Dyer, 1998; Wootton and Power, 1993). Congruently, exclusion and observational studies have provided evidence that large-bodied, apex predators can also profoundly affect community structure and ecosystem function (reviewed in: Terborgh and Estes, 2010). These larger-sized predators most often feed on larger prey species residing at higher trophic levels (i.e., mesopredators) and, in doing so, their effects on lower and basal trophic levels may be stronger and more widespread than smaller bodied predators (Terborgh and Estes, 2010). To date, however, no studies have manipulated (via inclusions) a large-bodied apex predator and tested experimentally this widely accepted theory of strong top-down control (Terborgh and Estes, 2010). As a consequence, many ecologists remain skeptical of the importance of and mechanisms by-which top-down forcing proceeds via apex predators, because alternative hypotheses cannot be ruled out from observational studies (Kuker and Barrett-Lennard, 2010; Terborgh and Estes, 2010). For example, Kuker and Barrett-Lennard (2010) propose that declines in sea otter populations and the resulting transition of kelp forests to urchin barrens can be explained by a combination of shark predation, high contaminant levels, and/or disease rather than predation by killer whales, as suggested by Estes et al. (1998). Similarly, Kauffman et al. (2010) found strong evidence that behavioral effects of wolf on elk foraging did not translate into aspen tree declines within Yellowstone National Park as suggested by a number of previous studies (e.g., Ripple and Beschta, 2004). As large-bodied, apex predators are in rapid decline in most ecosystems worldwide, gaining a better understanding of their community effects is key for predicting how their changes in density will influence ecosystem structure and function (e.g. Duffy, 2003; Heithaus et al., 2008; Miller et al., 2001).

Even if apex predators commonly cause trophic cascades, the magnitude of the effects and mechanisms driving these effects are not well understood (Estes et al., 2011). Because apex predators are hard to manipulate, no experiments have explicitly isolated the species-specific effects of large-bodied apex predators on mesopredator abundance and behavior and assessed the potential indirect consequences of...
these direct impacts on lower trophic levels (Elmhagen et al., 2010; Estes et al., 2011). While a number of studies have employed large-bodied, predator removals or exclusions to test and provide evidence for the mesopredator release hypothesis (reviewed in: Brashares et al., 2010) and more recently attempted guild–specific, predator removals (Maron et al., 2010), these experiments have not allowed for direct assessment of underlying mechanisms by which specific apex predators affect mesopredator abundance and behavior. Manipulative experiments that employ large-bodied apex predator inclusions and manipulate predator access to prey can help provide key insights needed to advance a mechanistic understanding of how apex predators affect communities.

There are two, top-down mechanisms by which predator can affect food webs. First, predators consume prey (Estes and Palisano, 1974; Menge, 1995; Menge et al., 1994; Paine, 1980). Alternatively, predators can also induce changes in prey behavior (Abrams et al., 1996; Power et al., 1989; Werner and Peacock, 2001). These non-consumptive (i.e., non-lethal) predator effects can influence the habitat use, growth, and competitive ability of prey, which can then cascade to affect lower trophic levels and ecosystem function (Lauri et al., 2010; Preisser and Bohnick, 2008; Schmitz et al., 2004, 2010).

Thus, when evaluating the net effects of a predator on its prey, both consumptive (CE) and non-consumptive (NCE) effects should be considered (Abrams, 1995; Peckarsky et al., 2001).

In this study, we build upon an emerging understanding of top-down control in Southeastern US salt marshes (Silliman and Bertness, 2002; Silliman and Zieman, 2001) and ask if a large-bodied, apex predator, the American alligator commonly consumes and, if so can a marsh mesopredator (blue crabs) abundance, habitat use, foraging efficiency and behavior. Because blue crabs are known to feed on both keystone marsh grazers (the Periwinkle snail, Littoraria irrorata Say 1822, hereafter Littoraria) and mutualist (the Atlantic ribbed mussel, Geukensia demissa Dillwyn 1817, hereafter Geukensia) (Lin, 1989; Sloan, 1987; Silliman and Bertness, 2002; Silliman and Newell, 2002; Silliman et al., 2004), alligators may indirectly affect these trophic levels as well.

Over the past decade, experimental research in southern U.S. salt marshes has revealed that a trophic cascade regulates salt marsh primary production (Griffin and Silliman, 2011; Silliman and Bertness, 2002; Silliman et al., 2005). In this tri-trophic interaction, estuarine mesopredators (e.g. blue crabs, salt marsh terrapins) indirectly facilitate the dominant cordgrass, Spartina alterniflora Loisel [hereafter Spartina], by controlling densities of plant-grazing snails, Littoraria (Griffin and Silliman, 2011; Silliman and Bertness, 2002; Silliman and Newell, 2002; Silliman et al., 2004). When mesopredator numbers decrease and soil salt stress increases during drought years, snail numbers can dramatically increase and overgraze stressed grasses (Silliman et al., 2005).

Intense predation by crabs is also thought to limit distribution and abundance of plant-facilitating mussels, Geukensia (Lin, 1989; Stiven and Gardner, 1992). By providing nutrients and increasing habitat heterogeneity, Geukensia locally enhances Spartina growth and infaunal species richness (Bertness, 1984, Bertness and Hacker 1994); in turn, Spartina provides Geukensia with shade and substrate for attachment (Altieri et al., 2007, 2010).

Alligators, which commonly occur in estuaries in the southeastern U.S., could be an important predator on snail- and mussel-consuming blue crabs. Numerous surveys have revealed that blue crabs are often a major diet component of estuarine-occurring alligators and occur in more than 50% of individual gut contents (Table 1). Other studies have shown that blue crabs respond behaviorally to the presence of their predators (e.g. Woodbury, 1986, crabs; Diaz et al., 1999; Gerald and Powers, 2011, redfish). Based on these food web observations, we hypothesize that alligators also cause behavioral responses in blue crabs and that these effects, in addition to CE’s, could cascade through the marsh food web and influence ecosystem processes.

To test our hypothesis we combine an observational study of dietary patterns with a mesocosm experiment. Specifically, we ask:

1) What is the strength of alligator–blue crab consumptive interactions (CE’s)?
2) Is there potential for the propagation of non-consumptive interactions (NCE’s)?
3) Can an apex predator generate a trophic cascade that enhances densities of two a potent grazer (Littoraria) and mutualist (Geukensia) in a simplified salt marsh food web?

2. Material and methods

2.1. Field study and literature survey: stomach content analysis

Alligators were captured using standard techniques (e.g. snatch hook, locking snare) in salt marsh habitats surrounding Sapelo Island, Georgia (31.453797 N, 81.259655 W) from 01–Mar–2008 to 30–Aug–2009 (West et al., 2008). Stomach contents were obtained from adult alligators (> 1.75 m total length [TL]) using the hose–Heimlich lavage technique (Fitzgerald, 1989), washed through a 1 mm mesh sieve, and stored in 70% ethanol until processing. All remains were later identified to the lowest taxonomic division possible, in most cases genus or species. Wet mass was taken (to 0.01 g) of prey items once separation and identification was complete. Additionally, we performed an in–depth search of literature through various databases and collections (i.e., Web of Science, BIOSIS, Florida Museum of Natural History Herpetology Library) for studies of alligator food habits in salt marsh and estuarine ecosystems (N = 10, published studies; n = 1359 individual stomach contents). From each study, we extracted the reported frequency of occurrence (number of stomachs containing prey item/total number of stomachs sampled) and prey mass (mass of prey item/total mass of all prey) of blue crabs. We present both frequency of occurrence and prey mass where possible, but consider 1) studies differed in the collection technique employed to remove stomach contents (e.g.,avage, necropsy, culled animals), 2) prey type frequency was the only consistent metric reported across all studies, and 3) digestion rate of blue crabs in alligator stomachs can bias results when mass is used (Nifong et al., 2012). Furthermore, we only report findings from studies that explicitly report alligators were captured in estuarine habitats.

2.2. Mesocosm experiment

To test whether alligators consume and/or influence the behavior of blue crabs and to evaluate the resulting effects on snails and mussels, we conducted a mesocosm experiment. Experiments took place from 25–Aug to 2–Oct 2010 at the Whitney Laboratory for Marine Bioscience in Marineland, Florida USA (29.669750 N, 81.21451 W). All trials consisted of two paired experimental treatments (alligator addition or no alligator-control), using two of the three available concrete/ fiberglass mesocosms (7 m diameter x 2 m total depth)
and alternating active mesocosms during each trial. Treatments were randomly assigned to individual mesocosms. Each mesocosm was populated with 18 pots (15 cm diameter) of Spartina plugs (15 cm diameter, stems > 45 cm total height), arranged in 3 stands of 6 pots each, 1000 periwinkle snails, 100 ribbed mussels, and 8 or 10 blue crabs (standardized by total biomass). The density and spatial distribution of prey within the mesocosms simulated a natural creek bank (Fitz and Wiegert, 1991; Wiegert and Freeman, 1990) such that snails were placed in Spartina stands, representative of their distribution on the marsh platform and mussels were allowed to fix to a flat tray opposite Spartina stands, to represent their sometimes exposed position on creek bottoms. Concrete blocks, aligned in groups of three associated with each Spartina stand, served as refuge for blue crabs from predation and enabled us to simulate tidal fluctuations by moving Spartina stands on and off blocks every 6 h to mimic low and high tides, respectively. Water depth was held constant at 1 m, measured in the center of the enclosures, via a consistent slow flow of fresh seawater into the mesocosms and modified drain-pipe. All blue crabs were haphazardly assigned to treatments, with sexes in equal proportions, and individuals were never used in more than one trial. Two blue crabs were found dead and were immediately replaced with an individual of same sex and similar size. Individual alligators were only used once during all trials (identified by unique Passive Integrated Transponder-PIT Tag). Trials lasted 3 days and upon termination all living crabs, snails, and mussels were collected and counted. Furthermore, mesocosms were drained and thoroughly washed between experimental trails.

Adult blue crabs were obtained from local trappers (ranging from 11.7 to 16.7 cm carapace width, measured spine tip to spine tip), transported to concrete holding tanks (2 x 1.5 x 1 m, L x W x D) and fed a mixed diet of shrimp, mussels, and snails once daily prior to use in experimental trials. Blue crabs were introduced to mesocosms 4 h prior to the introduction of an alligator in predator addition treatments. Adult crabs, Littoraria, (14 to 18 mm TL, measured from tip of spine to termination of siphonal canal) and adult mussels, Geukensia, (30 to 50 mm shell length, measured from anterior to posterior margin) were collected from nearby salt marshes and held in flow-through tanks that were stocked with senesced Spartina for food. Spartina was also collected locally, placed in 15 cm diameter pots, kept in full sun, and watered daily until being placed inside experimental enclosures.

Alligators were received on-loan from the St. Augustine Alligator Farm Zoological Park in St. Augustine, Florida USA (29.881973 N, 81.288550 W) prior to each experimental trial. Individuals were allowed to acclimate to their new surroundings for 4–8 h in smaller concrete/fiberglass holding tanks (2.4 x 1.8 x 1.2 m, L x W x H). Following this acclimation period, individuals were captured by hand and transported on-site to outdoor concrete/fiberglass mesocosms. Because alligators are chiefly sit-and-wait predators in salt marsh ecosystems (J. Nifong, unpublished data), the size (7 m dia.) of our experimental enclosures closely resembles the scale at which alligators forage within marsh creeks. Alligator total length (TL, measured from snout tip to tail tip) averaged 212 ± 17 cm (SD) and sex ratio was 4:3 (male: female). All alligators were returned to their origin following termination of each experimental trial.

To assess apex predator consumptive effects (CEs) on blue crab survival and resulting consumption of prey, we compared measures of blue crab mortality, foraging capacity (total number of snails and mussels consumed), and per capita foraging rate (number snails and mussels consumed/number living crabs) in control treatments to predator addition treatments containing one alligator (N = 7). To evaluate the potential for non-consumptive effects (NCEs) we observed blue crab behavior throughout mesocosm trials. Mesocosms were observed each for 5 min approximately every 3 h for the duration of each trial (providing 12 to 16 observations per trial). At each observation, we counted the number of consumed crabs, and for each of the remaining live crabs, noted their location (i.e., open space, in Spartina, hidden in blocks), activities displayed (i.e., swimming, defensive posturing), and specific foraging behaviors employed (i.e., consuming snails or mussels, prey searching). We used the average (per replicate) proportion of living blue crabs displaying a specific behavior (e.g., active/not active, in-open/hiding, etc.) of interest as our response variables.

2.3. Statistical procedures

We assessed treatment differences in per capita foraging rates of blue crabs and mortality of blue crabs by alligators with Generalized Linear Models (GLMs). We used a Gaussian error distribution with identity link function. Treatment effects on mesopredator foraging and behavior were assessed with a GLM using quasi-binomial error distribution (due to over-dispersion) with logit link function to estimate probability of mortality for snails and mussels, and the probability of blue crab behavioral responses (in open versus in refuge; active individuals foraging versus not; and active individuals vigilant or not). To assess the effects of abiotic factors (e.g., temperature, precipitation) on blue crab foraging and behavior we used Likelihood Ratio Tests to examine whether inclusion of experimental temperature and precipitation significantly reduced the deviance in our GLM fits. All analyses were performed using R 2.13 statistical software (R Core Development Team, 2011).

3. Results

3.1. What is the strength of alligator—blue crab consumptive interactions (CEs)?

Using stomach content analysis performed on 25 adult alligators (> 1.75 m TL) from Sapelo Island, Georgia, we found 35% of individuals sampled contained blue crab remains, comprising 32% of the total recovered prey mass across all individuals (Figs. 1 and 2a). Blue crabs comprised 52% of prey mass when considering only salt marsh inhabiting prey species (Fig. 2b). Our literature survey of 10 studies all performed in brackish or salt marshes in Louisiana revealed that 20 to 83% of alligator stomach contents contained blue crabs (mean ± SD, 48 ± 20%, n = 1334, Table 1).

In our mesocosm experiment, alligators consumed 3.5 ± 1.9 (mean ± SD) blue crab over the 3-day experimental trial, but none died in their absence, resulting in significantly higher blue crab mortality (Fig. 3a, P = 0.0009). Alligator size (total length) was not significantly correlated to the total number of blue crabs consumed (P = 0.28).

3.2. Is there potential for the propagation of non-consumptive interactions (NCEs)?

Alligator presence reduced the probability of observing a blue crab in the open (e.g., foraging or swimming) as opposed to taking refuge by ~44% relative to controls (alligator absent) (Fig. 3b, P = 0.03). Furthermore, when blue crabs were observed in the open, the probability of being observed foraging on prey (either snails or mussels) was reduced by ~62% in alligator treatments (Fig. 3c, P = 0.04) relative to controls. Temperature and precipitation did not significantly improve the deviance explained by the GLM for either probability of being active (P = 0.06) or probability of foraging when found active, (P = 0.10).

3.3. Can an apex predator generate a trophic cascade in a simplified salt marsh food web?

Per capita consumption of snails and mussels by blue crabs, did not differ in the presence vs. absence of alligators (P = 0.57, and P = 0.08, respectively). However, GLM analyses revealed strong effects of alligator presence on overall mortality (via blue crab consumption) of both
snails and mussels (P = 0.04 and P = 0.02, respectively). Probability of mortality for snails in the presence of alligator decreased by ~47% (Fig. 3d) and by ~64% for mussels relative to controls (Fig. 3e). Neither water temperature nor total precipitation significantly improved our GLM fit for either snail or mussel mortality (P = 0.39, P = 0.44, respectively).

4. Discussion

For nearly a century, food web theory has predicted that predators can exert strong top-down control on ecosystems (Elton, 1927; Leopold, 1949). Over the past 50 years, many researchers have experimentally tested this idea with small- and medium-bodied predators and found predators often elicit cascading effects within food webs and have worked to understand the conditions under which top-down effects are most likely to occur (e.g., decreased physical stress, simple, low diversity food webs) (e.g. Carpenter et al., 1985; Fretwell, 1977; Hairston et al., 1960; Menge and Sutherland, 1976; Mumby et al. 2006; Paine, 1969, 1980; Polis and Strong, 1996; Polis et al., 2000; Strong, 1992; Wootton and Power, 1993). Moreover, observational and exclusion studies over this same time period have suggested that large-bodied apex predators, such as killer whales and wolves, can also elicit cascading effects. These effects may be particularly important because apex predators are suggested to strongly control populations within trophic levels that are directly linked to the regulation of ecosystem functions (for review see, Terborgh and Estes, 2010). Although these studies are convincing and provide much evidence to eliminate alternative hypotheses, manipulations using large-bodied, apex predators are needed to advance and experimentally test our understanding of the mechanisms by which these species can influence both food chains and ecosystem processes. Our results provide correlational evidence that alligators and blue crabs commonly interact in salt marsh...
ecosystems and experimental confirmation that these large-bodied, apex predators can directly impact the density, behavior, and foraging of blue crabs, and thereby indirectly influence the density of a grazer and mutualist of the dominate primary producer in this system, *Spartina*. Cumulatively, these results suggest that alligators have the potential to exert previously unacknowledged top-down forcing in salt marsh communities, where there remains considerable skepticism that consumers can significantly influence these expansive and productive intertidal grasslands (Kiehn and Morris, 2009).

4.1. Can an apex predator generate a trophic cascade in a simplified salt marsh food web?

Through stomach content analysis of 25 captured individuals and literature survey of past studies (10 studies, n = 1334), we found that alligators consumed blue crabs in high frequencies in both Louisiana and Georgia salt marshes, with 20 to 83% of individual stomach contents containing blue crab remains. In the wild, alligators were found to consume up to 14 individual blue crabs within a two-week period, as determined from status of blue crab remains in stomach contents (Nifong et al., 2012). Alligators’ natural range extends along coastal habitats of Texas to Virginia and can reach high densities (i.e., 6 adult individual/km of shoreline) in salt marsh creeks (J. Nifong, unpublished data), although data on naturally occurring densities in salt marshes is limited. Given that blue crabs are an important prey species for alligators and occupy the same habitat, alligators within high density areas can potentially deplete blue crab densities. The suggested strength of these consumptive interactions was substantiated in our mesocosm study, wherein single adult alligators were able to reduce blue crab abundance in mesocosms up to 80% over a 3-day period. The net effects of alligator presence on blue crabs cascaded to lower trophic levels, increasing probability of survival for both snails and mussels, by ~26% and ~190% relative to controls, respectively. These results provide experimental evidence for the potential of an expanded salt marsh trophic cascade, where a large-bodied, apex predator influences the cascading effects of keystone mesopredators.

Though alligators indirectly enhanced survival of snails and mussels by reducing consumption by blue crabs, they did so differentially. Specifically, alligators improved mussel survival far more than snail survival (190% vs. 26% increase in alligator presence relative to controls). Two explanations could account for this differential facilitation 1) energetics (i.e., cost of prey searching, capture, and handling) or 2) trade-offs between predation pressure and prey preference. Our results seem to support the latter. In our study, the two prey species provided separate microhabitat choices for blue crabs, in which mussels were highly exposed on the benthos of the mesocosm (i.e., high risk of alligator predation) while snails were distributed within *Spartina* transplants that provided some protection from alligator predation. As a result, blue crabs probably experienced a both higher risk and longer handling time foraging on mussels than snails. Thus, blue crabs appeared to regulate their risk and seek prey with lower handling time in presence of alligators. Similarly, West and Williams (1986), found that blue crabs preferentially consumed snails opposed to mussels and attributed these differences to increased energy and time investment required to excavate and consume infaunal mussels opposed to epifaunal snails. In natural salt marsh creeks, where refuge habitats are plentiful (e.g., oyster reefs, deep holes) and *Spartina* canopies along banks are dense, we expect blue crabs would either retreat to deeper habitats to forage within oyster beds or flee to higher marsh elevations within *Spartina* canopies where vulnerability to alligator predation would be minimized. Consequently, in the wild alligators may have a relatively stronger effect on snails than mussels, as blue crabs may preferentially avoid the creek edge, preferred habitat for mussels, to evade alligator predation. The outcome of these indirect effects on *Spartina* growth and productivity in the more spatially complex field, however, is not clearly predictable and will depend on 1) the relative magnitude of effects resulting from increased grazing potential by snails and facilitation by ribbed mussels and 2) the spatial extent of alligator interactions with blue crabs across the marsh surface. The 3 day duration of our experimental trials was too short for cascading effects on *Spartina* growth to emerge.
4.2. Is there potential for the propagation of non-consumptive interactions (NCEs)?

We found evidence supporting the hypothesis that apex predators can propagate NCEs on their prey via perception of predatory risk cues. Blue crabs responded to alligator consumptive effects and predatory risk cues by 1) seeking refuge more often and 2) by reducing foraging activity. Additionally, differences between the indirect effects on survivorship of mussels versus snails suggest that blue crabs can perceive predatory risk cues transmitted by alligators and shift prey preference in relation to risk associated with habitat choices. A common metric of risk perception by prey is vigilance, which in terms of blue crabs behavior is increased alertness or defensive posturing. Vigilance is a metric of risk perception by prey is vigilance, which in terms of blue crabs behavior is increased alertness or defensive posturing. Vigilance can influence prey behavior in many ways including reducing foraging rates and alterations in habitat use (Lima and Dill, 1990; Lind and Creswell, 2005). In this study, we did not find significant treatment effects on blue crab vigilance when measured as the proportion of active individuals displaying defensive postures. We hypothesize that this result was either due to low replication, inadequate observation time, or because the vigilance response may have been masked by the propensity of crabs to seek refuge instead of displaying defensive postures while remaining active in the open. The behavioral responses of blue crabs coupled with losses due to predation resulted in significantly greater survivorship of both snails and mussels; however, the relative importance and magnitude of consumptive versus non-consumptive pathways in driving this pattern are yet to be determined. In this experiment, CEs appear to be the main driver of prey consumption by blue crabs.

4.3. Role of American alligators in salt marsh communities

In southeastern US salt marshes, alligators can occur in high densities (up to 6 adult individuals per kilometer of creek edge, J. Nifong, unpublished data) during seasons of peak activity and movement (April–November). In the case of blue crabs, two temporal constraints limit the use of salt marsh habitats 1) season and 2) tidal stage (Fitz and Wiegert, 1991; Hettler, 1989). Blue crabs can also become highly abundant during spring and summer months and often migrate off-shore to deeper waters during winter months. Within creeks, alligators chiefly use marsh edge and benthic habitats to search and acquire prey items (J. Nifong, personal observation). These temporal and spatial constraints concentrate the window for alligator–blue crab interactions on both a seasonal basis (Spring and Summer) and within marsh creeks, as opposed to higher elevation marsh platforms. Thus, the indirect effects of alligators revealed in this study are likely to be spatially confined in the marsh to the creek bank grasses, unless alligators can suppress blue crab densities so much that they do not enter marsh watersheds, a possibility that may not be likely given lower energetic demands of a large-bodied ectotherm, such as the American alligator. To determine the effects in natural settings large-scale inclusion or exclusion experiments should be performed and results compared to mesocosm findings.

5. Conclusion

Our results demonstrate using predator inclusions that a large-bodied, apex predator can affect its mesopredator prey and that these effects can indirectly propagate through a food chain to affect a keystone grazer and mutualist. Additionally, this study generates a data-supported hypothesis, that marshes, like other marine systems (e.g., kelps, seagrasses, corals), can be influenced by the activities of large-bodied, apex predators. When and where possible, manipulative approaches like the one we have employed with large-bodied predators should be scaled-up to real-world field scenarios (e.g., manipulations of alligators in salt marshes and mangroves, wolves in aspen communities, or Tiger sharks in seagrass ecosystems). In salt marshes (this study) and other systems, large-bodied apex predators are believed to modulate mesocommunity behavior via non-consumptive pathways (Terborgh and Estes, 2010). For example, wolves in North America are hypothesized to mediate mesocommunity (i.e., elk) grazing via NCEs on habitat choice and foraging behavior influenced by the threat of predation by wolves (Beschta and Ripple, 2009). Future apex predator research should concentrate on determining the relative importance of CEs versus NCEs in driving top-down effects and should highlight any differences between the effects of large-bodied apex predators and those of medium- or small-bodied predators. In this study, our findings were congruent with those of previous studies performed on smaller sized predators.

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References


