Megafauna Utilization of and Impact on Salt Marshes

by

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Marine Science and Conservation
Duke University

Date: March 22, 2024

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Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Marine Science and Conservation in The Graduate School of
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ABSTRACT

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Abstract

Megafauna (>45kg) are known to inhabit and reshape freshwater, terrestrial, and marine systems throughout the globe through consumptive and engineering pathways. Following long-term conservation, large consumers have expanded and recolonized regions thought to be beyond their niche space. By re-entering these systems, these large consumers may restructure these new habitats. The goal of this dissertation research was to document what megafauna use salt marshes and examine the effects of megafauna recolonization of salt marshes. We first conducted a literature review and found that a variety of megafauna utilize salt marshes, a total of 34 species including sharks, manatees, pinnipeds, crocodilians, sea otters, hippos, and large terrestrial animals, such as lions, bears and water buffalo. Next, we examined the impacts of 2 species of megafauna that recolonized salt marshes in Elkhorn Slough using observational and experimental studies. We conducted a control-impact study to understand the potential effects of harbor seals (*Phoca vitulina*) hauling out of the water on the structure of salt marsh edges. We found that sites with harbor seal haul outs had significantly more compressed soil, that the foundation plant species were heavily denuded, and that animal diversity shifted strongly - burrowing crabs were almost eliminated entirely from the edges of marshes, while birds congregated in high number. Erosion is a pressing issue in Elkhorn Slough at 0.5 m/yr, and despite the vast differences in regions with seal haul outs and denuded surface, we found no increase in erosion rate, likely due to compensatory effects of an intact root system, lack of crab burrows, and highly compressed sediment. These findings suggest that harbor seals act as ecosystem engineers in salt marshes by hauling out onto marsh platforms and generating large disturbances. Though megafauna can reshape systems and potentially drive erosion, they are not the only major drivers within estuarine systems – eutrophication is another major factor that reshapes salt marshes and is known to cause erosion. Recent studies showed that sea otters (*Enhydra lutris*) consume root-eating marsh crabs and through this trophic cascade, lower edge erosion rates. Using a factorial experimental design (sea otter presence x nutrient addition) at the edge of the creek banks, we examined the relative impact of otters and fertilization on erosion rates. We did not detect differences in marsh erosion rates or crab burrows or activity from otters or fertilization but did find effects of both main factors on plant communities. These findings do not match previous studies that show significant effects of both otters and eutrophication on erosion rates, but this mismatch likely stems from the interaction of differences in duration, scale, and erosion rates that vary greatly along creek banks. Taken together, this work highlights the importance of studying the impacts of megafauna on salt marshes, and variability in their effects.

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1. Introduction

Megafauna (>45kg) strongly shape ecosystems and their functions globally (Martin and Klein 1989). Through ecosystem engineering (Laws 1970), volume of consumption (Waldram et al. 2008), trophic cascades (Estes and Palmisano 1974), and increasing plant species resilience (Hughes et al. 2013), megafauna can fundamentally alter habitat structure and function. In addition, there is also a growing body of literature showing that large consumers are now appearing in places they were not expected to live (Silliman et al. 2018), indicating that megafauna can inhabit and shape a wider range of systems than has been previously appreciated. This mismatch in expectation and current range is likely a result of historical human activity, particularly hunting and extirpation efforts (Silliman et al. 2018), which led to modern ecologists starting to study these large animals in habitats that served as refuge from human hunting (e.g. tops of mountains, swamps, offshore kelp beds, rivers in isolated catchments). But following long-term conservation, populations of many large bodied consumers have been able to recover and rather than colonizing new habitats, are simply recolonizing parts of their previous range (Silliman et al. 2018). Fossil records and bone evidence from human middens show this is the case for alligators and sea otters (Crook 1978, Reitz 1982, Broughton 1999, Jones et al. 2011) and it is likely the case for other large animals as well, such as European Brown bears. While these general phenomena of large consumer expansion into unexpected ecosystems has been now been documented in many different habitats, the presence and impact of megafauna in shallow-water coastal systems, such as salt marshes, has only recently begun to be explored and appreciated.

Throughout the world, there are examples of large consumer expansion and reintroduction increasing the health and resilience of their ecosystems through promoting key plant species. Examples include sea otters with seagrass in California (Hughes et al. 2013), wolves with woody vegetation in Yellowstone National Park (Beschta and Ripple 2012), tiger sharks with seagrass in Australia (Burkholder et al. 2013), and sea otters in kelp systems in Alaska (Estes and Palmisano 1974). However, there is relatively little work examining how megafauna directly alter the geomorphology of the ecosystems they inhabit, particularly in coastal ecosystems such as salt marshes, which face intense edge erosion (Van Dyke and Wasson 2005). Given the dramatic transformations of other ecosystems with the introduction or recolonization of top predators, it is possible that through promoting plants by controlling herbivores, megafauna that utilize and are recolonizing salt marshes can also control the geomorphology of these ecosystems. Salt marshes have declined by 50% globally (Barbier et al. 2008) and a large portion of that has been to erosion of marsh edges. By better understanding how megafauna can impact the geomorphology and erosion rates of these ecosystems, we could harness this information to help restore these imperiled ecosystems.

Megafauna could play a variety of roles in salt marsh ecosystems. One is to protect plants through trophic cascade. For example, sea otters protect marshes from overgrazing burrowing crabs (Hughes et al. 2024). In turn, marshes that are facilitated by predators could provide important services for these large animals. Habitats such as estuaries and other nearshore shallow marsh habitats could provide nursery grounds (Kovacs et al. 1990, Wetherbee et al. 2007, Davy et al. 2015), breeding grounds (McCarthy 2010), feeding areas (Hughes et al. 2013, Nifong and Silliman 2013) and/or safe places to rest or sleep (McCarthy 2010, Eby et al. 2017). Additionally, megafauna could serve to physically reshape the ecosystems they live in and alter usage patterns by other animals not just by controlling plants but also by physically altering the environment. This could arise from large animals moving throughout the marsh or resting on top of plants – two actions that could kill vegetation in heavily used areas. This denuding of the marsh surface could in turn impact other animals whose ease of movement is altered by marsh sediment compression and plant presence. Though work in other ecosystems shows megafauna can play important roles through consumption and ecosystem engineering, their presence in and impacts on salt marshes systems has rarely been studied, and my dissertation aims to address this gap.

The first chapter of this dissertation, “Megafauna in salt marshes,” was published Frontiers in Marine Science in 2020. I am the lead author, and my coauthors are Avery B. Paxton and Brian R. Silliman. Together, we all came up with the design of the study. Dr. Paxton helped to complete the literature review and analysis, and all three of us drafted and edited the manuscript.

2. Megafauna in salt marshes

This chapter was published in Frontiers in Marine Science in November 2020, and my coauthors are Avery B. Paxton and Brian R. Silliman. All authors contributed to the conception and design of the study, and I was the lead on the study and lead author. Dr. Paxton and I performed the literature review and analysis. All authors contributed to manuscript initial drafts, revision, read, and approved the submitted version. This work is open access and under Creative Commons Attribution License.

2.1 Abstract

Megafauna shape ecosystems globally through trophic interactions, ecology of fear, and ecosystem engineering. Highly productive salt marshes at the interface of terrestrial and marine systems have the potential to support megafauna species, but a recent global meta-analysis of consumer-plant interactions in marshes found few studies investigated impacts of wild megafauna. We conducted a literature review to document the variety of megafauna in salt marshes and found that 34 species utilize salt marshes, including sharks, manatees, pinnipeds, crocodilians, sea otters, hippos, and large terrestrial animals, such as lions, bears and water buffalo. The use of salt marsh habitats by a variety of megafauna may have implications for both the conservation of these large consumers and for the resilience of coastal wetlands through stabilizing feedbacks on plant ecosystems. Future studies should quantify the occurrence and impacts of megafauna in salt marshes, and how their conservation can help restore these valuable ecosystems.

2.2 Introduction

Megafauna are animals > 45 kg (100 lbs) and shape ecosystem structure and function throughout the world (Martin and Klein 1989). As consumers, megafauna often regulate ecosystems through feeding. Elephants, for instance, eat and remove trees and thereby promote competitively inferior grasses and grasslands ecosystems (Laws 1970). Megafauna predators can also control their prey, and in doing so, can generate cascading effects by indirectly facilitating plant communities. For example, sea otters, by controlling densities of hold-fast grazing urchins, indirectly facilitate entire kelp communities (Estes and Palmisano 1974). The indirect effects of predators can also manifest through the fear they impose on their prey. In Shark Bay, Australia, tiger sharks create cascading impacts through fear by driving dugongs and sea turtles to spend extended periods in unvegetated, shallow areas thereby generating top-down release on seagrasses in deeper waters (Burkholder et al. 2013). Large herbivores can also shape ecosystems through their non-feeding activities. Elephants can generate animal-driven nutrient fluxes by translocating nutrients through their feces, and models predict this activity constitutes an important nutrient supply for plants in savannah ecosystems (Wolf et al. 2013). Rhinos consume such a large volume of grass that they alter the fire regime in savanna ecosystems by significantly lowering the amount of fuel available to burn in large patches (Waldram et al. 2008). Historically, the vast influence of megaherbivores has also played an important role in shaping ecosystems, as their elimination by human hunters likely reshaped the ecosystem types and impacted small herbivore diversity (Owen-Smith 1987). In systems where megafauna can occur in high densities, their impacts can be tremendous, and their loss or gain can change ecosystems and their resilience (Waldram et al. 2008, Hughes et al. 2013). For instance, the reemergence of sea otters on the west coast of the U.S. has revitalized seagrass habitats, as sea otter consumption of crabs facilitates sea slugs that protect seagrasses from algal overgrowth (Hughes et al. 2013).

Megafauna are well-known to occur in a diversity of ecosystems, including terrestrial, freshwater, and marine. Despite their abundance in many ecosystems that occur juxtaposed to temperate coastal shorelines, including bays, nearshore oceanic shelves, maritime forests, and grasslands, megafauna are not mentioned in major text books about salt marshes nor included in the food-web models presented therein (Nybakken and Bertness 2005, Bertness 2007, Mitsch and Gosselink 2007, Bertness et al. 2014). To examine whether this pattern is prevalent not only in textbooks but also in peer-reviewed literature, we analyzed a global dataset of 163 studies on marsh consumer effects (He and Silliman 2016) extracted from 178 studies of consumer-marsh plant interactions. This dataset revealed that 27% of studies (44) included a species of megafauna but that only 5 unique megafauna species were reported in total (Figure 1A). Within the subset of studies reporting megafauna, 89% of studies (39) investigated 3 unique species of domesticated livestock (horses, cows and sheep) while even fewer studies (5, 11%) focused on wild megafauna (Figure 1B), and all were terrestrial megafauna species. These results suggest that both the number of megafauna species and the diversity of megafauna that utilize salt marsh habitats globally is low.

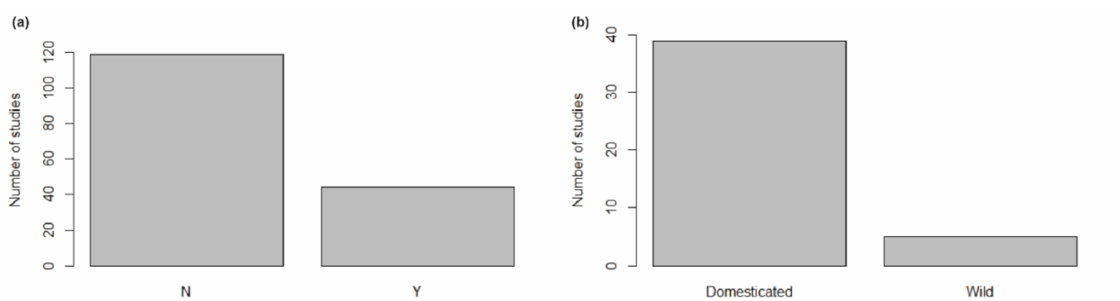

Figure 1: Megafauna studies within a consumer effects dataset. (A) Number of consumer effects studies which examine megafauna species, based on the He & Silliman 2016 data set. 163 marshes studies were examined total, with 44 studies that focused on megafauna (27%). (B) The number of studies that examined domesticated or wild megafauna species within the He & Silliman 2016 consumer effects data set. Of the 44 total megafauna studies, 5 looked at wild animals (11%), and 39 looked at domesticated animals (89%).

The notable and relatively recent expansions of American alligators and sea otters into salt marshes, along with a recent review study that found salt marshes are home to at least a few more megafauna (e.g. crocodiles, harbor seals) (Sievers et al. 2019), indicate that there are likely more megafauna species that utilize salt marshes than is represented in this global meta-analysis of top-down effects in salt marshes (He and Silliman 2016). In southeastern US salt marshes, for example, researchers found that in marine protected areas, densities of the American alligator *(Alligator mississippiensis*) were higher than in comparable freshwater systems (Nifong and Silliman 2017, Silliman et al. 2018). Alligators not only fed on marine animals in salt marshes, but more than 50% of the gut contents were marine animals, such as blue crabs (*Callinectes sapidus*), shrimp, and string rays (Nifong and Silliman 2013). In Elkhorn Slough in California, sea otters (*Enhydra lutris*) have recolonized seagrasses and salt marshes and, like alligators, have thrived. After colonization of these new habitats, sea otters quickly started eating marsh invertebrates, with burrowing crabs now making up 19% of the diet of the 131 otters in the slough (Tinker et al. 2018). Taking into account the variation in body size and that otters consume 4.53-11.34 kg daily, this means the Elkhorn Slough otters consume between 112.75-282.25 kg daily of burrowing marsh crabs alone (Riedman and Estes 1990, Tinker et al. 2018), which could have profound impacts on the salt marsh, as marsh plants and geomorphology can be highly regulated by crabs when their densities are high (Escapa et al. 2007). Given the outsized impact that megafauna can have on ecosystems, it is important to understand and quantify their impacts in marshes. However, whether a large number of megafauna species or a high diversity of megafauna occasionally or commonly occur in salt marshes has yet to be examined on a worldwide scale. To examine if textbooks and consumer effects studies truly capture the number or diversity of megafauna species in salt marshes, we conducted a literature review to search for additional megafauna species that commonly use salt marsh ecosystems as habitat.

2.3 Methods

To investigate megafauna occurrence in salt marshes globally, we conducted a literature review to search for documented instances of megafauna in salt marshes. We conducted our search with the Web of Science on 18 December 2018 using the search query: TS = (shark* AND marsh*) OR TS= (crocodil* AND marsh*) OR TS=(mammal* AND marsh*) OR TS=(megafauna AND marsh) OR TS=(top predator AND marsh*) OR TS=(apex predator AND marsh*) OR TS=(top consumer AND marsh*). This search yielded 765 potentially relevant papers. For each of the papers, we imported the title and abstract to Colandr (Cheng et al. 2018) where we first reviewed titles and abstracts to screen articles for inclusion. Articles were retained for additional screening within Colandr if they included observations of any animal in salt marshes. We excluded articles that were not in English or were in freshwater but not saltwater marshes. After the initial screening, which yielded 214 papers, we conducted a second round of screening and retained articles where one or more species of megafauna is documented in salt marshes. We included animals that can reach over 45 kg (100 lbs) at some point in their life as megafauna, as most literature does not report the size or weight of animals in marshes. Though we recognize some records may have been of juveniles under 45 kg, if a species has previously been documented to reach our 45 kg threshold, the species was included. For example, this drove our decision for sea otters, which can reach over 45 kg in Alaska, and hence were included (Estes et al. 2016). This definition of megafauna as > 45 kg (100 lbs) is commonly accepted in the scientific literature (Martin and Klein 1989), and mass is the most commonly used way of defining megafauna (Moleón et al. 2020). We included wild, domesticated, and semi-domesticated animals. Following the second round of screening, which produced 31 papers that were directly from the literature search or referenced in these texts, we conducted a final review to extract the species name and salt marsh location where megafauna have been documented. We then conducted a final verification that the animals were classified as megafauna and that the animals were documented in salt marshes, rather than solely near salt marshes. With this final verification, we reduced the number of applicable papers to 23. Though our search captured many megafauna species in salt marshes, there are likely more contained in peer-reviewed literature that were not identified in our literature search, or grey literature not searched. In multiple cases, salt marshes and other ecosystems were mentioned in papers. In these cases, we included the megafauna only if the species was clearly documented as occurring in salt marshes. For example, one paper referencing green turtles (*Chelonia mydas*) primarily focuses on mangroves, but explicitly states that *Spartina alterniflora*, a salt marsh grass, was important to the diet and ecology of green sea turtles, so this megafauna species was included (Nagaoka et al. 2012).

We also incorporated visual observations of additional megafauna that were not discovered in the literature search but have been observed in salt marshes by ourselves or a subset of our colleagues. For example, a colleague provided photographs documenting megafauna in South African salt marshes. While our approach likely is not exhaustive, our goal was not to find every instance of megafauna occurrence in salt marshes, but to test whether the diversity of megafauna that utilize salt marshes is greater than suggested by past studies. When compiling megafauna species that use salt marshes, we did not require density data, as these data were rarely reported. Instead, we opted for presence data. When density data were available, however, we recorded them, as well (Table 1). Future studies should conduct a more systematic survey of marsh scientists for a more comprehensive view into megafauna use of salt marshes.

Table 1: Megafauna documented in salt marshes through a literature review and through personal observations. Each animal includes the common name, scientific name, density (when available), reference(s), and the country where the animal was observed in a salt marsh.

English Common name	**Scientific name**	**Density**	**Reference(s)**	**Country**
African Buffalo	*Syncerus caffer*		JB Adams pers obs	South Africa
Alligator Gar	*Atractosteus spatula*		(Selman 2018)	USA
American Alligator	*Alligator mississippiensis*	0.3-6.3 indiv/km of creek, average of 3.45 ind/km (salt marsh), 2.25 ind/km (lake, river, swamp, freshwater marsh)	(Nifong and Silliman 2013, Nifong et al. 2014, Murray et al. 2015), (Nifong et al. 2015), (O'Brien and Doerr 1986), Webb unpublished data, (Wood et al. 1985)	USA
American Crocodile	*Crocodylus acutus*		(FNAI 2010)	USA
Black Bear	*Ursus americanus*	0.16-0.30 bears/km^2, average of 0.23 bears/km^2 (salt marsh), 0.258 bears/km^2 (forest)	(Lombardo 1993, Smith et al. 2012), (Lombardo 1993), (Schwartz and Franzmann 1989)	USA
Bottlenose Dolphin	*Tursiops truncatus*	3.7-5.4 indiv/km^2, average of 4.55 indiv/km^2 (salt marsh), 6.4-14.6 indiv/km^2, average of 10.5 indiv/km^2 (gulf)	(Young and Phillips 2002, Balmer et al. 2011), (Mullin 1990) (both densities)	USA
Broadnose Sevengill Shark	*Notorynchus cepedianus*		(Russo 2015)	USA
Brown Bear	*Ursus arctos*		(Smith et al. 2004)	USA

Bull Shark	*Carcharhinus leucas*		(Bangley 2016)	USA
Cattle	*Bos taurus*	0.5-2 indiv/ha (salt marsh)	(Jensen 1985, Amaral and Jablonski 2005), JB Adams pers obs, (Andresen et al. 1990)	Denmark, Brazil, South Africa
Common Warthog	*Phacochoerus africanus*		JB Adams per obs	South Africa
Common Zebra	*Equus quagga burchellii*		JB Adams per obs	South Africa
Donkey	*Equus africanus asinus*		JB Adams pers obs	South Africa
Florida Panther	*Puma concolor coryi*		D Onorato pers obs	USA
Gemsbok	*Oryx gazella*		JB Adams pers obs	South Africa
Goat	*Capra aegagrus hircus*		JB Adams per sobs	South Africa
Gray Wolf	*Canis lupus*		(Smith et al. 2004)	USA
Green Turtle	*Chelonia mydas*		(Nagaoka et al. 2012)	Brazil
Harbor Seal	*Phoca vitulina*	18.42 ind/km shoreline (salt marsh), 10.1 ind/km shoreline (outer coast)	(Eby et al. 2017), (Form 2016), (Akeman and Akeman 2016)	USA
Hippopotamus	*Hippopotamus amphibius*		JB Adams per obs	South Africa

Lion	*Panthera leo*		(Stander 2019)	Namibia
Loggerhead Turtle	*Caretta caretta*		(Stoneburner et al. 1982)	USA
Mule Deer	*Odocoileus hemionus*		LC Gaskins pers obs	USA
Nile Crocodile	*Crocodylus niloticus*		JB Adams pers obs	South Africa
Ostrich	*Struthio camelus*		JB Adams pers obs	South Africa
Sea Lion	*Zalophus californianus*		LC Gaskins pers obs	USA
Sea Otter	*Enhydra lutris*	0.61 indiv/ha (salt marsh), 0.0445 indiv/ha (kelp forest)	(Eby et al. 2017), (Tinker et al. 2018), (Nicholson et al. 2018)	USA
Sheep	*Ovis aries*	1.5-10 indiv/ha (salt marsh)	(Ranwell 1961, Laffaille et al. 2000), JB Adams pers obs, (Berg et al. 1997)	England, France, South Africa
Springbok	*Antidorcas marsupialis*		JB Adams pers obs	South Africa
Water Buffalo	*Bubalus bubalis*	1.0-1.3 indiv/ha (salt marsh)	(Amaral and Jablonski 2005), (Sweers et al. 2013)	Brazil
West Indian Manatee	*Trichechus manatus*		(Wingard and Lorenz 2014)	USA

White-tailed Deer	*Odocoileus virginianus*		JP Morton pers obs	USA
Wild Boar	*Sus scrofa*		(Sharp and Angelini 2016)	USA
Wild & Domesticated Horse	*Equus ferus, Equus ferus caballus*	0.39 indiv/ha low marsh (wild horse salt marsh), 0.035 indiv/ha (wild horse mountainous national park)	(Beeftink 1977, Turner 1987) (wild horse), JB Adams pers obs (domesticated horse), (Taggart 2008) (density, wild horse), (Dawson and Hone 2012) (density, mountains)	N&W European countries, USA, South Africa

2.4 Discussion

In total, the literature review yielded 34 megafauna species that utilize salt marshes (Figure 2, 3, 4, 5). This richness of megafauna represents a great expansion beyond the diversity of megafauna represented in the global meta-analysis of consumer-plant interactions in salt marshes (He and Silliman 2016), and demonstrates that there are a large variety of megafauna taxa that utilize salt marshes throughout the globe (Table 1). While most studies reported megafauna presence, several studies from the literature review reported megafauna densities, which were comparable to or higher than those in habitats in which they are established (Table 1). For example, density of black bears in salt marshes (0.23 bears/km^2) was similar to black bear density in Alaskan forests (0.26 bears/km^2). Sea otter, harbor seal, wild horse, and alligator densities had a higher relative abundance in salt marshes than in other established habitats (Figure 6). We predict that salt marshes, because of their high primary and secondary productivity, could be generally attractive ecosystems for megafauna in search of food and/or nursery grounds and that the diversity of megafauna using marshes will continue to increase as megafauna recover from overexploitation, as occurred with sea otters and alligators (Silliman et al. 2018).

Additionally, the large difference between the diversity of animals within consumer effects studies and those who use salt marshes globally indicates that, while there are several megafauna species, such as alligators and hogs, whose impacts have been documented, there are likely animals impacting salt marshes whose effects have not been quantified.

Figure 2: Megafauna in southeastern salt marshes. Including 1) white-tailed deer (*Odocoileus virginianus*), 2) Florida panther (*Puma concolor coryi*), 3) wild boar (*Sus scrofa*), 4) wild horse (*Equus ferus*), 5) black bear (*Ursus americanus*), 6) American crocodile (*Crocodylus acutus*), 7) bottlenose dolphin (*Tursiops truncatus*), 8) bull shark (*Carcharhinus leucas*), 9) American alligator (*Alligator mississippiensis*), and 10) west Indian manatee (*Trichechus manatus*). These are artistic illustrations and do not represent actual spacing among or abundance of megafauna. Artwork by Alex Boersma.

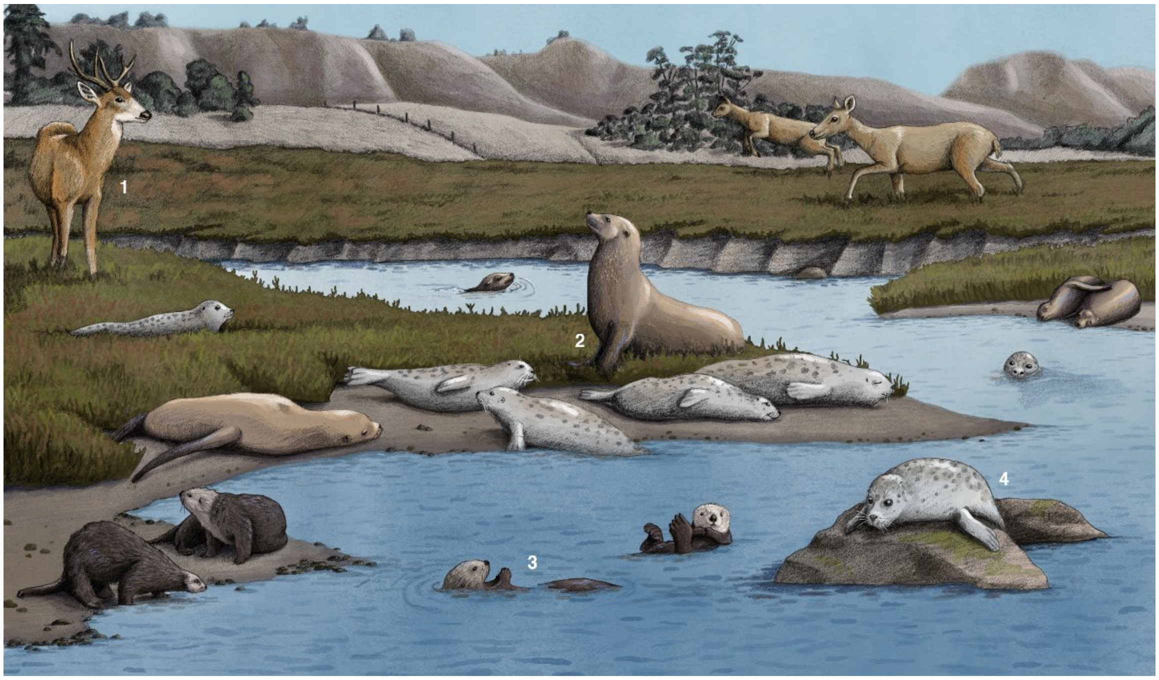

Figure 3: Megafauna in Elkhorn Slough, California salt marshes. Including 1) mule deer (*Odocoileus hemionus*), 2) sea lions (*Zalophus californianus*), 3) sea otters (*Enhydra lutris*), and 4) harbor seals (*Phoca vitulina*). These are artistic illustrations and do not represent actual spacing among or abundance of megafauna. Artwork by Alex Boersma.

Figure 4: Megafauna in South African salt marshes. Including 1) ostrich (*Struthio camelus*), 2) domesticated horse (*Equus ferus caballus*), 3) African buffalo (*Syncerus caffer*), 4) sheep (*Ovis aries*), 5) cattle (*Bos taurus*), 6) Nile crocodile (*Crocodylus niloticus*), 7) hippopotamus (*Hippopotamus amphibius*), 8) common zebra (*Equus quagga burchellii*), 9) lion (*Panthera leo*), 10) springbok (*Antidorcas marsupialis*), 11) common warthog (*Phacochoerus africanus*), 12) gemsbok (*Oryx gazella*). These are artistic illustrations and do not represent actual spacing among or abundance of megafauna. Artwork by Alex Boersma.

Figure 5: Photos of megafauna in salt marshes. Including (A) American alligator (*Alligator mississippiensis*; photo: J. Nifong), (B) sea lion (*Zalophus californianus*) and harbor seals (*Phoca vitulina*; photo: L. Gaskins), (C) sea otter (*Enhydra lutris*; photo: R. Eby), (D) mule deer (*Odocoileus hemionus*; photo: L. Gaskins).

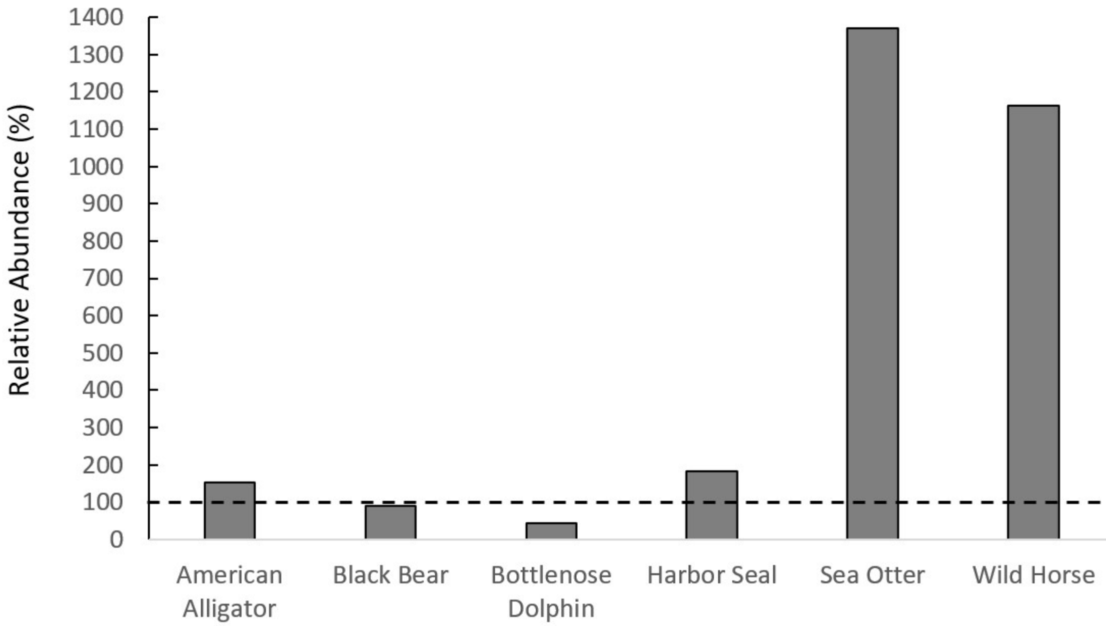

Figure 6: Relative abundance of megafauna in salt marshes compared to other habitats in which they are found. If above the dashed horizontal line, the species of megafauna is more abundant in salt marshes than other habitats.

Feral and introduced megafauna have been documented to impact saltmarsh structure and function. For example, feral hog activity not only leads to highly trampled areas and loss of vegetation, but also changes in soil organic carbon, marsh elevation, soil anoxia, higher concentrations of ammonium-nitrogen in porewater, and changes in carbon cycling (Persico et al. 2017, Sharp and Angelini 2019). Studies on feral horses show that they can also greatly alter salt marsh communities, increasing bird diversity and crab densities, but lowering the amount of vegetation biomass and the fish species richness in grazed marshes (Turner 1987, Levin et al. 2002). Additionally, overpopulated feral horses can graze the marsh so extensively it cannot recover (Turner 1988). These strong indirect impacts on salt marsh structure, resilience, and function are noteworthy and important to understand and preserve important salt marsh functions. Future work should focus on managing and mitigating the impacts of introduced and feral animals. This would not only aid in the recovery of native wild megafauna in these spaces but also protect the marsh ecosystems themselves. While impacts of feral and introduced megafauna on marshes are relatively well understood, the impacts of recovered, native megafauna species are less well understood.

The presence of a diversity of megafauna in salt marshes, including recovered native megafauna, has a range of potential implications for salt marsh ecosystem structure and function. First, megafauna may exert positive or potentially negative influences on foundational salt marsh species, such as grasses. Evidence that consumptive and non-consumptive impacts of alligators can trigger trophic cascades that indirectly promote snail and mussel populations supports this hypothesis (Nifong and Silliman 2013). Second, direct vegetation consumption by cattle and horses in Europe provides important insight into the impact of grazing on salt marshes (Menard et al. 2002, Nolte et al. 2014). Because of differences in nutritional requirements and plant species preferences, cattle and horses contribute differently to structural diversity and ecosystem management, and this information can be used to minimize negative impacts on foundational marsh plant species (Menard et al. 2002). Third, megafauna may stabilize feedbacks of predators on plant ecosystems, thereby providing increased coastal ecosystem resilience. For example, wetland predators, such as blue crabs and sea otters, induce trophic cascades through mesopredator and grazer consumption that promote plant populations (Silliman and Bertness 2002, Hughes et al. 2013). These more robust foundational plant populations could improve ecosystem resilience by stabilizing sediment with their roots and lowering erosion rates, improving coastal protection by wetlands (Silliman et al. 2019). Fourth, megafauna facilitation of foundational plant species (Hughes et al. 2013) could improve restoration approaches, leading to cost and effort savings, as facilitation of plant foundational species could proceed on its own with the proper restoration design. For example, through a trophic cascade, sea otters restored hectares of seagrass, the foundational plant species in the system, by consuming crabs that eat sea slugs which clean algae off the seagrass. The end result was that seagrasses were restored in the estuary without human intervention (Hughes et al. 2013). Fifth, large animals like hippos, water buffalo, and manatees could severely suppress standing plant biomass and/or create ponds within marshes, similarly to the way invasive feral hogs do now (Frederick 1998, Arrington et al. 1999). Because these five potential influences of megafauna on salt marsh ecosystems remain largely theoretical and hypothetical, future studies should focus on quantifying effects of megafauna on salt marsh structure and function and whether megafauna presence can be harnessed for conservation and restoration of these important coastal ecosystems. Additionally, we defined megafauna on the basis of mass (e.g., 45 kg) but recommend that as future studies gain more insight into the roles of megafauna in salt marshes that salt marsh megafauna be classified functionally, as proposed by Moleon et al. (2020).

The use of salt marshes by a variety of megafauna suggests that marshes could provide important ecological functions for these animals – including providing additional habitat for feeding and raising young, and refugia from human impacts. For example, sea otters, an endangered species, likely use salt marshes as nursery grounds for several reasons, including that the marshes are relatively free from otter predators, that 'hauling out' on salt marshes can be metabolically favorable for otters because body heat is lost more slowly in air than in water, and Elkhorn Slough marshes are low relief and otters can easily haul out onto them (Estes et al. 1998, Eby et al. 2017, Tinker et al. 2018). The degree of megafauna impacts on marshes likely depends upon species life stage. For example, if megafauna use salt marshes as juveniles, then their impacts may be reduced relative to those of larger, adult megafauna, yet additional research is necessary to test this. In terms of protection from human impacts, salt marshes likely serve as a refuge for the American crocodile and West Indian manatee, which are both listed as vulnerable by the IUCN Red List (Deutsch et al. 2008, Ponce-Campos et al. 2012, Sievers et al. 2019). The recognition that megafauna can be supported in marsh systems adds to and strengthens the list of known ecological services that salt marshes provide, such as increased coastal protection and erosion control through trophic cascades that positively impact foundational plant species, and water purification and carbon sequestration from marshes under less stress from overgrazing (Barbier et al. 2011, Silliman et al. 2019). Given the importance of salt marshes to species of megafauna, future marsh restoration and management plans should consider the ecological functions that marshes can provide for megafauna.

3. Comparative studies suggest harbor seals act as ecosystem engineers on salt marsh edges

3.1 Abstract

Following long-term conservation efforts, marine megafauna populations have recovered and expanded into new habitats. In these newly colonized systems, large animals have been shown to affect systems through top-down, consumptive effects. For example, sea otters have facilitated seagrass recovery through a trophic cascade in a California estuary. However, marine megafauna effects on newly colonized ecosystems are not well understood and their role as non-consumptive ecosystem engineers has not been robustly explored. In California estuaries, harbor seals (*Phoca vitulina*) have increased in numbers over the past decade and recently expanded into salt marshes, an ecosystem long thought to be beyond the habitat niche breadth of seals. Although seals do not feed in estuarine or marsh systems, they gather on the shorelines in haul-out areas. To begin to test whether seals could be having a large non-consumptive engineering effect on vegetated marshes, we set up a control-impact study to evaluate the potential effects of concentrated seal haul-out areas on the structure of salt marsh edges. Our findings indicate the potential for strong effects of seal haul-out locations on foundational plants, diversity and distribution of animals, and geomorphology of salt marsh edges. Salt marsh edges with seals were composed of heavily compacted soil with a mud surface almost entirely denuded of marsh plants and invertebrates in comparison to control sites. Specifically, haul-out areas were 69% lower in plant percent cover and 87% lower in crab burrow density at the edge in comparison to non-haul-out areas. In contrast, seal haul-out areas functioned as hot spots for bird diversity, as haul-out regions hosted five times more birds at the marsh edge and 23 times more at the interior of the marsh than controls. Bird communities may choose to congregate at seal-haul out sites because they represent favorable denuded and compressed platforms to forage and/or rest. Despite the

denuded edges, the erosion rates at seal haul-out sites were not significantly higher, likely due to the compensatory effects of intense soil compression, few crab burrows, and a surprisingly intact root network under the compacted soils. These findings from spatial comparisons suggest that harbor seals act as ecosystem engineers in salt marshes by creating large disturbances by hauling out onto marsh platforms. To further test this, future studies should exclude seals from the edges of the haul-out areas and conduct a before-after comparison (before seals colonized the estuary vs after with aerial photographs). As conservation continues to succeed and large marine consumers expand into new habitats, future research should examine the generality of marine animals acting as ecosystem engineers in wetland systems.

3.2 Introduction

Megafauna (>45 kg) have long been known to have significant effects across terrestrial, freshwater, and marine systems, and can reshape ecosystems through both consumptive and non-consumptive pathways (Martin and Klein 1989, Waldram et al. 2008, Coverdale et al. 2016, Estes et al. 2016, He et al. 2024). For example, sea otters (*Enhydra lutris*) facilitate kelp forest ecosystems by consumption by controlling the density of urchins that graze hold-fasts, generating a trophic cascade (Estes and Palmisano 1974). Megafauna can also indirectly impact systems non-consumptively through fear. For example, tiger sharks non-consumptively facilitate seagrass by scaring sea turtles and dugongs and driving them into unvegetated shallow areas (Burkholder et al. 2013). Finally, megafauna can have large, non-consumptive effects on communities and their functioning through ecosystem engineering. Whales can engineer ocean systems by transferring nutrients (Roman et al. 2014), and alligators create wallows that act as refugia for 81 species including birds, mammals, reptiles, and amphibians (Campbell and Mazzotti 2004, Rainwater et al. 2024).

Through the success of long-term conservation efforts, megafauna are expanding into and recolonizing habitats formerly thought to be beyond their niche breadth (Silliman et al. 2018). For instance, surveys of estuaries and palaeoecological records show that alligators are recolonizing marine ecosystems (seagrass, oyster reefs, estuaries) in the southeastern US that they once inhabited (Nifong 2014, Fujisaki et al. 2016, Silliman et al. 2018). This conservation success presents ecologists with an opportunity to explore how the re-entry of large consumers impacts ecosystems. The impacts of megafauna recolonization have rarely been explored, but in cases where it has been studied, the effects can reshape systems significantly. Sea otters recently recolonized and facilitated seagrass ecosystems by consuming crabs, which released sea slugs from predation, and allowed them to clear algal overgrowth (Hughes et al. 2013). Sea otters also recently recolonized salt marshes, and facilitate foundational marsh plants through a trophic cascade that lowers erosion rates (Hughes et al. 2024).

Harbor seals (*Phoca vitulina*) have also recolonized salt marshes in California as a result of decades of successful conservation and policy efforts (Broughton 1995, Braje and Rick 2011, Silliman et al. 2018). Historically, harbor seals were heavily exploited and commercially hunted for their pelts and meat, only ending with the passage of the Marine Mammal Protection Act in 1972 (Cammen et al. 2019). As a result, their population rebounded, to 400,000-500,000 individuals overall (Carretta et al. 2015). Due to this recovery, populations of harbor seals within Elkhorn Slough in Monterey Bay, California, increased from 30 individuals in 1975 to 345 individuals in 2009 (Harvey et al. 1995, Oxman 1995, McCarthy 2010). At night, harbor seals use areas near the mouth of the slough to forage but obtain the majority of their food out in Monterey Bay (Harvey et al. 1990, Oxman 1995, Eguchi and Harvey 2005). Marshes serve as a nursery, breeding, molting, socializing, and sleeping ground for harbor seals, where they use predictable areas to "haul out" of the water (Van Parijs et al. 2003, ESNERR 2016).

Generally, little is known about the impacts of pinnipeds on the dynamics of ecosystems (Bowen 1997, Estes et al. 2016), and no study has quantified the impact of harbor seal haul-outs on salt marsh ecosystems. Adult harbor seals in Elkhorn Slough average 81.3 kg (Eguchi 1998) and reach ~2 m in length (McCarthy 2010); when these large marine mammals repeatedly haul out onto the edge of marshes, this could create high magnitudes of disturbance and reshape marshes. Because harbor seals feed mostly offshore and at the mouth of Elkhorn Slough, their impacts within marshes are likely non-consumptive engineering effects, as seals may transfer nutrients to the marsh from Monterey Bay through feces and/or create disturbance in vegetated marshes through the formation of concentrated haul out areas. However, seals do not use the marsh uniformly, and are most concentrated right at the edge. Thus, we would hypothesize that the impact of seals will be highest right at the edge where they are most dense, and lower in the interior of the marsh where the seal density is lower. Though the marsh edge is only a small portion of the overall marsh, this transition zone is important, and by acting as ecosystem engineers at the edge, harbor seals could thus have a disproportionate impact on salt marshes (Minello et al. 1994, Peterson and Turner 1994, Cicchetti and Diaz 2000). The goal of this study was to understand whether harbor seals could potentially impact the structure and diversity of salt marshes through the establishment and maintenance of large haul out areas.

3.3 Methods

3.3.1 Site Description

Elkhorn Slough is a 1200 hectare estuary in Monterey Bay, California, containing vast salt marshes between Mean High Water (MHW) and Mean Higher High Water (MHHW) (Wasson et al. 2013). The salt marsh is dominated almost entirely by pickleweed (*Salicornia pacifica*). The climate is Mediterranean, and this semidiurnal and ebb-dominated system has a mean diurnal tidal range of 1.7 m (Caffrey and Broenknow 2002). The intertidal region of Elkhorn Slough, including tidal mudflats and salt marshes, hosts a vast biodiversity of invertebrates and birds, along with marine mammals, including harbor seals and sea otters (Harvey and Connors 2002, Wasson et al. 2002, Van Dyke and Wasson 2005, Eby et al. 2017). Elkhorn Slough has been designated as a “wetland of international importance” and is a bird diversity hotspot along the Pacific Flyway, with over 265 species of birds recorded in the estuary (Harvey and Connors 2002).

3.3.2 Site Selection

Our study design was a replicated, comparative study with control and impact sites (n=5). We conducted the study between June to September 2021. To address both how different densities of harbor seal haul outs affect marshes, we included transects at the edge and interior of each site as a proxy for density. Edge surveys were conducted between 0-1 meters from the end of the marsh platform closest to the water, and interior surveys were conducted between 2-3 meters from the end of the marsh platform (Fig 7.). This was driven by the results of boat counts, where we noted that seals were almost all at the edge of the marsh, and at most 3 meters into the marsh. Thus, to capture how their impact on marshes might change across different densities of seals within impact sites, we established these two zones: edge and interior.

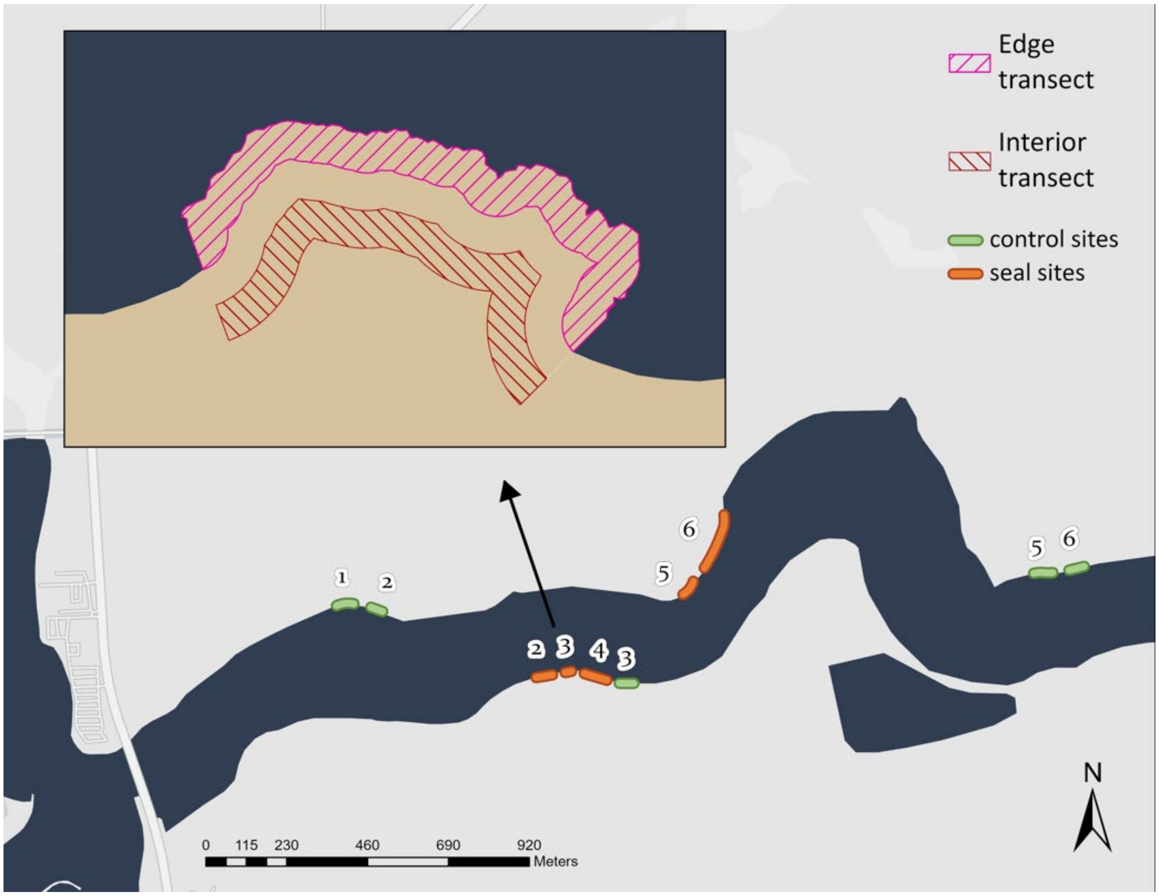

Figure 7: Locations of harbor seal haul out (orange) and control (green) sites within Elkhorn Slough. Inset shows the edge transect 0-1 m from the water, and edge transect 2-3 m from the water. An ID number for each site is also provided.

When selecting seal and control sites, each site had to meet a set of three criteria: 1) sites had to be along the main channel, and not up a tidal creek; 2) marshes could not have consistent accumulation of algal mats (*Ulva spp.*), because *Ulva* can strongly impact marsh communities (Wasson et al. 2017); and, 3) each site had to have a marsh platform accessible to seals, and the potential haul range of harbor seals is 0.8 to 1.65 m in elevation (ESNERR 2019). Additionally, at seal haul out sites, we eliminated sites where seals only used the mud platform in front of the site but not the marsh platform itself, and we only included sites where on at least one boat survey, we counted 8 or more seals in the marsh. If we saw one seal at a potential control site, but no more than one, that was deemed acceptable as it demonstrated that the marsh could be used by seals and was within the range of elevation they could climb onto.

To verify that our study sites met all of the above criteria, we conducted five boat surveys throughout the main channel of Elkhorn Slough over the course of four weeks in June 2021. We performed these counts across a range of tides to capture seal haul out patterns more accurately, and to verify that control sites were not used across all tides. On each boat survey, we counted the overall number of seals at each site, and for each individual seal, recorded if it was 0-1, 1-2, or 2-3 meters from the water's edge. Seal counts from the boat were conducted from the middle of the channel of Elkhorn Slough through binoculars to maximize our distance from the seals. No seals ever left the haul out sites during these counts, and we did not note any visible change in behavior. At control site five, there was one seal during two of the boat surveys, and later, we noted 1 seal at control site three on the trail cameras, and we kept all these sites. At the conclusion of these boat surveys, we selected five seal haul out sites and five control sites that met all the criteria. Sites adjacent to each other are separated by tidal creeks, which act as natural borders.

3.3.3 Characterizing marsh plant communities

To determine percent plant cover at each site, we randomly placed a quadrat in the marsh five times in the edge and interior (5 quadrats per site and 5 sites per treatment per location in marsh). We used a 0.5 m^2 quadrat elevated off the ground within which we dropped a metal rod at 16 intercept points (Wasson et al. 2017), noting when the rod touched plants, and which species. Then, we added up the number of times out of 16 where we recorded any species of marsh plant to get the overall percent plant cover for each individual quadrat. In these same 0.5 m^2 quadrats, we measured canopy height at 3 of the intercepts per quadrat (n=75) by selecting the tallest plant in the vicinity of the intercept as it stood naturally, then we noted the species. We removed all measurements with no plants present before analysis. Therefore, the number of measurements changed for each group. Out of a potential 75, at the marsh edge zone, there were 7 measurements for seal sites, and 74 for control, and at the marsh interior zone, 52 measurements for the seal sites, and 75 measurements for the interior.

Because algal mat (*Ulva spp.*) accumulation was part of the selection criteria for sites, we verified that *Ulva* was not covering our sites by conducting visual percent cover surveys on the ground rather than visually from the boat. We used five 1 m^2 quadrats placed randomly throughout each edge and interior region (5 quadrats per site and 5 sites per treatment per location in marsh). We conducted this survey separately from the percent plant cover survey because *Ulva* distribution is patchy, and a 1 m^2 quadrat would be more likely to represent *Ulva* accurately, whereas the 0.5 m^2 intercept survey would be more likely to accurately account for pickleweed, which has thin overground runners.

To determine the belowground biomass of plant roots, we collected 5 cores for each site at the edge and interior. Cores were collected randomly throughout these transects to assure they were representative of the whole site. We used the same sized corer device for these samples, soil samples, and bulk density, and it produced a cylindrical core that was 22 cm long, and 2.5 cm in diameter. To analyze the samples, we placed the 5 cores into a mesh strainer, and agitated them with our hands and water to wash away all mud from the roots. We then divided by 5 to get an average root mass per core, then divided by the corer volume (107.94 cm^3) to get root density in g/cm^3. In the analysis, there was only a single value per site because the samples were combined.

To understand differences in soil chemistry, we randomly collected 3 cores from the edge transects only. We combined the 3 cores and ground them up, then analyzed them for percent and amount of nitrogen and carbon and performed a Mehlich 1 test (Mehlich 1953) to examine the presence and concentration of common elements within soil.

3.3.4 Characterizing sediment geomorphology

To understand differences in sediment geomorphology, we calculated bulk density and soil penetration resistance. We measured bulk density by collecting five cores at the edge and interior of each site. Each core was dried in an oven, and weighed, then divided by core volume (107.94 cm^3) to calculate bulk density. We measured soil penetration resistance by taking 5 measurements at the edge and interior of each site using a soil compaction meter (Spectrum Technologies Inc). Applying a steady level of pressure on device, the soil compaction tester device was pushed into the soil down to the same depth, and measurements were taken at the same 8 discrete points that were equally spaced (7.62, 15.24, 22.86, 30.48, 38.10, 45.72, 53.34, 60.96 cm).

3.3.5 Calculating average annual erosion rates

To measure annual horizontal erosion, we used 2011 and 2018 Lidar digital elevation models (DEMs) to create 1.41 m (NAVD88) elevation contours for each year and calculated the perpendicular distance between the two contours. We selected this range of years because, according to historic maps, seals utilized all the haul out sites in this study since 2008, and so we attempted to capture erosion in the following decade (McCarthy 2010).

The 2011 data was a combination of 2010-2011 Coastal Lidar and CSUMB bathymetry in the main channel of Elkhorn Slough, and the 2018 data is FEMA Lidar Region 9 CA downloaded from NOAA Digital Coast using geoid 12b to match the 2011 Lidar. We clipped the DEMs to the main channel and created contour sets for both DEMs, selecting the 1.41 m contour for comparison because it is the approximate elevation of the top of the channel bank in the Elkhorn Slough main channel. We confirmed the positional accuracy of the contours by noting the tight alignment in areas of hard substrate (i.e. riprap) that would not have changed between

2011 and 2018. We used a mask polygon to clip both sets of contours along the edge of the main channel and eliminated any contour segments that did not contain both sets of contours. We also eliminated contour segments where the 2011 contour was landward of the 2018 contour since we know channel banks are not prograding in Elkhorn Slough and would have likely represented artifacts in the Lidar data (C. Endris personal communication). We then segmented the 2011 contour (the most seaward contour due to erosion) into 1-m segments and applied a custom-built toolset, using ArcGIS Desktop v.10.7 ModelBuilder, to create polylines normal to the azimuth of each 1-m contour segment. We selected a maximum polyline distance of 5 m to ensure all lines spanned the distance between the 2011 and 2018 contours. We then buffered each contour dataset, 2011 buffered to landward and 2018 buffered to seaward, and intersected these buffers to create a polygon that represented the zone between the two contours. This polygon became the mask from which we extracted (using the Clip tool) all the polylines normal to the 2011 contour, totaling approximately 8,750. We then selected and removed any polylines that appeared to be at extreme angles between the two contours, and which may not have represented a true distance of erosion. Finally, all polyline distances were calculated. We then divided by seven to get the average annual erosion rate.

3.3.6 Characterizing marsh invertebrate communities

To quantify differences in the marsh invertebrate community, we first measured crab burrow density by counting every burrow over 1 cm in diameter (Beheshti et al. 2021). At each site, we collected ten 1m^2 quadrats of data (five at the edge and five in the interior region). Then, we characterized the meiofauna community at each site (n=5, one core per site) in the edge region of the marsh only, by taking a 5ml core of soil using a Luer Lock Syringe with the tip cut off. Samples were processed in the lab on the same day using a 500 micron then 63 micron sieve and stained with Rose Bengal (Somerfield and Warwick 2013). The meiofauna were counted under a microscope on a slide, and grouped by type (i.e., nematodes, foraminifers, turbellarians, mites, copepods, polychaetes, or ostracods).

3.3.7 Characterizing bird communities

For 12 days, between August 24 to September 4, 2021, one trail camera (Bushnell Trophy Camera E3 Essential) was placed at one of the ends of each site, facing perpendicular to the shoreline. All on the ground field measurements of plant and animal communities and geomorphology were conducted when harbor seals were not present, and trail cameras were all placed and retrieved at tides when seals were not at sites. Cameras were programmed to take one photo every 30 minutes for a total of 46 photos a day (there are no photos at 9:30am or 11:30pm due to a camera programming issue). Across 12 days, cameras took 552 photos per site.

The 5,520 photos were graded by four people. First, each grader was trained in bird identification, then completed an identical set of photos to verify that each person graded the photos and reported the data in a standardized fashion. To limit potential bias, photos from each site were distributed among each of the graders, so no one person completed any one site alone. Each photo underwent a screening by a single grader who documented various details: the photo's number, the time of day, whether it was taken during day or night, the presence of foraging birds along with their species, and the count of birds and seals observed in both the edge and interior transects of each photograph. For each site, we had a visual map showing the boundaries of each transect which the grader used for reference. Birds were identified down to the lowest taxonomic level possible in 15 groupings (brown pelican, white pelican, cormorant, great blue heron, egret, long billed curlew, marbled godwit, willet, whimbrel, plover/sandpiper, seagull, mallard, California quail, tern, and black-necked stilt). If a bird was sitting at a boundary edge, we counted them as being in the region where their feet were planted. For seals, we counted the number and noted location. Seals were counted as being in the edge or interior transect if the majority of their body was laying in the edge or interior, the same protocol as the boat-based count surveys. Thus, it was possible for them to be in-between the two transects. Because pickleweed has a low canopy height (predicted canopy heights ranged from 10-23 cm in this study), we do not believe that vegetation occluding bird detection was an issue.

3.3.8 Statistical analysis

Statistical analyses were conducted using R version 4.2.3 (Team 2023). We fit generalized linear mixed effects models (GLMMs) to model the relationship between our response variable and two fixed effects - treatment (control or seal site) and location in marsh (edge or interior). Site was included as a random effect in all models to account for multiple measurements per site and thus their lack of independence. Distance from the mouth of Elkhorn Slough in meters was also added to every model as a fixed effect to account for sites that are closer together. We used GLMMs with an ordered beta dispersion for percent plant cover and percent Ulva cover, since that family is designed to handle proportional data. We used GLMMs with a negative binomial family for burrow density and bird density because they are both count data. We used GLMMs with a Gaussian distribution for canopy height, root density, bulk density and horizontal erosion, since they are all non-count data that was roughly symmetrical and we verified that model error terms were approximately normally distributed.

To build the GLMMs, we used the package glmmTMB (Brooks et al. 2017). We began by running 5 nested models for each set of data, increasing complexity with one added term in each model. The models started with only the random effects, added scaled distance from mouth, then added treatment (seal/control), then an additive model with the addition of location in marsh (edge/interior), then an interactive model between treatment and location. We conducted likelihood ratio tests on these four nested models, to examine if adding a new term significantly improved the model. When selecting models, we chose between the additive model or interactive model, since treatment and location (edge/interior) are fundamental to the study design. We ran all the models though in the likelihood ratio testing to get the individual p-values.

We plotted the selected model's residuals with a qq plot, and used the ranef function to examine if there were site outliers and plotted them as a qq plot. Both were evaluated visually. For count metrics, crab burrow density and bird counts, we used the DHARMa package (Hartig 2018) to test for zero-inflation. We then used the predict function to create a data frame that calculate the mean and standard error with the selected model. For crab burrow density and bird density where we used a negative binomial distribution, we used a log link for these models. To create the figures, we plotted the data using ggplot2 (Wickham 2016). We plotted the mean and standard error of the predicted data from the models instead of the raw data in our figures because the modeled data accounts for the non-independence of the data points since there are multiple measurements per site along with other factors in some specific analyses.

We consistently used this process for every type of data evaluated using a GLMM, but in a few cases, there were additional considerations to add in the model. For canopy height, multiple measurements were taken per quadrat where we measured plant cover. To account for this within quadrat-correlation, we added an additional random effect and gave each quadrat a Plot ID, nested within site. When evaluating horizontal erosion rate, we averaged every individual erosion measurement per site to a single value, then added a weight to account for the different number of erosion measurements per site. In erosion models, there is no location within marsh term, only treatment since horizontal erosion only happens at the edge. When evaluating daily bird density, we added an offset term for site surface area, because each site was not uniformly sized.

To analyze soil penetration resistance, we used the same overall process to select models, but with linear mixed effects models (LMM). We included first order autoregressive (AR1) error terms within an ordered depth term and we used nlme::lme() to fit these models (Pinheiro et al.

2012). Because the data is ordered and taken at discrete depths with each push of the machine, there is an AR1 term ordering the depths within each push of the soil compaction meter, and the ID of each push nested within site is the random term. We created nested models: 1) a base model with only depth and the random term, 2) added scaled distance from mouth, 3) treatment added as an interactive term with depth, 4) location incorporated as additive term, 5) location and treatment interaction term added, 6) location and depth interactive term added, 7) fully interactive model between treatment, location, and depth, and compared these models using likelihood ratio tests. To accurately represent soil penetration resistance by depth across factors visually within our figure, we selected the fully interactive model for graphing and used it to predict the soil penetration resistance. For this specific metric, we used the predictSE.lme function to get standard error from the AICmodavg package (Mazerolle and Mazerolle 2017), but the other metrics were computed with the regular predict function.

Across all data analyzed with GLMMs and LMMs, the figures and reported means and standard errors, I am reporting the model predicted means and standard errors within the manuscript and in the figures. I decided not to directly report the raw data, because averaging of the raw data does not effectively represent the lack of independence of repeated measurements per site. All p-values reported are from likelihood ratio testing.

To evaluate differences in meiofauna communities and soil chemistry by treatment, we used a Welch's two-sample t-test. We tested for normality using the Shapiro-Wilk test, and homogeneity of variance using the Bartlett test. For manganese and carbon amount, these assumptions were not met, so we conducted a Mann-U Whitney test. For meiofauna measurements along with soil chemistry measurements, the reported and graphed values are the raw data since the measurements are independent.

3.4 Results

Our comparative observational study of five seal haul-out and five control sites in Elkhorn Slough in Monterey Bay, California, shows that there are marked differences in plant communities, geomorphology, and animal communities associated with harbor seal haul outs. While these observed differences in plants, animals, and geomorphology associated with harbor seal haul out sites were strongest along marsh edges, similar patterns occurred in the marsh interior, but with lower intensity. The strongest differences in biological communities and geomorphology occurred at the edge and correspond to where the majority of harbor seals hauled out – 63% of seals counted through trail cameras and 95% of seals counted from boat surveys were at the edge vs. interior transects (Fig 8).

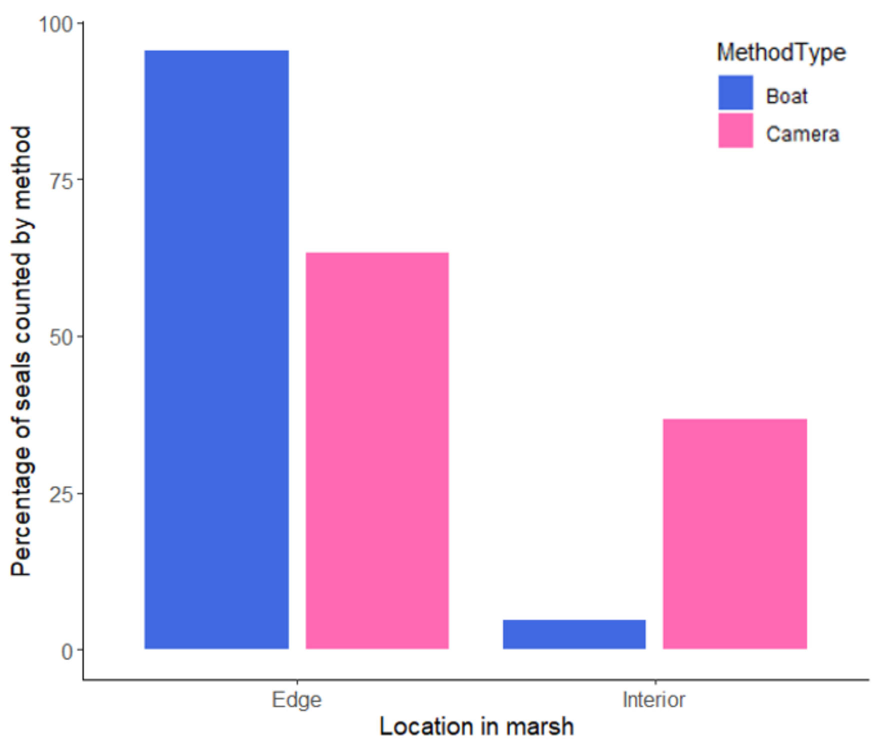

Figure 8: Percentage of total number of seals counted from boat surveys (n=5) and trail camera photos (12 days) in edge and interior transects. Because of the differences in methodology between the boat counts and the photos taken every 30 minutes, we kept them

separate. Also, we present both to demonstrate that the number of seals taper from the edge to the interior of the marsh.

Plant communities were nearly denuded in association with harbor seal presence. Mean percent plant cover differed with harbor seal presence ($p = 0.002$) and transect location in the marsh ($p < 0.0001$, edge vs, interior) (Fig 9, Table 2, ordered beta distribution). These effects were most extreme at the edge transect, where percent plant cover was 78.3% ± 5.1 in the control sites and only 9.1% ± 4.5 at seal sites. At the interior of the marsh, mean percent plant cover was also lower but to a lesser extent - a 22% difference from 99.2% ± 0.5 at control sites to 77.1% ± 5.7 at seal sites. Where plants remained, their canopy height was shorter at seal sites than control sites ($p = 0.02$) and differed by location in marsh ($p < 0.0001$), with shorter plants located in edge than interior transects across both seal and control treatments (Table 2, Table 3, Gaussian). In contrast to the aboveground results, root density did not differ by treatment ($p = 0.44$), but did differ by location in marsh ($p = 0.02$), increasing from the edge to the interior of the marsh (Fig 9, Table 2, Table 3, Gaussian, GLMM). *Ulva* cover was not different between treatments ($p = 0.78$) but did vary by location in marsh ($p < 0.0001$) (Fig 9, Table 2, Table 3, ordered beta distribution, GLMM). The mean *Ulva* percent cover was lower than 5% in both seal and control sites in the edge and interior (Fig 9, Table 3, ordered beta distribution, GLMM).

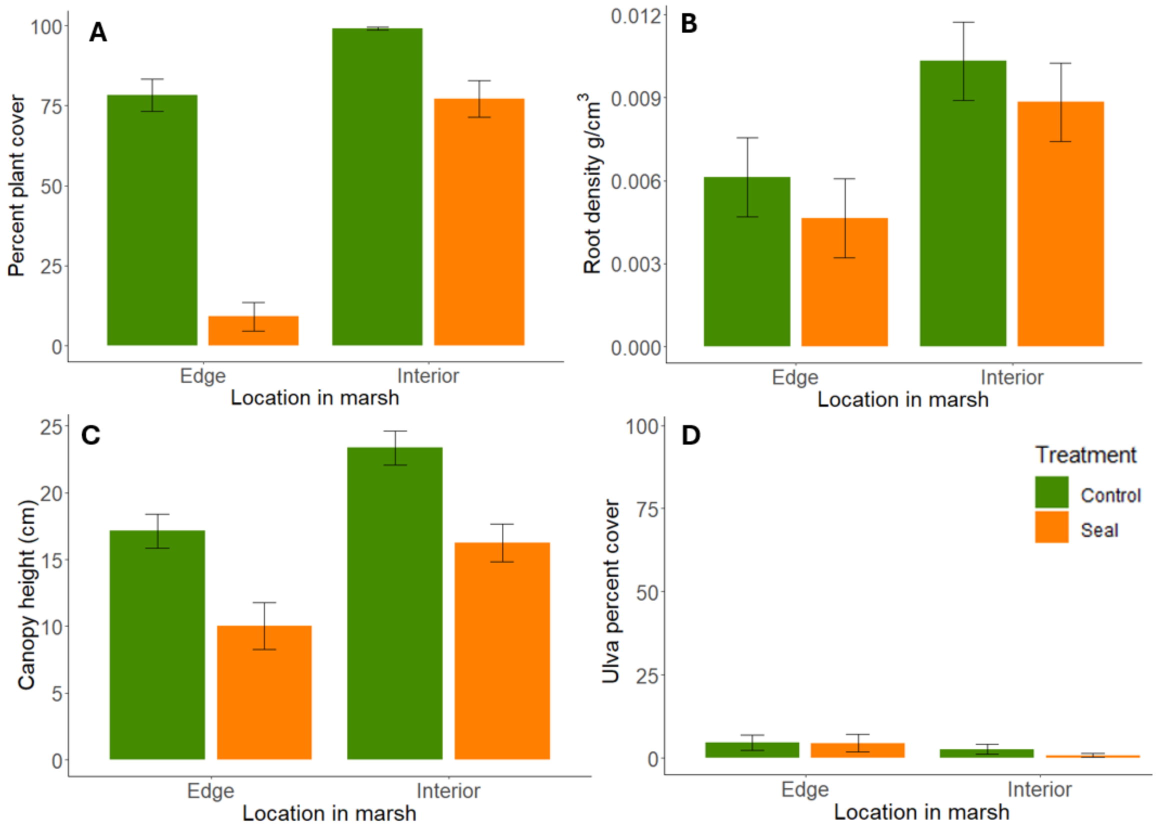

Figure 9: Vegetation metrics in harbor seal haul out regions versus control regions at the edge and interior of the marsh. A) Percent plant cover, B) root density (g/cm^3), C) canopy height (cm) and D) *Ulva* algal mat percent cover. Data are mean ± standard error.

Table 2: The model selections, p values, and chosen models for metrics analyzed with GLMMs.

Measurement and units	**Model family**	**Treatment p-value**	**Location in Marsh (Edge &Interior) p-value**	**Interaction p-value**	**Model Chosen**
Percent plant cover (%)	Ordered beta	0.002	<0.0001	0.67	Additive
Canopy height (cm)	Gaussian	0.02	<0.0001	0.46	Additive
Root density (g/cm^3)	Gaussian	0.44	0.02	0.60	Additive

Percent *Ulva* cover (%)	Ordered beta	0.78	<0.0001	0.03	Interactive
Bulk density (g/cm^3)	Gaussian	0.08	<0.0001	0.26	Additive
Horizontal erosion (cm)	Gaussian	0.12	NA	NA	Treatment only
Crab burrow density ($burrows/m^2$)	Negative binomial	<0.0001	0.29	0.40	Additive
Daily bird count for $50m^2$ site	Negative binomial	0.01	<0.0001	<0.0001	Interactive

Table 3: Sample sizes, means, and standard errors of metrics analyzed with GLMMs. * = the mean is exponentiated since the model predictions are on the log scale, and the values in parentheses are the mean minus and plus the standard error, then exponentiated, representing the lower and upper bounds of the error bars on the graphs. The transformation is non-linear so it's not symmetric.

Measurement and units	**Replication**	**Treatment type**	**Edge Mean ± SE**	**Interior Mean ± SE**
Percent plant cover	n=25	Seal	9.1% ± 4.5	77.1% ± 5.7
		Control	78.3% ± 5.1	99.2% ± 0.5
Canopy Height	n=7 edge, n=52 interior	Seal	10.0 cm ± 1.8	16.3 cm ± 1.4
	n=74 edge, n=75 interior	Control	17.1 cm ± 1.3	23.4 cm ± 1.3
Root density	n=5	Seal	0.005 g/cm^3 ± 0.002	0.009 g/cm^3 ± 0.002
		Control	0.006 g/cm^3 ± 0.002	0.01 g/cm^3 ± 0.002
Percent *Ulva* cover	n=25	Seal	4.5% ± 2.7	0.8% ± 0.6
		Control	4.6% ± 2.3	2.7% ± 1.5
Bulk Density	n=15	Seal	0.73 g/cm^3 ± 0.04	0.60 g/cm^3 ± 0.04
		Control	0.63 g/cm^3 ± 0.04	0.51 g/cm^3 ± 0.04
Horizontal erosion	n=442	Seal	27.1 cm ± 0.6	
	n=172	Control	25.3 cm ± 0.9	
Crab burrow density	n=25	Seal	1.0 $burrows/m^2$ (0.7, 1.5)*	1.3 $burrows/m^2$ (0.9, 1.9)*

		Control	7.7 burrows/m^2 (6.0, 10.0)*	9.8 burrows/m^2 (7.7, 12.5)*
Daily bird count for $50m^2$ site	n=60	Seal	50.4 birds (30.3, 84.0)*	23.4 birds (13.9, 39.2)*
		Control	9.2 birds (5.3, 15.8)*	1.0 birds (0.5, 2.0)*

Examinations of patterns in marsh geomorphology demonstrated that sites with seals were more compressed and had higher soil penetration resistance than controls. Soil bulk density did not differ by treatment (p = 0.08) but increased 16% at the edge and 18% in the interior in areas with seals relative to controls at the same location in the marsh (p<0.0001, Fig 10, Supp Table 2, Table 3, Gaussian, GLMM). Soil penetration resistance, however, differed by treatment, with increased resistance at seal sites (p=0.0007) (Fig 10, Table 4, Table 5, LME). Annual horizontal erosion rate was not different between seal and control sites (p=0.12), at 27.1 cm ± 0.6 at seal sites, and 25.3 cm ± 0.9 for control sites, an overall difference of just 1.8 cm (Fig 10, Table 2, Table 3, Gaussian, GLMM). We also quantified soil chemistry in the edge transects of all sites, and in any cases where the differences were significant, control sites had higher values (Table 6, Welch's two sample t-test and Mann-Whitney U test).

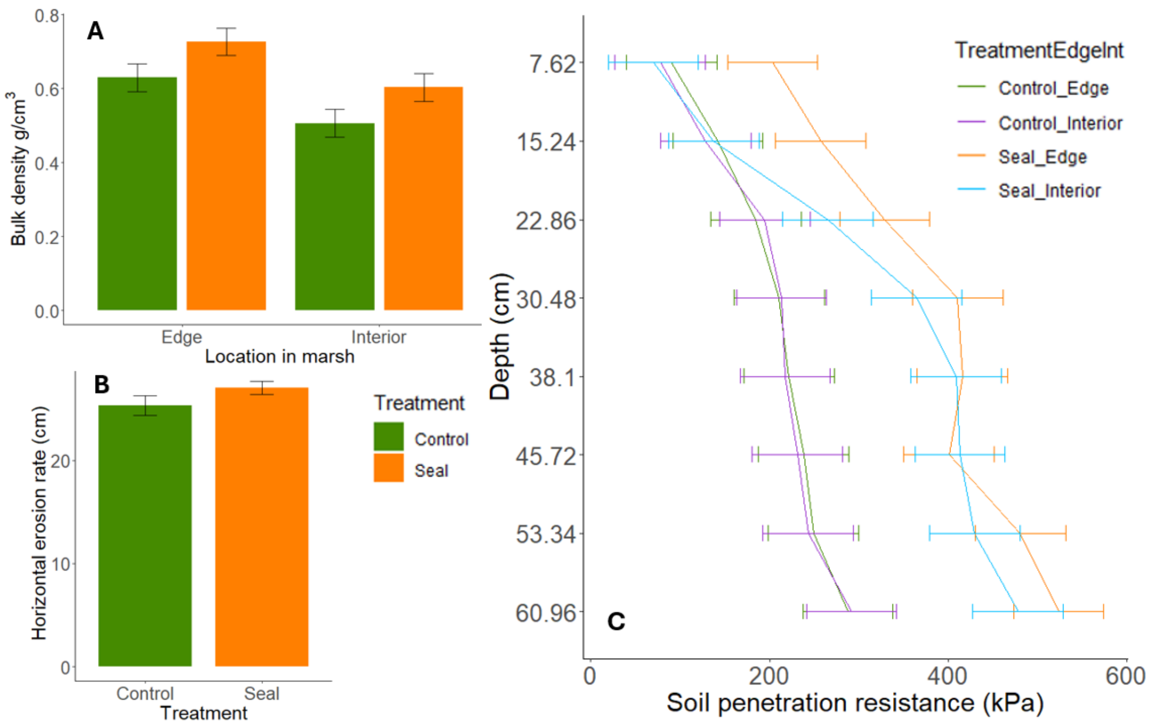

Figure 10: Sediment geomorphology in seal haul out versus control sites at the edge and interior of the marsh. Differences in average A) bulk density (g/cm^3), B) soil penetration resistance (cm) at 8 depths, and C) average annual horizontal erosion (cm) between 2011-2018. Data are mean ± standard error.

Table 4: Soil penetration resistance linear mixed effects models likelihood ratio testing results. The base model has depth as a fixed effect, and individual soil compaction tester push nested in site as a random term, along with a correlational term, the ordered depth metric. P-values in this table are the nested tests where we added the variables in the table's rows to the base model along with the variables listed in the rows above.

Term added in model	Associated p-value
Treatment added as an interactive term with depth	0.0007
Location incorporated as additive term	0.06
Location and treatment interaction term added	0.08
Location and depth interactive term added	0.58
Fully interactive model between treatment, location, and depth	0.77

Table 5: Soil penetration resistance predicted means. Predicted standard error across all means was 50.5 kPa.

Depth (cm)	Treatment	Edge Mean (kPa)	Interior Mean (kPa)
7.62	Control	90.4	78.0

	Seal	203.3	70.1
15.24	Control	142.2	128.4
	Seal	257.1	137.4
22.86	Control	184.7	194.6
	Seal	328.8	265.4
30.48	Control	210.6	213.4
	Seal	410.2	364.7
38.10	Control	221.6	217.5
	Seal	415.7	408.8
45.72	Control	238.2	231.0
	Seal	400.5	412.9
53.34	Control	249.2	243.4
	Seal	480.5	429.5
60.96	Control	287.6	291.7
	Seal	523.3	477.8

Table 6: The mean, standard error, p-values of all soil chemistry tests done in the edge transect only. Welch's two sample t-test used unless indicated otherwise. † = exact ties in data so p-value not presented. * = ran a Mann-Whitney U test. ^ = had all the same value for seal sites, so because there was no variance, we cannot compute a p-value.

Measurement (Units)	Seal Mean ± SE	Control Mean ± SE	p-value
LBC (ppm CaCO3/pH)	710.6 ± 45.5	742.8 ± 42.8	0.62
LBCeq (ppm CaCO3/pH)	2060.8 ± 132.1	2154.2 ± 124.0	0.62
pH	6.0 ± 0.3	6.2 ± 0.2	0.62
Calcium (mg/kg (ppm))	868.6 ± 41.6	1109.6 ± 74.8	0.03
Potassium (mg/kg (ppm))	684.4 ± 94.7	643.2 ± 60.8	0.73
Magnesium (mg/kg (ppm))	932.8 ± 63.2	1375.0 ± 72.9	0.002
Manganese (mg/kg (ppm))*	2.9 ± 0.5	20.0 ± 9.9	0.008
Phosphorus (mg/kg (ppm))	202.2 ± 20.0	157.6 ± 17.7	0.13
Zinc (mg/kg (ppm))	3.4 ± 0.8	3.3 ± 0.4	0.88
Nitrogen Amount (mg)†	0.01 ± 0.002	0.02 ± 0.004	---
% Nitrogen^	0.1 ± 0.0	0.2 ± 0.05	---
Nitrogen to Carbon Ratio	0.04 ± 0.001	0.03 ± 0.001	0.003
Carbon Amount (mg)*	0.1 ± 0.02	0.2 ± 0.06	0.02
% Carbon†	1.1 ± 0.1	2.7 ± 0.5	---

Animal communities, including both invertebrates and vertebrates, demonstrated differences between seal and control sites. Burrowing crab densities were lower at seal sites (p<0.0001) with an average of 1.0 and 1.3 crabs per m^2 in the edge and interior at seal sites from

7.7 and 9.8 in the control sites respectively, a drop of 87% in both locations in the marsh (Fig 11, Table 2, Table 3, negative binomial, GLMM). Numbers of total meiofauna counted in seal sites were 87% lower than control sites, with a mean of 1002 ± 131 in the controls, and a mean of 132 ± 53 at seal sites (p = 0.001) (Fig 11, Welch two sample t-test). Because the majority of the meiofauna we counted were nematodes, nematodes are where we saw the largest differences in count (Table 7). The predicted daily density of birds was higher in seal sites (p=0.01) and also at the edges than interior (p<0.0001), and the interaction was also highly significant (p<0.0001) (Fig 12, Table 2, negative binomial, GLMM). At the edge, the seal sites had a predicted mean 5 times greater than control sites, jumping from 9.2 to 50.4 birds (Table 3). In the interior marsh transects, the predicted mean was 23 times greater in the seal sites, jumping from 1.0 to 23.4 birds (Table 3).

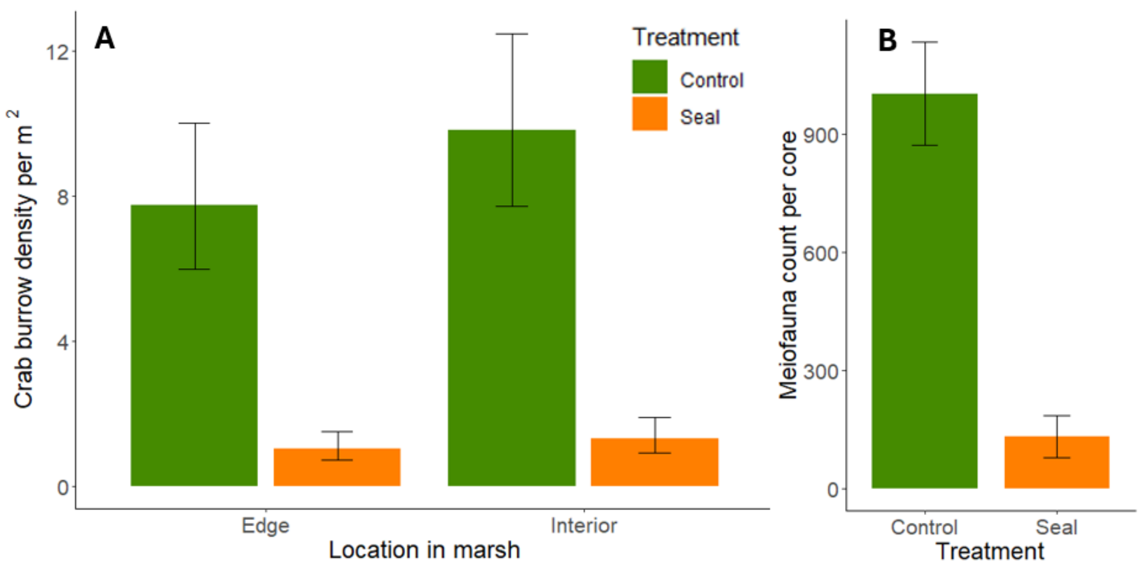

Figure 11: Animal communities in harbor seal haul out regions versus control sites. A) Crab burrow density (per m2) and B) meiofauna count (per soil plug). Crab burrow density (A) is provided at the marsh edge and interior, whereas meiofauna count (B) is provided only at marsh edges. Data are mean ± standard error.

Table 7: The counts of meiofauna by type and treatment. Meiofauna cores were only taken in the edge transects.

Treatment	Site	Total	Nematodes	Foraminifers	Turbellarians	Mite	Copepods	Polychaetes	Ostracods
Seal	2S	58	18	34	6	0	0	0	0
Seal	3S	340	110	201	26	0	2	0	1
Seal	4S	71	32	21	18	0	0	0	0
Seal	5S	128	0	127	1	0	0	0	0
Seal	6S	64	48	7	9	0	0	0	0
Control	1C	947	898	16	12	17	4	0	0
Control	2C	825	563	111	38	4	25	84	0
Control	3C	1519	1293	161	63	0	2	0	0
Control	5C	873	772	52	25	1	6	17	0
Control	6C	845	435	354	23	7	22	4	0

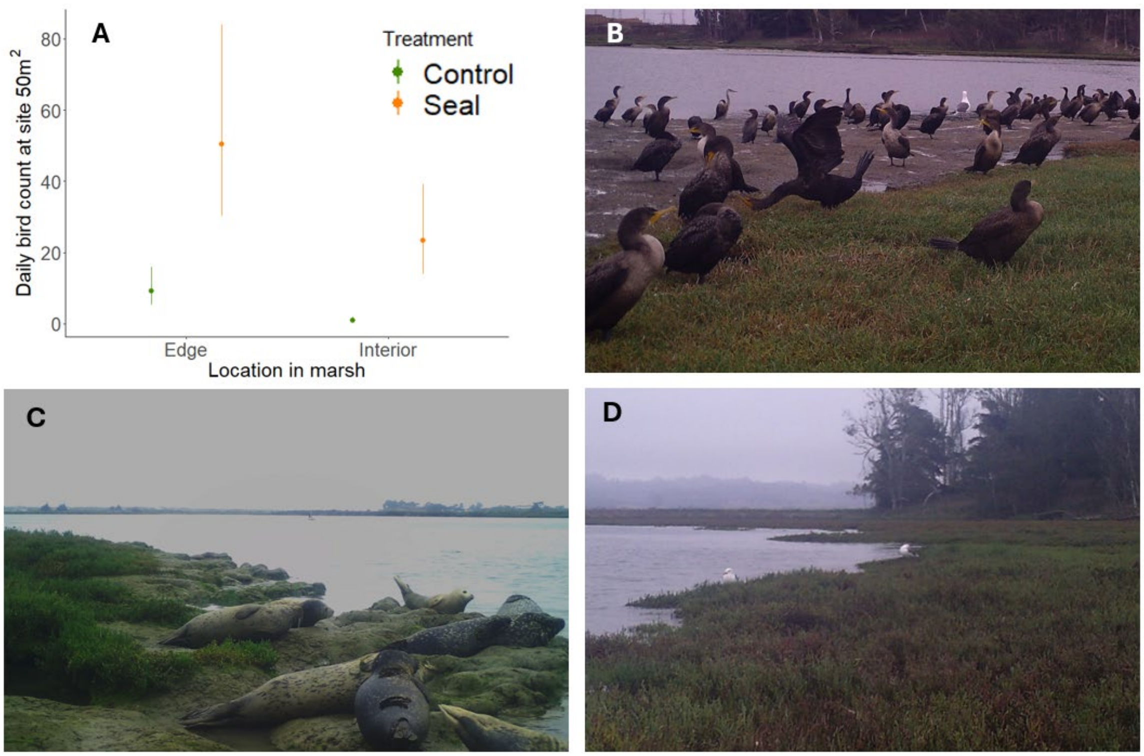

Figure 12: A) The model predicted density of birds per day at a single 50 m2 site. The means and standard error were transformed from the original log model scale, and the bars show one standard error. B and D) Visual depictions of the difference between the abundances of birds at seal haul out sites (C) and control sites (D), along with what seals look like hauled out onto these regions (A). Though the types of bird species are similar, the magnitudes differ significantly at the edge and interior of sites.

3.5 Discussion

By providing correlational evidence that pinnipeds can be ecosystem engineers in salt marshes, this study challenges and expands our understanding of what types of megafauna can act as engineers in intertidal systems. Our replicated comparative surveys indicate that harbor seals may reshape salt marsh edges by repeatedly hauling out of the water into the edge of marshes. Haul out of seals likely creates a very large disturbance both because of their concentrated numbers and because each harbor seal weighs an average of 81.3 kg in Elkhorn Slough (Eguchi 1998). In comparison to control sites, edge areas with seal haul outs display large differences in both plant and animal communities, as well as geomorphology. Seal sites were characterized by hard compacted marsh soil, largely devoid of marsh plants and burrowing crabs but served as hot spots for bird diversity. Seal sites also had higher bulk density, but the same root biomass, two effects that likely explain the observation that marsh edge erosion was not higher in their presence. These results contribute to a growing body of evidence that salt marshes are critical habitats for megafauna (Gaskins et al. 2020) and that these megafauna can have strong impacts on salt marshes, both positive and negative. To provide definitive assessment of whether seals create and/or maintain bare areas at the edge, future studies of harbor seals in marshes should attempt to exclude them from the marsh banks and assess their effects with before and after studies – two approaches that would complement the control impact study conducted here and definitively test causation.

A major difference between seal haul out regions and control regions was the extensive denuding at the edge, with 69% lower plant cover at the edge, and 22% lower plant cover at the interior of the marsh. These differences are significant and likely resulted from the repeated disturbance that seal haul outs cause. Because the dominant foundational marsh plant, *S. pacifica*, is a succulent plant with fleshy, delicate tissue, it could be particularly susceptible to damage and destruction from large animals hauling out, rolling, and smashing the plant tissue over time. Also, likely due to the disturbance created by haul outs, sites with harbor seal haul outs were characterized by highly compressed marsh sediment. Soil penetration resistance is significantly higher in seal sites, likely due to the repeated, downward pressure and disturbance from the weight and rolling movement of seals in the seal haul out areas over time. The denuding likely explains the pattern we see within the soil penetration resistance data in the seal interior. At the edge of seal haul out sites, the penetration resistance is consistently higher than the other predicted values, and both the control edge and interior are highly similar and consistently lower resistance, but the seal haul out interior initially is similar to the controls, and upticks at the 15cm reading. This corresponds to the approximate 10 cm depth of *S. pacifica* roots and crab burrows in Elkhorn Slough (Moffett et al. 2012, Hughes et al. 2024) and suggests that when the living plants and crab burrows are no longer present like in the seal edge, that they no longer help loosen the top of the soil. Bulk density is also higher than controls in both edge and interior regions, reaching 0.7 g/cm^3 at the edge. Due to these high levels of sediment compression, it is possible for animals (and field researchers) to traverse these haul out regions without sinking into the mud.

Marsh invertebrate communities may be responding to lower plant cover and highly compressed sediment conditions at seal haul out sites, as we found significantly lower densities of burrowing crabs and meiofauna within haul out sites. Burrowing crab densities were 87% lower. This lower density is likely in response to multiple changes induced by seal presence: 1) dense soil conditions that make it challenging to create and maintain burrows, 2) lack of plant cover that lowers protection from avian predators and desiccation stress, 3) higher numbers of bird predators in the areas, and 4) physical threat of being crushed by seals. Burrowing crabs are a marsh ecosystem engineer and influential bioturbator (Moore 2019, Beheshti et al. 2021), and the removal of a key marsh engineer in seal sites alone is likely to have a myriad of downstream impacts. Other studies have also noted that burrowing crabs significantly lower bulk density and belowground biomass, alter erosion rates, increase CO_2 and CH_4 efflux, oxygenate marsh plant roots, and create niches for other animals (Beheshti et al. 2021, Agusto et al. 2022, Grande et al. 2022), which then would become cascading indirect impacts of harbor seal haul outs. The lack of crab burrows also may drive the significant drop in meiofauna density at the edge. With compressed sediment, lack of crab burrows, and no plant cover, these soils are very likely harder to move through for meiofauna and therefore less hospitable (Bell et al. 1978, Bell 1979, DePatra and Levin 1989, Rutledge and Fleeger 1993).

This negative correlational pattern of seal haul outs and biodiversity, however, is reversed with avifauna. We observed significantly higher bird abundance in both the edge and interior of the marsh where seals were hauling out. Birds may use haul out regions at higher rates because of the combination of denuded and compressed sediment that creates an ideal platform for marsh birds to land, rest, forage, and congregate in great number. The two birds recorded in highest number, brown pelicans and cormorants, are piscivorous, and thus likely using the marsh platform to rest. However, marbled godwits, plovers, sandpipers, seagulls, and long-billed curlews were all noted foraging within photos at seal sites, along with standing, so these platforms could serve a dual purpose for them to obtain food and also rest and congregate. This is consistent with marsh literature, showing that birds often forage in non-vegetated areas and cue in on mudflats (Burger et al. 1997, Maccarone and Brzorad 2005, Rush et al. 2009). Additionally, the tangled canopy structure of pickleweed marsh likely impedes wading bird mobility. We note that these denuded platforms at seal haul out regions are not likely to bring more birds into Elkhorn Slough, but rather, create an ideal spot for birds to concentrate/aggregate, an important function none the less. Specifically, haul out sites may function like a high elevation mudflat, which is possible for birds to access during a larger percentage of the tidal cycle than other lower elevation mudflats. Additionally, these haul out sites are a region within Monterey Bay where wetland birds can rest and where it is unlikely that they will be harassed by people or dogs, unlike many of the surrounding beaches, marinas, and towns. Elkhorn Slough is widely regarded as a bird diversity hotspot, with hundreds of species a year, and having places for birds to aggregate may facilitate and help maintain their populations. Ecosystem engineers can facilitate diversity by creating new niches for a larger diversity of species (Wright et al. 2002, Ripple and Beschta 2012), and our work suggests a similar pattern between seals and birds.

Given the vastly higher numbers of birds at seal haul out sites, it is possible that the combination of bird and seal feces would enrich the soil, but we found no evidence to support this. Previous research has showed that seabirds and pinnipeds can alter the soil chemistry (Ma et al. 2013, Lavery et al. 2014, Ramírez-Fernández et al. 2019), and especially within ornithogenic soils in Antarctica in penguin colonies, they are especially rich in carbon, nitrogen, and phosphorus (Beyer et al. 1997, Tatur and Myrcha 2002, Zhu et al. 2011, Guo et al. 2018). In this study, we took soil samples at the edge transects. Very few of the soil measurements were significantly different than controls, and the few that were significant were all higher at control sites than seal sites. Therefore, we have no evidence of a nutrient enrichment signal within the soil at seal sites, in contrast with studies on seal and bird colonies in other regions of the world. The hypothesized mechanism for how this could have occurred despite the immense animal activity is that seal haul out regions act as a highly efficient fecal slide. With almost no plants or crab burrows to snag fecal matter, and flattened and compressed soil, along with an incredibly strong set of tides that washes over the marsh twice a day (Broenkow and Breaker 2005), seal haul out sites may have the perfect set of conditions to efficiently clear feces before they are absorbed and enrich the soil. Alternatively, because Elkhorn Slough is highly polluted with fertilizer runoff (Hughes et al. 2011, Wasson et al. 2017), it is also possible that the soil is already saturated with nutrients, and animal feces do not create a detectable differences in soil chemistry. To test the fecal slide hypothesis experimentally, one could create a bird poop mimic with a distinctive chemical signature, distribute it in seal and control sites at regular intervals, and test whether the chemical signature is later detectable in soil samples.

The combination of differences we observed at seal haul out sites could also have a significant effect on erosion rates. Generally, denuded marshes erode more quickly than less denuded marshes (Silliman et al. 2019), but again, haul out sites defy this expectation, and erosion rate was not significantly higher. Coastal erosion is a serious concern within Elkhorn Slough, where erosion rates are 0.5 meters a year (Van Dyke and Wasson 2005), so this finding is especially important. Given the magnitude of the differences in geomorphology and plant and animal communities that we observed between seal and control sites, the nearly identical erosion rates suggests that there are likely a set of compensatory effects that keep the overall erosion rate similar. Despite having significantly lower plant cover, seal sites have an intact root structure and the same root density as control sites, which likely helps hold soil in place. Loss of root structure was the reason that plant denuding increased erosion in other studies (Silliman et al. 2019). In combination with higher soil compression and few crab burrows, these factors could compensate for the disturbance of the seals, and denuding. In addition, bulk density is known to be an important factor in soil erosion rate (Jepsen et al. 1997, Lick and McNeil 2001). On a high level, it is possible that the differences that we found between seal and control sites are the byproduct of switching the dominant marsh engineer from burrowing crabs to harbor seals, and that these changes balance out in terms of erosion rate. Burrowing crabs are an engineer that aerates soil, generates burrows which act as erosion vectors, lowers bulk density, and lowers amount of belowground root biomass (Bertness 1992, Escapa et al. 2007, Grande et al. 2022), all factors that could impact erosion. In contrast, our study suggests that harbor seals increase bulk density and soil compression, drastically lower crab burrow density, and do not lower root biomass, all factors that could potentially impact erosion.

We also addressed an alternative/interactive hypothesis that could explain denuded marsh edges in Elkhorn Slough: i.e., that *Ulva* algal mats rather than harbor seal haul outs may generate the observed changes of denuding on marsh edges. We tested this alternative hypothesis because previous research showed that these *Ulva* mats can denude the edges of salt marshes in the main channel at Elkhorn Slough through shading (Wasson et al. 2017). Algal mats appear in predictable locations due to wind, and hydrodynamics within estuaries (Van Hulzen et al. 2006, Wasson et al. 2017), and in Elkhorn Slough, algal mats accumulate predominately in south and west facing marshes (Wasson et al. 2017). Every site we selected for our study faced north and east, and at both control and seal sites, all regions had an average *Ulva* percent of less than 5% throughout our study period, so we find it unlikely that it was a significant driver in shaping these marshes across both seal and control sites. However, we cannot rule out that *Ulva* cleared sites before seals arrived, and that would require further study and temporal comparisons of aerial imagery. But in the site selection process for this study, areas clear of algal mat accumulation was a key criterion, and we conducted this study in summer months when *Ulva* are most prevalent within Elkhorn Slough (Wasson et al. 2017), so if *Ulva* was impacting the sites, we would have observed this during the study. At most, our findings suggest that *Ulva* was a low-level stressor that was consistent across seal and control sites.

This study demonstrates marked differences in foundational plants, animal communities, and sediment geomorphology between seal haul out sites and control sites, which suggests that harbor seals act as ecosystem engineers in salt marshes. To fully test seal impacts and rule out other causes, future studies should exclude seals from these areas and conduct before after studies. Although we do not have these data, we do have gradient data that provides further inference that seals indeed are a major driver of these patterns. Specifically, harbor seals are associated with the biggest differences in marsh structure where their densities are highest at the marsh edge and are associated with smaller differences moving into the marsh interior as their densities get lower (Fig 8). Even though the edge of the marsh is not a huge portion of marshes, ecologically, the edge of the marsh is incredibly important for its functioning. The edge has the highest amount of nutrient transformation and energy transfer to the open water estuary and is one of two locations (the other at the land-marsh interface) where the ecosystem either grows or recedes. By engineering this location, seals could create a disproportionate impact on the ecosystem (Minello et al. 1994, Peterson and Turner 1994, Cicchetti and Diaz 2000).

Megafauna re-entry into ecosystems, and the subsequent impact on food webs and ecosystems is a key question for ecology in the coming decades. This study contributes to recent work in marshes showing that these ecosystems are likely hotspots for megafauna and their impacts (Gaskins et al. 2020). For instance, recent work demonstrates that sea otters facilitate marshes and geology through a trophic cascade, and hogs have also been shown to do this (Hensel et al. 2021, Hughes et al. 2024). This study contributes to this growing body of evidence and shows that megafauna can also have primarily engineering effects and those effects can be large and vary between species of megafauna. As long-term conservation efforts continue to succeed, megafauna expansions will likely continue and megafauna need to be factored into future conservation and restoration plans (Silliman et al. 2018, Gaskins et al. 2020).

4. Highly variable and elevated erosion rates likely obscure detection of nutrient enrichment and predators on erosion of salt marsh edges

4.1 Abstract

Past studies have individually revealed that trophic cascades and nutrient enrichment can lead to increased erosion on the edge of salt marshes, but no studies have tested their relative importance. In Elkhorn Slough, the second largest estuary in California, erosion of marsh edges is a pressing issue, with average horizontal loss of marshes at ~ 0.5 m/yr. Recent work has shown that recolonization of sea otters (*Enhydra lutris*) slows the erosion of marsh edges by suppressing densities of root-eating marsh crabs. In contrast, elevated nutrient levels from vast fertilizer runoff into Elkhorn Slough waters is thought to be having the opposite effect on marsh edge erosion. To test the relative effects of this trophic cascade and nutrient enrichment on marsh edge erosion, we conducted a two-year, fully-factorial experiment (sea otter presence x nutrient addition) and examined the effects on marsh edge erosion rates. We found main effects of both factors on foundational plants, but not on erosion rates. Specifically, we found sea otter exclusion affected aboveground biomass, and nutrient addition affected root biomass. We did not, however, find that these effects cascaded to affect shoreline erosion rates. We attribute the incongruent finding of our study with past studies showing strong effects of nutrients and predators on marsh edge erosion rates to an interaction between the differential scales of the studies and highly variable erosion rates along creek banks. Our study occurred on $1m^2$ areas, while past studies looked at erosion rates averaged over entire creeks. Because erosion rates are highly variable from meter to meter, but more consistent when compared creek to creek, there is a potential to not detect top down and bottom up effects on marsh edge erosion at the small scale.

4.2 Introduction

The decline of top predators is a major concern in ecology and conservation. Resulting long-term efforts to protect and restore predators have led to local recovery of predator populations, and the expansion of their ranges into habitats previously thought to be beyond their niche breadth (Silliman et al. 2018). Observational data suggest top predator recovery can dramatically alter ecosystem structure, function, and stability (Estes and Palmisano 1974, Mittelbach et al. 1995, Ripple and Beschta 2012). However, current understanding of the ecological impacts of top predator recovery remain limited, and more experimental studies are necessary to demonstrate when and where top predator recovery and range expansion may affect ecosystems. One system where understanding the ecological impacts of top predators is critical are salt marshes, which are high productive habitats that provide critical ecosystem services but are being lost globally at alarming rates (Silliman et al. 2009).

Coastal erosion is a pressing threat within salt marshes. Salt marsh erosion has accelerated worldwide due to human-driven environmental change, impacting the ability of these systems to provide important functions and services (Deegan et al. 2012). For instance, experimental studies in U.S. east coast marshes have demonstrated that anthropogenic nutrient loading accelerates marsh erosion (Deegan et al. 2012). The hypothesized mechanism is that when nutrients are no longer limiting, marsh plants shift tissue allocation from roots that both acquire nitrogen and stabilize the marsh soils to aboveground structures that gather more light. Grazer-driven marsh vegetation loss is another increasingly recognized cause of marsh erosion. Studies on multiple continents have shown that marsh grazers, including many burrowing crabs, can strongly suppress marsh vegetation and lead to wholesale vegetation loss when their abundance increases in the absence of predator control (Silliman and Bertness 2002, Holdredge et al. 2009, Beheshti et al. 2021). Marsh systems therefore represent an ideal system to study the relative impacts of top predators and nutrients on erosion rates.

Excitingly, recent work on the west coast of the U.S. has shown that top-down control of grazers due to the predator recovery can abate marsh erosion due to runaway grazer-driven vegetation losses (Hughes et al. 2024). Using temporal, spatial, and experimental data, Hughes et al 2024 demonstrated that the recent expansion and recolonization of sea otters (*Enhydra lutris*) generates a trophic cascade that slows creek bank erosion in Elkhorn Slough, California. Elkhorn Slough is a west coast estuary where marshes are experiencing high rates of loss due to intense edge erosion (0.5 m/yr) without regrowth (Van Dyke and Wasson 2005). Burrowing crabs (*Pachygrapsus crassipes*) are known to regulate marsh vegetation biomass and soil structure (Beheshti et al. 2021). Importantly, burrowing crabs make up 65% of the diet of sea otters within tidal creeks (Espinosa 2018). By consuming these vast amounts of crabs and signficantly lowering their densities, sea otters promote marsh vegetation through a trophic cascade (Hughes et al 2024). This is particularly important within Elkhorn Slough, which is intensely polluted by fertilizer runoff from surrounding agriculture, which likely accelerates rates of erosion (Hughes et al. 2011, Wasson et al. 2017). By consuming burrowing crabs, sea otters might mitigate the negative effects of eutrophication on erosion in marshes. In fact, there is a strong correlation over time between otter expansion into tidal creeks and lowered erosion rates (Hughes et al. 2024), although such a relationship has not been directly tested experimentally.

Here, we conducted an experimental field manipulation testing the hypothesis that top predator trophic control can mitigate nitrogen loading and lessen bank erosion rates. We also tested the hypothesis that the strength of top-down control and consequences for erosion depend on ambient nutrient concentrations. Consistent with these hypotheses and recent work (Beheshti et al. 2021, Hughes et al. 2024), we predict that top predator control of runaway grazers will release marsh plants from grazing pressure and allow plant growth, in turn slowing edge erosion despite heavy nitrogen loading. We predict that additional nutrient addition will shift tissue allocation to higher aboveground and lower belowground biomass, causing bank instability and increasing erosion rates (Deegan et al. 2012). We used a factorial experiment to examine the relative impacts of top predators and nutrient loading on erosion rates *in situ* over two years.

4.3 Methods

4.3.1 Experimental Setup

We examine the relative importance of nutrient loading and megafauna on marsh plant structure and edge erosion within Elkorn Slough. Elkhorn Slough is in the center of Monterey Bay, California, and is a 1200 ha estuary with vast salt marshes dominated by pickleweed (*Salicornia pacifica*) (Wasson et al. 2013). We employed a fully factorial experiment, manipulating nutrients and otter access to marsh edges in the field. Our experiment was conducted across three tidal creeks, which were selected to account for variation across the slough (Fig. 13). In each of the three creeks, 1 m^2 plots were established 15 cm from the marsh edge. Plots were assigned to the following 5 treatments (n = 9): control with otters excluded and no nutrients added, otters included with nutrients added, otters excluded with no nutrients added, otter exclusion with nutrient addition, and a two-sided partial cage control. We established 45 plots total, with 15 per creek. Within each creek, there were 3 blocks of 5 plots, one for each treatment. Treatments were blocked at each site to account for natural differences across each tidal creek.

Figure 13: Map showing the location of the three tidal creeks in Elkhorn Slough.

Otters were included or excluded via caging, and nutrients were held at ambient levels or increased via fertilizer additions of 30g per month during the summer growing season (Holdredge et al. 2010, Nelson and Zavaleta 2012). Fertilizer (Osmocote slow-release balls) was delivered into the sediment in nine 15-ml Falcon tubes with 16 holes drilled into them (1/16th of an inch) (Williams and Ruckelshaus 1993, Silliman and Zieman 2001), centered in the plot in a 0.5m^2 grid and secured with lawn staples. Regardless of treatment, all plots had these tubes placed within them to control for sediment disturbance, and the caps of the tubes were exposed so the tubes did not have to be pulled out of the ground for the monthly fertilizer addition. Caged plots to exclude otters were constructed out of hardware cloth (45 cm in height) that was attached to four wooden poles; cages were roofless. All caging was raised 10 cm from the marsh sediment to allow crabs to move freely into and out of caged plots. Open plots had one 92 cm wooden pole and three smaller 23 cm poles. Smaller poles were used in order to mark plot bounds while not deterring potential predator use, as little showed once they were secured into the mud. The plots were installed in July 2019, and slow release fertilizer was added once a month during the growing season of pickleweed (July and August 2019; May, June, and July 2020; June and July 2021).

4.3.2 Quantifying geomorphology

During the initial experimental setup in July 2019, we took measurements every 25 cm along the front edge of the cages (resulting in four measurements per plot); at each point we measured the distance from the front of the plot to the edge of the marsh platform. To calculate total horizontal erosion, we measured the same distance at the end of the study to calculate the change in erosion at the four points. We then calculated the difference in distance between the initial and final measurements, and averaged the four points to get the erosion rate by plot. Elkhorn Slough marshes are not prograding (C. Endris pers comm), but there were several instances where our end measurements indicated gain in bank. This could be due to measurement error – if the banks within our plots eroded and slumped over the course of the study, resulting in difference in angle could have made the distance measurements with a ruler slightly different, but we left this data as is for analysis. We calculated the bulk density of the soil in each plot at the end of the study by taking one core (22 cm long and 2.5 cm in diameter) per plot, then drying and weighing it.

4.3.3 Quantifying animal communities

At the beginning of the study, we counted the number of crab burrows in the center $0.5m^2$ of the plot, and at the end of the study, we counted all crab burrows in the remaining plot. We converted both numbers into densities to calculate change over the course of the study. We counted all burrows over 3 cm in diameter (Hughes et al. 2024), as these are most likely to be *P.*

crassipes burrows, the crabs that sea otters consume within tidal creeks (Espinosa 2018). To further characterize the animal communities in the plots, we used pitfall traps to collect crabs to measure their activity per plot. Pitfall traps were made of tennis ball cans with holes drilled in the bottom and buried in the ground (Beheshti et al. 2021, Hughes et al. 2024), then left out for 5 days in August 2021 at the close of the study. One pitfall trap had vegetation fall in it that was high enough for crabs to climb out and escape, and we removed this data point. We also did not install a trap in a plot that was entirely eroded by the end of the study. We did not count *Hemigrapsus oregonensis* crabs (n = 5) we caught because sea otters do not consume them (Espinosa 2018), and only counted the *P. crassipes* crabs (n = 191).

To confirm that the caging treatments were successful and to characterize the diversity of fauna that utilize the marsh and tidal creeks around these plots, we installed 9 trail cameras (Bushnell Trophy Camera E3 Essential) along the shoreline of the creeks, one per block. Cameras were programmed to take three photos when motion was sensed. The photos were first sorted to remove blank photos where a non-animal triggered the sensor (e.g. waves, wind). The animals were identified to the lowest taxonomic level possible; in some cases, birds with similar characteristics were identified to the broader groups (Table 8). For example, three species of white egrets were classified in one group, and all cormorant species were another group. We also recorded date, time, temperature, whether the marsh was flooded, and if it was day or night.

Table 8: List of all animals and total number counted across trail cameras from June 13 to August 3, 2021.

Common name	**Scientific name**	**Total counted**
Swallow	Family Hirundinidae	81
Brown pelican	*Pelecanus occidentalis*	270
Cormorant	*Phalacrocorax spp.*	141
Great blue heron	*Ardea herodias*	68
Cattle, great, and snowy egrets	*Bubulcus ibis*, *Casmerodius albus*, *Egretta thula*	250

Human	*Homo sapiens*	102
Sea otter	*Enhydra lutris*	54
Gull	*Larus spp.*	35
Whimbrel	*Numenius phaeopus*	26
American white pelican	*Pelecanus erythrorhynchos*	210

4.3.4 Quantifying plant communities

At the beginning and the end of the study, we recorded the overall percent plant cover of each plot. At the end of the study, we also measured canopy height, collected belowground root biomass cores and aboveground plant biomass, and analyzed the roots for percent nitrogen. The belowground root biomass core was 8 cm in diameter and 23 cm deep. We washed off soil into a sieve and dried it in oven, then weighed the root mass. For aboveground plant biomass, we cut 15 by 15 cm areas of pickleweed plants at the soil line from the plot, then rinsed and dried it. We separated succulent and woody parts and processed them separately, then combined the masses for an overall total aboveground biomass. Canopy heights were measured at three points within each plot, measuring the tallest plant in the vicinity of the ruler as it stood naturally and noting the species. The values were averaged by plot before analysis. To obtain total plant biomass, we standardized aboveground and root biomass to the size of a 1 m^2 area and then summed them per plot. One plot was eroded almost entirely by the end of the study, and thus was not included in any plant community analyses.

4.3.5 Statistical Analysis

To evaluate the differences in horizontal erosion by treatment and block, we used R version 4.2.3 (Team 2023) to run linear models. To test for differences in the main factors, we removed the partial cage treatment, then used an interactive model with otters and fertilizer, along with creek and scaled distance from creek mouth for each plot to account for the blocked design. We also tested for caging effects by comparing the treatment with no fertilizer addition and no cage to the partial cage. All analyses were done with linear models (LM) and crab counts in pitfall traps were done with the Poisson family and a generalized linear model (GLM). Assumptions were tested visually with plots.

4.4 Results

We did not find differences in geomorphology between treatments. Across the duration of the experiment, erosion rate was not significantly different across treatments with otters ($p = 0.12$) and fertilizer ($p = 0.30$) but was significantly impacted by distance from creek mouth ($p = 0.02$) and creek ($p = 0.006$) (Fig 14, Table 9). Otters ($p = 0.94$) and fertilization ($p = 0.97$) did not significantly alter bulk density (Table 9).

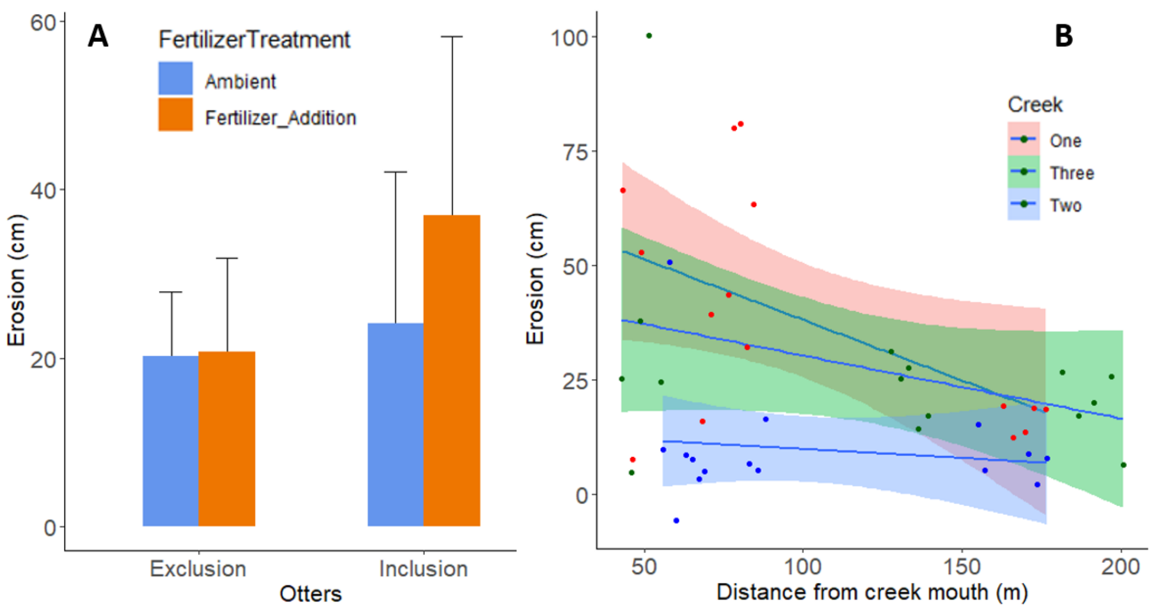

Figure 14: Overall horizontal erosion rate. A) From the beginning to end of the study by treatment. The error bars represent twice the standard error. B) Horizontal erosion by tidal creek (n=3) and distance from mouth.

Table 9: P-values associated with each model component. Green indicates p values < 0.05.

Measurement and units	Otters p-value	Fertilizer p-value	Interaction p-value	Distance from creek mouth p-value	Creek p-value
Erosion (cm)	0.12	0.30	0.34	0.02	0.006
Bulk density (g/cm^3)	0.94	0.97	0.98	0.87	0.35
Change in crab burrow density per m^2	0.16	0.86	0.13	0.06	0.04
Pitfall trapping crab count	0.58	0.78	0.29	0.54	0.11
Aboveground biomass (g)	0.004	0.16	0.08	0.81	0.91
Belowground root biomass (g)	0.68	0.004	0.27	0.006	0.44
Canopy Height (cm)	0.0002	0.06	0.65	0.91	0.88
Change in percent cover (%)	0.78	0.59	0.49	0.04	0.02
Total plant biomass	0.92	0.003	0.20	0.005	0.43

We also did not find differences in the animal community from otter inclusion/exclusion, or fertilizer addition. Neither otters ($p = 0.16$) nor fertilization ($p = 0.86$) significantly impacted crab burrow density (Fig. 15, Table 9). Crab activity measured as crabs caught in pitfall traps was not different based on otter ($p = 0.58$) or fertilizer treatment ($p = 0.78$) either (Table 9).

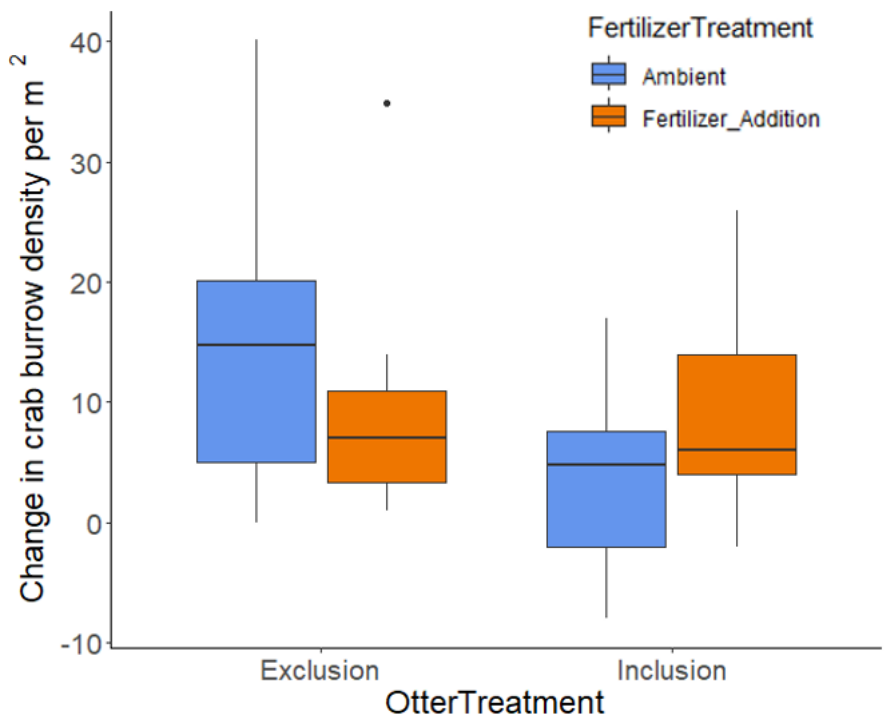

Figure 15: Change in crab burrow density from beginning to end of the study.

Across plant community metrics, otter exclusion increased canopy height and aboveground biomass of plants, and fertilizer additions increased root biomass. Otter exclusion significantly increased canopy height ($p = 0.0002$) and aboveground biomass ($p = 0.004$) but did not have a significant impact on belowground biomass ($p = 0.68$) (Fig. 16) or change in percent plant cover ($p = 0.78$) (Table 9). Canopy height increased from an average of 22.6 ± 1.4 cm in otter inclusion plots to 29.7 ± 0.9 cm in exclusions. Aboveground biomass increased from 12.6 ± 0.8 grams in otter inclusion plots to 16.7 ± 1.0 grams in otter exclusions. Fertilization significantly increased belowground biomass ($p = 0.004$) but did not have a significant effect on canopy height ($p = 0.06$), aboveground biomass ($p = 0.16$), or change in percent plant cover ($p = 0.59$) (Fig 16, Table 9). Belowground biomass increased from 22.6 ± 1.8 grams in controls to 31.7 ± 2.7 grams in fertilizer addition plots. Fertilization also significantly increased total plant biomass (p = 0.003), but otters do not have a significant effect (p = 0.92) (Fig 16, Table 9).

Across all metrics, we detected no significant caging effects.

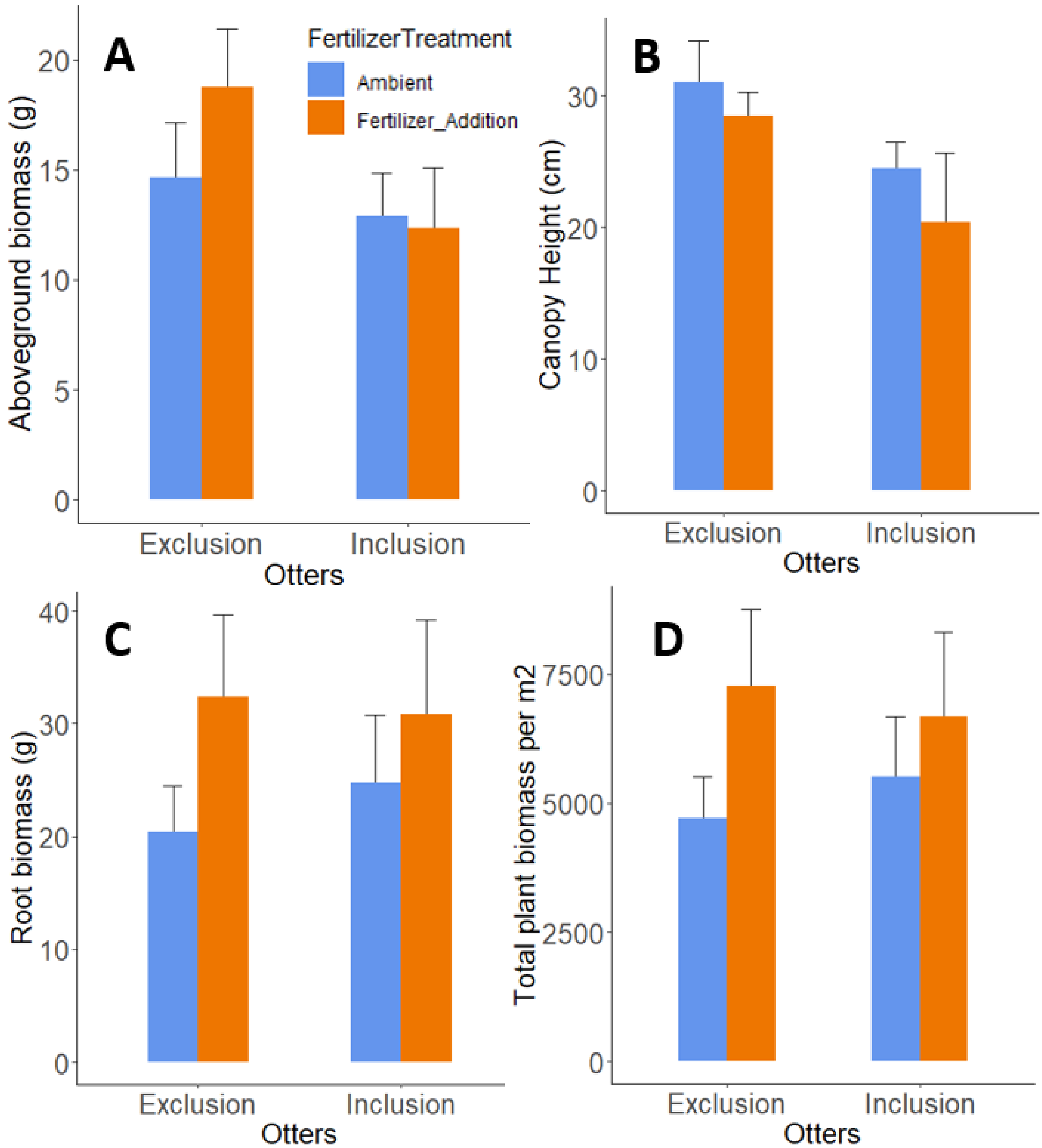

Figure 16: Impact of otters and fertilization level on plant communities at the end of the study. The error bars represent twice the standard error, which represents a 95% confidence interval. A) Aboveground biomass. B) Canopy height. C) Root biomass. D) Total plant biomass per m2.

4.5 Discussion

Over the two-year time scale of our experiment, we did not detect a significant impact of sea otters and nutrient loading on erosion rates. Though this stands in contrast with the findings of previous studies (Deegan et al. 2012, Nelson and Zavaleta 2012, Hughes et al. 2024), erosion within Elkhorn Slough is highly variable and very high across each meter of the creek bank. As a result, even variables that are known to strongly affect erosion like top predators and eutrophication were likely dwarfed and difficult to detect at the scale and duration we chose (Van Dyke and Wasson 2005, Deegan et al. 2012, Hughes et al. 2024). Previous studies showing that eutrophication and sea otters can drive erosion rates measured the effect across entire tidal creeks instead of 1 m^2 plots (Deegan et al. 2012, Hughes et al. 2024). We found few significant results of sea otters and nutrient loading across metrics including burrowing crab density and activity, bulk density, and plant communities. Overall, our findings suggest that longer term, larger scale experimental studies are needed to detect effects of otters and fertilizer on edge erosion.

In contrast to recent studies in Elkhorn Slough showing sea otters generate a trophic cascade through crab consumption, we did not detect any effect of otters or fertilizer on burrowing crab density or activity through pitfall traps (Hughes et al. 2024). Previous work found significant increases in burrow counts within otter exclusion plots, and higher densities of crabs within pitfall traps (Hughes et al. 2024). Likely because we did not detect significant differences in crab activity or density, we also did not find differences in bulk density, which burrowing crabs are known to regulate (Beheshti et al. 2021). An important factor that may have influenced this lack of effect is the time that it takes for crab burrows to close after their inhabitants have left, because crab burrows take longer than 2 years to fill in; for example, burrows in one study did not fill in during the five year duration of the study (Beheshti et al. 2021). Notably, we do not believe that this lack of effect is due to sea otters and other predators not using these tidal creeks during the study. We observed a range of avian predators and otter activity across the three tidal creeks (Table 8), and the cameras also demonstrated that the caging was highly effective, with no animals going inside the exclusion plots. Though the exclusion cages were effective, our plots were half the size of other studies that examined the effects of sea otters and burrowing crabs; our study also took place over two years, while others ran for longer, at three years (Hughes et al. 2024), and five years (Beheshti et al. 2021). It is also possible that the timing of the study impacted our ability to detect changes in crab communities: otters were undergoing a major expansion into tidal creeks during the course of the Hughes et al. (2024) study from 2013 to 2016, and likely had the largest impact on crab density during this expansion. Otters were well established in the tidal creeks by the time our study was conducted in 2019 –2021. If the populations of burrowing crabs had already been greatly reduced by this time, then an overall effect may have been much more difficult to detect. Also, this experiment unintentionally was running throughout the height of Covid-19, and the behavior of sea otters in tidal creeks or their use of different regions of the slough could have changed in unique ways based on human use during that time. This could have impacted the outcome of the experiment in ways that we cannot account for.

The only significant differences we observed as a result of otter treatments were significant increases in aboveground biomass and canopy height in otter exclusion plots. This could be due to the caging protecting the plants from trampling by otters, preserving the tissues and increasing canopy height and aboveground biomass. Our study was more likely to detect a trampling effect, because of the placement of plots relative to the edge – our plots started at only 15 cm from the edge, but Hughes et al. placed their plots starting between 50-150 cm from the edge of the bank. Therefore, our plots being close to the edge meant the otter inclusion plots were more likely to experience trampling when otters hauled out of the water than plots further into the marsh. Also, differences in cage size and height may have impacted plants and caused differences in our findings, as our plots were 1 m^2 with caging up to 55 cm, and Hughes et al 2024 used 2 m x 1 m plots, with 35 cm tall caging. Though we did not statistically detect a caging effect, plants may have benefited from the structure, since pickleweed is a floppy succulent that often falls over, and a four-sided cage may have helped prop the plants up. Consistent with this, we observed pickleweed weaving up through the cages throughout the study. Partial caging may show more variability in this metric because measurements taken near the two sides with caging were higher and away from the sides with caging were lower. Additionally, if canopy height was higher due to this structural benefit, this may have also impacted aboveground biomass measurements because of our methodology. We collected aboveground by measuring a 15 cm by 15cm area and cutting at the root, so the more upright the plants were, the more biomass we were likely to collect. This may have contributed to higher aboveground biomass in exclusion plots, since pickleweed is not a naturally rigid foundational marsh plant like *S. alterniflora* or *Juncus roemerianus*. Despite otters' effect on aboveground biomass and canopy height, otters did not have a significant impact on total biomass (combined above and belowground). Consequently, otters could have shifted above/belowground biomass allocation, which may have occurred not through changing crab numbers but because they are no longer trampling the pickleweed in the exclusion plots. Taken together, our findings and previous studies indicate that otters have a mixture of positive and negative effects on marshes, positively impacting the marsh through a trophic cascade that lowers the crab burrow density and erosion rates (Hughes et al. 2024), but negatively impacting the aboveground plant biomass through trampling.

Though otters did not impact belowground biomass, we found that fertilizer significantly increased root biomass, but not aboveground biomass or canopy height, results that are opposed to Deegan et al. 2012. However, the Deegan et al. 2012 study was conducted on *Spartina* *alterniflora*, whereas our study examined pickleweed, a succulent plant. But even fertilization studies done on pickleweed within Elkhorn Slough do not match our findings, with previous work finding significant increases in aboveground biomass and modest but not significant increases in belowground biomass (Nelson and Zavaleta 2012). Our results could be due to differences in fertilizer delivery methods. Deegan et al. 2012 enriched entire tidal creeks by adding nitrate to the water directly at 15x the natural level, but because we had to target individual plots and could not fertilize a whole creek, we chose to do a belowground addition of fertilizer in tubes with holes in them (Williams and Ruckelshaus 1993, Silliman and Zieman 2001). We used the same amount of fertilizer as Nelson and Zavaleta 2012, but they delivered it by combining fertilizer with water and pouring it over the plots bi-weekly, and we added slow-release fertilizer monthly in belowground tubes (as that was the only practical way to do this logistically, and we wanted to limit potential disturbances in an erosion study). Outside of methodology, a potential issue is simply that Elkhorn Slough is so highly polluted by fertilizer runoff that we did not add enough fertilizer to see a measurable effect on erosion given how high the ambient nutrient levels are (Hughes et al. 2011, Wasson et al. 2017).

Though our study did not detect differences in erosion from fertilizer additions or otters, our results highlight that studies conducted at different scales and durations can produce incongruent results. The difference between an experiment at the scale of a 1 m^2 plot and erosion rates across entire creeks mattered greatly (Deegan et al. 2012, Hughes et al. 2024). Future work could build upon these findings, and those of Deegan et al. and Hughes et al. To improve the ability to detect the relative effects of fertilizer and otter access on bank erosion, researchers should conduct a study at least five years in length, use larger cages than we did, and modify the cage design to exclude predators from the bank underneath the plots as well to prevent otters from scratching the banks to forage for crabs. We hope future studies will disentangle the effects of eutrophication and sea otters on marsh edge erosion and take lessons from our work.

5. Conclusion

Megafauna can serve a variety of roles within ecosystems and generate cascading effects through consumption or engineering that reshape systems, including salt marshes. This work suggests that harbor seals are ecosystem engineers, and by hauling themselves out of the water to rest, thermoregulate, molt, and socialize, they may have impacts that reshape the entire edge of the marsh. This is an interaction that had not been previously studied and calls for experimental studies to follow up and confirm these impacts on the marsh. Though the experiment on sea otters and fertilization did not yield significant results on erosion as predicted by previous work (Hughes et al. 2024), it reminds us how study duration, and scale can alter the ability to detect effects.

Despite how charismatic and widely known that megafauna are within scientific circles and by the public, and how much time, effort, and money are spent on conserving them, we still do not know much about the effects of megafauna within salt marshes. The contribution of this dissertation research is important, but there is still much more to be done in terms of understanding the impacts of megafauna on salt marshes. In the future, we also need to develop methods to integrate the impacts of megafauna into conservation and restoration work and harness any potential positive species interactions, which we know make systems more resilient and most important under stress (Bertness and Callaway 1994).

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