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Madeleine S. Gillis
Coastal Carolina University

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SHELL REPAIR IN *GEUKENSIA DEMISSA* AND PREDATION PREFERENCES OF *CALLINECTES SAPIDUS*: DO CRABS TARGET MUSSELS WITH WEAKENED SHELLS?

Madeleine S. Gillis

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Dr. Keith Walters Advisor	Dr. Charles Martin Committee Member
Dr. Blaine Griffen Committee Member	Dr. John Hutchens Committee Member
Dr. Richard Viso Graduate Studies Coordinator	Dr. Michael Roberts Dean of Science

Dedication:

This thesis is dedicated to Sammy Gillis (1999 – 2016).

I will forever be grateful for the love you brought into my life.

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I would first like to thank my major advisor, Dr. Walters, for providing me with advice and support throughout the thesis process. His dedication to precision may have prolonged my graduate tenure, but his sense of humor made my time at CCU enjoyable and (hopefully!) the resulting contribution to science made the time spent worthwhile. I would also like to thank my committee members, Dr. Blaine Griffen, Dr. Charles Martin, and Dr. John Hutchens, for their valuable insight and suggestions.

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Abstract:

Atlantic blue crabs, *Callinectes sapidus*, are voracious predators that often leave damage on the shells of unconsumed ribbed marsh mussels, *Geukensia demissa*. The extent of shell damage and size-dependent tradeoffs in marsh mussel growth and repair, as well as the effects of shell damage on crab predation preferences, were determined in this thesis.

A preliminary experiment investigated characteristics of damaged mussels in the field. Mussels (n = 30) were collected in the fall of 2011 within two ocean-dominated inlets along the South Carolina coast and were measured for size (length, width, height), area of damage, shell thickness, mass, and strength (crushing resistance). Shell damage was significantly different between inlets and shell repair was evident in damaged mussels.

During the summer of 2012 three sizes of field-collected mussels (small: 20-30 mm, medium: 50-60 mm, large: >60 mm) were damaged (undamaged 0%, moderate 33%, extensive 66% shell surface removed), caged in the mid-marsh, and sampled monthly. Changes in mussel characteristics (e.g., shell length, strength), were measured. In most cases, increased damage suppressed growth, however, only medium, moderately-damaged mussels repaired shells. Medium, moderately-damaged mussels also experienced a greater mortality rate, suggesting mussels enter a critical stage around 55 mm with increased energy demands for both growth and repair. Small mussels eschewed repair and focused entirely on growth, as larger sizes create a refuge from predation. Large mussels did not exhibit any signs of shell repair and had minimal growth, possibly instead prioritizing reproduction.

A series of wet lab mesocosm experiments and field trials were conducted to determine if blue crabs target damaged mussels. In the wet lab mesocosms, crabs showed a significant preference for damaged and first-touched mussels. Crab consumed damaged mussels in 68% of all successful predation attempts and mussels touched-first in 73% of successful predation attempts. Unsuccessful crabs targeted undamaged mussels first more frequently than successful crabs (55% vs 33%). However, a preference for damaged mussels was not observed consistently in the field and may have been masked by various mitigating factors. Undamaged mussels survived significantly longer than damaged mussels in the mid-marsh but were consumed at equal rates on mudflats, oyster reefs, and in the low-marsh. Mussel survival was greater overall in the mid-marsh with large mussels (> 60 mm) surviving significantly longer than medium (50-60 mm) and small (20-30 mm) mussels. Limited tidally-influenced inundation and densely distributed *Spartina alterniflora* stems likely increased survival by impeding access of large predators (e.g., blue crabs). The generally thicker shells of larger mussels also will increase predator time and effort required to breach shells successfully and should increase survival rates for large mussels.

Both mussels and crabs play a vital role in maintaining healthy salt marsh systems and reductions in either population have dramatic consequences. Salt marshes are structured in part by the top-down control of blue crabs and recent "die-offs" of *Spartina* is suspected to be caused by declining blue crab numbers while salt marsh loss due to sea level rise is suspected to be exacerbated by declining mussel numbers. Pollution, overfishing, habitat destruction, and the various effects of climate change (e.g., temperature rise, ocean acidification, sea level rise, etc.) threaten crab and mussel populations. Mussel response to shell damage and the ability of crabs to detect weakened mussels may be increasingly important as environmental conditions deteriorate.

Further research should investigate the effect of shell damage on mussel pumping and if changes in pumping influences crab predation. The latitudinal differences in crab and mussel growth and behavior should also be examined, as additional insight into mussel-crab dynamics would be useful for salt marsh conservation.

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Introduction:

Predators have dramatic impacts on community structure and ecosystem stability directly by reducing prey populations through consumption (consumptive effects) and indirectly by altering prey characteristics including morphology and behavior (non-consumptive effects) (Weissburg et al. 2014). Sometimes direct predation has indirect consequences leaving the prey item still alive but damaged. The damage, or sublethal predation, often results in the loss of varying amounts of prey tissue during unsuccessful attempts by predators that usually consume prey whole. Sublethal effects on prey are both direct, the loss of biomass, and indirect, the loss of function. Although not included in Menge and Sutherland's (1987) classic model for community structure, Harris (1989) proposed sublethal predation is an important factor regulating population size and consequently the structure and stability of communities and ecosystems.

Predator consumptive effects (CEs) also are known as density-mediated interactions (DMIs) because the primary effect is a reduction in prey density (Hairston et al. 1960, Oksanen et al. 1981, Abrams 1995). Consequences of DMIs extend across population (e.g., Connell 1970, Micheli 1997), community (e.g., Paine 1966, Kerbes et al. 1990, Hixon and Beets 1993) and ecosystem scales (e.g., Worm et al. 2006, Heithaus et al. 2008, Estes et al. 2011). DMI-induced top-down forcing and trophic cascades often have dramatic effects on abundance and species composition, and can even lead to alternate states of ecosystems (Terborgh 2010, Carpenter et al. 2011). The collapse of

North Pacific subtidal kelp systems is attributed to a top-down cascade in which increased killer whale predation on otters enabled urchin numbers to increase creating "urchin barrens" in place of kelp forests (Estes and Palmisano 1974, Estes and Duggins 1995, Estes et al. 1998, Williams et al. 2004). Urchins are also important in the Caribbean where grazing controls algal abundance; following the infamous mass mortality of 1983-84, where 95-99% of urchins in the Caribbean died, algal biomass increased by 20% and algal primary productivity dropped by 61% (Carpenter 1988). Freshwater lakes are structured by the cascading effect of predator control on plankton which changes along a nutrient and depth gradient (Jeppesen et al. 2003); when planktivorous fish were removed from eutrophic lakes, zooplankton populations increased while phytoplankton populations (and chlorophyll *a*) declined substantially (Jeppesen et al. 2000, Carpenter et al. 2001). Top-down control also has a major impact in terrestrial ecosystems: the reintroduction of grey wolves in Yellowstone National Park resulted in decreased elk populations but increased plant populations (Ripple and Beschta 2012), reduced cougar populations in Zion National Park led to higher mule deer densities, decreased riparian plant densities, increased bank erosion, and reductions in both terrestrial and aquatic species abundance (Ripple and Beschta 2006), and the introduction of arctic foxes to the Aleutian archipelago transformed grasslands to dwarf shrub/forb-dominated ecosystems by reducing seabird populations which reduced the nutrients transported from ocean to land (Croll et al. 2005). In Atlantic salt marsh systems crabs exert a strong top-down control on herbivores to the benefit of plants (Marczak et al. 2011). A suspected decline in blue crab and terrapin numbers, native predators on marsh periwinkles, likely led to an increase in snail abundance (Silliman and

Bertness 2002) that contributed to the seeming “die-off” in *Spartina* marshes (Silliman et al. 2005).

Non-consumptive effects (NCEs) include a number of possible indirect interactions documented to affect all ecological scales. A category of NCEs, trait-mediated interactions (TMIs) between predators and prey or predators and other predators are essential to the complete explanation of many classic predator-prey systems, especially in spatially-structured multispecies systems (Preisser et al. 2005, Peckarsky et al. 2008, Preisser and Bolnick 2008, Schmitz et al. 2008). Meta-analysis found effects of TMIs are equally as strong or stronger than the effects of direct consumption (Bolker et al. 2003, Werner and Peacor 2003, Preisser et al. 2005, Preisser et al. 2007), although in accordance to the "sensory stress model" (Smee et al. 2008) the strength of the TMI will vary depending on environmental conditions that modify sensory abilities of predators and prey (Weissburg et al. 2014). In TMIs prey enact strategically defensive behavioral or morphological changes in response to the presence of a predator. Consequently, these trait changes alter the population density or fitness of affected species (Werner and Peacor 2003). In general, more elusive prey have a greater chance of survival since prey only can be consumed by predators once discovered. Methods for reducing an organism’s visibility to predators are costly energetically and result in suppressed rates of growth and reproduction (Fraser and Gilliam 1992, Harvell 1992, Sheriff et al. 2009).

Many studies found significant TMIs in simple three trophic level systems where the presence of a predator suppressed the activity of the intermediary species to the benefit of the prey species. For example, the presence of spiders shifted grasshopper feeding time budget, caused the same level of grasshopper mortality as direct predation, and decreased grass biomass loss (Beckerman et al. 1997, Schmitz et al. 1997); in the presence of a top predator dragonflies consumed less than half of the damselflies consumed when foraging alone (Wissinger and McGrady 1993); and the presence of fish reduced the foraging activity of salamanders on isopods (Huang and Sih 1991). When exposed to predatory risk cues snails exhibited more refuge-seeking behavior, increased shell thickness, and consumed less than conspecifics feeding in the absence of risk cues (Appleton and Palmer 1988, Turner 1996, 1997, Trussell and Smith 2000, Trussell et al. 2003). Periphyton benefited from reduced snail grazing and had greater abundances in habitats with predator cues (Turner 1996, 1997).

Anti-predator behavior reduces the immediate risk of predation but often comes at the cost of lower energy intake (i.e., refuge-seeking reduces feeding), which reduces reproductive output or long-term survival. Mayflies are the classic example: decreased consumption in the presence of predators led to slower growth, smaller adults, and fewer eggs (Peckarsky et al. 1993, Scrimgeour and Culp 1994). Similar results have been found for dipterans (Ball and Baker 1996), odonates (Van Buskirk 2000), and squamates (Dial and Fitzpatrick 1981). Snails exposed to predator cues experienced decreased shell and tissue growth, which was attributed to the costs associated with decreased consumption and increased shell thickness (Turner 1996, 1997, Trussell et al. 2003). Whelks with tumid ridges (localized regions of increased shell thickness) experienced less severe shell damage in encounters with stone crabs and significantly higher overall survival rates than whelks without tumid ridges, but had much slower growth rates throughout ontogeny (Kosloski 2012).

TMIs also can have cascading effects on the structure of habitats and function of ecosystems (Ripple and Beschta 2012). In the aforementioned example of the reintroduction of grey wolves to Yellowstone, not only did wolves affect elk directly through predation (reduction in density), the threat of wolf predation altered elk behavior including habitat use, movement, group size, and vigilance, which had significant cascading affects throughout the entire ecosystem (Laundré et al. 2001, Fortin et al. 2005, Beyer et al. 2007, Halofsky and Ripple 2008). Elk avoided "high risk" areas such as valley bottoms and riparian areas, and as a result plant heights increased in those areas (Ripple and Beschta 2003). The resurgence of riparian willow increased the stability of formerly eroding stream banks (Beschta and Ripple 2006), allowed for greater songbird richness (Baril 2009), and nourished the population increase of beavers by providing food and dam-building materials (Smith and Tyers 2008, Smith and Tyers 2012). The increased beaver population may increase the waterfowl population, as streams in Wyoming with beaver ponds had 75 times more abundant waterfowl than streams without beaver ponds (McKinstry et al. 2001). A TMI between a carnivorous whelk and an intertidal barnacle had a dramatic effect on the structure of the mid-intertidal community in the northern Gulf of California (Raimondi et al. 2000). Whelks increased the space available for settlement and growth of mussels and algae by consuming adult barnacles and inducing a "bent morph" in juvenile barnacles (Raimondi et al. 2000).

Interactions within trophic levels (i.e., predator-predator or prey-prey) also affect the outcomes of TMIs across ecological scales (Sih et al. 1998). Increased densities of a single predator species can result in interference competition and decreased predation rates. The increase in agonistic encounters with conspecifics impedes both blue crab

(Clark et al. 1999b) and mud crab foraging (Grabowski and Powers 2004). Interspecific interactions among predators also have both negative and positive influences on predation rates. For example, toadfish positively influence bivalve survival by reducing mud crab foraging (Griffen et al. 2012) while stone crabs negatively influence oyster survival by facilitating drill predation on oysters previously damaged by failed crab predation attempts (Fodrie et al. 2008). Overall oyster mortality is increased even though crabs also consume drills and affect drill numbers (Fodrie et al. 2008). Similarly, the threat of intraguild predation (IGP) can reduce predation rates (Griffen and Byers 2006). IGP is when competing predators within the same guild (i.e., species that perform similar functions within a community) consume each other (Polis et al. 1989). In situations with only competition and without IGP, predation on amphipods was consistent with predictions from a risk model (Griffen and Byers 2006), but when IGP was present (e.g., when large Asian shore crabs capable of consuming small European green crabs were experimentally forced to forage together) amphipod survival increased (Griffen and Byers 2006). Sometimes behavioral changes by the prey to avoid predation by one type of predator unintentionally reduces vulnerability to another predator. Juvenile spot in the presence of two predators had a survival rate greater than expected based on adding separate predator effects (Crowder et al. 1997). Spot moved into shallow water to avoid southern flounder and aggregated to avoid birds, but the aggregating behavior also reduced mortality from flounder (Crowder et al. 1997). The nonlethal presence of an odonate changed the behavior of small green frog tadpoles which then became less vulnerable to a different odonate predator (Peacor and Werner 1997). The presence of a predator can also affect the competitive interaction between two prey species: green frogs reduced activity levels more than bullfrogs in the presence of odonate predators, and consequently mass gain was higher for bullfrogs than green frogs (Peacor and Werner 1997). When competing without predators, wood frogs grew faster than leopard frogs, but in the presence of caged predators the outcome of frog competition was reversed (Relyea 2000). The addition of alternate prey sources can weaken effects of existing TMIs: large predatory beetles positively affect fly egg survival by reducing foraging activity of small beetles but when aphids are also present large beetles opportunistically eat both aphids and fly eggs, increasing fly egg mortality (Prasad and Snyder 2006). Similarly, the addition of a second prey species in a rocky subtidal reef increased the predation rate on both species because the predators aggregated to the area with both prey species (Schmitt 1987). Alternatively, agonistic interactions between prey species can disproportionally increase predatory risk and subsequent mortality rates beyond those predicted by typical food web interactions. For example, blue crabs were displaced from seagrass refuge by mud crabs and remained active (i.e., did not attempt to hide) from toadfish predators while exposed in an unstructured sand habitat (Toscano et al. 2010). The effects species have within food webs are complicated and cannot be predicted by simply summing individual interactions.

Competition for enemy-free space is also an indirect effect of predation that sets limits to community structure. Enemy-free space is defined as ways of living that reduce or eliminate a species' vulnerability to enemies (Jeffries and Lawton 1984). When multiple prey species are attacked by one or more shared enemies competition between prey species for enemy-free space can arise, almost identical to more conventional forms of interspecific competition for limited resources (Holt and Lawton 1994). Many studies have documented the importance of enemy-free space in arthropods (Berdegue et al. 1996). The association of Lycaenid butterflies with ants was considered a refuge since the ants protected the larvae and pupae against potential predators and parasitoids (Atsatt 1981). The refuge from centrarchid predators in lakes is the space between the thermocline and the zone of anoxia; the seasonal community change within lakes was best predicted by loss of refuge size, as different daphnid species dominated when refuges were large or small (Tessier and Welser 1991). Invasive species that better compete for enemy-free space can trigger extirpations of natural-occurring fauna. For example, in the Mascarene Islands endemic night geckos suffered increased predation after being displaced from refuges by invasive house geckos (Cole et al. 2005). Similarly, in estuaries of the Gulf of Mexico endemic redspotted sunfish are threatened by invasive Nile tilapia (Martin et al. 2010). Laboratory experiments demonstrated that sunfish are displaced from structured habitats by the more agonistic tilapia and consequently suffer increased mortality by piscivorous predators (Martin et al. 2010). In the case of many bivalves, enemy-free space takes the form of size refuges, where an animal achieves a size at which it is safe from predation by a particular predator (Jeffries and Lawton 1984).

Sublethal predation is a CE that has both direct and indirect effects on a variety of taxa, from plankton (Allan and Spero 1981) to whales (Pitman et al. 2001). Although capable of influencing population and community dynamics (e.g., Lawrence and Vasquez 1996, Meyer and Byers 2005), consequences of sublethal predation at the ecosystem scale are likely substantial but have not yet been experimentally tested. On bryozoan colonies, sublethal predation is similar to herbivory with patterns of regeneration and tolerance to consumers paralleling terrestrial plants (Lidgard 2008). Sublethal predation slows growth, reduces reproduction, and increases the risk of subsequent predation or parasitism in species with relatively soft, unarmored bodies such as polychaetes (Zajac 1985, Lindsay and Woodin 1992, 1995, Hentschel and Harper 2006, Berke et al. 2009), echinoderms (Bowmer and Keegan 1983, Lawrence and Vasquez 1996), amphibians (Figiel Jr and Semlitsch 1991, McCollum and Leimberger 1997, Johnson et al. 2006, Bowerman et al. 2010), and squamates (Dial and Fitzpatrick 1981, Dial and Fitzpatrick 1984).

In bivalves, such as clams (e.g., Salas et al. 2001, Lomovasky et al. 2005, Meyer and Byers 2005, Cledón and Nuñez 2010), oysters (Loosanoff and Nomejko 1955), scallops (Schejter and Bremec 2007), and mussels (Alexander and Dietl 2001, Hillard and Walters 2009), sublethal predation is common and results in direct tissue loss or damaged shells. Both tissue loss and shell damage affects bivalves negatively by reducing growth rates and increasing mortality (Coen and Heck 1991, Kamermans and Huitema 1994, Irlandi and Mehlich 1996, Lomovasky et al. 2006, Hillard and Walters 2009). Sublethal predation can also facilitate lethal predation by altering the behavior of damaged bivalves (Kamermans and Huitema 1994, Meyer and Byers 2005) and may increase detection of bivalves by olfaction-guided predators if metabolites are able to leach through damaged shells (Vermeij 1983).

Siphon and foot nipping are primary means of direct tissue loss from sublethal predation and, along with the loss of tissue, often result in subsequent effects on the damaged bivalve. In clams, siphon nipping reduces growth and reproductive output (Peterson and Quammen 1982, Coen and Heck 1991, Kamermans and Huitema 1994, Irlandi and Mehlich 1996). Clams with nipped siphons are also forced to bury shallower in the sediment, facilitating discovery and consumption by predators (Meyer and Byers 2005, Cledón and Nuñez 2010). Siphon nipping is frequent and ranges between clam populations from 4-11% in Massachusetts to 15-20% and 15-25% in Alabama/Florida and New Jersey (Coen and Heck 1991). Individual clams lose an average of several siphon tips per day (De Vlas 1985) and a single juvenile stone flounder preys on approximately 370 clams in a season (Sasaki et al. 2002). Sublethal foot predation is also common; up to 48% of Donacidae clams suffer from nipped feet during peaks of predation (August - September) resulting in a >20% loss of biomass (Salas et al. 2001). Foot cropping occurs in 14-34% of New Zealand cockles with an ensuing 9-21% loss of foot area (Mouritsen and Poulin 2003). Foot regeneration in cropped cockles is required for burial and cockles are exposed to thermal and desiccation stress and a five-fold greater risk of predation during the up to eight weeks required for regeneration (Mouritsen and Poulin 2003, Mouritsen 2004). Sublethal predation via siphon and foot nipping is likely an important force in structuring benthic ecosystems.

Shell damage generated by failed predation attempts is prevalent within bivalve populations and often results in an increased susceptibility and vulnerability to future predation (Fodrie et al. 2008) along with requiring increased efforts to repair shells (Palmer 1992). Sublethal shell damage is identifiable by the breakage pattern (Cintra-Buenrostro 2007) and ranges from 58% in scallops (Schejter and Bremec 2007), to 73% in clams (Lomovasky et al. 2005), and up to 90% in mussels (Hillard and Walters 2009). Shell damage assessments are used by paleoecologists to infer the historical prevalence and types of biotic interactions between ancient predators and molluscan prey (Vermeij

1983, Bond and Saunders 1989, Kowalewski 2002, Baumiller 2013), and when compared with contemporary assemblages (e.g., Alexander and Dietl 2001) evolutionary responses to predation can be distinguished. Damage in some species of bivalves makes the shell easier to breach, increasing the probability of mortality (Covich et al. 1981, Geller 1990, Roy et al. 1994, Zuschin and Stanton 2001, Beadman et al. 2003a, Fodrie et al. 2008). For example, crayfish were only able to consume small (<6 mm) undamaged clams, but were able to consume larger (24-35 mm) clams if they were damaged (Covich et al. 1981), and drill predation on oysters was facilitated by shell damage inflicted by stone crabs (Fodrie et al. 2008). Clams reduce pumping (Smee and Weissburg 2006a) and barnacles withdraw cirrals (Palmer et al. 1982) in efforts to curtail metabolite release and remain hidden from predators; shell damage, however, may increase susceptibility to predators by enabling metabolite leaching into the surrounding environment even when valves are shut (Vermeij 1983). Even if shell damage doesn't increase the frequency or success of subsequent predator attacks, damaged shells require additional energy to repair (Geller 1990, Palmer 1992, Brown et al. 2004, Lomovasky et al. 2005). Energy required to repair shell damage also affects growth and, possibly, reproduction (Dietl 2003). Reproduction and somatic growth should decrease as a consequence of shell repair because of energy reallocation (Dietl 2003, Brown et al. 2004). However, documented responses to shell damage vary; mussels (Hillard and Walters 2009) and snails (Geller 1990) with damaged shells grew slower than undamaged conspecifics, but oysters grew faster with damaged than non-damaged shells, although returned to typical growth rates after repairing the damage (Loosanoff and Nomejko 1955). Shell damage that removes the protective organic periostracum layer also leaves the underlying crystalline structure vulnerable to erosion and microbial colonization, potentially culminating in shell dissolution and microboring (Glover and Kidwell 1993, Freiwald 1995). The prevalence and biological consequences of sublethal shell damage likely reaches beyond the organism level, affecting communities, populations, and even ecosystems.

In South Carolina populations of the ribbed marsh mussel (*Geukensia demissa*), an important resident in North American intertidal estuarine environments, over 90% of individuals and up to 60% of the total shell area are damaged (Hillard and Walters 2009). Even though such a large percentage of the population survives with damage scars, experimentally damaged mussels had significantly greater mortality than undamaged mussels and reduced tissue mass (Hillard and Walters 2009), indicating that shell damage, although prevalent, is detrimental to mussel survival. *Geukensia demissa* living in soft marsh sediments are unlikely to incur shell damage from burrowing (Checa 1993, Alexander and Dietl 2001, 2005, Lomovasky et al. 2005) or erosion (Day et al. 2000), and unless adjacent to commercially important species (e.g., oysters) should not be damaged by harvesting methods (Mensink et al. 2000, Schejter and Bremec 2007). A leading cause of shell damage in *G. demissa*, as with many other bivalves, is failed decapod predation. Blue crabs (*Callinectes sapidus*) are primary predators of *G. demissa* and can leave shells with extensive chips, nibbles, and scallops (Alexander and Dietl 2001, Cintra-Buenrostro 2007).

The interaction between tidal inundation duration and habitat structure controls predation success on intertidal denizens, such as *G. demissa*, in salt marsh systems. Typically, predation intensity declines inland (Kneib 1984, West and Williams 1986, Schindler et al. 1994), with the greatest frequency of lethal predation occurring in low marsh zones characterized by long inundation times and a lack of obstacles (e.g., vegetation) (Schindler et al. 1994, Silliman and Bertness 2002). Dense stands of *Spartina* act as a filter excluding large predators and reducing access of blue crabs to the marsh interior (Vince et al. 1976, Arnold and Kneib 1983, Minello and Zimmerman 1983, Lin 1989b, Lee and Kneib 1994, Tucker et al. 1995, Tucker et al. 1997). The mid-marsh, with intermediate vegetation densities allowing predator access for limited durations, is where sublethal predation is most ubiquitous and shell damage is most prevalent (Gregory and Richard 2009, Hillard and Walters 2009).

Mussels with shell damage may be at a greater risk of incurring subsequent successful predation attempts by blue crabs because damaged mussels may be easier to locate and easier to open than undamaged mussels. Blue crabs primarily are olfactory-driven predators and can detect homogenates prepared from tissues of bivalve prey at concentrations as low as 10^{-15} g/L (Pearson and Olla 1977, Weissburg and Zimmer-Faust 1993). Crabs actively migrate to maximize foraging efficiency (Griffen 2009) and are responsive to the overall quality of prey, altering prey patch use depending on the quality (e.g., calories, health, and species) and quantity of available prey items (Clark et al. 2000). Crabs navigate turbulent plumes by moving upstream in response to odor (odor-gated rheotaxis) while maintaining contact with the plume through spatial sampling (tropotaxis) (Keller et al. 2003). When crabs reach sedentary bivalve prey, such as *G. demissa*, tactile sensory organs on the inner faces of the crabs' walking legs and chelae allow the crabs to detect and pick out individual mussels (Seed and Hughes 1997). Damaged mussels involuntarily may release more metabolites compared to undamaged mussels (Vermeij 1983) so may be easier for blue crabs to detect. Thinner, more easily cracked shells resulting from sublethal predation also may lead to preferential selection of damaged mussels by crabs (Hughes and Elner 1979, Boulding 1984, Tucker et al. 1997, Beadman et al. 2003a, Fisher et al. 2011). Molluscivore decapods, including blue crabs, frequently forage selectively on prey with thinner shells (e.g., Palmer 1985, Robles et al. 1990a, Haugum et al. 1999, Caro and Castilla 2004) or smaller sizes (e.g., Hughes and Seed 1981, Boulding 1984, Robles et al. 1990b, Juanes 1992, Aronhime and Brown 2009, Silva et al. 2010, Canton 2011) even if capable of consuming thicker, larger prey. Increased mechanical costs (e.g., claw damage) or longer handling times can explain why crabs choose smaller, thinner-shelled prey (Dietl 2003, Rutten et al. 2006, Aronhime and Brown 2009). Crabs also are able to detect and exploit weakened areas on shells (Elner 1978, Hughes and Seed 1981). Even inconspicuous damage weakens shells (Blundon and Vermeij 1983) likely resulting in targeting by crabs.

In response to predation risk, many bivalves exhibit predator-induced defenses that confer some degree of resistance to attacks (Harvell 1990) such as thickening shells (e.g., Hughes and Elner 1979, Leonard et al. 1999, Lewis and Magnuson 1999, Reimer and Harms-Ringdahl 2001, Caro and Castilla 2004, Cheung et al. 2004, Freeman and Byers 2006), increasing byssus production (e.g., Leonard et al. 1999, Reimer and Harms-Ringdahl 2001, Caro et al. 2008), increasing the size and strength of adductor muscles (Reimer and Tedengren 1996, Reimer and Harms-Ringdahl 2001), and altering shell morphology (Reimer et al. 1995, Reimer and Tedengren 1996, Smith and Jennings 2000, Reimer and Harms-Ringdahl 2001). Thicker shells are stronger (Zuschin and Stanton 2001) and are thus more difficult (i.e., require longer handling times) and dangerous (i.e., risk of damage to predator) for crabs and other predators to crack open (e.g., Hughes and

Elner 1979, Boulding 1984, Reimer and Tedengren 1996, Anton et al. 1997, Leonard et al. 1999, Cheung et al. 2004, Fisher et al. 2011). Increased byssal threads make it more difficult to remove mussels (Lin 1991, Leonard et al. 1999, Reimer and Harms-Ringdahl 2001, Caro et al. 2008), and increased adductor muscles make it more difficult to pry valves apart (Reimer et al. 1995, Reimer and Harms-Ringdahl 2001). Bivalves are capable of altering shell allometry through differential deposition of calcium along shell dimensions (Reimer and Harms-Ringdahl 2001). For example, when exposed to starfish, blue mussels became more globular in shape than control mussels (Reimer and Tedengren 1996, Reimer and Harms-Ringdahl 2001). Globular, dome-shaped shells are stronger than flatter shells against crushing predators (Wainwright 1969, Vermeij 1987). However, bivalves with flatter, more streamlined-shaped shells may be able to escape from predators faster (e.g., bury in the sediment) than more "obese" conspecifics (Luttikhuizen et al. 2003).

Many molluscs are also capable of repairing damaged shells by adding internal layers (e.g., Bond and Saunders 1989, Ramsay et al. 2000, Alexander and Dietl 2001, Dietl and Alexander 2005, Lomovasky et al. 2005, Schejter and Bremec 2007, Hillard and Walters 2009). Shell repair is a relatively modern adaptation, and has increased in incidence through Phanerozoic time as shell-breaking fish and crustaceans become more prevalent (Vermeij et al. 1981). Repaired shells have similar strengths or resistance to crushing as undamaged shells (Blundon and Vermeij 1983), but shell repair is energetically costly (Palmer 1992) and not an automatic response (Alexander and Dietl 2001). Consequently, shell repair frequencies vary greatly between species and habitats (Vermeij et al. 1981, Schmidt 1989, Cadée et al. 1997, Alexander and Dietl 2001).

Frequencies of shell repair (the percentage of shells with at least one repair scar) in Upper Mississippian ammonoids ranged between species from 9% to 38% (Bond and Saunders 1989), substantially lower than modern *Nautilus* populations where 57% had minor repaired breaks and 18.1% had major repaired breaks (Saunders et al. 2010). In gastropods, repair frequencies can range from 7.6% to 87.9% between species and 11.9% to 64.9% between habitats (Cadée et al. 1997). In bivalves, repair frequencies are typically highest in species with retractable mantle edges (Vermeij 1983), such as the Pinnidae (pen shells), where repair frequencies (defined in this study as the number of repairs in a sample divided by the number of specimens) ranged from 0.31 to 1.14 (Dietl and Alexander 2005). However, shell repair has been observed in a wide assortment of bivalve species, even those without retractable mantle edges: in an assemblage of New Jersey bivalves repair frequencies ranged from zero to 0.3 (Alexander and Dietl 2001), in the Argentine Sea scallops had an overall repair frequency of 55% (Schejter and Bremec 2007), in Argentinian coastal lagoons 73% of clams sampled had repaired shell damage (Lomovasky et al. 2005), and in the closely-related brachiopods, shell repair frequencies ranged from 3.7% in Antarctic populations to 43.9% in temperate populations (Harper et al. 2009).

Shell repair frequencies also vary between age groups or size classes within populations. In some species, such as in the brachiopods *Liothyrella uva*, *Magellania venosa*, *Terebratella dorsata*, and *Magellania venosa* (Harper et al. 2009), the oyster *Crassostrea virginica* (Alexander and Dietl 2001), and the surf clam *Spisula solidissima* (Alexander and Dietl 2001), shell repair occurs predominantly in smaller individuals that are at increased risks of predation. Shell repair is absent in larger individuals that have reached a "size refuge" from predation because either attacks are unable to cause shell damage or predators actively avoid large prey items (Alexander and Dietl 2001). In other species, such as the scallop *Zygochlamys patagonica* (Schejter and Bremec 2007), and the limpet *Nacella concinna* (Cadée 1999), repaired damaged is concentrated on larger individuals, but not on smaller individuals that may be too fragile to survive predation attempts (Schejter and Bremec 2007). Similarly, although Ammonoid shell repair was recorded across all size classes, shell repair was positively correlated with shell thickness, indicating that thick-shelled forms survived a higher frequency of injury than thin-shelled forms (Bond and Saunders 1989). The repair rate in a New Jersey assemblage of live and dead *G. demissa* was 0.1, and most repairs were concentrated in the smaller sizes (Alexander and Dietl 2001). The average size at repair was 46 mm, significantly less than the average size at death (63 mm), indicating the majority of shell repairs occurred before mussels reached the larger size classes in which increased burial and size were thought to dissuade predation attempts (Alexander and Dietl 2001). However, research on a South Carolina population of *G. demissa* suggests small individuals may forgo shell repair and instead focus on growth, possibly in an attempt to reach a size that provides a refuge from predators, while larger individuals tend to expend the energy necessary to repair damaged shells (Hillard and Walters 2009).

Critical, unstudied aspects of decapod sublethal predation on *G. demissa* were examined in the following studies. The temporal progression and damage dependence of mussel shell repair during the summer, the period of increased growth (Bertness and Grosholz 1985, Stiven and Gardner 1992, Hillard and Walters 2009) and predation (Virnstein 1977, Virnstein 1979, Holland et al. 1980, Hines et al. 1990, Stiven and

Gardner 1992), were measured in a field enclosure experiment. Results from experiments are presented in Chapter 1. Medium- (~50 mm) and large-sized (~70 mm) mussels with greater shell damage were predicted to exhibit a more rapid rate of repair, a priority if damage increases the risk of future mortality. Additionally, small (~30 mm) mussels with varying amounts of shell damage were expected not to differ in the rate of shell repair but may exhibit different growth rates in an attempt to reach an anticipated size refuge.

The ability of Atlantic blue crabs (*C. sapidus*) to distinguish between damaged and undamaged mussels was examined in a series of wet lab mesocosm experiments. "Weakened" mussels are exploited by blue crabs (Elner 1978, Hughes and Seed 1981), but the origins of mussel "weaknesses" (e.g., shell damage) were not stipulated. Damaged mussels should be selected preferentially by blue crabs and the time required to breach mussel defenses should be shorter.

The effects of crab predation preferences on mussel distributions across the salt marsh environment also were examined in the field. Mussels in low marsh zones, small mussels, and damaged mussels should all experience increased mortality. Mussels in low marsh sites should experience increased mortality because prolonged tidal inundation will increase exposure to predators. Small mussels should experience increased mortality because blue crabs preferentially select smaller individuals. Damaged compared to undamaged mussels also should experience increased mortality because crabs are able to detect quickly and more easily consume damaged mussels. Results from crab selection and predation experiments are presented in Chapter 2.

Chapter 1: Effects of shell damage on growth and repair

Abstract:

Sublethal decapod predation on the ribbed marsh mussel, *Geukensia demissa*, significantly affects shell strength and individual survival and growth. A preliminary experiment investigated characteristics of damaged mussels in the field. Mussels (n = 37 and n = 29) were collected in the fall of 2011 within two ocean-dominated inlets along the South Carolina coast. Each mussel was measured for size (length, width, height), shell thickness, mass, area of damage, and strength (crushing resistance). The prevalence and extent of shell damage was significantly different between inlets. Mussels with the most damage were significantly thicker than the mussels with no damage suggesting shell repair had occurred.

Effects of size and extent of shell damage on mussel growth and shell repair were examined experimentally during the 2012 summer season. Three sizes of field-collected mussels (small 20-30 mm, medium 50-60 mm, large >60 mm) were damaged (0, 33, 66% shell surface removal), caged in the mid-marsh, and sampled monthly. Changes in mussel characteristics (e.g., shell length, strength) were calculated between estimated or measured initial and final values. Increases in shell length, width, or height and tissue mass indicated mussel growth while increases in shell thickness or strength indicated shell repair. Shell damage typically suppressed shell and tissue growth but only medium, moderately-damaged mussels appeared to repair shells. Medium, moderately-damaged mussels also experienced greater mortality suggesting mussels enter a critical stage around 55 mm where abilities to supply the energetic demands of normal growth and reproduction are exceeded by the need to repair shell damage. Small mussels only increased in length and tissue mass and did not repair shell damage suggesting increasing size, perhaps as a refuge from predation, is more important than attempting to counteract the negative effects of shell damage. Large mussels unexpectedly exhibited no signs of shell repair and also experienced minimal growth, possibly instead prioritizing reproduction.

Mussels are vital to the health of coastal ecosystems and may be the key to preventing salt marsh loss to sea level rise by stimulating vertical marsh accretion. As rising global temperatures lead to increased predation pressure and decreased mussel defenses (via reduced calcification rates), mussel response to shell damage becomes increasingly important. Further investigation into the causes of varied metabolic allocations within mussels and the latitudinal differences in mussel behavior and population structure will provide helpful insight that can be used to protect salt marshes in the future.

Introduction:

Sublethal predation on bivalves is a common occurrence across a range of species and habitats. Burrowing bivalves, such as clams, experience soft tissue loss via siphon nipping, where predators only consume the exposed siphons (Peterson and Quammen

1982, Coen and Heck 1991, Kamermans and Huitema 1994, Irlandi and Mehlich 1996). Siphon nipping is frequent and ranges between clam populations from 4-11% in Massachusetts to 15-20% and 15-25% in Alabama/Florida and New Jersey (Coen and Heck 1991). Individual clams lose an average of several siphon tips per day (De Vlas 1985) and a single juvenile stone flounder preys on approximately 370 clams in a season (Sasaki et al. 2002). Sublethal foot predation is also common; up to 48% of Donacidae clams suffer from nipped feet during peaks of predation (August - September) resulting in a >20% loss of biomass (Salas et al. 2001). Foot cropping occurs in 14-34% of New Zealand cockles with an ensuing 9-21% loss of foot area (Mouritsen and Poulin 2003). Sublethal predation on bivalves can also result in shell damage and is identifiable by the breakage pattern (Cintra-Buenrostro 2007). The prevalence and degree of shell damage ranges greatly within and between bivalve populations. Fifty-eight percent of scallops sampled in Argentina had some degree of shell damage, ranging from one small scar to several large scars completely deforming the shell (Schejter and Bremec 2007). In clams, 73% of individuals were damaged: 70% of damaged clams had scars on both valves around the shell margin, 55% had posterior shell area damage on one or both valves, and 30% had more than one scar (Lomovasky et al. 2005). In mussels, over 90% of individuals and up to 60% of the shell surface area were damaged (Hillard and Walters 2009).

The direct consequences of sublethal predation include tissue loss and shell damage that ultimately affects future survival and growth. Tissue loss from siphon and foot nipping increases the risk of subsequent lethal predation (Mouritsen and Poulin 2003, Mouritsen 2004, Meyer and Byers 2005, Cledón and Nuñez 2010) and reduces growth and reproductive output (Coen and Heck 1991, Kamermans and Huitema 1994, Irlandi and Mehlich 1996). Clams with nipped siphons are forced to bury shallower in the sediment, facilitating discovery and consumption by predators (Meyer and Byers 2005, Cledón and Nuñez 2010). Foot regeneration in cropped cockles is required for burial and can take up to eight weeks. During the regeneration period cockles are exposed to thermal and desiccation stress and a five-fold greater risk of predation (Mouritsen and Poulin 2003, Mouritsen 2004). Damage in some species of bivalves makes the shell easier to breach, increasing the probability of mortality (Covich et al. 1981, Geller 1990, Roy et al. 1994, Zuschin and Stanton 2001, Beadman et al. 2003a, Fodrie et al. 2008). For example, crayfish were only able to consume small (<6 mm) undamaged clams, but were able to consume larger (24-35 mm) clams if they were damaged (Covich et al. 1981) and drill predation on oysters was facilitated by shell damage inflicted by stone crabs (Fodrie et al. 2008). Clams reduce pumping (Smee and Weissburg 2006a, Smee and Weissburg 2006b) and barnacles withdraw cirrals (Palmer et al. 1982) in efforts to curtail metabolite release and remain hidden from predators; shell damage, however, may increase susceptibility to predators by enabling metabolite leaching into the surrounding environment even when valves are shut (Vermeij 1983). Shell damage that removes the protective organic periostracum layer also leaves the underlying crystalline structure vulnerable to erosion and microbial colonization, potentially culminating in shell dissolution and microboring (Glover and Kidwell 1993, Freiwald 1995). The effects of shell damage on growth and reproductive output, however, vary greatly between species and even between size/age classes within populations.

Repair of damaged bivalve shells typically occurs through addition of internal layers (e.g., Bond and Saunders 1989, Ramsay et al. 2000, Alexander and Dietl 2001, Dietl and Alexander 2005, Lomovasky et al. 2005, Schejter and Bremec 2007). Shell strength, or resistance to crushing, are similar to undamaged shells once repair has occurred (Blundon and Vermeij 1983), but shell repair is costly energetically (Geller 1990, Palmer 1992, Brown et al. 2004, Lomovasky et al. 2005) and not an inevitable response in all bivalves (Alexander and Dietl 2001). Energy required to repair shell damage also affects growth and, possibly, reproduction (Dietl 2003). Reproduction and somatic growth should decrease as a consequence of shell repair because of energy reallocation (Dietl 2003, Brown et al. 2004). However, documented responses to shell damage vary: mussels (Hillard and Walters 2009) and snails (Geller 1990) with damaged shells grew slower than undamaged conspecifics, but oysters grew faster with damaged than non-damaged shells, although returned to typical growth rates after repairing the damage (Loosanoff and Nomejko 1955). The size/age of individuals also affects whether shells are repaired. In some species repair occurs predominantly in smaller individuals that are at increased risks of predation (Harper et al. 2009). In those species, shell repair is absent in larger individuals that have reached a "size refuge" from predation because either attacks are unable to cause shell damage or predators actively avoid large prey items (Alexander and Dietl 2001). In other species, repaired damage is concentrated on larger individuals, but not on smaller individuals that may be too fragile to survive predation attempts (Cadée 1999).

Within Southeastern U.S. marshes sublethal predation on the mussel *G. demissa* occurs more often within mid-marsh elevations (Hillard and Walters 2009) likely as a result of unsuccessful predation attempts by decapod crustaceans. *Geukensia demissa* living in soft marsh sediments are unlikely to incur shell damage from burrowing (Checa 1993, Alexander and Dietl 2001, 2005, Lomovasky et al. 2005) or erosion (Day et al. 2000), and unless adjacent to commercially important species (e.g., oysters) should not be damaged by harvesting methods (Mensink et al. 2000, Schejter and Bremec 2007). The majority of shell damage on *G. demissa*, as with many other bivalves, is likely caused by failed decapod predation. Crabs (e.g., *Callinectes sapidus, Panopeus herbstii*) frequently found within salt marshes (Teal 1962, Archambault et al. 1990) are known predators on *G. demissa* (Seed 1980, Laughlin 1982, Lin 1990, Canton 2011, Toscano and Griffen 2012) and can leave shells with extensive chips, nibbles, and scallops (Figure 1; Alexander and Dietl 2001, Cintra-Buenrostro 2007). The reduced frequency of tidal coverage common at mid-marsh elevations may contribute to the prevalence in shell damage; semidiurnal tides limit the time to feed successfully on mid-marsh mussels.

The greater prevalence and extent of shell damage on mid-marsh mussels (Hillard and Walters 2009) should increase the risk of subsequent successful predation attempts because damaged mussels are easier to locate and easier to open. Many crabs are olfactory-driven predators and *C. sapidus* are able to detect homogenates prepared from bivalve tissues at concentrations as low as 10^{-15} g/L (Pearson and Olla 1977, Weissburg and Zimmer-Faust 1993). Crabs actively migrate to maximize foraging efficiency (Griffen 2009) and are responsive to the overall quality of prey, altering prey patch use depending on the quality (e.g., calories, health, and species) and quantity of available prey items (Clark et al. 2000). Similar to other bivalves (Vermeij 1983), damaged *G. demissa* likely leach homogenates into the environment facilitating detection by blue crabs. Damaged mussels also should be easier for crabs to open because thinner compared to thicker shells are less crush-resistant (e.g., Hughes and Elner 1979, Boulding 1984, Tucker et al. 1997, Beadman et al. 2003a, Fisher et al. 2011). Molluscivore decapods, including blue crabs, frequently forage selectively on prey with thinner shells (e.g., Palmer 1985, Robles et al. 1990a, Haugum et al. 1999, Caro and Castilla 2004) or smaller sizes (e.g., Hughes and Seed 1981, Boulding 1984, Robles et al. 1990b, Juanes 1992, Aronhime and Brown 2009, Silva et al. 2010, Canton 2011) even if capable of consuming thicker, larger prey. Crabs also are able to detect and exploit weakened areas on shells (Elner 1978, Hughes and Seed 1981). Even inconspicuous damage weakens shells (Blundon and Vermeij 1983) likely resulting in targeting by crabs.

Sublethal predation on mid-marsh mussels increases non-predatory mortality and decreases growth in *G. demissa* (Hillard and Walters 2009). Shell damage increased non-predatory mortality by 4-10% and decreased both shell and tissue growth by 7-12% to 31-43% respectively. The individual effects of sublethal predation also varied with mussel size given most physiological functions (e.g., growth, maintenance, and reproduction) are size dependent in organisms (Brown et al. 2004). In the mid-marsh, *G. demissa* reduced tissue relative to shell growth in medium (~ 50 mm) compared to large (~70 mm) mussels suggesting smaller size classes allocate greater energy to increasing shell size (Hillard and Walters 2009). Small mussels possibly forego shell repair in an attempt to reach a putative size refuge (e.g., Paine 1976, Jeffries and Lawton 1984, Bertness and Grosholz 1985, Stiven and Gardner 1992). The differential ontogenetic allocation of energy to repair or growth in *G. demissa* also may vary with latitude and time. Repairs of shell damage were observed to predominate in small (<50 mm) *G. demissa* from fossilized populations in New Jersey (Alexander and Dietl 2001).

Two major aspects of shell damage effects previously not investigated in *G. demissa* populations are examined in this study: the relationship of shell damage to shell integrity and shell repair. To test if damage affects shell strength, the crushing force for *G. demissa* collected in the fall of 2011 within marshes in two ocean-dominated inlets along the South Carolina coastline was measured. Exterior damage was expected to affect shell strength negatively and damaged compared to undamaged mussels were expected to require less force to crack open. Effects of shell damage on size-dependent tradeoffs between growth and repair were examined experimentally during the 2012 summer season. Summer typically is the period of increased growth (Bertness and Grosholz 1985, Stiven and Gardner 1992, Hillard and Walters 2009) and predation (Virnstein 1977, Virnstein 1979, Holland et al. 1980, Hines et al. 1990, Stiven and Gardner 1992), on *G. demissa.* Monthly shell and tissue growth and changes in shell strength were determined in a field enclosure experiment. Medium- (~50 mm) and large (~70 mm) mussels with greater amounts of shell damage were predicted to exhibit a more rapid rate of shell repair, a priority if damage increases the risk of future mortality. Both damaged and undamaged small (~30 mm) mussels were expected to exhibit low shell repair rates and similar growth rates in an attempt to reach the hypothesized size refuge.

Methods:

Shell strength differences among mussel populations:

Mussels were collected between September to November 2011 from two inlets along the northern South Carolina coast: Hog Inlet (33.83389 °N, 78.6011 °W) and Murrells Inlet (33.5517 °N, 70.0489 °W). Locations were selected to collect from sites where mussels previously were observed to have no or minimal, Hog Inlet, to extensive shell damage, Murrells Inlet (Hillard and Walters 2009). Hog Inlet mussels (n = 37) were gathered at a mid-marsh elevation within and around the bulkheading supporting the causeway across Dunn Sound onto Waties Island. Murrells Inlet mussels (n = 29) were excavated from bare sediments surrounded by dense stands of *Spartina alterniflora* at a mid-marsh site in Huntington Beach State Park. Mussels from both locations were haphazardly collected without regard for size or damage. Individuals were sized with digital calipers (shell length or umbo to lip, width, and height across both valves), dissected to remove tissue, dried at 60˚C for >24 hours, and tissue and shell dry mass measured to the nearest 0.1 mg. Right and left valves were photographed digitally and image analysis software (ImageJ, v.1.46b) used to measure the total surface and damaged area on valves. Damage was defined as any area where the periostracum visibly was removed exposing the inner calcite layers of the shell. One valve from each mussel was cut in half perpendicular to the long axis and shell thickness measured at the lip, midline, and hinge regions. The other valve was crushed in a homemade device designed to measure the compression strength of shells (Figure 2). The device consisted of a mobile pressure plate attached to a rounded dowel (6.2 mm dia.) that rested as close as physically practical on the X-Y midpoint of the shell. Weight was added incrementally to the pressure plate until the shell broke. The force (Newtons) required to break a shell was calculated from the mass loading and acceleration of gravity constant. Compression forces measured are not an exact simulation of every type of crab predation (Tokeshi et al. 2000), but the dowel was shaped to resemble the teeth on crab chelae and the force was exerted consistently on the midpoint of each shell. Differences in compression force between shells with different levels of external damage were considered a reasonable, relative measure of differences in shell strength (e.g., Blundon and Vermeij 1983, Beadman et al. 2003b, Aronhime and Brown 2009). Phytoplankton availability within the various inlets from which mussels were sampled was determined to assess if any differences among mussels could be attributed to differences in food availability. Multiple (n = 3-4) 1L samples were collected on three dates in late summer of 2010 and 2011. A 50 mL subsample from each sample was filtered immediately after collection through a Whatman GF/F filter and frozen at -20°C until extraction. Phytoplankton pigments (e.g., chlorophyll *a*) retained by the filters were extracted in 90% acetone and flourescence determined after 48 h on a Turner Trilogy laboratory fluorometer.

Consistency of shell damage treatments:

An experiment was conducted to determine if consistent shell damage treatment levels could be produced on mussels. Visibly undamaged mussels (n = 75) were collected from rock bulkheads protecting a causeway over Eden Saltworks Creek near Waties Island, South Carolina, numbered, and length, width, and height measured with digital calipers. Collected mussels either were left undamaged (n = 15) or processed to create treatments on only a single valve varying in area and intensity of damage from limited to moderate to extensive (n = 20 ea.). The limited damage treatment removed the middle 1/3 of the shell surface or periostracum but left shell ridges intact. The moderate damage treatment removed the middle 1/3 of the shell along with any ridges to keep area the same but vary damage intensity. In extensively-damaged mussels 2/3 of the shell furthest from the umbo along with all ridges were removed. The valve on each mussel was damaged using a Dremel® rotary tool and sanding drum (Hillard and Walters 2009). Previous studies creating shell damage in an attempt to mimic the effects of crab predation examined a variety of approaches, but dremeling produced damage similar to that observed in the field in the least amount of time without unduly stressing mussels (Hillard and Walters 2009). After damaging, mussels were dissected, dried at 60ºC for >24 h, and shell and tissue mass measured to the nearest 0.1 mg. Both valves in 50% of each mussel treatment were bisected carefully and shell thickness measured with calipers (see *Shell strength differences among mussel populations*). The force required to crush both valves was determined in the remaining 50% of treated mussels. Each valve was processed in the device designed to measure compression force (see *Shell strength differences among mussel populations*).

Effects of shell damage on growth and repair:

Effects of shell damage on mussel survival, growth, and shell repair were investigated in a seasonal field enclosure experiment. Undamaged mussels (n = 300) were collected in May 2012 near Waties Island, South Carolina (see above) and separated into small (20-30 mm), medium (50-60 mm) and large (>60 mm) size classes. In each size class 1/3 of the individuals were left undamaged while remaining mussels were damaged using a Dremel® rotary tool (Hillard and Walters 2009). Damage treatments included removing the periostracum layer on both valves from 1/3 of the shell in the mid-region removing ridges, moderate damage, or 2/3 of the shell closest to the growing lip, extensive damage (Figure 3). After damaging, individuals were numbered and sized (length, width, height). Although indications are shell removal using a Dremel® does not affect survival (Hillard and Walters 2009) all mussels were maintained in the lab for one week prior to deployment in the field to monitor any possible treatment-induced mortality. Mussels of each size class and damage treatment (n = 9 total) were placed into 0.64 cm Vexar® mesh cages 10-15 cm in diameter and ≈50 cm tall that were buried ≈25 cm in the sediment at a mid-marsh site near Clambank Landing in the North Inlet-Winyah Bay National Estuarine Research Reserve (NERR), South Carolina. The Clambank Landing site was ≈75 km south of the original Waties Island collection site. An initial sample of mussels from each size class and damage treatment was frozen at -20°C until processed. Monthly from June to September six cages were collected and the mussels frozen until processed. Wet mass and shell length, width, and height of all frozen mussels were remeasured. Individual mussels were dissected and the shell and tissue mass determined after drying at 60°C for >48 h. One valve from each mussel was bisected lengthwise and shell thickness measured with a digital caliper to the 0.01 mm at the hinge, midline, and lip. The other shell valve was crushed using a Humboldt HM-3000 Unconfined Compression Tester to measure the force required to crack the shell. A 2 kN load cell was used on the compression tester that crushed shells with a flat steel plate moving at 1 mm s^{-1}, a procedure similar to previous shell strength studies (e.g., Blundon and Vermeij 1983, Kennedy and Blundon 1983, Singh et al. 2000, Beadman et al. 2003a, MacDonald et al. 2007, Aronhime and Brown 2009, Fisher et al. 2011, Coleman et al. 2014).

Statistical Analyses:

Shell strength differences among mussel populations:

Size-adjusted differences in shell characteristics between undamaged Hog Inlet and damaged Murrells Inlet mussel populations and relationships between the extent of damage and measures of strength were analyzed with various general linear models. All requisite assumptions (e.g., covariate-dependent variable correlation, homogeneity of slopes) were tested prior to analyses (Quinn and Keough 2002). For ANOVA/MANCOVA analyses data were edited to omit mussels < 40 mm, sizes not collected at the Murrells Inlet location. Shell length was used as the covariate and all variables were $\log_{10}$ transformed in shell and tissue mass analyses to adjust for power function relationships among linear (length) and volume measurements (mass). Data were transformed as the focus was on assessing population differences and not estimating parameters, but alternative approaches related to the ongoing debate over effective analyses for allometric relationships were considered (e.g., Packard et al. 2011, Glazier 2013, Packard 2014). Shell length, thickness, and compression force data were not transformed in analyses. Differences in shell thickness between inlets were analyzed by MANCOVA incorporating lip, midline, and hinge measurements as dependent variables in the model. Significance of the MANCOVA model was evaluated with Pillai's trace, which is both conservative and robust to violations (Berkman and Reise 2011). Relationships among area of shell damage and other mussel characteristics (e.g., shell thickness, mass) and compression force were analyzed in a multiple regression. Only data from Murrells Inlet were included in the multiple regression since Hog Inlet shells were not damaged. Differences in pigment amounts reflecting the availability of food for mussels were analyzed with a nested ANOVA. Year and date were random effects nested within inlet locations.

Consistency of shell damage treatments:

Within and among treatment consistency of manufactured shell damage effects were tested by ANOVA. Differences in shell mass and thickness and requisite crushing force among treatments (undamaged, limited, moderate, and extensive) were analyzed in a one-way model after violations of model assumptions were assessed and if significant differences determined Tukey’s HSD post hoc test applied. Tukey's HSD test was used over other stepdown procedures, such as REGWQ, because of unequal sample sizes; Tukey's is reliable and controls the Type I error rate to no more than the 0.05 level (Quinn and Keough 2002). Paired t-tests were used to determine differences in shell mass between damaged and undamaged valves from the same individuals.

Effects of shell damage on growth and repair:

Damage effects on survival, repair, and growth were analyzed with hierarchical loglinear and general linear models. Total numbers of alive or dead mussels across damage treatments (undamaged, moderate damage, extensive damage), and size classes (small, medium, large), were analyzed with hierarchical loglinear models using a backward elimination approach (Agresti and Kateri 2011). Effects of shell damage on total and change in shell length, thickness, strength, mass, and tissue mass were analyzed using ANOVA models and if significant differences determined Tukey's HSD post hoc test applied (see above) (Quinn and Keough 2002). Cages containing the mussels in the field did not have a significant effect on growth ($F_{23,160}=0.652$, $p>0.05$), so cages were not used as a blocking factor in analyses. Starting shell and tissue mass for mussels deployed in the growth experiment were estimated with a nonlinear regression approach calculated from the initial sample of mussels (Packard 2014). In all cases shell length and a power equation proved the best fit for the data ($R^2>0.98$). Growth rates were defined monthly and calculated by dividing the change in each variable (e.g., shell length) by the number of growing months. Models for shell thickness and strength were not sufficiently accurate to predict starting condition, therefore "growth" was examined through the differences in shell thickness and strength between damage treatments for each size class of mussel over the growing period using appropriate ANOVA models. Measurements of shell thickness and strength were standardized by total shell length prior to analyses. Dead mussels were excluded from analyses of growth, but were analyzed in log-linear models (see above) to assess differences in survivorship. Negatively growing mussels, however, were still included in all analyses, unlike in Hillard and Walters (2009), because of the increased prevalence and relationship with shell damage. All data used in ANOVA models were tested for assumptions (e.g., normality, homogeneity), and all statistical analyses were run using SPSS (v.20).

Results:

Shell strength differences among mussel populations:

Shell damage affected some but not all characteristics associated with the strength of individual mussels collected from field populations (Figure 4). Total shell mass was significantly different between undamaged, Hog Inlet, and damaged mussels, Murrells Inlet (Figure 4a; $F_{1,53} = 5.385$, $p < 0.025$), when shell length was included as a significant covariate ($F_{1,53} = 374.8$, $p < 0.001$). Undamaged mussels were 17.2% heavier at an average length of 72.6 mm. Tissue mass (Figure 4b; $F_{1,52} = 2.866$, $p > 0.05$) and compression force (Figure 4c; $F_{1,48} = 0.096$, $p > 0.05$) were not significantly different between inlets. Damaged mussels had slightly greater tissue mass and required slightly more force to break shells. Shell thickness was significantly different between undamaged and damaged mussels (Figure 4d; $F_{3,51} = 5.675$, $p < 0.003$). Murrells Inlet mussels were thicker across the middle of the shell in the region typically exhibiting damage. Shell thickness at the hinge region was the only shell characteristic including area of damage that entered and remained in the multiple regression ($F_{1,24} = 25.834$, $p < 0.001$). The model fit was modest, $R^2 = 0.518$, and both fit and inclusion of additional variables were not improved by transformation. There were no differences in pigment amounts between the two inlets ($F_{1,3} = 0.236$, $p>0.05$).

Consistency of shell damage treatments:

Experimental removal of shell material resulted in measurable differences among damage treatments (Table 1, Figure 5). Shell thicknesses (Figure 5a) differed significantly between damage treatments at the midline ($F_{3,40}$=6.474, $p<0.001$) and hinge ($F_{3,40}$=14.074, $p<0.01$). Undamaged shells were significantly thicker than extensive and moderate damage shells ($p<0.05$), but there were no significant differences in shell thickness between undamaged and limited damage shells ($p>0.05$), or between moderate and extensive damage shells ($p>0.05$). There were no significant differences in shell mass between the treatment groups (Figure 5b; $F_{3,70}$=0.841, $p>0.05$) even when shell mass was adjusted for total shell length ($F_{3,70}$= 0.896, $p>0.05$). However, all damage treatments significantly reduced the shell mass for individual mussels when comparing the mass of the damaged versus undamaged valve (limited damage: t_{19}=-2.479, $p<0.05$; moderate damage: t_{19}=-3.997, $p<0.01$; extensive damage: t_{19}=-6.672 $p<0.01$), while the left and right valves for undamaged mussels had similar masses (t_{13}=0.355, $p>0.05$). The extensively- damaged mussels required the least amount of force to crush, but the differences in force between all of the damage treatments was not significant (Figure 5c; $F_{3,38}$=0.801, $p>0.05$). The limited and moderate damage mussels required more force to break than the undamaged mussels, but again, the difference was not significant.

Effects of shell damage on growth and repair:

Combined mortality for all mussel treatments was 11.7%. Mortality was dependent on the extent of shell damage but not size (Figure 6; $X^2 = 8.129$, $p < 0.05$, df=2). The majority (86%) of deaths were split equally between the moderate and extensive damage treatments. Out of all combinations of size classes and damage treatments, large undamaged mussels had the lowest mortality rate (3% of large undamaged mussels died) while medium moderately-damaged mussels had the greatest mortality rate (35%).

Shell damage only significantly affected the linear growth of large mussels. Large undamaged mussels grew significantly more than large moderate and extensive damage mussels (Figure 7; $F_{2,61}=3.282$, $p<0.05$). Similarly, although insignificantly, small undamaged mussels grew more than small damaged mussels ($F_{2,61}=2.076$, $p>0.05$). There were no significant differences in linear shell growth between damage treatments in medium mussels ($F_{2,53}=2.101$, $p>0.05$), but mussels with moderate damage grew more than undamaged mussels, while mussels with extensive damage had the lowest growth rate out of all combinations of size and damage treatments.

Shell mass growth was significantly affected by damage treatment. Extensively-damaged mussels had significantly reduced shell mass growth in all size classes (Figure 8; small: $F_{2,61}=7.168$, $p<0.01$; medium: $F_{2,53}=8.661$, $p=0.01$; large: $F_{2,61}=9.682$, $p<0.01$). There were no significant differences in growth rates between undamaged and moderately-damaged mussels ($p>0.05$); undamaged large mussels had greater rates of shell mass growth than moderately-damaged large mussels, while moderately-damaged small and medium mussels had greater rates of shell mass growth than undamaged small and medium mussels.

Tissue mass growth was not significantly affected by damage treatment for any size class of mussels (Figure 9; small: $F_{2,61}=1.239$, $p>0.05$; medium: $F_{2,55}=1.013$, $p>0.05$; large: $F_{2,61}=1.778$, $p>0.05$). Medium, moderately-damaged mussels had the greatest tissue mass growth rate while large, extensively-damaged mussels had the lowest tissue mass growth rate. Undamaged mussels had the greatest tissue mass growth rates within small and large mussel size classes.

Shell thickness differences between damage treatments dissipated by the end of the summer in small and medium mussels, however differences increased in large mussels (Figure 10). Initially, undamaged small and medium mussels had significantly thicker shells than moderately and extensively-damaged mussels (small: $F_{2,19}=9.056$, $p<0.01$; medium: $F_{2,11}=11.573$, $p<0.01$). Undamaged shells continued to be thicker throughout the summer, however, final thickness measurements were not significantly different (small: $F_{2,14}=0.778$, $p>0.05$; medium: $F_{2,12}=0.403$, $p>0.05$). Large undamaged mussels were not significantly thicker than damaged mussels at the start of the experiment ($F_{2,16}=2.805$, $p>0.05$), but were significantly thicker than both damage treatments by the end of the summer ($F_{2,13}=6.650$, $p<0.05$).

Shell strength was significantly affected by mussel size and time, but not damage. There were significant differences in force between all size classes of mussels ($F_{2,196}=51.579$, $p<0.001$), with increased mussel size requiring more force to break shells. Mussels also increased in strength over the summer, as final shell strengths were significantly greater than initial shell strengths ($F_{4,196}=4.547$, $p<0.01$). Mussel shell thickness was positively, and significantly, correlated with shell strength (Figure 11; $F_{2,32}=146.843$, $p<0.001$, $R^2=0.3876$), however, there were no differences between damage treatments within size classes even in the initial sample of mussels (Figure 12; small: $F_{2,71}=1.071$, $p>0.05$; medium: $F_{2,71}=0.303$, $p>0.05$; large: $F_{2,68}=0.371$, $p>0.05$). When standardized for mussel size (force/mm shell length), no differences were detected within size classes between initial and final measurements (Figure 13; small: $F_{1,33}=0.383$,

$p>0.05$; medium: $F_{1,38}=1.114$, $p>0.05$; large: $F_{1,29}=1.119$, $p>0.05$) or between damage treatments (small: $F_{2,33}=0.122$, $p>0.05$; medium: $F_{2,38}=2.281$, $p>0.05$; large: $F_{1,29}=1.119$, $p>0.05$).

Discussion:

Mussels with exterior shell damage collected from Murrells Inlet appeared to contain internal layers of shell repair. Freshly damaged mussels, as demonstrated in the consistency of shell damage treatments experiment, have significantly reduced shell thicknesses. However, mussels collected with exterior shell damage were thicker and equally as strong as undamaged mussels. Differences between mussel populations were not caused by food availability, as chlorophyll *a* levels were similar in both inlets, but were most likely caused by the effects of and responses to shell damage. Damaged mussels selectively added internal layers to achieve similar shell strengths with undamaged mussels. Undamaged mussels still had significantly greater shell masses than damaged mussels post repair, indicating repair material may be less dense and needed in greater thicknesses than shell material produced through normal growth. The cell biology underlying biomineralization is not perfectly understood, but these results support recent findings of different pathways for shell repair and shell growth (Mount et al. 2004, Fleury et al. 2008).

During the seasonal field enclosure experiment, shell damage significantly increased non-predatory mortality across all size classes of mussels and reduced growth. Overall, mussel mortality was low (12%), but consisted mainly of damaged mussels

(86%). The size class of mussels did not affect mortality, and there was no difference in mortality rates between moderately and extensively-damaged mussels. Extensive damage significantly reduced shell mass growth rates across all size classes of mussels. Increases in shell mass were caused by the linear growth of the shell and shell repair. Mussels with extensive shell damage had suppressed linear shell growth and thus reduced shell mass growth. Many medium and large extensively-damaged mussels also had negative shell mass growth, indicating that not only was growth stunted by shell damage, but shell mass was being lost via erosion or microboring. Moderate shell damage did not have a significant effect on shell growth and actually increased shell mass growth rates in small and medium mussels and shell length growth in medium mussels. Shell damage decreased tissue mass growth in large mussels but differences between damage treatments were not significant. In general, mussels that survived with moderate damage grew more over the course of the summer than mussels with extensive damage.

During the summer the increase in food availability and prevalence of predators should stimulate shell repair, however, repair was only widespread in medium, moderately-damaged mussels. If repair occurred in mussels, shell thickness should have increased proportionally more than shell thickness increases observed during normal growth (i.e., shell thickness should have increased in damaged mussels more than undamaged mussels to be considered “repair”). Increases in shell mass were also expected, although did not have to be at a greater rate than undamaged mussels because the repaired mussels collected in the shell strength differences among mussel populations experiment had significantly reduced shell masses compared to the undamaged mussels. Undamaged large mussels remained significantly thicker than moderately and extensively-damaged mussels throughout the summer, and although shell strength varied greatly, undamaged mussels were the strongest most months. Shell and tissue growth also were minimal, indicating a focus on reproduction rather than repair, as many large mussels lose tissue mass during spawning season (Kuenzler 1961b). Large mussels are capable of shell repair, as evident in the damaged mussels collected from Murrells Inlet, but repair may only be a priority during non-reproductive months. The lack of significance in shell thickness per shell length between damage treatments in small mussels most likely does not indicate shell repair is occurring. In small mussels, lateral shell growth occurred at a greater rate than the rate of increasing shell thickness. Therefore, when small mussels with damaged shells, which suffered reduced growth rates, are compared with undamaged mussels, the undamaged mussels are actually decreasing in thickness per length because of the increases in lateral growth instead of damaged mussels increasing shell thickness via shell repair. In both small and large mussels, the moderately-damaged mussels typically mimicked the growth rates of the undamaged mussels, although at a slightly reduced rate. In medium mussels, the moderately-damaged mussels grew more than undamaged and extensively-damaged mussels, had the greatest tissue mass growth rates, the greatest shell mass growth rates, and the greatest mortality rate out of any other combination of size class and damage treatment (35%). Because medium, moderately-damaged mussels grew more than the undamaged mussels, the increased shell thickness per shell length is not just reflective of growth, but of repair. Medium, moderately-damaged mussels appear to be at a critical point where the mussel attempts to balance growth and repair, consequently suffering increased mortality when overwhelmed by the dueling pressures. Some extensively-damaged medium mussels showed visual signs of shell repair along the shell margin (Figure 14). On the inside of such shells there was an elevated ridge that ran along the previous edge of the shell, and shell growth appeared discontinuous when viewed from the outside- the new section of shell was not attached to the farthest edge of the old shell but instead grew out at a different angle from a point ~2 mm towards the umbo. Not all extensively-damaged mussels had discontinuous shell growth patterns, however, and it appeared that shell repair only occurred if the shell growth margin was sufficiently damaged, and only occurred along the shell edge and not throughout the entire damaged area. Unlike the repairs observed in moderately-damaged mussels that most likely are defensive responses with the intent to increase shell strength, repairs in extensively-damaged mussels appear to only occur if they are needed for continued shell growth. Otherwise, extensively-damaged mussels incur too much loss to attempt shell repair and instead focus only on growth and survival.

Shell damage reduces growth directly by increasing energy needed to thermoregulate and possibly indirectly through a TMI. When temperature exceeds 25˚C, filtration rates fall significantly in similar mussel species, *Mytilus galloprovincialis* and *Mytilus edulis* (Gonzalez and Yevich 1976, Anestis et al. 2007). As estuarine residents that contend with substantial fluctuations in abiotic conditions (e.g., inundation, salinity, temperature, etc.), *G. demissa* have increased physiological plasticity and can tolerate temperatures up to 36˚C (Lent 1969). However, there was a heat wave during the course of this experiment and air temperatures reached 36˚C. There was also a historic "heat burst" on July 1st when temperatures briefly reached 49˚C. The mussels may have been exposed to even greater temperatures because the surrounding marsh grasses act as insulation and trap heat (Hofmann and Somero 1995, Jost and Helmuth 2007). Shell damage could exacerbate temperature stress on mussels and contribute to the observed decreased growth rates and increased mortality rates. Similar species reduce chemical excretions in order to remain hidden from olfaction-guided predators (Palmer et al. 1982, Smee and Weissburg 2006a, Smee and Weissburg 2006b). Mussels may leach metabolites into the surrounding water when shells are damaged (Vermeij 1983) and as compensation reduce pumping even further. The exact mechanism for the reduced growth observed in damaged mussels in this experiment is unclear. Continued research should examine the effects of shell damage on mussel filtration rates in the presence and absence of predators.

Direct measures of shell strength did not reflect treatment differences. Larger, thicker shells were, as expected, stronger than smaller, thinner shells. However, strength differences between damage treatments at each size class, even for preliminary mussels, were not significant, even when adjusted for total length and shell thickness. Also, although the overall relationship between shell midline thickness and shell strength was significant, thickness alone could not be used as an accurate predictor of strength because only 39% of the variation could be explained by the model. Differences between damage treatments could explain some of the variation; although extensively-damaged mussels had twice as much shell surface area removed compared to moderately-damaged mussels, the thickness of shell removed was the same for each treatment. So, even though the thickness of a moderately-damaged mussel may be the same as an extensively-damaged mussel, the strength of the two mussels may not be identical because the extent of shell damage differs.

Strength results likely were confounded by the method for measuring strength as well as shell geometry. Only one valve was measured for strength so the other valve could be used to determine shell thickness. Valves were placed with the inside facing down on the compression tester and crushed against a flat surface. Many shells were uneven and did not lay flat on the surface of the compression tester. The shells were not adjusted to lay flat because altering the edges could possibly cause damage and reduce overall strength (Currey et al. 1988). Having fewer points of contact, from either the compression tester surface or from the descending crushing plate, would put additional stress on the parts of the shell that were in contact. Therefore, shells with varying shapes and with different contact areas would have differences in strength regardless of shell thickness just because of differences in how the compression force is distributed. The crushing methodology used was designed to determine differences between the damage treatments, not necessarily to determine the true strength of the shells. In the consistency of shell damage treatments experiment, extensively-damaged mussels took less force to break than all of the other damage treatments, although the differences were not significant. The lack of significance was presumed to be caused by the rudimentary nature of the hand-made crushing device that was used. It was expected that using the more precise Humboldt HM-3000 Unconfined Compression Tester variation would be reduced and clearer differences in shell strength would be found. However, even when using the HM-3000 there were no significant differences between damage treatments. Variation was still a complication and possibly other methods would have given significant results. Conversely, the damage experimentally inflicted on mussels may not actually have a significant effect on shell strength.

Shell strength has often been exclusively determined by the compression resistance of shells, but shell strength is not the only factor contributing to mussel defense. Previous studies also crushed shells against flat surfaces, but with the organism intact (Blundon and Vermeij 1983), while others pinned the mussels between two coarse blades (Aronhime and Brown 2009). Using the entire mussel, not just an empty valve, would probably have given more accurate results of shell strength. However, even using the entire mussel, the shape of the mussel would have an effect on the strength (Caill-Milly et al. 2012) and may continue to mask any effects of shell damage. Shell strength may not be as important to mussels as other methods of defense. Mussels are found in an aggregated distribution throughout the marsh (Bertness and Grosholz 1985, Lin 1989a), and in laboratory settings, clump together when exposed to chemical cues from predators (Côté and Jelnikar 1999). Byssal thread production increases and adductor muscles strengthen when threatened by predation (Leonard et al. 1999, Reimer and Harms-Ringdahl 2001, Garner and Litvaitis 2013). Mussel shells are also streamlined and ideal for rapid reburial instead of globular-shaped to maximize crushing resistance (Wainwright 1969, Vermeij 1987, Luttikhuizen et al. 2003). Clumped mussels are more difficult for crabs to target and pull apart, and mussels with stronger byssal threads and those buried deeper in the sediment suffer reduced mortality from crabs (Lin 1991). Bolstering shell strength may have been a low priority for mussels in this experiment because of the relative security brought about from being tightly clumped, partially buried, strongly attached to surrounding *Spartina* and conspecifics with byssus threads, and from the physical lack of predators (via exclusion cages).

The compression resistance of mussels is also only important to smaller size classes that are actually in danger of being crushed by crab claws. Larger mussels are more concerned with "chipping" strength, as crabs must chip away at edges before being able to pry the shell open. The relative strength of the shell against chipping attacks has been theorized to be a function of shell mass per unit surface area of soft tissue, or simply shell length or thickness as long as the ratio of tissue to shell mass remains constant (Tokeshi et al. 2000). In large mussels, the ratio of shell mass to tissue mass was significantly different between damage treatments. Using Tokeshi's (2000) theory, undamaged large mussels were significantly stronger than moderately and extensively-damaged mussels ($F_{2,80}=3.358$, $p<0.05$; post hoc $p<0.05$), however there was no significant difference in strength between moderately-damaged and extensively-damaged mussels (post hoc, $p>0.05$). Both crushing resistance and chipping strength are important to medium mussels which encounter both forms of attack. As previously mentioned, there were no significant differences in compression strength between medium mussel damage treatments. For chipping strength, undamaged medium mussels were stronger than moderately and extensively-damaged mussels, but were not significantly stronger ($F_{2,68}=1.599$, $p>0.05$).

Still, shell mass or thickness may not be appropriate indicators of strength in damaged mussels that have undergone shell repair because the layers of regenerated shell do not resemble the layers that were lost (Mount et al. 2004, Fleury et al. 2008). For example, exterior shell damage may have removed part of the periostracum and underlying outer prismatic layer. Mussels can increase shell thickness by adding internal layers, but cannot directly repair the exterior shell damage. The internal layer is nacreous aragonite, the middle layer is aragonite prisms, and the outer layer is calcite (Blackwell et al. 1977). So, although repaired shells have similar thicknesses to undamaged shells, because of the differences in shell composition shell mass may still be different, as observed in the damaged mussels collected from Murrells Inlet.

Shell strength may also differ depending on the thicknesses of the different shell layers. Layers composed of prisms oriented perpendicular to the surface of the shell, such as the outer calcite layer and alternating prismatic layers within the inner nacreous layer, are the weakest shell layers because the prisms are aligned in the same direction cracks travel (Currey et al. 1988, Watabe 1988). In contrast, nacreous layers are the strongest layers because the aragonite crystals are arranged almost parallel to the inner shell surface (Currey et al. 1988, Watabe 1988). Cracks that travel easily through the outer prismatic layer are brought to a halt when reaching the nacreous layer because the fracture path is forced to zig-zag between the nacre sheets, which requires considerably more force (~ 100,000 kN) (Currey et al. 1988). The entire shell is not composed of nacre because nacre takes much longer to form than calcite prisms (Currey et al. 1988). The outer layers that were removed when damaging the mussels may not have significantly contributed to overall shell strength.

Temperature-dependent shell formation processes in *G. demissa* and latitudinal variation in predator pressure may explain the differences in shell repair observed between New Jersey (Alexander and Dietl 2001) and South Carolina (Hillard and Walters 2009) populations. Mussels south of Cape Hatteras lack the granular structures (cold-water produced) found in northern populations, and as a result form shells with alternating layers of only irregular prisms and nacre (Lutz 1984, Lutz and Clark 1984).

Southern mussels typically are also faced with more intense predation pressure. Blue crab predation significantly reduces the abundance of *G. demissa* (Seed 1980) and causes shell damage when unsuccessful. In northern populations, such as in the Chesapeake Bay, predation pressure is increased during warm summer-fall months as *C. sapidus* become more active (Virnstein 1977, Virnstein 1979, Holland et al. 1980, Hines et al. 1990). In estuaries at lower latitudes, similar patterns of blue crab activity are evident although are less intense (Livingston 1976, Laughlin 1982). In the Apalachicola estuary in northern Florida, predation pressure on *G. demissa* may still be substantial in the winter despite reduced crab activity because of a shift in diet away from fish and crabs to being almost entirely comprised of bivalves (Laughlin 1982). Northern populations of *G. demissa* are characterized by large numbers of juvenile mussels with elevated mortality rates (40-50% per year) and smaller numbers of older (larger) mussels with decreased mortality rates from mainly abiotic factors (e.g., ice) (Franz 2001). Refuge from predators can occur as soon as 50 mm in length (Bertness and Grosholz 1985). Southern mussel populations form a bimodal distribution, with large numbers of juvenile and older (larger) mussels (Kuenzler 1961b). Older mussels that reached a size refuge from predation had lower mortality rates than northern populations because of the lack of winter ice (Bertness and Grosholz 1985). Unlike northern populations, refuge from predators is unlikely to occur at 50 mm, as even small (~90 mm CW) blue crabs are able to open mussels of this size (Stiven and Gardner 1992). Even large mussels (>60 mm) experienced significant mortality in low marsh areas. Shell repair in northern populations of mussels may occur earlier (at smaller sizes) than in southern populations because of these differences in refuge size. Shell repair may also occur at different rates and in different seasons since northern populations experience a more concentrated burst of predation during the summer, while southern populations experience predation year round.

Future studies should use scanning electron microscopy (SEM) to more accurately identify and quantify shell repair. Repaired shell layers are composed of very thin (~1μm) sheets of nacre. Even when completely repaired total shell thickness changes by <1 mm, so using midline shell thickness to measure shell repair becomes difficult when there is high variation in individual shell thicknesses and growth. SEM photographs have successfully been used to quantify repaired shell damage in previous experiments (Ramsay et al. 2000, Trinkler et al. 2010). The photographs produced by SEM would allow measurements of the individual shell layers and would clearly identify areas of shell repair. Using SEM, or a similar technique, further research should investigate whether shell repair is occurring in large mussels in different seasons, or if the evidence of shell repair in large mussels is just an artifact from repair when the mussel was smaller (medium).

Continued investigation in latitudinal differences in mussel life history characteristics would be beneficial to expand our current understanding of mussels and could potentially be used to predict coastal regime shifts in response to the effects of climate change (e.g., sea level rise and ocean acidification). Mussels play a critical role in maintaining water quality by removing pollutants, sediment, nutrients, algae, and *Spartina* detritus from the water column (Kreeger et al. 1988, Kreeger et al. 1990, Kreeger and Newell 1996). Unlike other mussel species (such as *M. edulis*) *G. demissa* also assimilate a significant amount of carbon from bacteria (Kreeger and Newell 1996) and is recognized as a good candidate for use in cultivation-based bioextraction purposes, especially for highly impacted coastal ecosystems (Kreeger et al. 2011, Galimany et al. 2013). In the Great Sippewissett Marsh in Massachusetts, *G. demissa* filter a volume of water in excess of the tidal volume of the marsh each tidal cycle (Jordan and Valiela 1982). Each year, the mussels filter 1.8 times the particulate nitrogen exported from the marsh by tidal flushing, half of which is absorbed by the mussels and half deposited as feces or pseudofeces (Jordan and Valiela 1982). In Georgia, *G. demissa* filter a third of the suspended particulate phosphorus daily, and deposit most of it as feces and pseudofeces (Kuenzler 1961a). Mussels reduce turbidity through feeding and physically trapping suspended particles. The large amount of pseudofeces deposited is then available as a food source for benthic organisms or is cycled into inorganic forms that *Spartina* can use for growth (Jordan and Valiela 1982, Espinosa et al. 2008). Soil nitrogen in tall form *S. alterniflora* is significantly increased when *G. demissa* are present (Bertness 1984). *G. demissa* play a vital role in preventing salt marshes from succumbing to sea level rise by preventing erosion and significantly contributing to vertical marsh accretion. Without mussels, vertical marsh accretion on the marsh flat is roughly 0.66 cm/year, while with mussels present accretion nearly doubles to around 1.16 cm/year (Bertness 1984). As global temperatures rise, predation pressure on mussels increases while mussel defense decreases. The ocean's pH has decreased by 0.1 units since the industrial revolution, and is predicted to decline by another 0.3-0.4 units by the end of the 21st century (Caldeira and Wickett 2005). A 0.4 change in pH corresponds to a 50% reduction in the concentration of carbonate ions required by calcifying organisms (e.g., bivalves) to create shells (Caldeira and Wickett 2005). Mussels grown in elevated

CO_2 conditions have reduced calcification rates, however, predators, such as blue crabs, show the opposite response and have elevated calcification rates in acidic conditions (Ries et al. 2009). The effect of pH on shell repair in mussels has yet to be determined, but in gastropods increased acidity depressed shell repair rate, compromised shell integrity, and reduced overall snail condition (Coleman et al. 2014). As oceans become more acidic, mussels become weaker and decapod predators become stronger, altering existing predator-prey dynamics and potentially creating an alternative stable state. However, effects of an altered CO_2 balance do not consistently favor decapod predators over bivalve prey. Mud crabs (*P. herbstii*) feeding on juvenile eastern oysters (*C. virginica*) consumed fewer oysters in elevated CO_2 treatments (Dodd et al. 2015a). The suggestion was crab sensory organs were damaged in the acidic conditions leading to a less effective predator. A consensus as to the effects of changing ocean pH on decapod predator and bivalve prey relations and community dynamics is yet to be reached but continued investigation would be beneficial. Decreases in mussel populations in coastal salt marshes is extremely detrimental to the health of coastal ecosystems; salt marsh degradation along the southern Gulf of St. Lawrence in Nova Scotia, Canada is correlated with declining *G. demissa* populations and sea level rise (Watt et al. 2011). Further research is needed for a fuller understanding of the changes in these systems and to aid in preventing population and subsequent ecosystem collapses.

Sublethal shell damage significantly affected survivorship and growth of mussels. In most cases, growth was further suppressed with increased damage. Shell repair was evident in damaged mussels collected from the field, but in the growth experiment only medium, moderately-damaged mussels repaired shells. Medium, moderately-damaged mussels also experienced the highest mortality rate, suggesting mussels enter a critical stage around 55 mm with increased energy demands for both growth and repair. Small mussels eschewed repair and focused entirely on growth, as larger sizes create a refuge from predation. Surprisingly, large mussels did not exhibit any signs of shell repair, and also had minimal growth. The variance in response to sublethal predation across size and damage treatments likely contributes to population and community dynamics in the important salt marsh denizen, *G. demissa*.

Chapter 2: Do crabs preferentially select damaged mussels?

Abstract:

Atlantic blue crabs (*Callinectes sapidus*) are voracious predators, yet routinely select prey, such as the ribbed marsh mussel (*Geukensia demissa*), that are the easiest to open instead of the most profitable (calories gained per unit effort). Crabs prefer smaller mussels with thinner shells, and can even detect and exploit weakened areas on shells. Weaknesses in shells may be from shell damage inflicted by previous predation attempts. Mussels with damaged shells may involuntarily leach metabolites into the surrounding environment, expediting the discovery by the olfaction-driven blue crabs. Once encountered, the damaged mussels would be easier for crabs to successfully open and consume than undamaged counterparts.

A series of wet lab mesocosm experiments and field trials were conducted to determine if crabs target damaged mussels. In wet lab mesocosms, crabs consumed damaged mussels in 68% of all successful predation attempts. However, this preference was not always observed in the field and may have been masked by various environmental factors. Undamaged mussels survived significantly longer than damaged mussels in the mid-marsh, but were consumed at equal rates on mudflats, oyster reefs, and in the low-marsh. Mussel survival was highest overall in the mid-marsh where limited inundation time and dense *Spartina alterniflora* stems impeded access of large

predators, such as blue crabs. Large mussels (>60 mm) also survived significantly longer than medium (50-60 mm) and small (20-30 mm) mussels. Larger and thicker shells are more difficult for crabs to break open and may even be avoided altogether.

Both crabs and mussels play important roles in maintaining healthy salt marsh systems; changes in either population or the dynamic of the predator-prey relationship could have dramatic consequences. Anthropogenic impacts on the environment such as pollution, overfishing, habitat destruction, and various effects of climate change (e.g., temperature rise, ocean acidification, sea level rise, etc.) threaten blue crab and mussel populations. The ability to detect weakened mussels may be increasingly important as environmental conditions deteriorate, therefore further investigation into the apparent dichotomy in crab preferences observed in the wet lab versus in the field is warranted. Continued research should examine effects of crab proximity to mussel metabolism, whether crabs can target damaged mussels using olfaction instead of touch, the maximum distance crabs are able to detect damaged versus undamaged mussels, and if the apparent lack of field preferences are similarly observed in areas with lower crab densities.

Introduction:

Optimal foraging theory predicts predators should select the most profitable prey: maximizing calories gained while minimizing time and expended energy (Charnov 1976). With some exceptions (e.g., humans), organisms that maximize caloric intake survive longer and reproduce more often than organisms consuming fewer calories (Lemon and Barth 1992). However, many organisms sacrifice short-term caloric gains in order to increase survivability. For example, mesopredators may select the prey easiest to obtain and consume because reduced handling and foraging times decreases the risk of being predated upon.

Blue crabs appear able to account for handling time, prey location, prey refuge use, and the risk of claw damage in assessing optimal prey, however, the importance of each factor in prey selection is not resolved. Juvenile blue crabs were able to select the most profitable snail species (in terms of calories per crushing resistance) in both laboratory and field settings, although the degree of selectivity varied by crab size and season (Cote et al. 2001). Molluscivore decapods, including blue crabs, frequently forage selectively on prey with thinner shells (e.g., Palmer 1985, Robles et al. 1990a, Haugum et al. 1999, Caro and Castilla 2004) or smaller sizes (e.g., Hughes and Seed 1981, Boulding 1984, Robles et al. 1990b, Juanes 1992, Aronhime and Brown 2009, Silva et al. 2010, Canton 2011) even if capable of consuming thicker, larger prey. Increased mechanical costs (e.g., claw damage) or longer handling times can explain why crabs choose smaller, thinner-shelled prey (Dietl 2003, Rutten et al. 2006, Aronhime and Brown 2009). Minimizing foraging time is beneficial to crabs because it reduces exposure to predators and allows for increased time spent on other activities, such as searching for mates.

Mussels with damaged shells may be preferentially selected by blue crabs because damaged mussels may be easier to locate and easier to open than undamaged mussels. Blue crabs primarily are olfactory-driven predators and can detect homogenates prepared from tissues of bivalve prey at concentrations as low as 10^{-15} g/L (Pearson and Olla 1977, Weissburg and Zimmer-Faust 1993). Crabs actively migrate to maximize foraging efficiency (Griffen 2009) and are responsive to the overall quality of prey, altering prey patch use depending on the quality (e.g., calories, health, and species) and quantity of available prey items (Clark et al. 2000). Crabs navigate turbulent plumes by moving upstream in response to odor (odor-gated rheotaxis) while maintaining contact with the plume through spatial sampling (tropotaxis) (Keller et al. 2003). When crabs reach sedentary bivalve prey, such as *G. demissa*, tactile sensory organs on the inner faces of the crabs' walking legs and chelae allow the crabs to detect and pick out individual mussels (Seed and Hughes 1997). Damaged mussels involuntarily may release more metabolites compared to undamaged mussels (Vermeij 1983) so may be easier for blue crabs to detect. Thinner, more easily cracked shells resulting from sublethal predation also may lead to preferential selection of damaged mussels by crabs (Hughes and Elner 1979, Boulding 1984, Tucker et al. 1997, Beadman et al. 2003a, Fisher et al. 2011). Crabs also are able to detect and exploit weakened areas on shells (Elner 1978, Hughes and Seed 1981). Even inconspicuous damage weakens shells (Blundon and Vermeij 1983) likely resulting in targeting by crabs.

Although "weakened" mussels are exploited by blue crabs (Elner 1978, Hughes and Seed 1981), the origins of mussel "weaknesses" (e.g., shell damage) were not stipulated. The objective of this experiment was to determine the Atlantic blue crab's ability to distinguish between damaged and undamaged mussels. Crab predation preference was examined in a series of wet lab mesocosm experiments as well as in controlled mesocosm experiments on mussel distributions across the salt marsh environment in the field. Damaged mussels should be selected preferentially by blue crabs in the wet lab mesocosms and the time required to breach mussel defenses should be shorter. Mussels in low marsh sites should experience increased mortality because increased tidal inundation will increase exposure to predators (Lin 1989b). Damaged compared to undamaged mussels also should experience increased mortality because crabs are able to detect more easily and quickly consume damaged mussels.

Methods:

Crab preference mesocosm experiment:

Crab feeding preference experiments were conducted at the Baruch Marine Laboratory in the North Inlet National Estuarine Research Reserve. Damaged and undamaged mussels were offered to blue crabs (*C. sapidus*) within flow-through seawater tanks in a series of trials. Undamaged mussels (50-60 mm) were collected from rock bulkheads protecting a causeway over Eden Saltworks Creek near Waties Island, South Carolina and either were left undamaged or were damaged extensively using a Dremel® rotary tool and sanding drum (Hillard and Walters 2009). Damage was generated on 2/3 of the shell closest to the growing lip on both valves by sanding the periostracum and underlying crystalline layers until ridges were no longer visible. Mussels damaged using this technique have significantly thinner shells than undamaged mussels (see experiment *Consistency of shell damage treatments* in Chapter 1). Blue crabs caught using hand dip nets at Oyster Landing in the North Inlet-Winyah NERR, SC were starved for three days in individual plastic containers (21x14x10 cm). Previously used crab starvation periods to standardize hunger levels range between one to four days (Weissburg and Zimmer-Faust 1993, Zimmer-Faust et al. 1996, Micheli 1997, MacDonald et al. 2007, Aronhime and Brown 2009). Initial trials identified three days as sufficient to motivate crab feeding without contributing to substantial crab mortality. After starvation, crab feeding preferences were tested in large circular flow-through tanks (1 m dia; 1 m ht sides with 10 cm of water) with the incoming flow of raw seawater restricted (could not be completely stopped, but was reduced to periodic dripping) to minimize the possibility of any directional flow effects on crab feeding. During experiments tanks were not filled with sediment because during initial trials sediment became suspended and restricted vision. Vision was also impaired if trials occurred during dawn and dusk, typical periods of increased crab feeding activity (Nye 1989, Wolcott and Hines 1989). Instead, feeding trials were conducted during the rising and early high tide, as 24 h stomach content sampling of crabs found the fullest stomachs during high tides (Ryer 1987). Six mussels were measured to determine length and width were spaced evenly around the circular tank walls alternating between damaged and undamaged treatments. A crab was placed in the center of the tank and the time and nature of all activity recorded. After a mussel was consumed the crab was removed and carapace width (from point to point) and dominant claw length measured. The majority of crabs tested were male (79%) simply because fewer females were captured in the field. Similar to MacDonald (2007), if a crab failed to attack a mussel within 30 minutes of being introduced into the tank, the trial was ended and the crab removed and measured. In preliminary trials crabs that did not eat within the first 30 minutes did not feed even after 4+ hours. After each trial any mussels handled by a crab were discarded and any untouched mussels were returned to the pool of potential mussels. To remove any lingering chemical cues between trials tanks were drained completely, flushed with raw seawater, and refilled for the next trial (see MacDonald et al. 2007). A total of 100 crabs were tested and each crab was allowed to consume only one mussel to prevent potential experience and satiation effects on prey selection (Jubb et al. 1983, Micheli 1997).

Predation on mussels across marsh zones:

Tethering experiments were conducted across four marsh zones to determine if size and shell damage affects mussel survivability and if those effects are consistently found throughout the different marsh zones. Undamaged mussels (n = 100) from each size class (small = 20-30 mm; medium = 50-60 mm; large = >60 mm) were collected from Waties Island, SC (see above), and half in each size class were damaged extensively (see above). Individual mussels were attached to a tether using marine epoxy, zip-ties, and twine, and the tethers attached along four 20 m transects at Clambank Landing in the North Inlet-Winyah NERR. Transects were located on an intertidal oyster reef, along a low-marsh mud flat, at the edge of a tidal creek within a stand of tall *Spartina alterniflora*, and in the mid-marsh within a stand of tall *S. alterniflora*. All transects were oriented parallel to the nearest tidal creek. Mussels haphazardly selected were buried every ≈25 cm within the sediment on alternate sides of the transect. Along each transect 12 damaged and 12 undamaged mussels of each size class were tethered. Additional mussels were tethered inside a mesh cage (0.64 cm Vexar® 10-15 cm in diameter and roughly 50 cm tall) to evaluate potential tether or mussel loss as a control. The size and treatment condition of individual mussels along the transect was recorded during placement. Tethers did not seem to restrict normal mussel behavior, including vertical burial within the sediments, but greatly aided in relocating individuals to determine survival. Each week for four weeks tethers were checked and surviving mussels identified. The weekly interval was selected based on a previous study where similarly tethered mussels left unburied reported 90% survival 5 days and 60% survival after 30 days (Walters 2009). Broken or empty shells still attached to tethers and tethers unattached to mussels after a search of the nearby vicinity did not locate the previously tethered individual all were classified as dead. Although missing mussels may not be dead, similar tethering approaches successfully have identified relative differences in predation pressure on bivalves using this technique (Clark et al. 2003, Eggleston et al. 2005, Orth et al. 2007, Walters 2009).

Refuge effect on mussel predation:

Tethering experiments were conducted on oyster reefs and adjacent mud flats to determine if shell damage and habitat complexity affects mussel survivability. Undamaged medium (50-60 mm) mussels (n = 72) were collected from Waties Island, SC (see above), and 50% were damaged extensively (see above). Mussels were tethered (see above) and placed in the field at three paired mud flat and reef sites along Bly Creek within the North Inlet-Winyah NERR, SC. Individual mussels were tethered around PVC stakes buried in the sediment on either side of each oyster reef or the paired, similarly sized mudflat areas. Damaged and undamaged mussels were attached to the stakes on either the left or right side of reefs and mudflats. Each stake was covered for a week with a Vexar® mesh cage (see above) and buried in the sediment to prevent predation and minimize any confounding effects during the experimental set-up (e.g., sediment disturbance attracting predators). After a week cages were removed and mussel survival monitored daily.

Shell damage effect on mussel predation in the mid-marsh:

Tethering experiments were conducted within the mid-marsh to determine if shell damage affects mussel survivability. Undamaged medium (50-60 mm) mussels (n = 36) were collected from Waties Island, SC, and 50% were damaged extensively (see above). Mussels were tethered with Loctite® Gel Super Glue and monofilament fishing line (see Puntila et al. 2012). PVC stakes were haphazardly placed in the mid-marsh along Bly Creek within the North Inlet-Winyah NERR, SC. Half of the stakes were tethered with damaged mussels and the other half were tethered with undamaged mussels. Mussel survival was monitored every low tide for seven tidal cycles.

Statistical Analysis:

Results from male and female crabs were combined for analysis because size (carapace width, t_{12}=0.926, $p > 0.05$) and handling times (t_9=1.064, $p > 0.05$) did not differ, similar to previous studies (Seed and Hughes 1997). Hierarchical Loglinear Analysis using a backward elimination approach (Agresti and Kateri 2011) was used to determine if crab size, mussel size, and mussel shell damage had an effect on crab predation preference, and a separate Hierarchical Loglinear Analysis was used to determine if mussel shell damage affected whether crabs consumed the first mussel touched. T-tests were used to compared crack times (time it took for crabs to crack mussels open) and handling times (time it took for crabs to open and completely consume mussels) between damaged and undamaged mussels.

Hierarchical Loglinear Analysis was also used for the various tethering experiments. The effect of mussel size (small, medium, large), shell damage (undamaged, damaged), habitat (mudflat, oyster reef, low-marsh, mid-marsh), and time (weeks) were analyzed in the predation of mussels across marsh zones experiment to determine effects on mussel survivorship. The effect of refuge was similarly analyzed and included shell damage (undamaged, damaged), habitat (mudflat, oyster reef), and time (weeks), but did not include mussel size in the model, as all mussels were the same size. Predation in the mid-marsh was simply analyzed with respect to time (tidal cycle) and damage (undamaged, damaged).

Results:

Crab preference mesocosm experiment:

Out of 100 crabs tested, only 44 successfully consumed a mussel. Twenty-two crabs attacked mussels but failed to open them and the remaining 34 crabs were inactive. Sixty-eight percent (30) of consumed mussels were damaged (Figure 15). Crab size and mussel size had no effect on crab predation preferences; only shell damage had a significant effect ($X^2 = 5.344$, df = 1, $p<0.05$). The first mussel the crab touched affected consumption ($X^2 = 112.0$, df = 1, $p<0.01$). Seventy-three percent of mussels that were consumed were the first mussels the crab attacked, but only 49% of first touched mussels were consumed. Shell damage, although significantly affecting mussel consumption ($X^2= 5.502$, df = 1, $p<0.05$), did not affect the first mussel chosen by crabs. Only 54% of the first-touched mussels were damaged, but 68% of mussels that were eaten were damaged. Crab handling and cracking times were longer for undamaged mussels than damaged mussels (handling: 18.4 vs 17.8 mins; cracking: 8.0 vs. 6.4 mins) though were not significantly different (Figure 16; handling: t_{42}=0.114, $p>0.05$; cracking: t_{41}=0.445, $p>0.05$). There was no crack time reported for one trial because the crab snuck up on a gaping mussel and inserted a chela between the shell valves. The crab was then able to rip the mussel in half without cracking or damaging the shell.

Predation on mussels across marsh zones:

After one week, only 11.8% of the 288 mussels deployed in the field were still alive and attached to tethers. Only one large undamaged mussel survived on the mud flat, three undamaged mussels (two large, one small) survived in the low marsh, and six mussels survived on the oyster reef (varying sizes and damage treatments). The mid marsh, as expected, had the highest survival rate (33.3%), but still experienced dramatic mortality, and after five weeks every tethered mussel had been consumed (Figure 17). There were no differences between damaged and undamaged survivors in the mid-marsh after one week- exactly half of the survivors were damaged (12 out of 24). There were significant differences in size, however (X^2= 10.28, df=2, $p<0.05$). The majority of survivors in the mid marsh were large mussels (62.5%). Only three (12.5%) small mussels were still alive after one week, but by the second week all of the small mussels had been eaten.

Refuge effect on mussel predation:

After one week only 9.7% of the 72 mussels deployed in the field were still alive and attached to tethers (Figure 18). All of the surviving mussels were damaged mussels on reefs. The habitat by week interaction (X^2= 16.489, df=2, p<0.001) and damage by week interaction (X^2=12.075, df=2, p<0.01) were both significant.

Shell damage effect on mussel predation in the mid-marsh:

After two low tides (one day), 72% of the mussels deployed in the field were still alive and attached to tethers (Figure 19). Shell damage significantly affected mussel survivability (X^2=27.83, df=1, p<0.001). Of the surviving mussels, 75% were undamaged and 25% were damaged. After three low tides all of the damaged mussels had been consumed, while 39% of undamaged mussels survived. By the end of the experiment, two undamaged mussels survived (11% of initial undamaged mussels).

Discussion:

In mesocosms, crabs did not always initially target damaged mussels but consumed significantly more damaged than undamaged mussels. The lack of water flow within the tanks made olfaction-guided prey selection difficult. Instead, it appeared weakened mussels were identified by touch. Typically, crabs would move around the perimeter of the tank and attack each mussel encountered (see Seed and Hughes 1997). If the crabs experienced motivational cues (Abby-Kalio 1989), such as shell cracking, the crabs would continue attacking the mussel until the motivational cues dissipated or until the mussel was successfully opened and consumed. Since damaged mussels had thinner (i.e., weaker) shells (Beadman et al. 2003a), damaged mussels were easier for crabs to damage further encouraging continued attacks. If crabs attacked an undamaged mussel first and were not able to damage the shell, the lack of motivational cues spurred the crabs to move on to the next mussel (58% of undamaged mussels that were touched first were not eaten). In almost every case, if a crab stopped attacking the first mussel touched but successfully opened a different mussel, the mussel consumed was a damaged mussel (83%).

The initial target of crab predation significantly affected consumption. The majority (73%) of crabs that successfully consumed a mussel ate the first mussel encountered. Similarly, starved *Carcinus maenas* indiscriminately consumed the first mussel encountered, but began rejecting certain prey within thirty minutes, preferring mussels ~25 mm (Jubb et al. 1983). Overall, however, only 49% of first touched mussels were consumed. Many crabs attacked one or more mussel without successfully opening any. Crab size did not influence success as the average size difference between successful and unsuccessful crabs was <1 mm. Instead, success appears predominantly influenced by the initial prey item. Undamaged mussels were targeted more frequently by unsuccessful crabs than by successful crabs (55% vs 33%). Attacks on undamaged mussels may produce fewer motivational cues discouraging prospective predation. However, 45% of unsuccessful crabs targeted damaged mussels and still failed. Crabs are able to improve handling efficiency through experience (Cunningham 1983, Abby-Kalio 1989, Hughes and O'brien 2001) and preferentially select familiar prey (Micheli 1995, 1997). The unsuccessful crabs may have lacked mussel expertise and consequently struggled with handling unfamiliar mussels, or could have given up after expending too much energy. Crabs handling less preferred prey also have shorter "giving-up" times than when handling favorite prey (Micheli 1995). Many crabs did not even attempt to open mussels even after being starved for three days. Crabs feed in distinct feeding bouts several times a day (Nye 1989, Wolcott and Hines 1989) and are attracted by chemical cues released by prey. When crabs are not feeding, prey effluent does not initiate foraging behavior, even at elevated concentrations and in close proximity (Zimmer-Faust et al. 1996). The mesocosms themselves may affect crab behavior; stressed, vulnerable crabs may intentionally reduce activity levels to hide from potential predators. To increase instances of crab predation attempts, future studies should consider only testing active crabs in a more natural setting.

Cracking and handling times did not reflect crab preference for damaged mussels. Differences in cracking and handling times between damaged and undamaged mussels were not significant. Abundance of prey items and lack of predators or competitors may have contributed to a leisurely foraging pace. Blue crabs are extremely antagonistic and the presence of conspecifics will often alter or disrupt foraging activity (Clark et al. 1999a, 1999b). There was also a great deal of variation in cracking and handling times between crabs. Some crabs were able to crack shells open within minutes, while others had to manipulate shells for up to 43 minutes before succeeding. There were also twice as many damaged mussels consumed than undamaged, so the average handling and cracking times of each group were not equally precise. If damaged mussels are not significantly easier to crack open, instead of responding to tactile cues crabs may be reacting more to olfactory or visual cues. Damaged mussels may leach more metabolites than undamaged mussels, and the white shells of freshly damaged mussels are strikingly visible compared to the dull brown/grey/green shells of the undamaged mussels. However, further examination into differences in handling times between damaged and undamaged mussels is needed before the mechanism governing crab prey selection can be resolved.

The presentation and size of mussels had minimal impact on crab choice. The size preference bias of the crabs was successfully mitigated in this study by using mussels within the same size class (50-60 mm). Blue crabs prefer smaller prey (e.g., Hughes and Seed 1981, Boulding 1984, Robles et al. 1990b, Juanes 1992, Aronhime and Brown 2009, Silva et al. 2010, Canton 2011), however in this study the crabs chose the smallest mussel in only 25% of successful predation events, and only initially targeted the smallest mussel in 13% of trials. Crab predation techniques differ when presented mussels individually or in groups (Burch and Seed 2000). When presented in groups, crabs do not use boring or edge-chipping techniques, handling times are reduced, and the percentage of flesh left uneaten on discarded shells is significantly greater than on mussels presented individually (Burch and Seed 2000). By presenting the crabs with multiple ungrouped mussels, individual predation techniques (e.g., edge-chipping, less uneaten flesh) were still observed. However, even if mussels were presented in groups (i.e., in piles instead of separately) the specific group predation techniques (e.g., crushing) may not have been observed because most of the crabs were not large enough to outright crush mussels.

Crab preference for damaged mussels was not always observed in the field experiments, although a size preference was. Large mussels, regardless of damage treatment, survived longer than medium and small mussels in the mid-marsh. Mortality was too great in the mudflat, reef, and low-marsh to distinguish effects of damage or size. Reduced access of large predators in the mid-marsh likely resulted in the increased survival of large mussels; dense *Spartina* stalks and limited inundation time made it more difficult for large predators to reach and consume the large mussels, while smaller predators were able to more easily move through the *Spartina* and reach the small and medium mussels. Atlantic mud crabs (*P. herbstii*) were even observed attacking small tethered mussels during low tide when the mussels were exposed. Mussels on the oyster reef survived longer than on mudflats in both the across marsh zones experiment and in the refuge experiment. The oyster reefs provided more refuge from predators than the mudflat because of the structural complexity- mussels are typically buried in sediment between clumps of oysters, which reduced predator accessibility (Seitz et al. 2001). Crabs foraging on oyster reefs also have a myriad of other prey items (e.g., oysters, other mussel species, fish) to choose from, however the strong chemical cues emanating from the abundant prey items on the reef may attract additional predators to the area, inflating predation rates.

The effect of shell damage on mussel predation in the mid-marsh varied by location. Damage did not have an effect on predation in the mid-marsh along a small tidal creek connected to Clambank Creek, since damaged and undamaged mussels were consumed at an equal rate. Within medium mussels, the damaged mussels even survived longer than the undamaged mussels, with 11% of damaged mussels surviving until week four while all of the undamaged mussels had been consumed by week two. However, in the mid-marsh along Bly Creek damaged mussels were consumed at a much greater rate than undamaged mussels, and it was the undamaged mussels that survived until the end of the experiment (similarly with 11% surviving until the end). The larger quantity of damaged mussels in the across marsh zones experiment may have attracted opportunistic predators to the area. In the mesocosm experiment crabs often consumed the first mussel touched, so maybe this preference was also occurring in the marsh. It is also possible that other predators, such as stone crabs (*Menippe mercenaria*), do not show preferences for damaged mussels, and so the non-selective predation of other predators could mask any preferences *C. sapidus* show in the field. The size and abundance of predators within the two creeks may also affect predation rates, however, the size of the creek channel did not reflect predation pressure as expected since the smaller creek experienced the greatest amount of mussel mortality. Clambank Creek is closer to the ocean than Bly Creek and so may have longer inundation times offering predators more time to access and consume mussels.

Caging tethered mussels prior to the start of the refuge experiment did not significantly reduce predation. Sediment disturbance caused by the initial setup of the across marsh zones experiment may have unintentionally attracted additional predators, artificially increasing mussel mortality. For the refuge experiment, cages were placed over mussels for a week prior to the start of the experiment, presumably so the mussels could acclimate (e.g., attach byssus threads, feed normally, reduce or eliminate excretions of potential stress/fear pheromones) and any environmental disturbance caused by the setup could dissipate. The acclimation period resulted in reduced, although still substantially high, mortality rates compared to the first tethering experiment (9.7% versus 4.9% surviving after the first week). In most cases (92%), mussel mortality within each site and treatment was greater than one mussel per day. And in many cases (75%), mussel mortality was over 80% after just one day. In one instance, it appeared as though the entire cluster of mussels had been consumed by a ray because the location of the mussels had been engulfed by a large pit, presumably a ray feeding pit. Damaged mussels survived longer than undamaged mussels both on the reef (e.g., 50% vs. 5.6% by day three) and the mudflat (e.g., 33% vs. 5.6% by day three), but neither damage or habitat type were predictors of mussel survivability, both had significant interactions with time (weeks).

The predation rates observed in this study were much greater than anticipated based on the results of a similar tethering study conducted in the Kamehameha salt marsh near Kings Bay, GA, wherein undamaged tethered *G. demissa* had a survival rate of 60% after 30 days (Walters 2009). Damaged mussels may have attracted predators to the area to inflate predation rates, or simply the study site may have been home to more predators than Kamehameha- North Inlet is a protected location where commercial and recreational crab harvesting is illegal. In either case, the elevated predation rates, although not expected, are not unusual. Estuarine shorelines with low water flow, such as the location of this study, are often characterized by high crab predation rates (Leonard et al. 1999). In the Gulf of Maine almost all (97%) tethered mussels (*M. edulis*) were consumed by crabs (*C. maenas*) after only two days at river low-flow sites, while only 29% of mussels were consumed at open-coast high-flow sites (Bertness et al. 2004).

Another factor that could have influenced the varied predation rates seen in the field trials is the patchiness of prey availability. Many prey species, such as *G. demissa*, are found primarily in an aggregated distribution throughout the salt marsh (Bertness and Grosholz 1985). The mussels clustered together form prey patches which crabs are able to analyze for quality and selectively forage upon (Clark et al. 2000). Crabs are also highly sensitive to consumption rates and will move to a more profitable prey patch when consumption rates drop (Griffen 2009). However, blue crabs are extremely agonistic and in high densities interfere with foraging success (Clark et al. 1999b). Even in low densities blue crab foraging is impeded by agonistic displays. In tank feeding trials with three crab species, *C. sapidus* lost to the other crab species in competition for food, and in many trials would go into an aggressive display with claws out while another crab found and consumed the food (MacDonald et al. 2007). On average, blue crabs spend 2% of time engaging in agonistic behaviors (e.g., meral spreading), and have been observed spending up to 40% of time in meral spread posturing, which is among the highest occurrence of threat display reported for arthropods (Clark et al. 1999a). When prey is partitioned into two patches, blue crabs at high densities disperse among the patches to minimize agonistic clashes (Clark et al. 1999b). When approached by conspecifics, crabs moved to adjacent prey patches instead of taking refuge in interpatch space (Clark et al. 1999b). In the mussel tethering experiments, blue crabs may have been attracted to damaged mussels, but when multiple crabs attempted to forage on the patch of damaged mussels, agonistic encounters, or retreat in the interest of avoiding agonistic encounters, led to crabs moving off the damaged patch and on to the adjacent undamaged patch.

Shell strength may not be the primary determinant of mussel defense. As discussed in Chapter 1, mussels rely on clumping, byssal thread and adductor muscle strength, and burial as defensive mechanisms. Mussels also may reduce pumping in the presence of predators to avoid detection. Although the purpose of this study was to single out the effects of shell damage on crab choice, a more holistic approach may be needed to translate those choices into actual crab predation strategies in the salt marsh.

Changes in predator-prey relations between blue crabs and mussels could have dramatic consequences to the health of salt marsh ecosystems. Atlantic salt marsh systems are structured in part by the top-down control of blue crabs. Plants benefit from crab predation on herbivores (Marczak et al. 2011), and the recent "die-offs" of Southeastern *Spartina* marshes is suspected to be caused by a decline in blue crab numbers (Silliman and Bertness 2002, Silliman et al. 2005). Anthropogenic impacts on the environment such as pollution, overfishing, habitat destruction, and the various effects of climate change (e.g., temperature rise, ocean acidification, sea level rise, etc.) threaten blue crab populations. Human development of watersheds reduces blue crab abundance (Seitz et al. 2003, King et al. 2005). Hypoxia initiation and expansion in many areas is accelerated by human activity, especially when related to eutrophication (Rabalais et al. 2010). Blue crab densities are zero in anoxic waters and both juveniles and adults avoid hypoxic waters (Pihl et al. 1991, Das and Stickle 1994, Bell et al. 2003). Impaired habitats support fewer individuals and exacerbate the problem of overfishing (Lipcius and Stockhausen 2002), which in turn can cause further damage to important habitats, such as oyster reefs (Toscano and Griffen 2012). Ocean acidification impairs crab predation (Dodd et al. 2015b) and reduces prey condition (Coleman et al. 2014). Ocean warming facilitates nonindigenous species invasions (Stachowicz et al. 2002), and even though estuarine species are typically hardy and can withstand great variations in temperature, estuaries are still susceptible to invasion (Cohen and Carlton 1998) and blue crabs have some disadvantages compared with exotic sympatric crab species (MacDonald et al. 2007). Despite the agonistic tendencies of blue crabs, when matched up against invasive crab species (*C. maenas* and *Haemigrapsus sanguineus*) blue crabs lost a disproportionate number of times (MacDonald et al. 2007). Crab invasions recently occurred in New England rocky intertidal habitats to the detriment of local fauna (e.g., Lohrer et al. 2000, Lohrer and Whitlatch 2002, Griffen and Byers 2009). The invasion by *H. sanguineus* of an earlier invader, *C. maenas*, resulted in reduced *C. maenas* and *M. edulis* populations (Lohrer and Whitlatch 2002). Although *H. sanguineus* is a relatively small crab, individuals can eat up to 215 juvenile mussels in a day and with densities occasionally exceeding 150 crabs m^{-2} are a significant threat to mussel populations (Lohrer and Whitlatch 2002). As discussed in Chapter 1, the ability of salt marshes to stave off sea level rise is directly affected by *G. demissa*, and reductions to mussel populations could be extremely detrimental to the entire ecosystem.

Although blue crabs are able to target damaged mussels in mesocosms, a preference for damaged mussels was not clearly observed in field tethering experiments. Further investigations into the cause of the dichotomy can look at effects of crab proximity to mussel metabolism, whether crabs can target damaged mussels using olfaction instead of touch, and if the apparent lack of field preferences are similarly observed in areas with lower crab densities. When crabs are nearby, mussel valves are shut to impede detection and consumption. However, damaged mussels may still produce noticeable chemical plumes if metabolites are able to leach through the damaged shell (Vermeij 1983). How close a crab needs to be to a mussel to induce the valve-shutting and if the crab can still detect and locate a damaged mussel will determine the ability of a crab to target damaged mussels in the field. Shell damage did not seem to have a significant effect on predatory-mortality in areas with high predator abundance, but perhaps would have more of an impact in areas with fewer (thus more selective) predators.

Conclusions:

Sublethal predation is consequential to salt marsh ecosystem dynamics. Survivors of predation attempts often suffer from reduced growth, reduced reproductive output, and increased mortality rates (e.g., Geller 1990, Coen and Heck 1991, Kamermans and Huitema 1994, Irlandi and Mehlich 1996, Lomovasky et al. 2006, Hillard and Walters 2009). Predators may also have greater success locating and consuming prey that had previously been predated upon (e.g., Covich et al. 1981, Kamermans and Huitema 1994, Meyer and Byers 2005, Fodrie et al. 2008, Cledón and Nuñez 2010). To ameliorate the negative effects of sublethal predation, the marsh mussel, *G. demissa*, can deposit internal shell layers to compensate for exterior shell loss (Alexander and Dietl 2001). Shell repair, however, is not an automatic response because it is energetically costly and must be evaluated against other priorities, such as reproduction and growth (Geller 1990, Palmer 1992, Alexander and Dietl 2001, Brown et al. 2004, Lomovasky et al. 2005). This thesis evaluated the interactions between the extent of shell damage and size-dependent tradeoffs in marsh mussel growth and repair, and determined if crabs target damaged mussels.

Damaged *G. demissa* collected from two South Carolina inlets displayed evidence that shell repair had occurred. Shell damage ranged from 0% (Hog Inlet) to 50% (Murrells Inlet). The presence of exterior shell damage was not a good predictor of strength, as damaged shells were equally as strong as undamaged shells. The damaged shells were, however, thicker than undamaged shells, indicating that shell repair had occurred. Shells damaged experimentally using a Dremel® rotary tool and sanding drum were significantly thinner than undamaged shells and had less shell mass. Using a rudimentary hand-made crushing device, damaged shells were slightly weaker than undamaged shells, but not significantly. Presumably using a more accurate strength-measuring instrument would reduce variation and either find significant differences between the damage treatments or confirm the lack of strength differences.

Shell damage reduced growth and increased non-predatory mortality in mussels during the summer. In most cases, increased damage suppressed growth, however, the data only found evidence of repair in medium, moderately-damaged mussels. Medium, moderately-damaged mussels also experienced the highest mortality rate, suggesting mussels enter a critical stage around 55 mm with increased energy demands for both growth and repair. Some medium, extensively-damaged mussels had repairs along the shell margin, but these repairs seemed to only occur if needed for continued growth, and repairs were not present throughout the rest of the damaged area. Small mussels eschewed repair and focused entirely on growth, as larger sizes create a refuge from predation. Surprisingly, large mussels did not exhibit any signs of shell repair, and also had minimal growth.

Blue crabs targeted damaged mussels in mesocosm experiments, but this preference was not always observed in the field. In mesocosms shell damage and the first mussel a crab touched were significant in determining whether a crab would consume a mussel. Crabs were more likely to consume the mussel first touched (73%) and damaged mussels (68%), and if the initial mussel was rejected the mussel eventually eaten was usually a damaged mussel (83%). The preference for damaged mussels was not as strongly observed in tethering experiments, although perhaps the preference for mussels touched first was. Shell damage did not have an effect on survivability in the across marsh zones experiment, although large mussels survived significantly longer than small and medium mussels in the mid-marsh as the dense *Spartina* stalks and shorter inundation time provided protection against larger predators (Vince et al. 1976, Arnold and Kneib 1983, Minello and Zimmerman 1983, Lin 1989b, Lee and Kneib 1994, Tucker et al. 1995, Tucker et al. 1997). Damaged medium mussels, surprisingly, survived longer on oyster reefs and on mudflats than undamaged medium mussels, but undamaged medium mussels survived longer than damaged medium mussels in the mid-marsh. Predation by other predators coupled with the blue crab's predisposition to attack and consume anything encountered likely overshadowed any blue crab predation preferences.

Future studies should investigate possible seasonal and marsh-specific trends in mussel shell repair as well as the cause for the perceived dichotomy in crab predation preferences. Large, damaged mussels collected from South Carolina marshes displayed signs of shell repair, but experimentally damaged large mussels did not repair shells over the summer, only moderately-damaged medium mussels, and to a lesser extent extensively-damaged medium mussels, repaired shells. Further research should investigate whether shell repair occurs in large mussels during non-summer (non-reproductively active) months, or if the repaired shell observed in large mussels was merely an artifact of repair that occurred previously (i.e., while medium-sized). Differences in shell thickness and repair between South Carolina marshes, and even greater latitudinal differences between South Carolina and New Jersey populations, should continue to be investigated. Shell thickening derived by predator-induced defenses, temperature-dependent shell formation processes, and various sizes of refuge may all contribute to the observed differences in shell repair between mussel populations. Although crabs were able to target damaged mussels in mesocosm experiments, a similar preference was not always observed in the field. Further investigations into the cause of the dichotomy should look at effects of crab proximity to mussel metabolism, whether crabs can target damaged mussels using olfaction instead of touch, and if the apparent lack of field preferences are similarly observed in areas with lower crab densities. When crabs are nearby, mussel valves are shut to impede detection and consumption. However, damaged mussels may still produce noticeable chemical plumes if metabolites are able to leach through the damaged shell (Vermeij 1983). How close a crab needs to be to a mussel to induce the valve-shutting and if then the crab can still detect and locate a damaged mussel will determine the ability of a crab to target damaged mussels in the field. Shell damage did not seem to have a significant effect on predatory-mortality in areas with high predator abundance, but perhaps would have more of an impact in areas with fewer (thus more selective) predators.

This thesis contributes to the burgeoning body of work on sublethal predation and its important, if sometimes subtle, effects on individual and community dynamics. Shell damage reduced growth and increased non-predatory mortality in mussels during the summer, and crabs targeted damaged mussels in mesocosm experiments but did not appear to target damaged mussels in field tethering experiments. Further investigation is warranted and could reveal telling information about mussel energy partitioning and crab predation strategies.

Tables:

Table 1. Experimental removal of shell material results. Means (±SE) are shown for each treatment.

	Light damage	Moderate damage	Extensive damage	Undamaged
Description of treatment	middle third of shell removed, ridges intact	middle third of shell removed, ridges removed	top two thirds of shell removed, ridges removed	none- left undamaged
Shell length (mm)	72.1 ± 1.2	71.90 ± 1.9	72.0 ± 1.7	72.0 ± 1.8
Shell thickness at midline (mm)	1.05 ± 0.1	0.75 ± 0.1	0.88 ± 0.1	1.16 ± 0.1
Shell thickness at hinge (mm)	1.21 ± 0.1	0.79 ± 0.1	0.87 ± 0.7	1.41 ± 0.1
Shell mass (g)	6.26 ± 0.4	5.69 ± 0.5	5.70 ± 0.3	6.45 ± 0.4
Force (kN)	1.95 ± 0.3	1.85 ± 0.2	1.49 ± 0.2	1.72 ± 0.2

Figures:

Figure 1: Typical shell damage from failed decapod predation. The pattern of shell damage pictured can be caused by crabs trying to pull mussels out of the sediment or from an attachment site.

Figure 2: The hand-made device designed to measure the compression strength of shells.

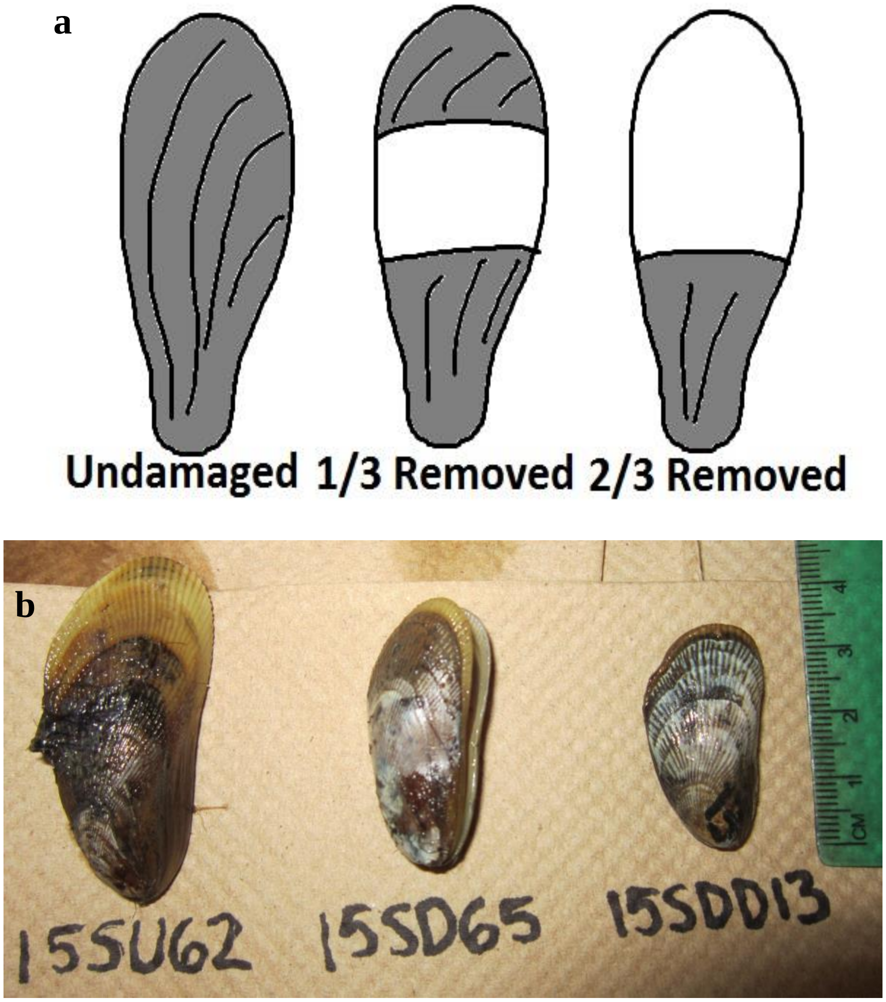

Figure 3: **a)** Diagram of the damage treatments used in the growth and repair experiment. Undamaged (left), moderate damage (middle), and extensive damage (right). **b)** Photograph of small mussels three months after damage (left = undamaged, middle = moderate damage, and right = extensive damage).

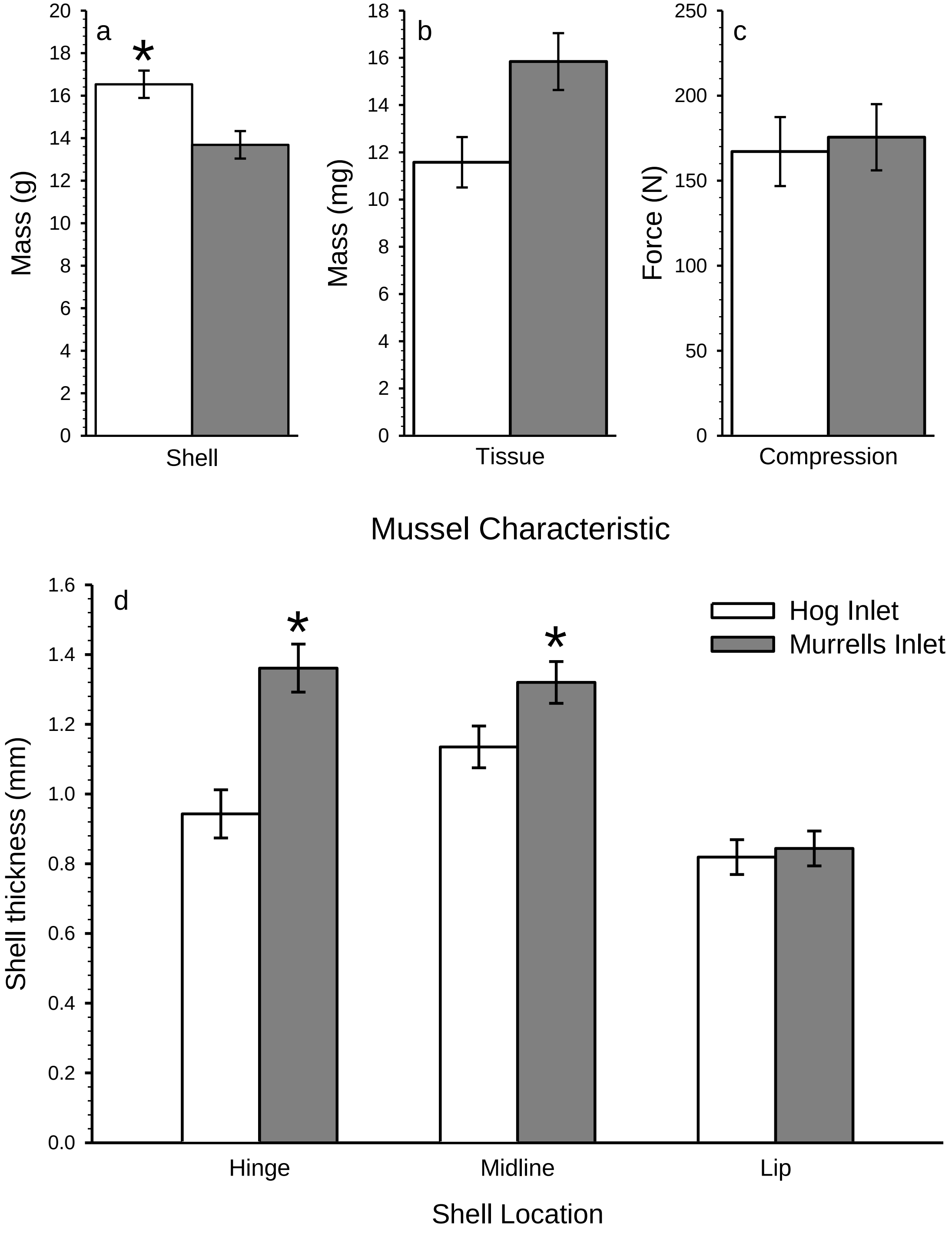

Figure 4: Characteristics of mussels collected from Hog Inlet (no damage) and Murrells Inlet (damage). Average mussel size was 72.6 mm. Means ± SE shown. Statistically significant differences are indicated with asterisks.

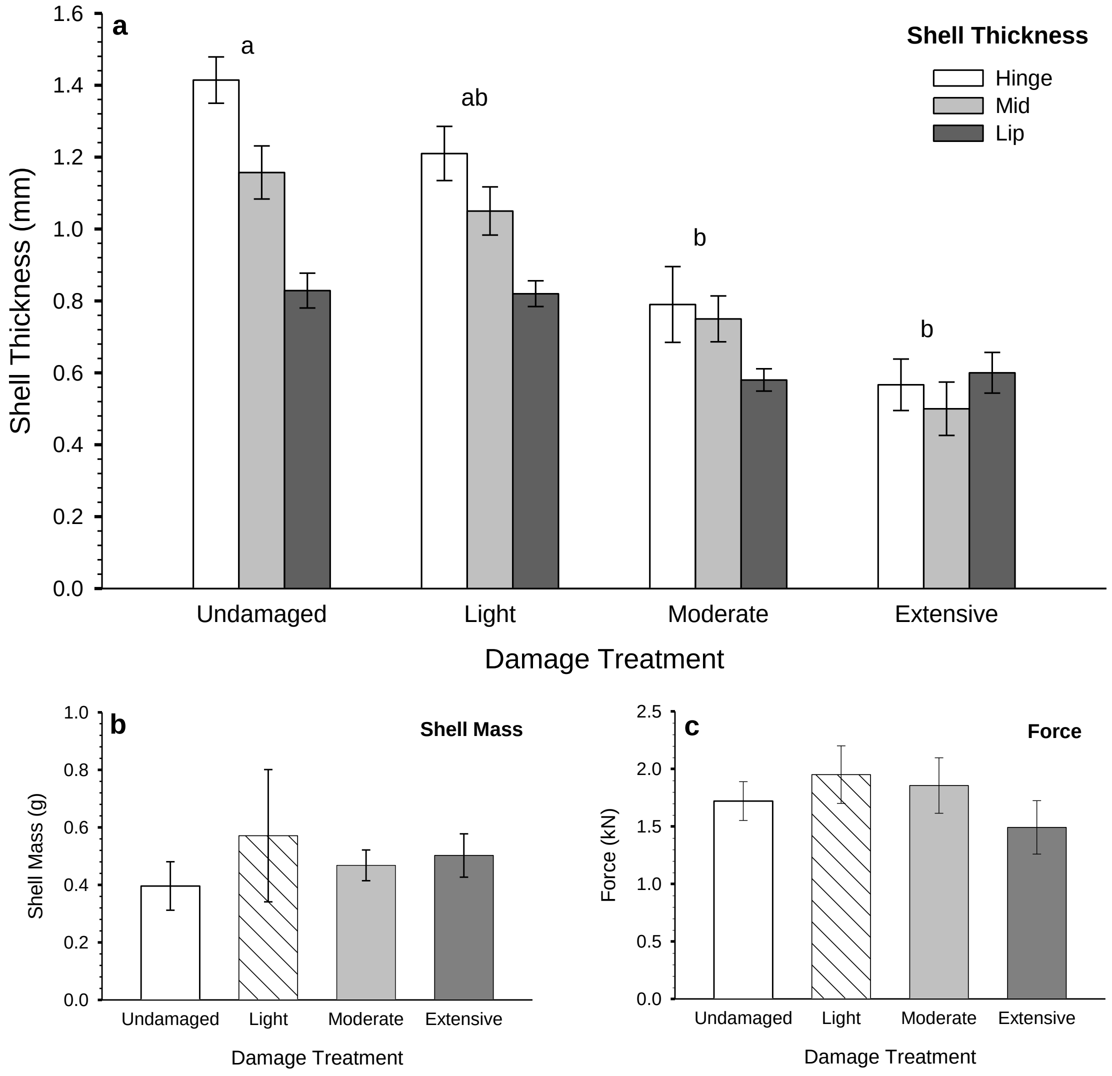

Figure 5: Consistency of shell damage treatment results (mean ± SE). Thickness (mm) measured at the umbo, mid, and lip, shell mass (g), and shell strength (kN) for mussels (~72 mm length) with no damage, light damage (33% removed, ridges intact), moderate damage (33% removed, ridges removed), and extensive damage (66% removed, ridges removed). Statistically significant differences are indicated with letters.

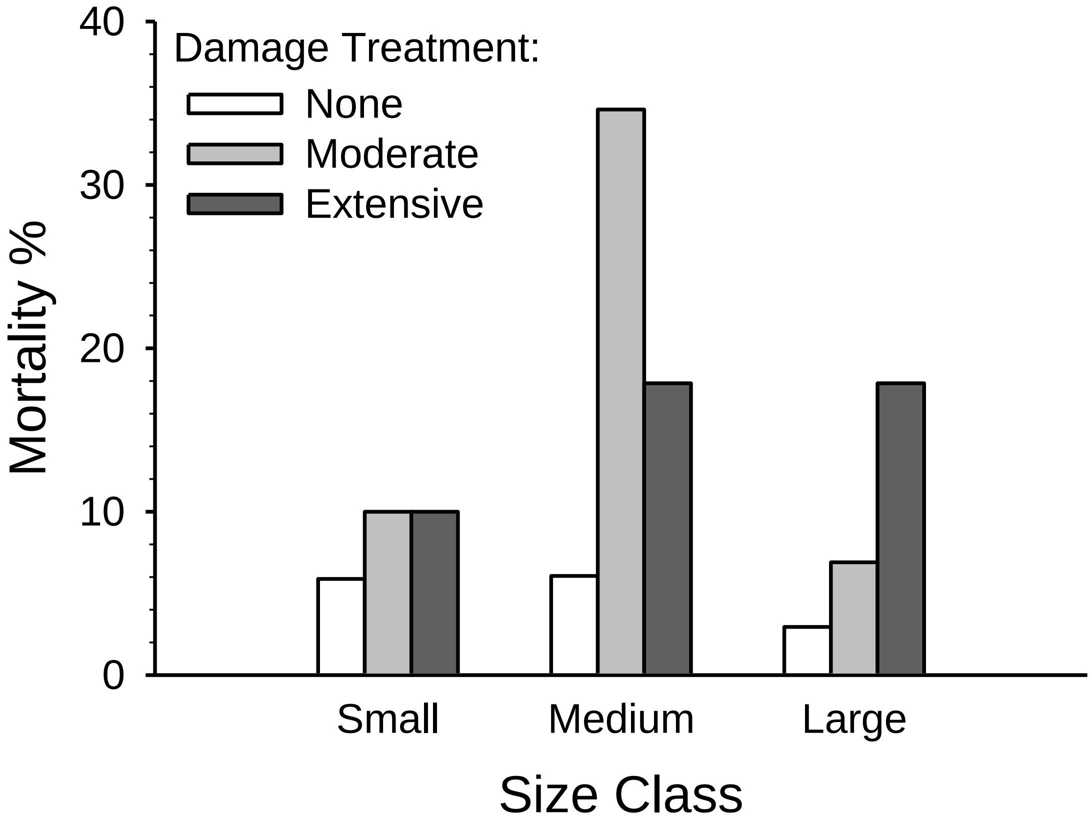

Figure 6: Total mortality (%) experienced over the growth and repair experiment for mussels of each size class and damage treatment.

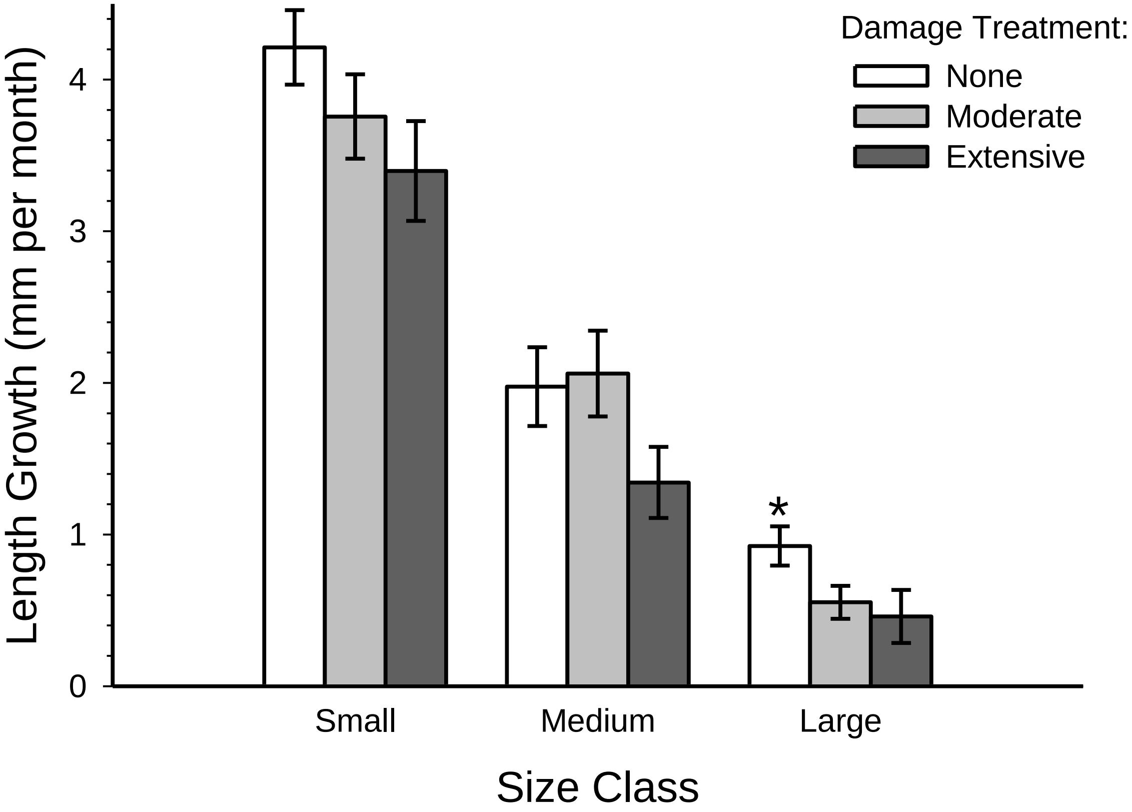

Figure 7: Mean (± SE) length growth (mm per month) for each size class and damage treatment of mussels from the growth and repair experiment. Statistically significant differences are indicated with an asterisk.

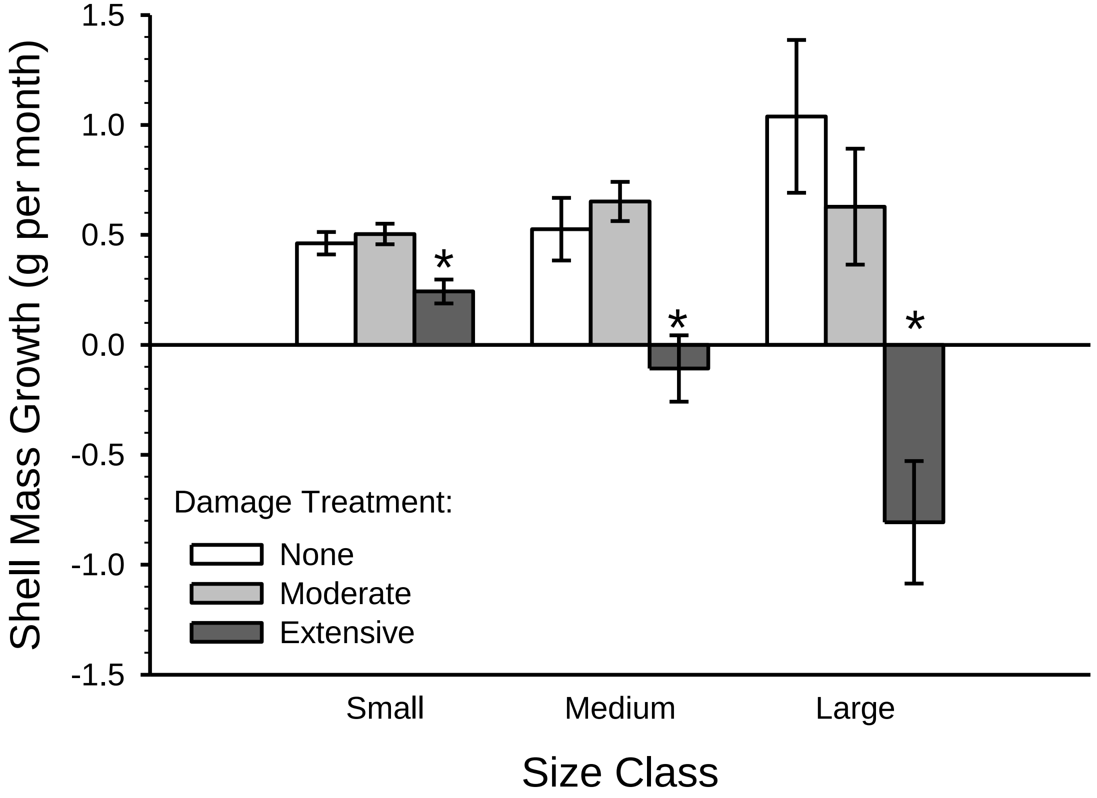

Figure 8: Mean (± SE) shell mass growth (g per month) for each size class and damage treatment of mussels from the growth and repair experiment. Statistically significant differences are indicated with asterisks.

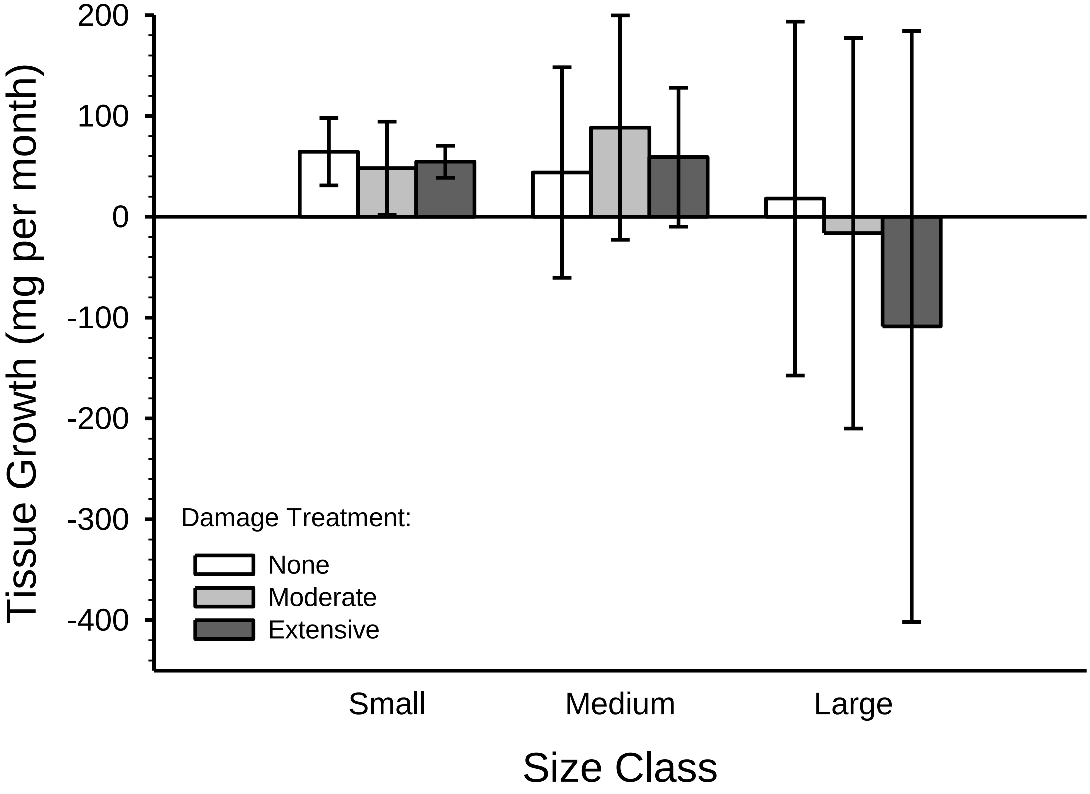

Figure 9: Mean (± SE) tissue mass growth (mm per month) for each size class and damage treatment of mussels from the growth and repair experiment.

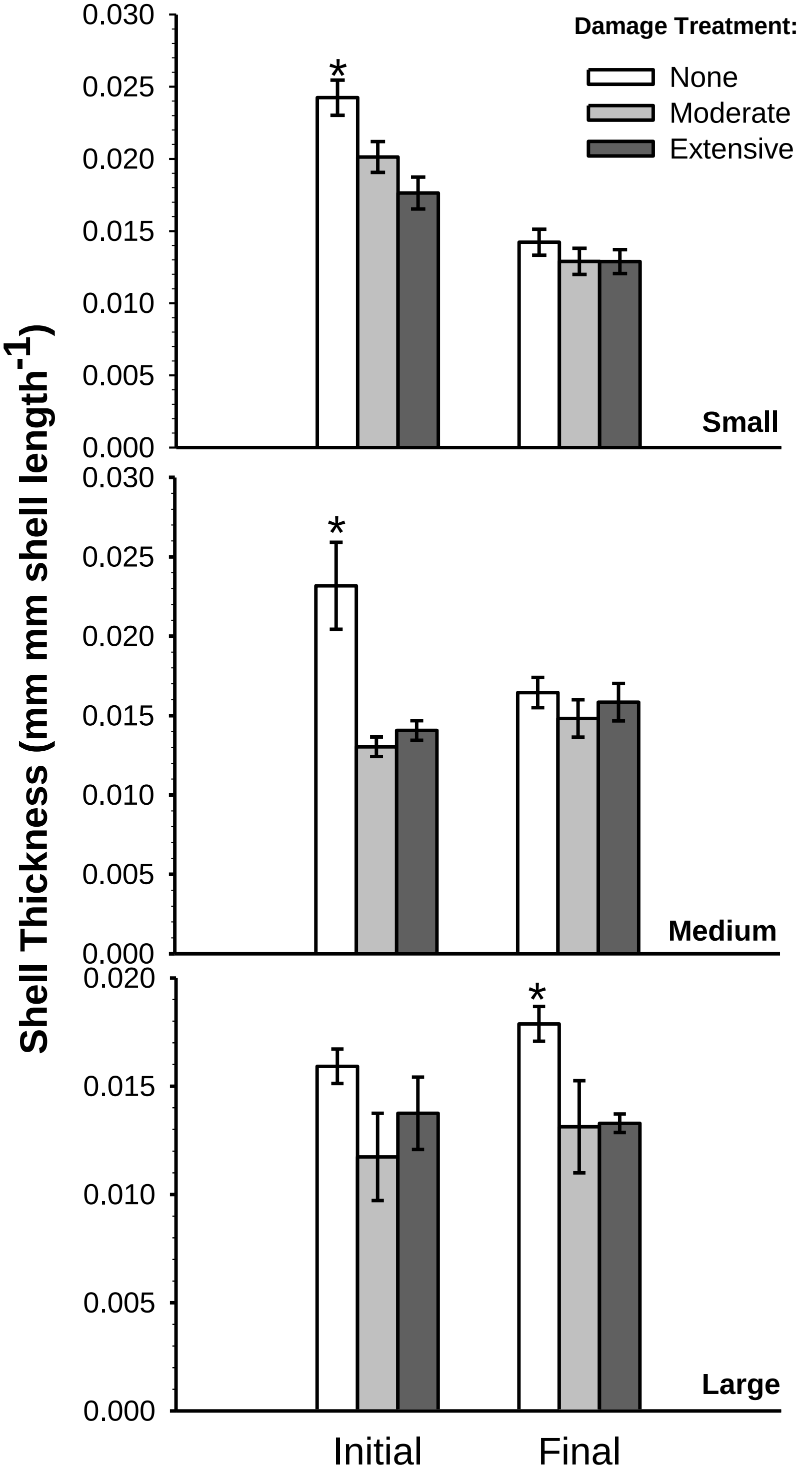

Figure 10: Initial and final mean (± SE) midline shell thicknesses (mm per mm shell length) for each size class and damage treatment of mussels from the growth and repair experiment. Statistically significant differences are indicated with asterisks.

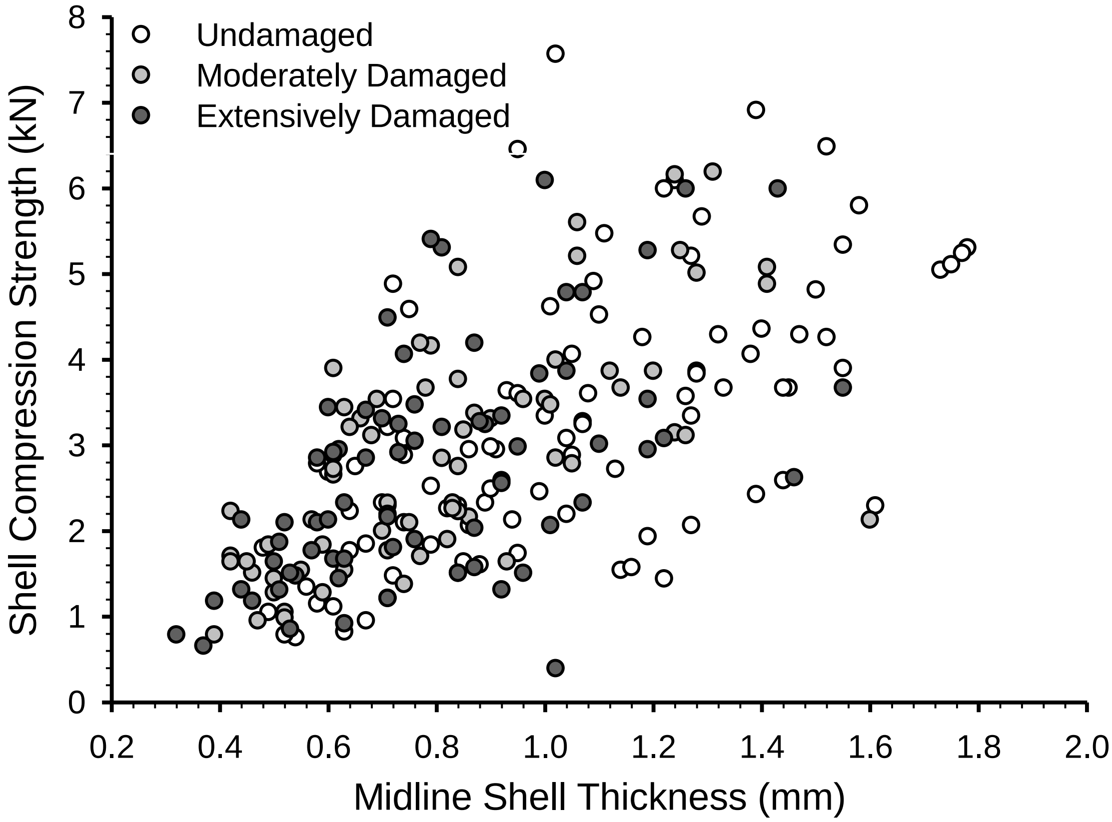

Figure 11: The midline shell thickness (mm) plotted against the shell compression strength (kN) of undamaged ($y = 2.8374x + 0.2932$; $R^2 = 0.3759$), moderately-damaged ($y = 3.197x + 0.2739$; $R^2 = 0.4664$), and extensively-damaged ($y = 2.8504x + 0.4542$; $R^2 = 0.312$) mussels from the growth and repair experiment.

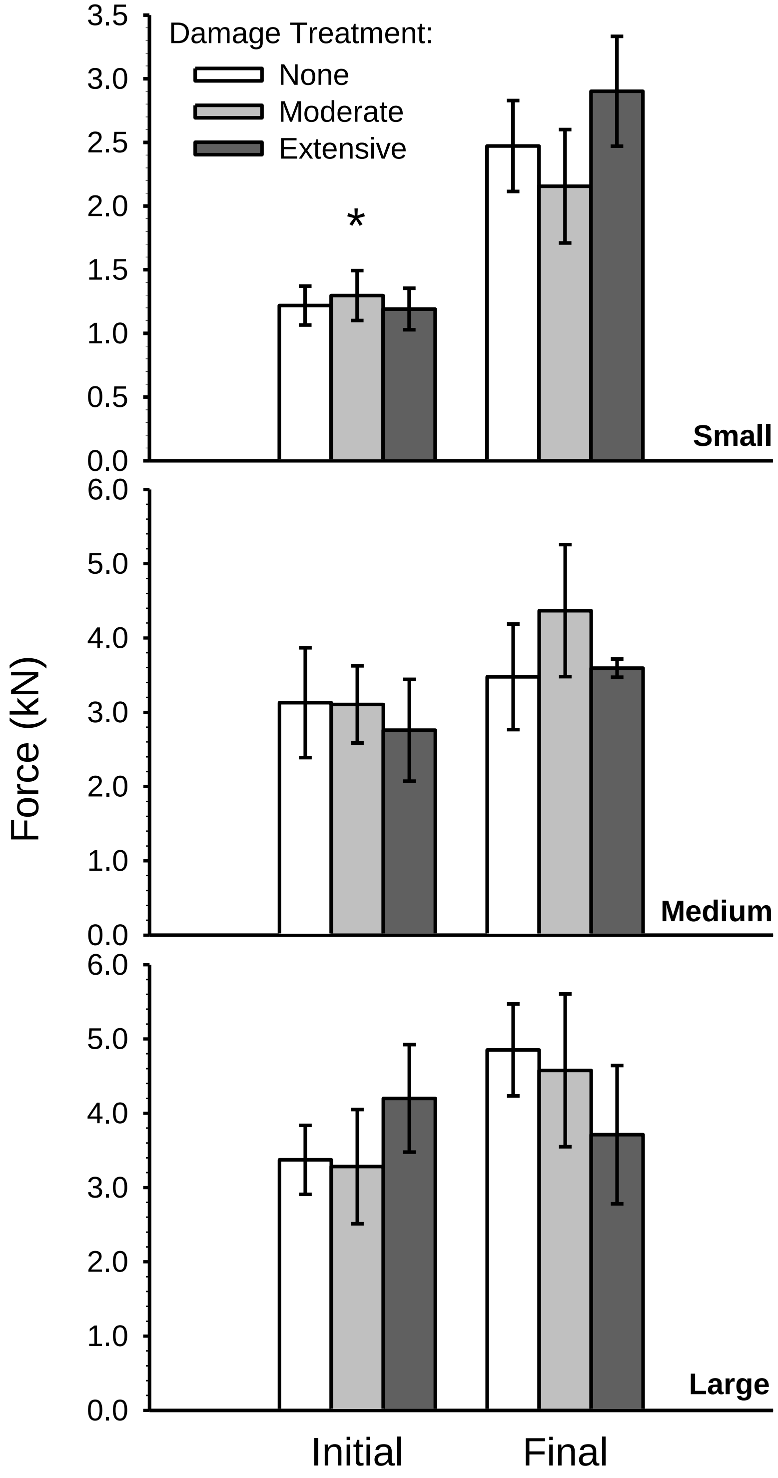

Figure 12: Initial and final mean (± SE) shell strengths (kN) for each size class and damage treatment of mussels from the growth and repair experiment. Statistically significant differences are indicated with an asterisk.

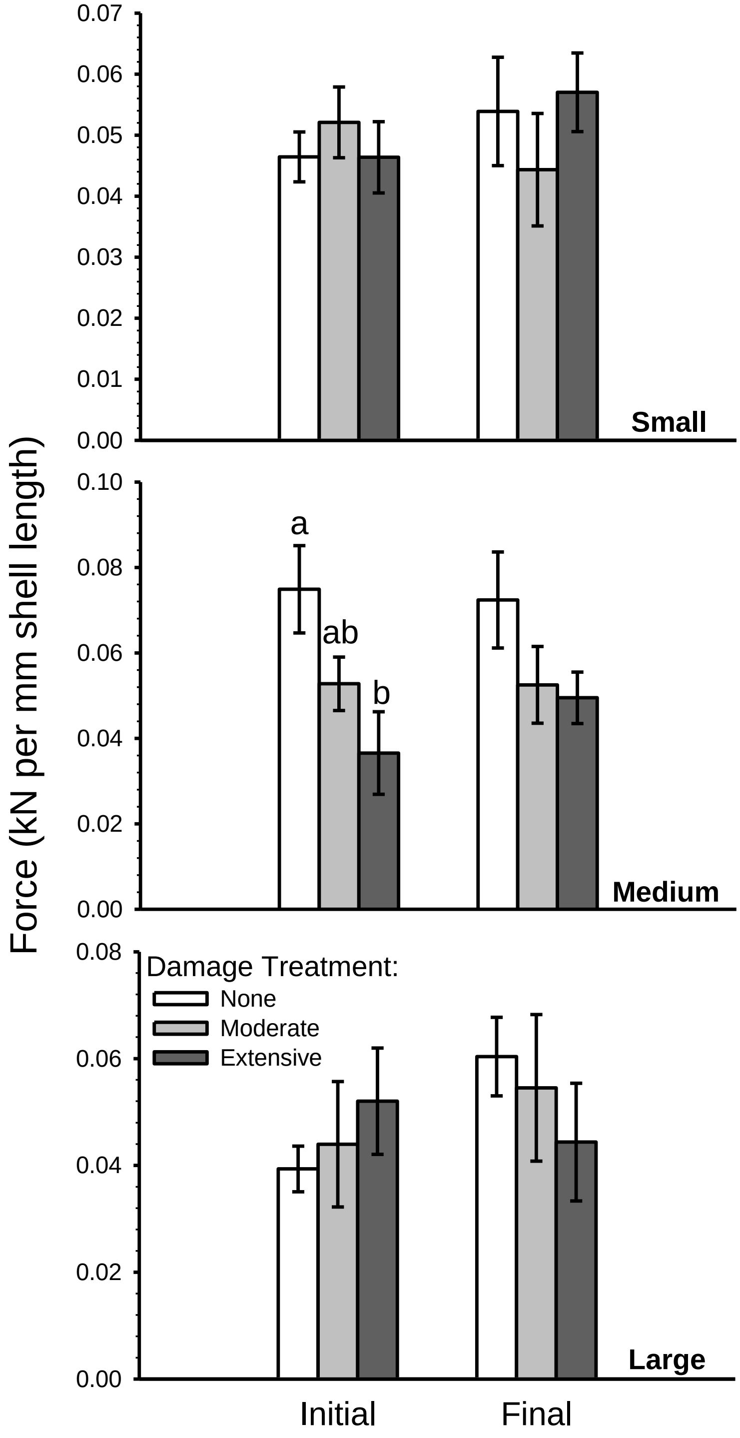

Figure 13: Initial and final mean (± SE) shell strengths (kN per mm shell length) for each size class and damage treatment of mussels from the growth and repair experiment. Statistically significant differences are indicated with letters.

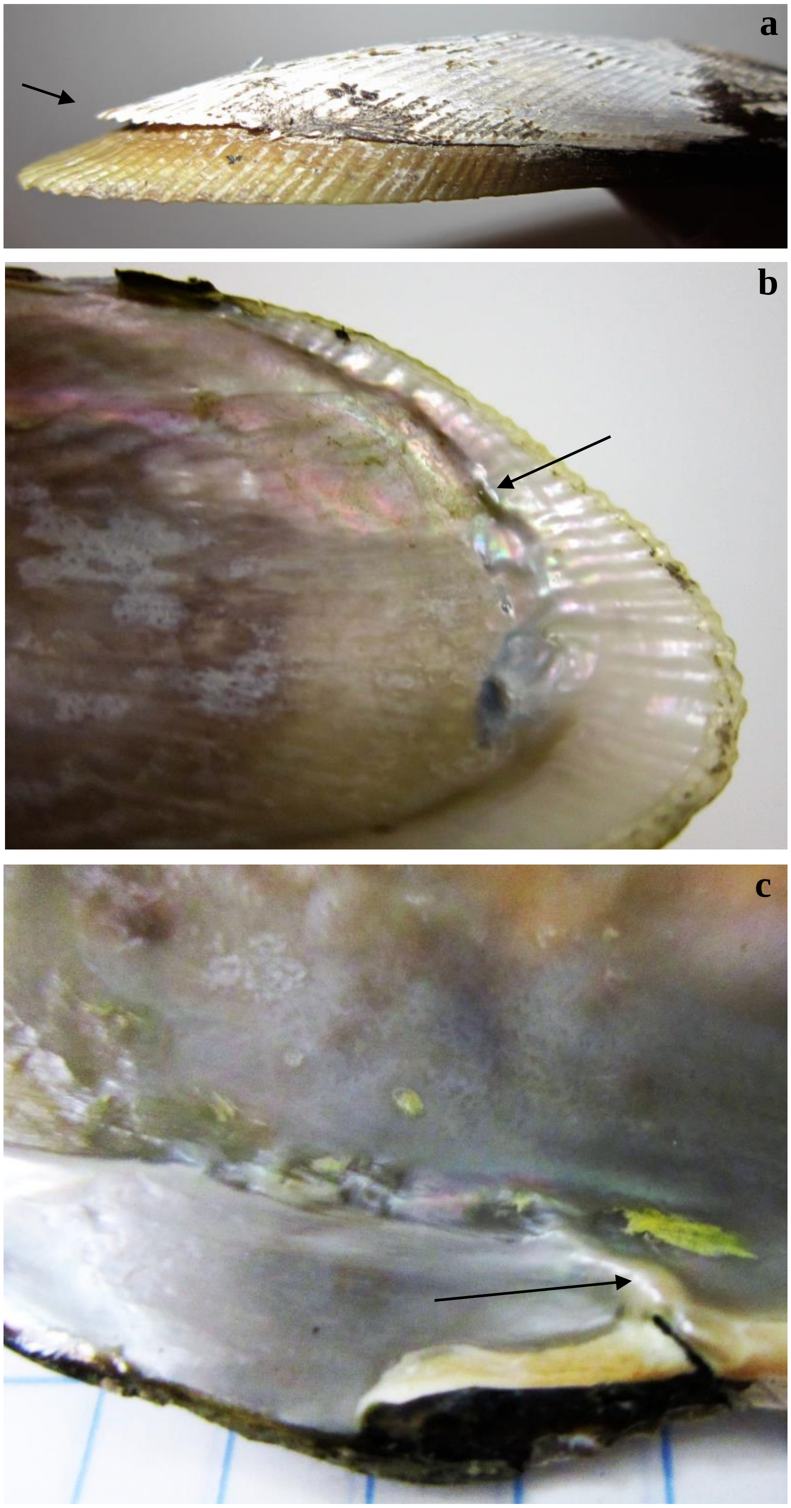

Figure 14: **a)** External view of discontinuous growth in a medium, extensively-damaged mussel. The white shell area on top is the original, damaged shell, and the brown/yellow area below is the new shell growth. **b)** Internal view of the same mussel. There is an elevated ridge of shell repair along the inside edge of the old shell. **c)** Internal view of another mussel with a repaired crack.

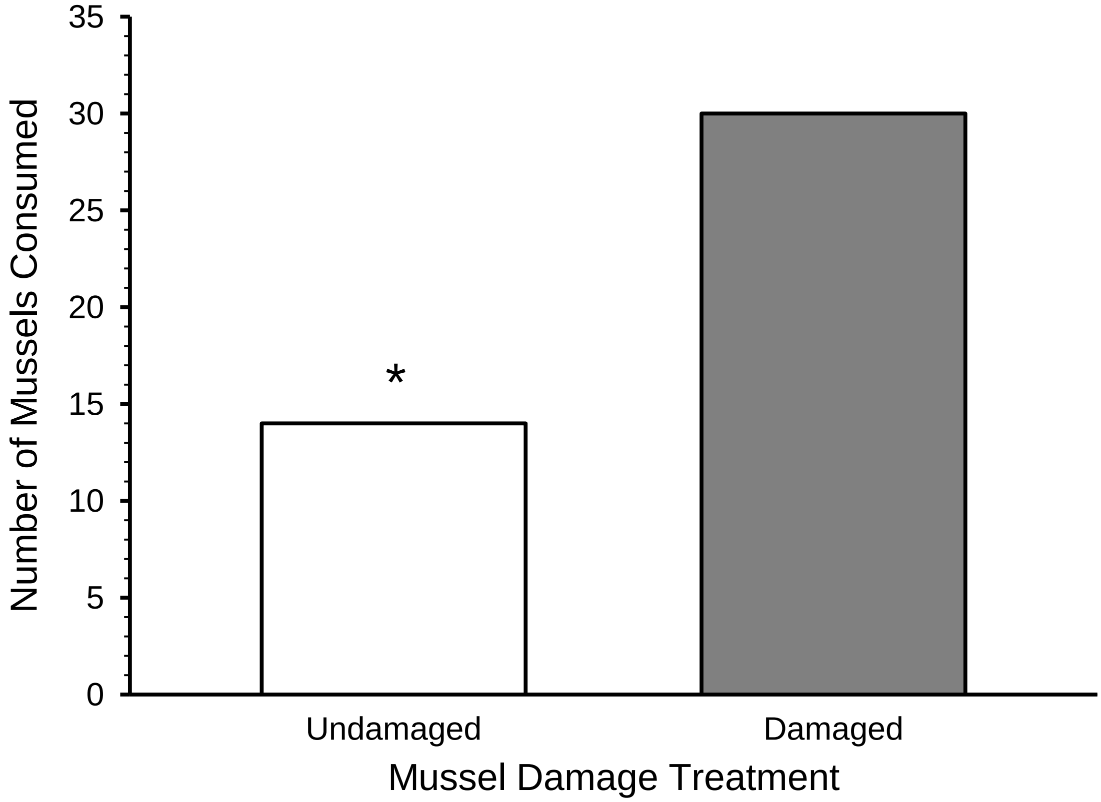

Figure 15: The number of undamaged and damaged mussels consumed by blue crabs in mesocosms. 68% of consumed mussels were damaged. Statistically significant differences are indicated with an asterisk.

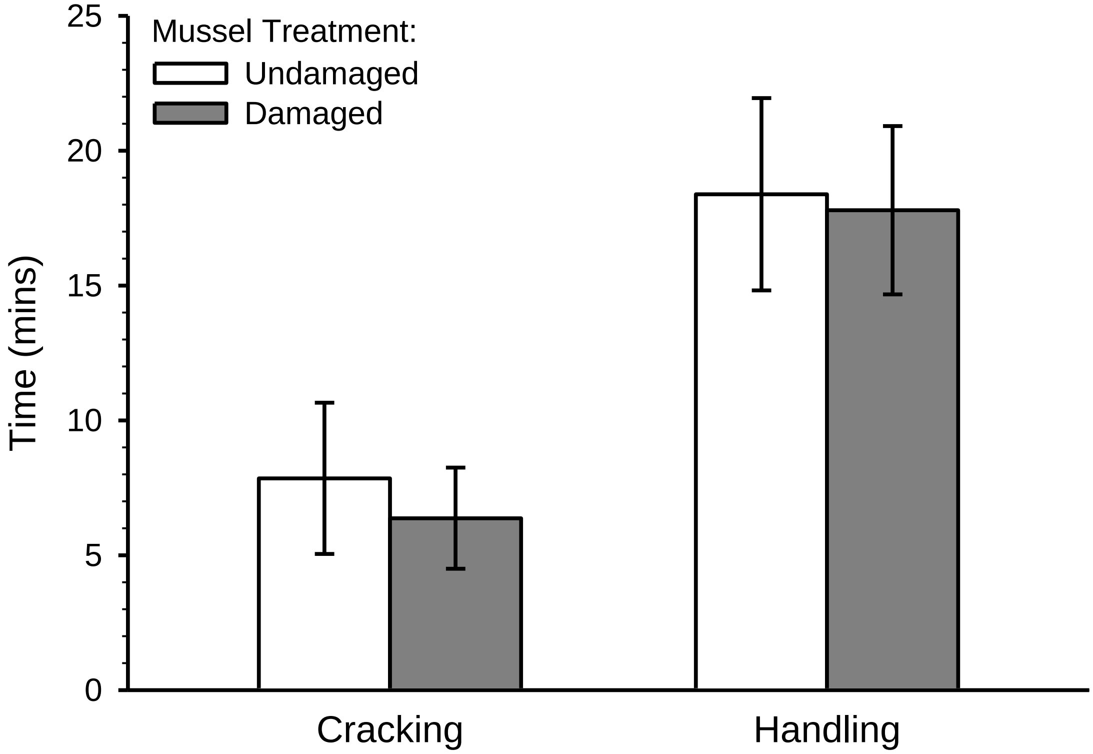

Figure 16: Mean (± SE) crab cracking and handling times of undamaged and damaged mussels.

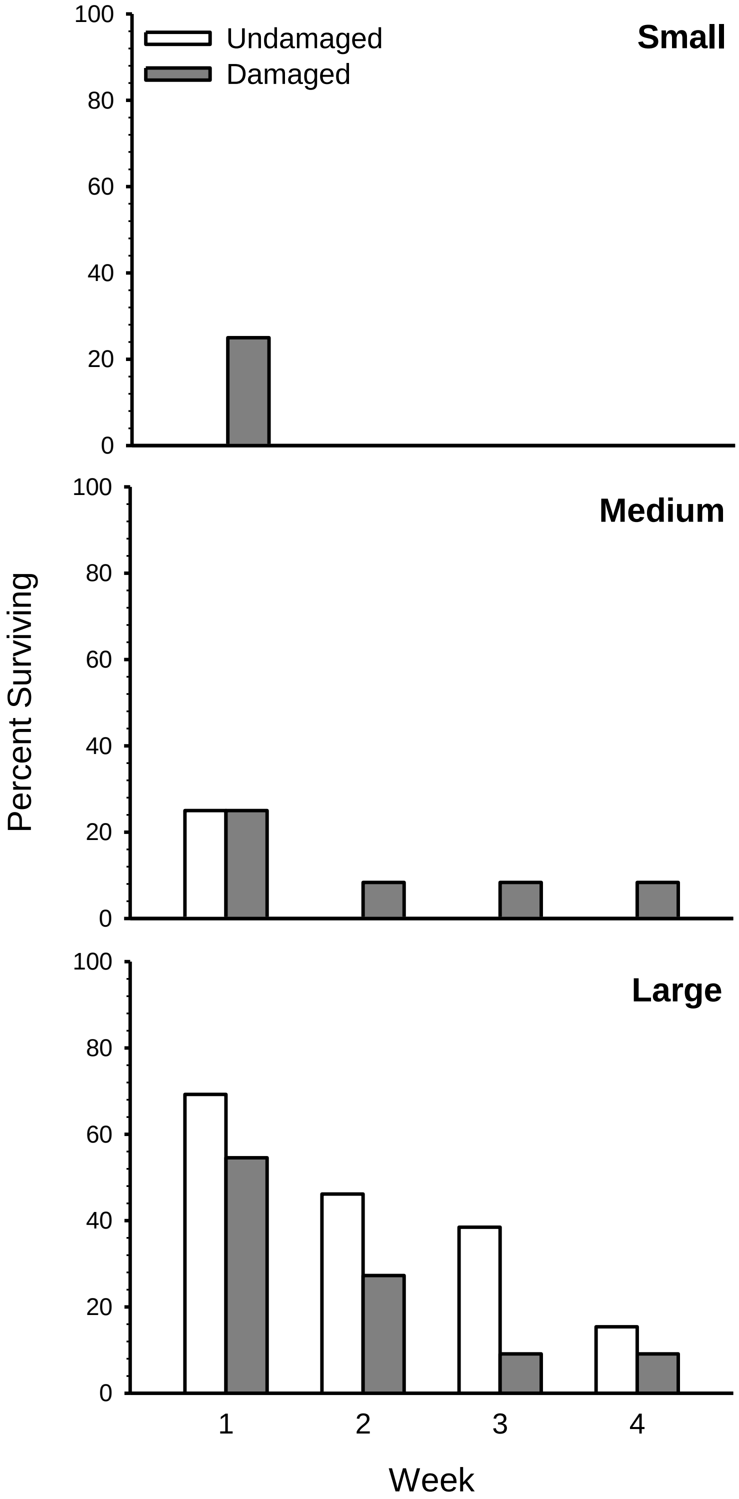

Figure 17: Mussel survival (%) in the mid-marsh during the predation across marsh zones experiment.

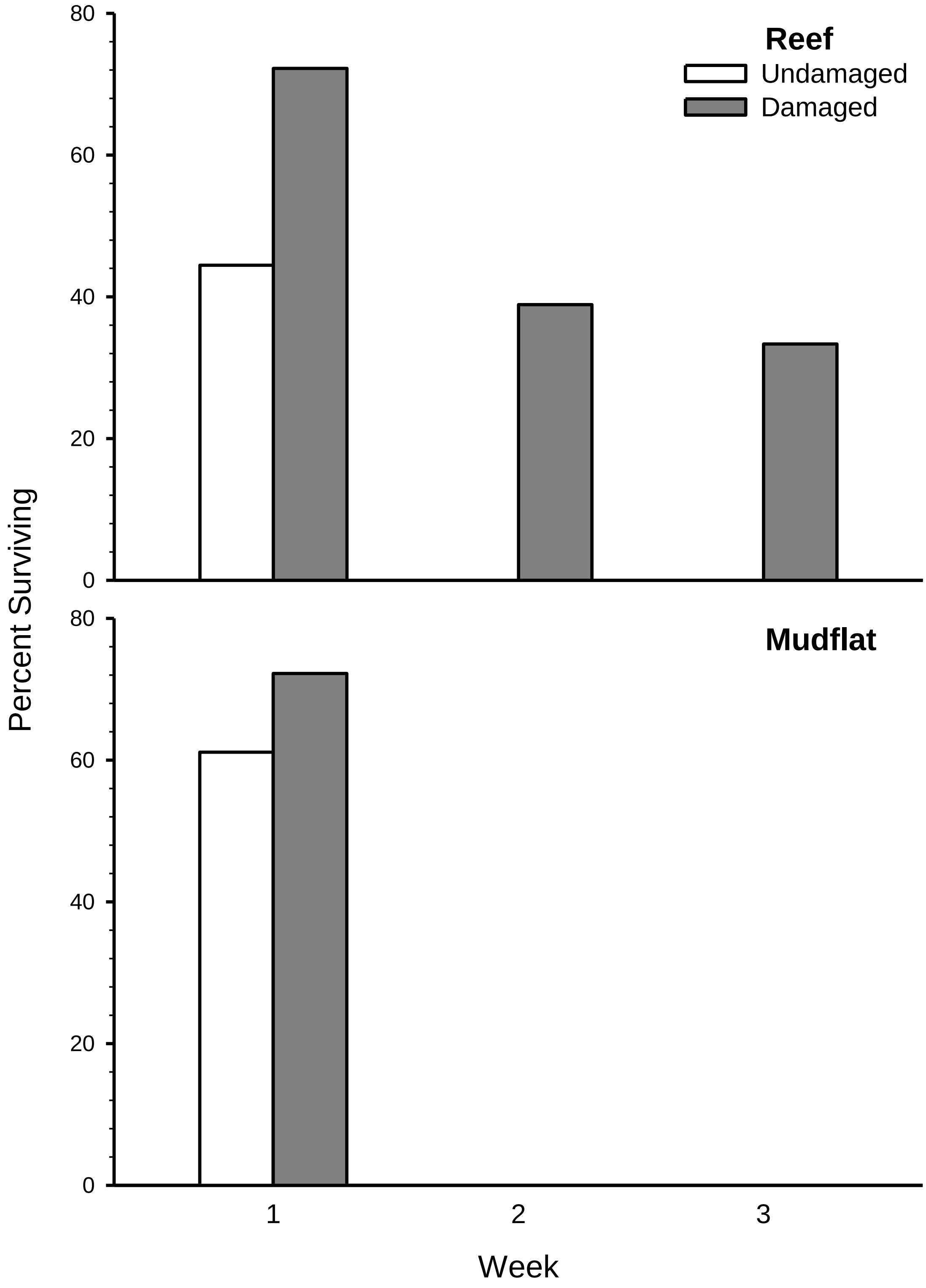

Figure 18: Refuge and damage effects on mussel predation. After one week <10% of mussels were alive. All surviving mussels were damaged mussels on reefs.

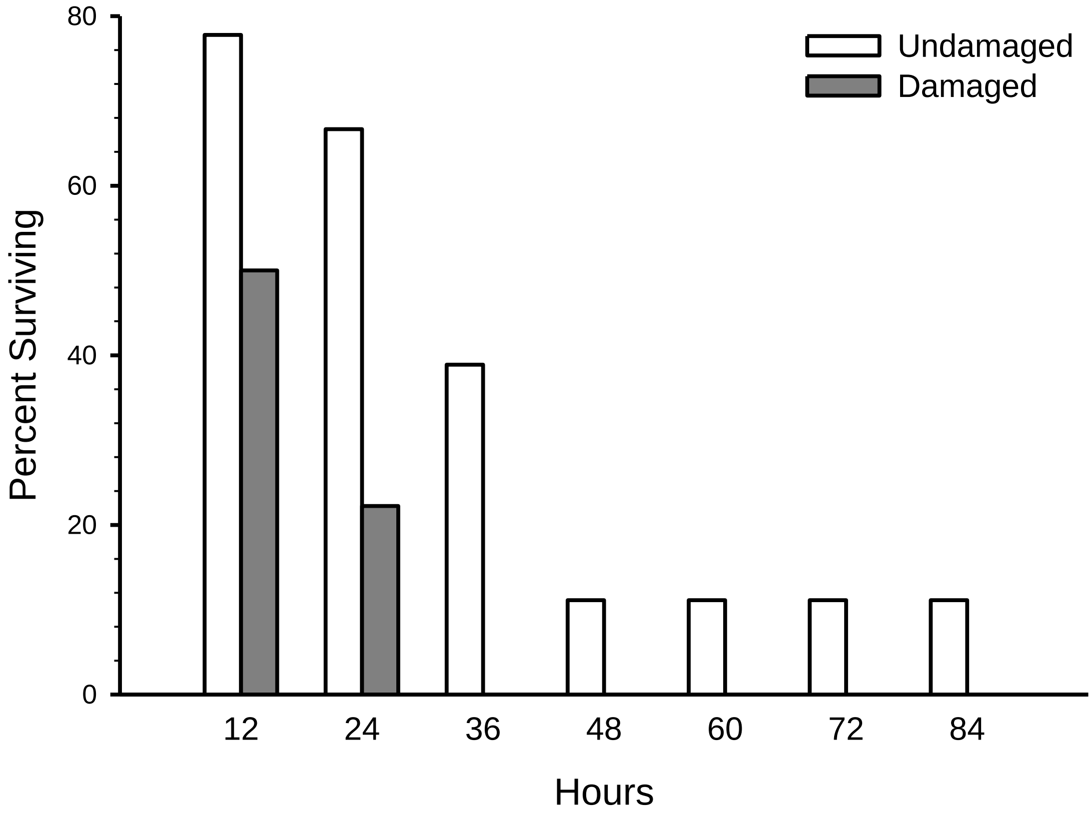

Figure 19: Survival (%) of damaged and undamaged medium (50-60 mm) mussels in the mid-marsh recorded every low tide for four days. After three low tides all damaged mussels had been consumed while 39% of undamaged mussels survived.

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