The Survival Benefit of Benthic Macroalgae Gracilaria vermiculophylla as an Alternative Nursery Habitat for Juvenile Blue Crabs

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The Survival Benefit of Benthic Macroalgae *Gracilaria vermiculophylla* as an Alternative Nursery Habitat for Juvenile Blue Crabs

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

by

Justin A. Falls

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This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Science

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ABSTRACT

The Chesapeake Bay blue crab is in decline. One of the threats to it is the loss of its once plentiful nursery habitat, seagrass, due to baywide eutrophication and climate change. The emergence of the non-native benthic macroalga *Gracilaria vermiculophylla* may offer the blue crab an alternative nursery if it can provide juvenile crabs a refuge from predation. The ability of *Gracilaria* to protect juvenile blue crabs was investigated in mesocosm and field survival studies, which were combined into a larger dataset. All of these studies used tethering and therefore a tethering validation study in mesocosms accompanied these experiments. In the validation study, there was no evidence for treatment specific-bias due to tethering, and mortality of free crabs was approximately half that of tethered crabs. In mesocosms, survival in a large algal patch of 80-cm diameter was 42-69 % greater than that of crabs in a 10-cm algal patch or unvegetated habitat. In the field, the survival benefits of a 40-cm-diameter *Gracilaria* patch varied with the size of juvenile blue crabs. In the combined data, larger algal patches increased the survival of smaller juvenile crabs. This survival benefit of macroalgae decreased with increased crab size such that survival of larger juveniles was inversely related to *Gracilaria* patch diameter. Consequently, the non-native *Gracilaria* may serve as a nursery for the blue crab, but its benefits will depend on crab and algal patch size.
INTRODUCTION

The Chesapeake Bay’s blue crab population has declined significantly. Spawning stock abundance decreased by 81% during the 1990s, and larval abundance decreased by an order of magnitude (Lipcius and Stockhausen 2002). Spawning stock, larval abundance, and recruitment are unlikely to rebound to former high levels without significant reductions in fishing and environmentally linked mortality, along with enhanced environmental conditions conducive to successful recruitment (Lipcius and Stockhausen 2002). The blue crab is very important to the Chesapeake Bay region economically and culturally (Warner 1976); therefore much effort is being directed at determining the causes of the blue crab’s decline and how the population can be restored.

The blue crab is facing the reduction and loss of eelgrass (*Zostera marina*), its primary nursery habitat in Chesapeake Bay (Orth and Moore 1984, Orth and van Montfrans 1990, Batiuk et al. 1992, Moore et al. 2000, Hovel and Lipcius 2001, Harwell and Orth 2002, van Montfrans et al. 2003, Moore and Jarvis 2008). Eelgrass is declining under increasing water turbidity and temperatures (Orth and Moore 1983, Moore and Jarvis 2008), and climate change has become a major threat to *Zostera marina* in the Chesapeake Bay, the southern part of its range.

The Bay’s other seagrass species, *Ruppia maritima* (widgeon grass) can also provide a nursery habitat for crabs and other fauna (Heck and Thoman 1984). Although widgeon grass is less sensitive to higher temperatures than eelgrass, the species is also in decline (Anderson et al. 1972, Stevenson and Confer 1978, Orth and Moore 1983, 1984). The major common cause in the decline in distribution and abundance of eelgrass,
widgeon grass, and all the submerged vascular plants of the Chesapeake Bay, is the eutrophication of the bay and increased water turbidity associated with eutrophication (Kemp et al. 2005).

Eutrophication in estuaries and coastal areas has led to local eradication of submerged vascular plants in many ecosystems (Kinney and Roman 1998, Silva-Santos et al. 2006). The major problem with eutrophication is that excess nutrients cause unchecked primary production, and the balance between primary producers in shallow-water systems is altered. Because seagrass has roots, it is adapted for low-nutrient waters. Thus seagrass can thrive in waters that have insufficient nutrients to support high densities of phytoplankton and macroalgae. When these phytoplankton and macroalgae proliferate after the introduction of excess nutrients, they shade out the seagrass (Valiela et al. 1997). However, some of the macroalgae that prosper under eutrophic conditions may also provide habitat benefits to blue crabs (Wilson et al. 1999, Epifanio et al. 2003, Dittel et al. 2000, 2006, Mahalak 2008, Johnston and Lipcius unpublished).

*Gracilaria vermiculophylla*, a particularly resilient macroalga that may prove useful to blue crabs, has greatly extended its local distribution within five years of its discovery in the North Atlantic Ocean (Bellorin et al. 2004, Thomsen et al. 2005, 2007, Freshwater et al. 2006, Mahalak 2008). *Gracilaria* attaches to biogenic and other substrates and sometimes breaks off and drifts to other places (Thomsen et al. 2007). This Asian species has the ability to form extensive mats and has dominated the biomass of shallow-water systems like Hog Island Bay, Virginia (Bellorin et al. 2004, Thomsen et al. 2005). *Gracilaria* may have benefits to local diversity, as it forms an attachment site for filamentous algae and adds structural complexity to relatively homogenous soft-bottom
Gracilaria is providing a nursery habitat to juvenile blue crabs (Mahalak 2008, Johnston and Lipcius unpublished).

The objective of this study was to determine if *Gracilaria vermiculophylla* can provide blue crabs with protection from predation. Since smaller crabs are in the greatest need of habitat refuges from predation, I also sought to determine if the size of the crab influences the refuge provided by *Gracilaria* and how much *Gracilaria* is required to protect individual blue crabs.

**BACKGROUND**

State of Seagrass in the Chesapeake Bay

Seagrasses are productive habitats that provide shelter to many animal species, specifically the blue crab *Callinectes sapidus* (Adams 1976, Wilson et al. 1987, Heck et al. 1995). *Zostera marina* (eelgrass) has historically been the dominant species of seagrass in the polyhaline zone of the Chesapeake Bay (Orth and Moore 1984, Moore et al. 2000) where blue crab megalopae settle in their initial migration from the continental shelf (Lipcius et al. 2007). The eelgrass beds are very important to megalopae and juveniles because they provide a refuge from the high predation rates these small animals experience in open habitats (Pile et al. 1996, Moksnes et al. 1997, Orth and van Montfrans 2002). Eelgrass also provides the crabs with abundant food (Perkins-Visser et al. 1996) and can have 5-15 times the macrofaunal production of adjacent habitats (Heck et al. 1995). This productive nursery habitat, however, faces an uncertain future in the Chesapeake Bay.
Eelgrass in Chesapeake Bay has been experiencing a severe decline in distribution and continues to face serious threats (Orth and Moore 1984, Moore et al. 2000, Kemp et al. 2005, Moore and Jarvis 2008). The decline began in 1931 when an eelgrass wasting disease was infecting eelgrass on both sides of the Atlantic Ocean (Renn 1934, 1935, Muehlstein et al. 1991). In parts of its range, *Zostera marina* has never recovered from this decline (Orth et al. 2006). This loss of habitat caused the extinction of the eelgrass limpet *Lottia alveus* (Carlton et al. 1991), and has been linked to the reduced abundance of other species (Milne and Milne 1951). Eelgrass in the Chesapeake Bay partially recovered from the worldwide decline but never again reached its former abundance (Orth and Moore 1984).

In more recent times climate change is causing an increased threat to *Zostera marina* in Chesapeake Bay, because *Zostera* is near the southern limit of its range. Unusually hot summers can cause die-offs linked to a carbon deficit attributed to increased respiration at temperatures above 25 °C (Bocci et al. 1997). In 2005, an unusually hot summer with little wind contributed to a bay-wide eelgrass defoliation (Moore and Jarvis 2008). Possible repetitions of this event are a concern especially when these affect already stressed seagrass plants.

Widgeon grass, in contrast, is more tolerant of higher temperatures (Stevenson and Confer 1978, Orth and Moore 1988) and also provide habitat for blue crabs (Heck and Thoman 1984). Widgeon grass is also a euryhaline plant, an adaptation that allows it to have an extensive range in Chesapeake Bay and dominate the Bay’s mesohaline zone (Anderson 1972, Stevenson and Confer 1978, Orth and Moore 1984). In the polyhaline zone of the Bay, *Ruppia* and *Zostera* often grow in mixed beds (Orth and Moore 1988).
Ruppia and Zostera limit competition with each other by having different growing seasons based on different temperatures. Eelgrass growth peaks in early summer, whereas widgeon grass growth peaks in late summer at higher temperatures during a time of year when the high temperatures causes eelgrass leaves to defoliate (Stevenson and Confer 1978, Orth and Moore 1988). Despite the association of these species, monospecific eelgrass beds historically dominated the polyhaline region of lower Chesapeake Bay (Orth and Moore 1984, Moore et al. 2000).

When eelgrass and widgeon grass grow in mixed beds, they inhabit different zones due to the differing tolerances and properties of the seagrass species (Orth and Moore 1988). The higher irradiance requirement of Ruppia confines it to the shallows while the lower heat tolerance of Zostera restricts it to deeper waters. In mid-depth zones, where both species can tolerate environmental conditions, Ruppia and Zostera occur in mixed-species beds (Orth and Moore 1988). The association between these plants may be beneficial to Ruppia which has a much lower tolerance to wave energy than does Zostera (Orth and Moore 1988). Higher wave energy excludes Ruppia from many areas of the lower Chesapeake Bay. However, its wave energy tolerance increases when eelgrass in deeper water muffles the wave energy in shallower waters (Orth and Moore 1988). The elimination of eelgrass would therefore also eliminate widgeon grass from these high-wave-energy environments. The other major threat to widgeon grass is the shading effects and loss of light due to the eutrophication of Chesapeake Bay (Gallegos and Bergstrom 2005, Kemp et al. 2005).

The Chesapeake Bay is home to not only two seagrass species but also to a variety of salt-tolerant freshwater species of submerged aquatic vascular plants.
(Anderson 1972, Stevenson and Confer 1978, Orth and Moore 1984, Moore et al. 2000, Gallegos and Bergstrom 2005). The abundance and range of submerged aquatic vegetation (SAV) species in the bay have declined greatly in the mid to late 20th century across all salinity ranges in Chesapeake Bay (Orth and Moore 1983, 1984, Moore et al. 2000, Kemp et al. 2005). The root cause of this SAV decline has been the eutrophication of Chesapeake Bay waters (Kemp et al. 2005). Many of the great declines in the ranges and abundances of the Chesapeake Bay’s SAV occurred at times when no comparable decline was occurring in other estuaries or coastal areas on the Atlantic Coast of North America (Orth and Moore 1983, 1984).

The decline of SAV in the Chesapeake Bay that was linked to eutrophication began in the 1960s when densely vegetated areas in the Patuxent and lower Potomac Rivers, as well as the upper sections of other bay tributaries, became devoid of vegetation by 1970 (Orth and Moore 1983). Similar reductions in SAV occurred in places like the Rhode River, Maryland, although these did not result in river systems that were devoid of vegetation (Southwick and Pine 1975). The baywide shifts from vegetated to unvegetated bottom was accelerated by tropical storm Agnes in 1972, which lowered salinity and increased turbidity throughout Chesapeake Bay (Orth and Moore 1984). Widgeon grass largely disappeared near Parsons Island in 1979, and many of the Bay tributaries in Maryland had sparse or no vegetation by 1982 (Orth and Moore 1983, Heck and Thoman 1984). The decline of *Ruppia* caused a decrease in many decapod crustaceans (Heck and Thoman 1984).

By the late 1980s and early 1990s there was a resurgence of SAV coverage in some portions of the Bay, particularly in areas dominated by *Zostera* and freshwater
species. Meanwhile, *Ruppia* and *Potamogeton* (a salt water tolerant SAV) communities of the mesohaline region continued to decline. The total baywide SAV coverage during this time was stable because the resurgence of eelgrass in the lower Bay was greater than the SAV loss in the mesohaline portions of the Bay (Moore et al. 2000). The SAV in the mesohaline portion of the Bay continued to decline throughout the 1990s. This region suffered and continues to suffer from a recurring bloom of the phytoplankter *Prorocentrum minimum*, which shades out the local SAV community (Gallegos and Bergstrom 2005). The eelgrass population that resurged in the 1980s and 1990s was devastated again in 2005 by a temperature-induced die-off (Moore and Jarvis 2008). Many shoal areas of the lower and middle Bay that once supported both eelgrass and widgeon grass are now predominantly widgeon grass. It is unclear whether this is an expansion of widgeon grass or simply a contraction of eelgrass or both (R.J. Orth personal communication).

**Proliferation of Macroalgae**

Macroalgae and phytoplankton are both natural components of healthy seagrass beds and play an integral role in the nutrient cycles of the seagrass community (Penhale and Thayer 1980, Sand-Jensen and Borum 1991, Duarte 1995). The addition of nutrients to coastal and estuarine systems stimulates the growth of opportunistic algae which compete with seagrass for light and space. Under these conditions macroalgae and phytoplankton can both bloom. Macroalgal blooms are like phytoplankton blooms in that they are both caused by cultural eutrophication where the addition of excess nutrients into the watershed releases primary producers from the control of otherwise limiting nutrients.
Macroalgal blooms can last for years or decades and have a broad range of ecological effects (Valiela et al. 1997). The appearance of macroalgal blooms can lead to the extinction of seagrass in some shallow areas (Kinney and Roman 1998, Hauxwell et al. 2001, Silva-Santos et al. 2005).

The excess nutrients of cultural eutrophication cause unchecked primary production and change the balance between primary producers in shallow-water estuarine systems. Seagrass has roots allowing it to sequester nutrients from the sediment. Such an advantage allows it to thrive in waters that are too low in nutrients to support high densities of phytoplankton and macroalgae. These same roots confine seagrass to the bottom where other more mobile producers can grow over seagrass in the water column or even on the leaves of the seagrass itself, shading out their less successful competitors. Seagrass also has the disadvantage of having a higher irradiance requirement than other primary producers. As a result, seagrasses are characteristic of shallow low-nutrient waters in which other competitors are excluded by low nutrient supply (Duarte 1995, Valiela et al. 1997).

As nutrient loading occurs, the seagrasses become replaced by macroalgae. At the highest levels of nutrient loading, macroalgae become replaced by phytoplankton. Phytoplankton are the fastest growing, most mobile producers. They occur high in the water column and have high nutrient demands. When allowed to proliferate they can shade out macroalgae. When there is a low water residence time, however, phytoplankton are flushed out of the system before they are allowed to respond to increasing nutrients in the system, allowing macroalgae to dominate. Macroalgal blooms can become the most prolific in high-nutrient shallow estuaries with short water residence
times (Valiela et al. 1997). Macroalgae can also proliferate when human activities aid in the introduction of non-native macroalgae species into new environments.

*Gracilaria vermiculophylla* is a non-native macroalga first described in Japan and native to eastern Asia (Ohmi 1956, Bellorin et al. 2004). It has colonized the coasts of California, Mexico, North Carolina, Virginia, and Western Europe (Bellorin et al. 2004, Thomsen et al. 2005, Freshwater et al. 2006, Thomsen et al. 2006, 2007). In Europe it has spread widely and quickly attaching itself to invertebrate shells in estuaries and bays along the Atlantic Coast (Thomsen et al. 2007). In other areas this species has formed extensive beds in the intertidal and shallow sublittoral zones attaching to rocks, pebbles, and anthropogenic substrates (Bellorin et al. 2004, Freshwater et al. 2006). *Gracilaria vermiculophylla* has even hampered fishing operations in North Carolina by fouling fishing nets (Freshwater et al. 2006). Intermediate levels of *Gracilaria* in Hog Island Bay, Virginia increased species richness by adding complexity to a homogeneous soft bottoms and providing an attachment site for other macroalgae and fouling organisms. However, *Gracilaria* biomass densities over 100 grams dry weight per square meter led to anoxia and an accompanying reduction in diversity and faunal biomass (Thomsen et al. 2006).

Nursery habitat of the juvenile blue crab

In Chesapeake Bay, seagrass is the primary nursery habitat of the blue crab (Heck and Thoman 1984, Orth and van Montfrans 1990, Hovel and Lipcius 2001, van Montfrans et al. 2003). This habitat provides young crabs with important benefits, including increased growth rates from the diverse prey in seagrass, as well as reduced
predation rates from cannibals and other predators that the crabs face in unvegetated habitats (Perkins-Visser et al. 1996, Moksnes et al. 1997, Orth and van Montfrans 2002). The reduction of cannibalism is particularly important because the presence of seagrass can prevent intercohort cannibalism from eliminating a large segment of the newly recruited year class (Pile et al. 1996, Moksnes et al. 1997). For juvenile crabs of 10-35 mm carapace width (cw), survival increases with increasing seagrass shoot density (Schulman 1996, Hovel and Lipcius 2001). In some cases, juvenile crabs may move from one species of seagrass to another (e.g., from Zostera and Ruppia) in search of high-density patches because shoot densities vary spatially and temporally (Pardieck et al. 1999). The survival of smaller crabs in the second and third instar stage (3.1-5.9 mm) is higher at lower eelgrass densities and this phenomenon is linked to the increased presence of larger juvenile crab cannibals and shrimp predators in the denser seagrass (Schulman 1996, Moksnes and Heck 2006).

After initially settling in seagrass beds, juvenile crabs often disperse to secondary nursery habitats (Orth and van Montfrans 1987, Reyns and Eggleston 2004, Lipcius et al. 2005, Seitz et al. 2005). The secondary dispersal allows early juvenile crabs to escape the high density of conspecifics in the seagrass beds (Reyns and Eggleston 2004). As the juvenile crabs increase in size, there is a smaller difference in the rate that they are preyed on in seagrass and unvegetated habitats (Pile et al. 1996). These factors allow the 25-35 mm crabs to leave the seagrass beds in search of bivalve and other invertebrate prey in unvegetated habitats such as muddy marsh coves, which become important feeding grounds for larger juveniles (King et al. 2005, Seitz et al. 2005, Lipcius et al. 2007).
When juvenile crabs leave the seagrass beds, they utilize various habitats (Everett and Ruiz 1993, Ruiz et al. 1993, Dittel et al. 1995, Lipcius et al. 2005, 2007). Shallow waters serve as an effective predation refuge for juvenile crabs because adult blue crabs and other large aquatic predators are mostly absent from waters less than 15-20 cm deep (Ruiz et al. 1993, Dittel et al. 1995). Shallow mud flats in lower salinity waters offer a particularly effective refuge, because mesohaline and oligohaline waters have less diverse and fewer predators than the polyhaline waters of the crab’s primary settlement habitats (Lipcius et al. 2005).

The current nursery habitat paradigm begins with crabs settling in seagrass beds in the shallows at the base of the estuary (Lipcius et al. 2007). Around 25 mm cw, crabs move upriver to exploit rich food resources and reduce density-dependent mortality (Lipcius et al. 2005). The expansion of *Gracilaria vermiculophylla* in Chesapeake Bay adds another layer to this situation because it occurs in both the primary and secondary nursery habitats. *Gracilaria* occurs in seagrass beds and inside shallow coves and marsh creeks where it offers an alternative nursery habitat for crabs and other structure-dependent species.

**Patch Size**

The patch area of a habitat can have differing effects on species richness and the relationships between competitors, predators, and prey within the habitat (Debinski and Holt 2000). Colonization rates of seagrass patches are species-specific and depend on patch area and body size (Eggleston et al. 1999). In general, smaller mobile species like grass shrimps and amphipods colonize smaller seagrass plots, whereas larger adult blue
crabs and fish predators congregate more in and around larger seagrass patches (Eggleston et al. 1999, Laurel et al. 2003). The attraction of predators to larger seagrass patches is believed to be the reason juvenile blue crabs and red rock crabs experience lower survival in larger seagrass patches than in smaller seagrass ones (Hovel and Lipcius 2001, Hovel 2003).

Many other species have the opposite relationship between habitat patch size and survival, where the survival of the animal increases as seagrass patch size increases (Wilcove 1985, Irlandi 1997, Laurel et al. 2003). The positive relationship between habitat patch size and survival has been linked to the decreasing edge to interior ratios of larger seagrass beds. The survival of clams is twice as high in the seagrass interior as along the edges, and 18 times higher in the interior than in unvegetated substrate (Irlandi 1997). Survival of scallops is lower on the seagrass edge than in the seagrass interior or away from seagrass beds (Bologna and Heck 1999). Another mechanism explaining the increase in survival of animals in larger habitat patches is the decreased detectability of a prey item to predators in the midst of increasing cover and places to hide (Lipcius et al. 1998, Bartholomew 2002)

Macroalgae as a Nursery Habitat

In the presence of eutrophication, macroalgae of the genera *Ulva* and *Gracilaria* are being observed more frequently within the Chesapeake Bay. Despite the damage these macroalgae can do in shading out seagrass beds in some areas, they may have benefits for blue crabs and other organisms that have historically relied upon seagrass. Macroalgal habitats, especially branching macroalgae like *Gracilaria vermiculophylla*,

...
are generally useful to decapod crustaceans because the branches provide juvenile
decapods with living spaces where they are concealed from predators (Herrnkind and
Butler 1986, Moksnes et al. 1998, Wilson et al. 1999). Algae with intermediate levels of
branching (which have more structure than unbranched algae and more living space
between branches than highly complex algae) provide a better predation refuge to crabs
than dense seagrass or bivalve habitats. Simple unbranched macroalgae like Ulva can
still provide crabs with some refuge (Moksnes 1998, Wilson et al. 1999).

In Rehoboth Bay, Delaware, there is a complete absence of eelgrass, and the
benthic macroalga Ulva has become the primary nursery habitat for the blue crab
(Epifanio et al. 2003). Crab abundance was seven times higher in the macroalgal habitat
than in the surrounding unvegetated habitats (Epifanio et al. 2003), probably due to a
relative refuge from predation (Wilson et al. 1999). The crabs that inhabit the macroalgal
habitats are trophically linked to the macroalgae through amphipod grazers and over time
the crabs adopt C_{13} and N_{15} ratios similar to those of macroalgae (Dittel et al. 2000,

Despite the advantage of Ulva compared to unvegetated bottom, it is likely that
the more complex structure of Gracilaria will provide a stronger predation refuge
(Moksnes et al. 1998). Studies in Chesapeake Bay have already yielded evidence that
blue crabs are using Gracilaria vermiculophylla as a nursery habitat (Mahalak 2008,
Johnston and Lipcius unpublished). When Gracilaria was placed in unvegetated mud
coves, the macroalgal patches were often colonized by wild crabs or by hatchery crabs
released in the vicinity (Mahalak 2008). Natural patches of Gracilaria in the field have
densities of blue crabs that are higher than those in unvegetated mud and equal to those in seagrass (Johnston and Lipcius unpublished).

Survival Patterns of Juvenile Crabs

The survival rates of juvenile blue crabs can be influenced by crab size and season as well as by habitat. As crabs grow larger they become less susceptible to conspecifics and other predators (Peery 1989, Pile et al. 1996, Orth and van Montfrans 2002). Crab predation mortality is usually highest in the summer due to a broader suite of predators and the higher metabolic rates of exothermic predators in warmer water temperatures causing the predators to eat more (Brett 1971, Leffler 1972, Elliot 1975, Bayne and Scullard 1978, Moody 2001, Murdy et al. 1997).

In some cases crab size and season interact with the effect of habitat to influence crab survival. Vegetated habitat, for instance, can have variable effects on the different sizes of crabs (Pile et al. 1996, Schulman 1996, Hovel and Lipcius 2001). Sometimes crab size and season appear to have additive effects on crab survival along with vegetated habitat (Moody 2001). In other cases, the effect of crab size or season can swamp the effect of habitat, which limits the benefit of structured habitat. Therefore, when investigating the effects of *Gracilaria* on crab survival in the field, the habitat effects must be integrated with the effects of crab size and season.

The possible emergence of a new and abundant nursery habitat for blue crabs will become increasingly important as their primary nursery habitat (eelgrass) becomes less available. This study is an investigation of the potential of the abundant benthic
macroalga *Gracilaria* to serve a nursery function for blue crabs by increasing blue crab survival.

**Tethering Technique**

Tethering has been used in many ecological studies to estimate relative survival of aquatic organisms in conditions where it can be difficult to measure survival directly (Aronson and Heck 1995). The technique has been used to compare how different habitats, latitudes, animal sizes, and seasons affect survival (Heck and Wilson 1987, Wilson et al. 1987, McIvor and Odum 1988, Rozas and Odum 1988, Aronson 1989, Schulman 1996, Pile et al. 1996). Results of tethering are usually reported as predation risk or relative survival. In some cases, tethering causes treatment-specific bias, where artifacts from the experiment change animal behavior or interact with habitat, species, or conditions of the prey animals (Barshaw and Able 1990, Peterson and Black 1994, Smith 1995, Micheli 1996, Curran and Able 1998). It is therefore recommended that tethering experiments be accompanied by some procedure to check for experiment-specific non-additive biases (Peterson and Black 1994).

Tethering has commonly been used to measure relative mortality rates of motile animals such as the blue crab (Heck and Thoman 1981, Lipcius et al. 2005, 2007), and to isolate predation mortality from emigration and non-predatory loss of animals (Zimmer-Faust et al. 1994). When tethered, an animal is secured to a monofilament line, which is anchored to the bottom by a hook, pole, or weight. The survival estimate obtained through tethering is expected to be biased low, because tethering increases the vulnerability of mobile animals to predation (Peterson and Black 1994, Zimmer-Faust et
al. 1994, Kneib and Scheele 2000, Bullard and Hay 2002); however, this technique can be useful to determine relative survival rates.

My work investigates the importance of *Gracilaria* habitat to survival of juvenile blue crabs, *Callinectes sapidus*. Blue crabs are highly mobile, and respond actively to avoid predation (Peery 1989). They are also highly cannibalistic, with larger crabs typically preying on smaller conspecifics (Peery 1989, Lipcius et al. 2007). Tethering has been used extensively to measure effects of crab size and habitat on blue crab survival (Heck and Wilson 1987, Ruiz et al. 1993, Pile et al. 1996, Moody 2001, Lipcius et al. 2005). Tethering elevates juvenile blue crab mortality by limiting the escape distance of the juvenile, which may encourage the predator to persist in its attack after the first escape response (Zimmer-Faust et al. 1994). Consequently, one component of this investigation was a tether-method validation study (1) to check for interactions between the effects of tethering and habitat on juvenile crab survival, and (2) to measure the reduction in survival of tethered crabs.

**OBJECTIVES**

The objectives of this research are as follows:

1. Validate a tethering technique used to estimate crab survival.

2. Measure the impact of different predators and algal patch sizes on the survival of 13-26 mm crabs in mesocosms.

3. Measure the impact of algal patch size and season on the survival of 11-34 mm crabs in the field.
4. Combine results of the mesocosm and field experiments to define quantitative relationships between crab size and algal patch diameter with crab survival.

**METHODS**

**Tethering Validation**

Tethered and untethered juvenile crabs (12-26 mm cw) were placed solitarily in mesocosm tanks with an adult crab. The tanks were 1-m-diameter flow-through tanks lined with mud. Tethered crabs were glued to a monofilament line approximately 10 cm long, which was attached to a PVC post via a cable tie. Untethered crabs were simply placed in the tank. In algae trials, a single 10-cm-diameter clump of algae was placed in the tank and pushed into the mud within reach of the tethered prey crab.

After the prey crab and habitat had been secured, a predatory crab > 80 mm cw was placed in the tank and the time and date were recorded. Crabs were checked twice daily until the juvenile crabs could no longer be found. When checking the crabs, tanks were partially drained and all of the mud was searched for the prey crab. In the case of the tethered crabs, the tether was checked. If the crab had survived, the water flow was resumed and the trial continued. If the prey crab could no longer be found, the time and date were recorded and the trial was stopped. Nine flow-through tanks were used concurrently, including one tank for control trials without predators. Control tanks were used to estimate crab recovery rate and non-predation mortality. Trials in which a crab molted were discounted. Fifty-nine trials were used in the analysis.
The data were analyzed using Akaike's information criterion (AIC), with an AIC\textsubscript{C} value correcting for low sample size (Anderson 2008), to compare four models including the effects of \textit{Gracilaria} presence or absence, tether presence or absence, and the interaction between these two factors on the number of hours prey crabs survived (Table 1). A ΔAIC\textsubscript{C} value was computed by subtracting the lowest AIC\textsubscript{C} value from the AIC\textsubscript{C} value of each of the other models. Model weights were then assigned based on the ΔAIC\textsubscript{C} values

\begin{equation}
    w = \frac{e^{-\frac{1}{2}ΔAIC_{C}}}{\sum e^{-\frac{1}{2}ΔAIC_{C}}}
\end{equation}

where \( w \) is the weighted probability of the model and ΔAIC\textsubscript{C} is the difference between the AIC values of individual model and the best model. Parameter estimates were then examined for all models where \( w > 0.07 \) (Anderson 2008) to determine which factors most influenced crab survival. The primary goal of this analysis was to determine whether there was an interaction between the effect of tethering the prey crab and the effect of \textit{Gracilaria} on survival. Such an interaction would invalidate subsequent tethering survival experiments due to treatment-specific bias (Peterson and Black 1994).

The other goal of the tethering validation experiment was to measure the magnitude of the bias in survival estimates. This was done with a Kaplan-Meier analysis comparing the percent survival of tethered crabs in algae, free crabs in algae, tethered crabs in open mud, and free crabs in open mud over time. The tethering bias was determined by comparing the survival of tethered and free crabs in the same habitat conditions.
Mesocosm Study

This experiment tested for the effects of three factors—predator presence, algal patch size, and substrate—on survival of juvenile blue crabs in mesocosm tanks. The predators were oyster toadfish and adult blue crabs greater than 90 mm cw. The three algae treatments were no algae, small algal patch (10-cm-diameter), and large algal patch (80-cm-diameter). The sediment treatments were mud and sand (Figure 1).

Juvenile crabs of 12-26 mm cw were placed in a 1-m-diameter flow-through tank with a predator for 24 hours. Nine outdoor flow-through tanks were used and checked simultaneously across a group of trials (Figure 1). Each juvenile crab was tethered to a PVC post in the tank with a monofilament line that permitted an approximately 10-cm-diameter space in which to move (Figure 2).

The small algal patch consisted of a single clump of algae 20 cm tall and approximately 10 cm in diameter, created by folding a 5 cm aggregate of *Gracilaria* thalli (the stem of the macroalga) 43 cm long around a hook. The hook was then driven into the substrate to hold the algal clump in place. To create the large algal patch, five contiguous algal clumps were spread out over half of a mesocosm tank.

Predator and algal treatments were randomly rotated among eight of the flow-through tanks while the substrate factor remained constant throughout the experiment (Figure 1). A control tank was kept free of predators, into which different algal and substrate treatments were rotated (Figure 1). The controls were not included in the analysis, but served as a check on retrieval rates and prey crabs escaping the tether...
without predation. After the habitats were set up, a predator was added to the tank and the time was recorded. The tethered crab was checked 24 hours later and its status was recorded. The crab was recorded as alive, if present, or eaten, if it had been completely removed from the tether or if only part of the crab remained. Each treatment combination had 12 replicates for a total of 144 trials in an orthogonal design that included two predators (oyster toadfish and blue crabs), two substrates (sand and mud), and three levels of algae (large patch, small patch, and no algae).

The binary responses (alive or dead) of the mesocosm experiment were analyzed using AIC to compare 11 models (Table 2). The AIC analysis was conducted as described for the tether validation study. Parameter estimates of all models with weighted probabilities greater than 0.07 were examined to distinguish influential factors.

All of the hypotheses in the models included crab size, because larger crabs are generally less susceptible to predators than smaller crabs (Peery 1989, Pile et al. 1996, Orth and van Montfrans 2002). Some of the models included an effect of predator ($g_2$, $g_5$, $g_7$, $g_9$, $g_{10}$) where adult blue crabs were expected to be more effective predators than the oyster toadfish. There is greater evidence for the prevalence and importance of blue crab cannibalism (Laughlin 1982, Peery 1989, Hines et al. 1990, Mansour 1992, Hines and Ruiz 1995, Moksnes et al. 1997, Moody 2003, Lipcius et al. 2007) than there is of predation on blue crabs by oyster toadfish (Gudger 1908, Schwartz and Dutcher 1963, Steele and Perry 1990, Moody 2003). Oyster toadfish are known mostly as predators on xanthid crabs (Schwartz and Dutcher 1963, Grabowski 2004, Shervette et al. 2004).

In addition to prey size and predator, the sediment type and algal habitats could affect the survival of blue crabs in the mesocosm tanks. Blue crabs were expected to
have a higher survival in mud than in sand ($g_3, g_6, g_7, g_8, g_{11}$) (Moody 2001). The increase of crab survival in mud is linked to increased water turbidity which may be more effective in protecting small crabs than larger juveniles, which would be easier to detect ($g_8, g_{11}$). A vegetated habitat like *Gracilaria* is also expected to increase the survival of juvenile crabs ($g_4, g_5, g_6, g_7, g_8, g_9, g_{10}, g_{11}$) (Heck and Wilson 1987, Wilson et al. 1987, Pile et al. 1996, Schulman 1996, Moksnes et al. 1997, Pardieck 1999). A vegetated habitat like macroalgae may be more beneficial to smaller crabs than larger crabs ($g_9, g_{11}$) for two reasons. The vegetated habitat becomes less important for larger crabs in part due to their size refuge (Pile et al. 1996). Larger animals would also be more detectable within the algae than would smaller crabs (Lipcius et al. 1998). If the high turbidity of mud and presence of algae both protect juvenile crabs by lowering the detectability of juvenile crabs, then algal habitat will become more important in sand because crabs in sand would be more detectable in the absence of algae than crabs in mud ($g_8$). The *Gracilaria* habitat may also be a greater defense against oyster toadfish than adult blue crabs if toadfish have more difficulty handling the prey within *Gracilaria* than blue crabs ($g_{10}$). The smaller claws may be more effective at reaching between the *Gracilaria* thalli than the large jaws of the oyster toadfish.

**Field Experiment**

This experiment was conducted in the summer and fall of 2007 in the subtidal zone (85-cm mean low tidal depth) off a sandy beach near VIMS in Gloucester Point, VA. There were three habitat treatments: sand, small algal patches (10 cm diameter), and large algal patches (40 cm diameter). Summer trials occurred in July and August, and fall
trials in October and November. The average temperature during the study period ranged from 12.5-30.0 °C (24.0-30.0 °C in the summer, 12.5-24.0 °C in the fall). The summer trials were 15 h in duration, whereas fall trials were 24 h in duration. Juvenile crabs of 11-34 mm cw were tethered with a monofilament line to a metal garden post driven into the bottom, which afforded a 20-cm-diameter area for movement. The garden posts were placed one meter in front of a PVC post used to locate the tether locations. This distance from the tethering post was presumed sufficient to prevent the PVC post from affecting the behavior of the predators (Lipcius et al. 2005).

The field habitat treatments were designed to match those in the earlier mesocosm experiment. The *Gracilaria* thalli used to create the algal patches in this experiment were 43 cm long. The small patch was created by wrapping a cable tie midway down the length of a 5-cm-wide clump of *Gracilaria* and folding the algae over the cable tie into a 10-cm-diameter algal patch. A small guard post and a garden staple were hooked around the cable tie and sunk completely into the sand bottom. The large patch of algae was secured with netting and monofilament line stretched across a 40-cm-diameter rebar ring. The netting and monofilament line were designed to secure the algae midway down the thalli, permitting one end of the thalli to drift freely while the base of the algae was bound together with the netting and weighed down by the rebar ring. At the end of the trial period, the tethers were checked and the crabs were recorded as either alive, or eaten, using the same basis of assessment described in the earlier mesocosm study.

Nine logistic regression models were run on the binomial response (alive or dead) (Table 3). Factors included algal patch size, crab size, season, and interactions amongst these factors where
\[
(3) \ln(survival) = \alpha + \beta_1 \otimes \text{Variable}_1 + \beta_2 \otimes \text{Variable}_2 \ldots \beta_n \otimes \text{Variable}_n
\]  

(Table 3). The AIC analysis was conducted as described for the tether validation study. Parameter estimates of all models with weights greater than 0.07 were examined to distinguish influential factors.

Most of the hypotheses in the models included crab size (Table 3), because larger crabs are generally less susceptible to predators than smaller crabs (Peery 1989, Pile et al. 1996, Orth and van Montfrans 2002). Against small predators that can maneuver between the spaces within structure, habitat may not be a refuge; only large size may protect juvenile crabs (Olmi and Lipcius 1991, Bartholomew 2002). Hypothesis g6 is an exception in not including crab size, because the mechanism behind the season $\times$ algae interaction involves finfish predation, and the role of crab size in finfish predation is unknown. In the fall, striped bass target blue crabs in vegetated habitats (J. van Montfrans personal communication) such that the effectiveness of algal habitat may be limited in the fall (g6 & g8). Striped bass predation may also cause an interaction between crab size and season if striped bass are less size-selective predators than the predators that kill juvenile crabs in the summer (g7) (Table 3).

While crab size and habitat may affect crab survival, season may also play an important role. Predation rates are usually higher in the summer than in the fall, because there are more predators in summer, and they eat more in warmer temperatures (Brett 1971, Leffler 1972, Elliot 1975, Bayne and Scullard 1978, Moody 2001, Murdy et al. 1997). Thus, season may influence crab survival rates (g4) (Table 3). In some instances crab size, habitat, and season all increase crab survival in a purely additive manner (g5) (Moody 2001). Within a season, both crab size and structured habitats will increase crab
survival ($g_2$) (Orth and van Montfran 2002). In other cases, the effect of crab size interacts with the effect of habitat. Larger crabs do not seem to receive the same benefits from structured habitat as smaller crabs ($g_3$, $g_7$, $g_9$) (Table 3) (Pile et al. 1996).

Cross Study Comparison

The mesocosm and field experiments were conducted with different crab sizes and algal patch diameters, yet there was some overlap in the treatments (Figure 3). Both studies had no-algae treatments and small algal patch treatments (10-cm-diameter). The large algal patch treatment was different in the mesocosm experiment (80-cm-diameter) than in the field study (40-cm-diameter). Another treatment distinction was that the field study had a larger size range (11-34 mm cw) of prey crabs than did the mesocosm study (13-26 mm cw) (Figure 3).

The data from the small algal patch and no-algae treatments with prey crabs between 13-26 mm cw were collapsed into one larger dataset and analyzed with experiment (field or mesocosm) as a factor. In all the analyses, the experiment factor was not significant (see results). Data from the two experiments were then combined into one meta-data set due to the non-significance of the experiment factor.

Combined Survival

For the combined dataset, algal patch treatment was converted into algal patch diameters: 0 cm, 10 cm, 40 cm, and 80 cm (Figure 4). Crab survival was modeled based on crab size and algal patch size where

$$\ln(survival) = \alpha + \beta_1 \otimes Variable_1 + \beta_2 \otimes Variable_2 \ldots \beta_n \otimes Variable_n$$
(Table 4). The models were analyzed using AIC statistics. The $\Delta$AIC$_C$ values and model weights were then assigned based on the AIC$_C$ values (Equation 1), and the parameter estimates of the top models were further examined.

RESULTS

Tethering Validation

Survival was highest when crabs were untethered in tanks with Gracilaria. The model that best explained the data included both habitat and tethering effects, but no interaction effect, and a weighted probability of 0.56 (Table 5a). Although the model that included an interaction effect had a weighted probability of 0.19 (Table 5a), there was little contribution of the interaction coefficient (effect size = 4.9, SE = 16.8) to the model (Table 5b). Consequently, I concluded that there was no treatment-specific bias due to tethering.

In the Kaplan-Meier Analysis at 24-25 h, untethered crabs had a survival of 80 % in tanks with algae, and a survival of 75 % without algae (Figure 5). Tethered crabs had a survival of 46 % in tanks with algae and 29 % without algae (Figure 5). Irrespective of algae, tethered crabs had a survival rate of 37 %, whereas the survival rate for the untethered crabs was 79 %.

Mesocosm Study

The best model for survival of juvenile crabs in mesocosms was determined by prey size, algal patch treatment and predator (Table 6):
where $s =$ probability of survival, $cw$ is the prey carapace width, $algaeb =$ small patch, $algaec =$ large patch, and $tf$ is the oyster toadfish predator (Table 6). The least likely models did not include predator or algae treatment parameters (Table 6).

Within the models the large algal patch and predator treatments were the only significant parameters, and they were greater in magnitude than any of the other parameters (Table 7). Crab size, small algal patch, sediment, and all the various interactions between factors never significantly affected the survival of juvenile crabs in mesocosm tanks (Table 7).

Cannibalistic adult blue crabs were far more effective predators on juvenile blue crabs than oyster toadfish, and the survival of juveniles in tanks with adult blue crabs was half the survival in tanks with oyster toadfish (Figure 6). Juvenile crabs were also 50 % more likely to survive when a larger algal patch was present in their tank than they were in tanks with a smaller or no algal patch (Figure 8).

**Field Experiment**

In the best model, juvenile crab survival was determined by crab size, algal patch treatment, season, and the interaction between crab size and algal patch treatment (Table 7):

$$s = \frac{e^{0.30-0.05cw-0.49a_{algaeb}+1.05a_{algaec}+0.39tf}}{1 + e^{0.30-0.05cw-0.49a_{algaeb}+1.05a_{algaec}+0.39tf}}$$

(5)

where $s =$ probability of survival, $cw$ is the prey carapace width, $algaeb =$ small patch, $algaec =$ large patch, and $tf$ is the oyster toadfish predator (Table 6). The least likely models did not include predator or algae treatment parameters (Table 6).
patch size had higher model probabilities than models where both of these variables were additive (Tables 8 and 9).

Within the models, only three parameters were consistently significant to crab survival in the field—crab size, large algal patch (40 cm in diameter), and the interaction between these two factors (Table 9). Both crab size and large algal patch became significant only when an interaction between these effects was included in the model. Models \( g_9 \) and \( g_5 \) were identical with the exception that model \( g_9 \) had an interaction between crab size and large algal patch size, and model \( g_5 \) did not. Consequently model \( g_9 \) had a much greater magnitude of the effect of large algal patch treatment (3.45 ± 1.24 \( \text{SE} \)) than did model \( g_5 \) (-0.05 ± 0.33 \( \text{SE} \)) (Table 9).

The interaction between large algal patch and crab size was also significant in the two highest weighted models, \( g_9 \) and \( g_3 \) (Table 9). In small algal patch and bare sand treatments, crab survival increased with increasing crab size. In the large algal patch, crab survival decreased with increasing crab size (Figure 8). Smaller prey crabs (11-18 mm \( \text{cw} \)) experienced higher survival in the large algal patch (0.54 ± 0.09 \( \text{SE} \)) compared to the smaller algal patch (0.41 ± 0.11) and bare sand (0.27 ± 0.10). Larger prey crabs (25-34 mm \( \text{cw} \)) experienced a lower survival in large algal patches (0.26 ± 0.08 \( \text{SE} \)), compared to small algal patches (0.45 ± 0.11) and bare sand (0.56 ± 0.10) (Figure 8).

Cross Study Comparison

The field vs. mesocosm experiment comparison failed to reveal any significant difference in crab survival between the mesocosm and field for the no algae and small algal patch treatments. The experimental setting (field vs. mesocosm) was not a
significant factor singularly (-0.21, SE = 0.29 in model $g_1$), nor was it a significant factor when added to other factors of algae and crab size (Table 10). The estimate of the value of the setting was almost always smaller than the standard error of that estimate (Table 10). I therefore concluded that the mesocosm and field experiments had no significant differences where the algae treatments and crab sizes overlapped. Thus, the data from the field and mesocosm survival experiments could be combined into a meta-dataset.

Combined Survival Analysis

Tethered crab survival in mesocosms and in the field was best explained by a model that included crab size, algal patch diameter, and the interaction between these two variables:

$$ (7) \quad \text{crab survival} = \frac{e^{-1.181+0.044x+0.058y-0.002xy}}{1+e^{-1.181+0.044x+0.058y-0.002xy}} $$

where $x$ is crab carapace width (mm) and $y$ is the diameter of the $Gracilaria$ patch (cm). When compared against the other nine models, this model had a weighted probability of 0.880 (Table 11).

Smaller crabs (11.0-17.9 mm) had increased survival in algae starting with a low in no algae (0.39 ± SE 0.06) and increasing in 10 cm (0.44 ± 0.05), 40 cm (0.58 ± 0.06), and 80 cm (0.75 ± 0.09) $Gracilaria$ patches as the patch diameter increased. The survival of larger crabs (25-34 mm) decreased with increasing algal patch diameter starting from a high of 0.51 ± 0.6 SE in no algae to a low of 0.31 ± 0.15 in the 80-cm-diameter $Gracilaria$ patch (Figure 9).
DISCUSSION

My tethered crab/non-tethered crab comparison in mesocosms validated the tethering method I used in the survival study. I found no significant interaction between the effects of algal habitat and the effects of tethering in this comparison. Generally, the 24-hour survival of free crabs was twice the survival of tethered crabs in the no algae and 10-cm-diameter *Gracilaria* patch conditions.

Predation pressure experienced by juvenile crabs has been significantly higher in the summer than in the fall (Moody 2001). In my field experiments, shortening the summer trials by 15 hours compared to the fall made the experimental survival rates in the two seasons similar, as evidenced by the non-significant effect of season in the field experiment. The predation pressure on juvenile crabs in the field in the fall was very similar in magnitude to the predation pressure created by crabs living in a tank 1-m-diameter tank with a single predator; thus I found no difference between the field and mesocosm predation rates in the cross study comparison.

Crabs greater than 25 mm cw, experienced a disadvantage from *Gracilaria* habitat. Despite the well acknowledged ability of vegetated habitats to lower predation mortality (Perkins-Visser et al. 1996, Moksnès et al. 1997, Wilson et al. 1999, Orth and van Montfrans 2002), there is growing evidence that this refuge benefit can decreases with increasing crab size (Pile et al. 1996, Moksnès et al. 1997, Lipcius et al. 2005). Moksnès et al. (1997) saw the differences in survival between crabs in vegetated and unvegetated habitats disappear when crabs reached the fifth instar (7.5-9.1 mm cw), while Pile et al. (1996) witnessed the difference decrease by the ninth instar (14.2-16.2
mm cw). The survival of 25-55 mm cw crabs was lower in unvegetated mud up-river than in seagrass beds near the mouth of the estuary (Lipcius et al. 2005). All of these findings support the idea that once crabs reach a certain size, seagrass beds and other vegetated habitats may no longer serve as a predation refuge and may even increase the prey’s vulnerability to predation.

Two different mechanisms can cause the increase in predation rates of crabs above a certain size in vegetated habitats. Crabs may become less able to maneuver through the structured habitat when they become larger than the inter-structural space within the habitat (Bartholomew et al. 2000). This is the very mechanism that inhibits predators from capturing smaller prey in structured habitats (Ryer 1988, Bartholomew et al. 2000), but makes larger crabs less mobile and more vulnerable to predation. The second mechanism for higher predation rates of the larger crabs in *Gracilaria*, compared to the smaller crabs, is the increased detectability of the animals. Larger opisthobranchs and larger amphipods both have higher encounter rates with predators in vegetated habitats than do smaller individuals (Ryer 1988, Pennings 1990). The combination of these mechanisms renders crabs greater than a certain size more likely to be seen and less able to evade predators in complex structural habitats.

The predators in both the mesocosm and in the field appeared to be drawn to *Gracilaria* patches. The attraction of predators to structural habitat explains the crab size × algae interaction in the combined dataset. In studies with shrimp, crabs, and scallops as prey, predation rates were higher at the edges of seagrass beds than in the seagrass interior or on unvegetated substrate (Bologna and Heck 1999, Peterson et al. 2001) because the predators were apparently targeting the structured habitat. Prey on the edge
were more likely to be detected and attacked by predators because they lacked the dense cover of the interior, and predators were drawn to the structure. I witnessed a predator’s preference for structure in my mesocosm trials, whereby oyster toadfish consistently preferred to reside in or near the *Gracilaria* patches. In cases where no algae was available, the toadfish dug holes in the sediment and rested there during daytime, prior to foraging at night (Gudger 1910). Consequently, larger crabs unable to use *Gracilaria* patches effectively may fall prey to the larger predators attracted to *Gracilaria*.

In conclusion, juvenile crabs had lowered predation rates and increased survival by utilizing *Gracilaria vermiculophylla* as a habitat. This finding offers new hope that the Chesapeake Bay’s blue crab may be adapting to the Bay’s shift from a seagrass-dominated system to one that includes widespread macroalgal abundance. Non-native vegetated species are often viewed as a concern, but this study reveals evidence that *Gracilaria* may provide benefits to native fauna. A vegetated species in sufficient quantity, whether it be native or non-native, will still help animals avoid detection and the ability to avoid detection is shown here to be a central strategy in prey animal survival.

Although *Gracilaria* is able to provide crabs similar survival benefits as seagrass and even supports similar densities of juvenile crabs, the ecosystem impacts of *Gracilaria* remain unresolved. Unlike seagrasses, *Gracilaria* does not possess roots, such that it will not have the same influence on the infaunal community as eelgrass. As infaunal invertebrates represent an important component of the blue crab diet (Seitz et al. 2005, Lipcius et al. 2007), degradation of the infaunal community during the shift from seagrass to macroalgae may have a negative impact on the blue crab population. There may, however, be some compensatory benefits provided by the invertebrate prey residing...
in *Gracilaria* patches. In some habitats, hypoxia associated with high biomass of *Gracilaria* may also negatively affect the benthic community, and therefore the blue crab as well.

Finally, temporal variation in the abundance of *Gracilaria* in the Bay has not been described quantitatively. I have observed population declines in July and December around the Goodwin Islands and other shallow coves off the York River, VA, in two successive years. It is possible that *Gracilaria vermiculophylla* may be too ephemeral to provide juvenile crabs with protection during critical parts of the year when large numbers of newly recruited juveniles are in need of refuge. It is clear from my experiments that the non-native macroalga *Gracilaria vermiculophylla* has the potential to serve as a beneficial habitat for blue crabs, but further work is necessary to understand its spatio-temporal patterns in abundance and its impact at the ecosystem level.
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Table 1. The parameters in the models of crab survival times in the tethering method validation where

\[ \text{survival} = \alpha + \beta_1 \otimes \text{Variable}_1 + \beta_2 \otimes \text{Variable}_2 \ldots \beta_n \otimes \text{Variable}_n, \]

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Table 2. Parameters of the models of blue crab survival in the mesocosm tanks. \( Sp = \) size of prey; \( Asp = \) small algal patch; \( Alp = \) large algal patch; \( P = \) predator; \( S = \) sediment.

\[
\ln(\text{survival}) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n
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Table 3. The parameters for the models of crab survival for the field experiment. Int = intercept, lp = large patch and sp = small patch.

\[ \ln(\text{survival}) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n \]

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<thead>
<tr>
<th>Model</th>
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<th>Crab</th>
<th>Algae(sp)</th>
<th>Algae(lp)</th>
<th>Season</th>
<th>C×Asp</th>
<th>C×Alp</th>
<th>Asp×S</th>
<th>Alp×S</th>
<th>C×S</th>
<th>C×Asp×S</th>
<th>C×Asp×S</th>
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</table>
Table 4. The parameters of the models explaining crab survival in the combined dataset.

C×A stands for the interaction of Crab size (mm) and Algal patch diameter (cm).

\[ \ln(\text{survival}) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n \]

<table>
<thead>
<tr>
<th>Model</th>
<th>Intercept</th>
<th>Crab size</th>
<th>Algae diameter</th>
<th>C×A</th>
</tr>
</thead>
<tbody>
<tr>
<td>g_1</td>
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<td>( \beta_1 )</td>
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<td>g_2</td>
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<tr>
<td>g_3</td>
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<td>( \beta_1 )</td>
<td>( \beta_2 )</td>
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</table>
Table 5a. The AIC values for the models of crab survival in the tethering validation study. Model labels (g₁- g₄) from Table 1.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Weight</th>
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<tbody>
<tr>
<td>g₃</td>
<td>555.40</td>
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<td>g₂</td>
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<td>g₄</td>
<td>557.53</td>
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<td>564.12</td>
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Table 5b. Means and standard errors of the parameters within the models of crab survival in the tethering validation study.

<table>
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<tr>
<th>Model</th>
<th>Algae</th>
<th>SE</th>
<th>Tether</th>
<th>SE</th>
<th>A×T</th>
<th>SE</th>
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Table 6. Akaike's Information Criterion values and weighted probabilities of the models of crab survival in mesocosm tanks.

<table>
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<th>Weighted probability</th>
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Table 7. Values of the parameters in the models of crab survival in mesocosm tanks. Int = intercept; SE = standard error.

<table>
<thead>
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<th>Model</th>
<th>Int</th>
<th>Size(prey)</th>
<th>SE</th>
<th>Algae(sp)</th>
<th>SE</th>
<th>Algae(lp)</th>
<th>SE</th>
<th>Predator</th>
<th>SE</th>
<th>Sediment</th>
<th>SE</th>
<th>Sp×Asp</th>
<th>SE</th>
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<th>Asp×S</th>
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</table>

54
Table 8. AIC table for models of crab survival in the field. Parameters in the model are contained in Table 2.

<table>
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<th>ΔAICc</th>
<th>Weight</th>
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</table>
Table 9. The parameters in the models of crab survival in the field. Shown here with means ± standard error.

<table>
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<th>Model</th>
<th>α</th>
<th>Crab size</th>
<th>Algae sp</th>
<th>Algae lp</th>
<th>Season</th>
<th>Factors in Crab survival</th>
<th>C×Asp</th>
<th>C×Alp</th>
<th>Asp×S</th>
<th>Alp×S</th>
<th>C×S</th>
<th>C×Asp×S</th>
<th>C×Asp×S</th>
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<td>-2.22</td>
<td>0.08±0.04</td>
<td>1.60±1.24</td>
<td>3.45±1.24</td>
<td>0.44±0.28</td>
<td>-0.08±0.06</td>
<td>-0.16±0.05</td>
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<tr>
<td>g_3</td>
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<td>0.08±0.04</td>
<td>1.39±1.24</td>
<td>3.33±1.23</td>
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<td>-0.07±0.05</td>
<td>-0.16±0.05</td>
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<tr>
<td>g_4</td>
<td>-0.44</td>
<td>0.01±0.02</td>
<td></td>
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<td>0.40±0.27</td>
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<td>g_1</td>
<td>-0.03</td>
<td>0.01±0.02</td>
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<tr>
<td>g_7</td>
<td>-4.89</td>
<td>0.19±0.07</td>
<td>3.67±2.00</td>
<td>6.18±2.00</td>
<td>5.13±2.15</td>
<td>-0.15±0.08</td>
<td>-0.26±0.08</td>
<td>-2.47±2.93</td>
<td>-4.74±2.88</td>
<td>-0.18±0.09</td>
<td>0.08±0.13</td>
<td>0.17±0.13</td>
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<tr>
<td>g_5</td>
<td>-0.37</td>
<td>0.01±0.02</td>
<td>-0.12±0.34</td>
<td>-0.05±0.33</td>
<td>0.40±0.27</td>
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<tr>
<td>g_6</td>
<td>-0.58</td>
<td>0.01±0.01</td>
<td>0.09±0.47</td>
<td>0.29±0.44</td>
<td>0.80±0.47</td>
<td>-0.45±0.69</td>
<td>-0.76±0.66</td>
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<tr>
<td>g_2</td>
<td>-0.22</td>
<td>0.01±0.02</td>
<td>-0.13±0.34</td>
<td>-0.07±0.33</td>
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<tr>
<td>g_6</td>
<td>-0.51</td>
<td>0.08±0.47</td>
<td>0.29±0.44</td>
<td>0.80±0.47</td>
<td></td>
<td>-0.37±0.68</td>
<td>-0.69±0.66</td>
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</tbody>
</table>
Table 10a. The parameters of the models that were run in the comparison between field and mesocosm data.

\[ \ln(\text{survival}) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n \]

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameters</th>
<th>Int</th>
<th>Field</th>
<th>Algae</th>
<th>Crab size</th>
<th>F×A</th>
<th>F×C</th>
<th>A×C</th>
<th>F×A×C</th>
</tr>
</thead>
<tbody>
<tr>
<td>( g_1 )</td>
<td>( \alpha )</td>
<td>( \beta_1 )</td>
<td>( \beta_2 )</td>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>( g_2 )</td>
<td>( \alpha )</td>
<td>( \beta_1 )</td>
<td>( \beta_2 )</td>
<td></td>
<td></td>
<td>( \beta_4 )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( g_3 )</td>
<td>( \alpha )</td>
<td>( \beta_1 )</td>
<td>( \beta_2 )</td>
<td>( \beta_3 )</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>( g_4 )</td>
<td>( \alpha )</td>
<td>( \beta_1 )</td>
<td>( \beta_2 )</td>
<td>( \beta_3 )</td>
<td>( \beta_4 )</td>
<td>( \beta_5 )</td>
<td>( \beta_6 )</td>
<td>( \beta_7 )</td>
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</tr>
<tr>
<td>( g_5 )</td>
<td>( \alpha )</td>
<td>( \beta_1 )</td>
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<tr>
<td>( g_6 )</td>
<td>( \alpha )</td>
<td>( \beta_1 )</td>
<td></td>
<td>( \beta_3 )</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>( g_7 )</td>
<td>( \alpha )</td>
<td>( \beta_1 )</td>
<td></td>
<td>( \beta_3 )</td>
<td></td>
<td>( \beta_5 )</td>
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</tr>
</tbody>
</table>

Table 10b. Results of models comparing the mesocosm and field experiments. *Crab* represents the crab’s carapace width (mm). *Field* was the setting factor where the mesocosm experiment = 0 and the field experiment = 1. *Algae* had two levels—no algae and 10-cm-diameter algal patches.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameters Including Setting</th>
<th>Parameter Value</th>
<th>SE of Parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>( g_1 )</td>
<td>Field</td>
<td>-0.207</td>
<td>0.290</td>
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<tr>
<td>( g_2 )</td>
<td>Field</td>
<td>-0.0438</td>
<td>0.407</td>
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<tr>
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<td>Field×Algae</td>
<td>0.475</td>
<td>0.582</td>
</tr>
<tr>
<td>( g_3 )</td>
<td>Field</td>
<td>-0.222</td>
<td>0.293</td>
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<tr>
<td>( g_4 )</td>
<td>Field</td>
<td>-2.166</td>
<td>2.161</td>
</tr>
<tr>
<td></td>
<td>Field×Algae</td>
<td>1.065</td>
<td>3.082</td>
</tr>
<tr>
<td></td>
<td>Field×Crab</td>
<td>0.087</td>
<td>0.107</td>
</tr>
<tr>
<td></td>
<td>Field×Algae×Crab</td>
<td>-0.029</td>
<td>0.156</td>
</tr>
<tr>
<td>( g_5 )</td>
<td>Field</td>
<td>-0.205</td>
<td>0.290</td>
</tr>
<tr>
<td>( g_6 )</td>
<td>Field</td>
<td>-0.241</td>
<td>0.292</td>
</tr>
<tr>
<td>( g_7 )</td>
<td>Field</td>
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<td>1.521</td>
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<tr>
<td></td>
<td>Field×Crab</td>
<td>0.063</td>
<td>0.077</td>
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</table>
Table 11a. AIC values and weighted probabilities of the models of crab survival in the combined data set.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Weight</th>
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</thead>
<tbody>
<tr>
<td>g3</td>
<td>494.9</td>
<td>0</td>
<td>0.888</td>
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<tr>
<td>g2</td>
<td>499.2</td>
<td>4.3</td>
<td>0.103</td>
</tr>
<tr>
<td>g1</td>
<td>504.3</td>
<td>9.4</td>
<td>0.008</td>
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</table>

Table 11b. Parameters of the models in the combined data set.

<table>
<thead>
<tr>
<th>Model</th>
<th>Crab size</th>
<th>SE</th>
<th>Diameter</th>
<th>SE</th>
<th>C×D</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>g3</td>
<td>0.044</td>
<td>0.026</td>
<td>0.058</td>
<td>0.020</td>
<td>-0.002</td>
<td>.001</td>
</tr>
<tr>
<td>g2</td>
<td>0.001</td>
<td>0.019</td>
<td>0.011</td>
<td>0.004</td>
<td>NA</td>
<td>NA</td>
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<tr>
<td>g1</td>
<td>-0.002</td>
<td>0.019</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>
FIGURE LEGENDS

Fig. 1. Experimental setup. The sediment lining the bottom of the tanks was kept fixed throughout the experiment, with the exception of the control tank.

Fig. 2. Setup of the tethered crabs and algal patch treatments within the mesocosm tanks. The prey crab was tethered with a 10 cm radius of free movement. When algal patches were present in the tank, they were arranged as shown.

Fig. 3. Crab sizes and algal patch diameters used in field and mesocosm survival experiments. The area of overlap is shown with both stripes and dots. The broken line shows inference of combined and individual data sets.

Fig. 4. Sizes and shapes of the algal patch treatments used in the field and mesocosm experiments.

Fig. 5. Kaplan-Meier survival measurements from the tethering validation experiment. The solid line represents untethered crabs in tanks with algae. The dashed line represents tethered crabs in tanks with algae. The line composed of dots represents untethered crabs in tanks without algae, and the line composed of both dots and dashes represents tethered crabs in tanks with no algae.
Fig. 6. Survival probabilities for 24 hours in the tanks with predators under the different habitat conditions. Error bars = 1 SE.

Fig. 7. Survival probabilities over 24 h in the tanks with predators. Error bars = 1 SE.

Fig. 8. Survival of different sized crabs in the field in various habitat treatments. The solid line represents crabs in no algae, the dashed line represents crabs in the small algal patches, and the dotted line represents crabs in the large algal patches.

Fig. 9. Crab daily survival rates in the combined dataset.
Figure 1.
Figure 3.
Figure 4.

<table>
<thead>
<tr>
<th></th>
<th>No algae</th>
<th>10 cm patch</th>
<th>40 cm patch</th>
<th>80 cm patch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Both</td>
<td>Both</td>
<td>Field</td>
<td>Mesocosm</td>
<td></td>
</tr>
</tbody>
</table>
Figure 5.
Figure 6.

![Bar chart showing survival rates for Oyster Toadfish and Blue Crab predators.](image-url)
Figure 7.

![Bar chart showing survival rate for different habitats. The x-axis represents habitat types: Small Patch, No Algae, and Large Patch. The y-axis represents survival rate ranging from 0.0 to 1.0. The chart indicates that the survival rate is highest for the Large Patch habitat, followed by No Algae, and then Small Patch.]
Figure 8.

[Graph showing the relationship between crab size and survival in different conditions.]

- Circles: No Algae
- Triangles: Small Patch
- Squares: Large Patch
- Dashed line: No Algae
- Dotted line: Small Patch
- Solid line: Large Patch

Survival is plotted on the y-axis, and Crab Size mm is plotted on the x-axis.
Figure 9.