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**The effects of habitat and predation on bay
scallop populations in New York**

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by

John Michael Carroll

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Abstract of the Dissertation

The effects of habitat and predation on bay scallop populations in New York

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Bay scallops once supported a vibrant fishery on Long Island. Populations crashed in the mid 1980s due to a series of brown tides, and while blooms haven't occurred within the Peconic Estuary since 1995, scallops have not naturally recovered. Concomitant with the loss of scallops due to the blooms was the disappearance of eelgrass, often called the "preferred" scallop habitat, possibly explaining the lack of recovery. Current restoration efforts have produced over 6 million scallops for deployment to the estuaries, leading to significant increases in the local scallop population. However, it is possible that the loss of seagrass might limit full recovery; this research aimed to investigate the impacts of eelgrass patchiness and alternative habitats on scallop recruitment, survival, and growth.

A common theme in marine landscape studies are edge effects, and seagrass edges can affect settlement, access to food, and survival of bay scallops, *Argopecten irradians*. Using artificial seagrass units, the settlement, recruitment, and survival of bay scallops was investigated across a variety of seagrass patch treatments. By simultaneously collecting settlers (those viable

larvae available to settle and metamorphose) and recruits (those settlers which survive some period of time, in this case, 6 weeks) on the same collectors, we were able to demonstrate a balance between positive and negative edge effects, resulting in a net neutral effect.

Another important aspect to be considered across a seascape is potential trade-offs between growth and survival. Despite different growth rates across the three years studied, the pattern in growth and condition remained the same – highest in unvegetated sediments, intermediate at patch edges and slowest in patch interiors, which suggests a biological cost for scallops associated with seagrass habitats. Survival of tethered scallops showed an opposite pattern, however, being highest in patch interiors and lowest over barren sediment, and thus showed a potential food-risk trade-off for the scallops in seagrass patches. Further, by examining the core area index (CAI), the data suggest that growth and survival intercept at a low CAI, suggesting that smaller and/or more complex shaped patches may maximize growth and survival.

While eelgrass is generally regarded as the preferred habitat of bay scallops, it is disappearing throughout its range, so alternative substrates may serve important ecological functions for bay scallops. One candidate is *Codium fragile*, a introduced macroalgal species with which bay scallops are known to associate in Long Island, New York. By using both free-released and tethered scallops for a period of 7 days within eelgrass and *Codium* habitats, this research demonstrated that the invader offers the same predation refuge value. Additionally, densities of naturally recruited 0+ yr scallops recovered by visual and suction dredge sampling were similar in the eelgrass and *Codium* substrates. This work suggests that *Codium* might be a viable alternative habitat for scallops.

However, since scallops exhibit a food-risk trade-off in their preferred habitat, the complex canopy can have impacts on scallop growth. Growth of scallops placed in *Codium* was compared to eelgrass and unvegetated sediments by placing caged scallops within each of 3 habitats at 2 hydrodynamically different sites over 2 years. Scallops were measured for long term (3 month) survival, growth, and condition. In 3 of the 4 experiments, scallops exhibited no negative effects of *Codium* association. In the only experiment where scallops in *Codium* were negatively affected, the results differed from natural scallops in invaded habitat. This reiterates that *Codium* may be a viable replacement habitat for bay scallops, although it highlights the complex relationships between invasive engineers and native species.

The general conclusions from this study suggest two major shifts from current paradigms in marine ecological literature. First, fragmented seagrass meadows may be beneficial for populations of associated fauna, such as bay scallops. Enhanced settlement and growth at edges, and similar densities of scallops across a seagrass landscape suggests that scallop population growth is reliant on these edge habitats. Second, invasive species may facilitate native species. In the absence of seagrass, this research has demonstrated that an invasive macroalgae may facilitate typically seagrass-associating fauna. Scallop survival is the same in *Codium* with no additional metabolic costs. These results, in sum, provide valuable information for management and restoration efforts.

Dedication Page

I would like to dedicate this dissertation to my family and friends who helped me achieve my goals.

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Vita, Publications and/or Fields of Study

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Carroll, J., C.J. Gobler, B.J. Peterson. Resource-restricted growth of eelgrass in New York estuaries: light limitation, and alleviation of nutrient stress by hard clams. Marine Ecology Progress Series 369:51-62

Chapter One

Introduction

Background

Estuaries are vital coastal ecosystems that provide critical habitats for a variety of wildlife, e.g., spawning and nursery grounds for numerous marine species, as well as naturally filtering and buffering the shoreline. Much of the world's population is concentrated near the coasts and relies on estuaries for food, employment and recreation. In fact, many commercially important fin and shellfish species spend part or ,most of their lives within these estuaries. Despite the ecological and economic importance of estuaries, negative human pressure on these ecosystems is increasing as human populations increase in the coastal zone.

Man's encroachment into coastal environments has led to alarming changes in ecosystem structure and function (Vitousek et al. 1997, Pandolfi et al. 2003). Human impacts on coastal marine systems first began thousands of years ago and escalated to rapid degradation during the colonial development periods and industrial revolution (Lotze et al. 2006). Examples include nutrient loading and eutrophication (Richardson and Jorgensen 1996, Paerl 1997, de Jonge et al. 2002, Lotze et al. 2006), land-use changes and coastal development, and overharvest (Pauly et al. 1998, Jackson et al. 2001, Pauly et al. 2003), these processes have reorganized the ecosystem structure of many coastal ecosystems.

Human impact on a coastal system is especially true in New York estuaries, which have been documented as some of the most productive in the country in terms of primary production and shellfish harvest (COSMA 1985). Oysters, *Crassostrea virginica*, hard clams, *Mercenaria mercenaria*, and bay scallops, *Argopecten irradians*, all supported vibrant fisheries, and yet, each fishery collapsed, in part, due to anthropogenic influences – overharvest, eutrophication, and/or harmful algal blooms. New York oysters were world renowned, but populations throughout the

state crashed between the early to mid 1900s (Kirby 2004). During the 1970s, two out of every three hard clams eaten on the east coast of the United States came from the Long Island South Shore Estuary system (LISSE) and accounted for 54% of the total US hard clam harvest (McHugh 1991). During the 1980s, Peconic bay scallops comprised of 1/4 of commercial US landings (see MacKenzie 2008). The reasons behind each collapse are slightly different, none-the-less, all have occurred in the past 100 years, a period of economic and industrial development, population growth, and land-use changes (Lotze et al 2006).

Among the reasons for formerly high fisheries productivity in these bivalve species were healthy seagrass meadows. In estuarine systems, seagrass is a foundation species and provides a variety of services that can determine ecosystem structure and function. Ecosystem services provided by seagrasses include: 1) sediment stabilization by roots and rhizomes; 2) reduce water flow through the leaf canopy which enhances particle deposition; 3) creation of critical nursery habitat by the 3D canopy structure which provides shelter for many juvenile fish and shellfish species; 4) absorption of water column nutrients; 5) oxygenation of sediments via root/rhizome complex; and 6) production of large quantities of biomass which can be a important component of coastal food webs (Hemminga and Duarte 2000, Green and Short 2003, Orth et al. 2006).

While each of these services can be beneficial to the many species inhabiting estuaries, there is a wealth of literature describing the nursery role of seagrass beds for many estuarines species (Heck and Orth 1980, Orth et al. 1984, Bell and Westoby 1986, Orth 1992, Heck et al. 1995, Irlandi et al. 1995, Irlandi 1997, Bell et al. 2001, Heck et al. 2003, Ford et al. 2010, Warren et al. 2010).

Eelgrass, *Zostera marina*, is the dominant seagrass species in the northeastern United States (Green and Short 2003), and within the Peconic estuary (Bortman and Niedowski 1998).

Eelgrass can be critical for multiple commercial species, including winter flounder, *Pseudopleuronectes americanus* (Phelan et al. 2000, Goldberg et al. 2002), blue crabs, *Callinectes sapidus* (Wilson et al. 1987, Thomas et al. 1995, Etherington and Eggleston 2000), hard clams (Irlandi 1994, 1996, Johnson and Heck 2007) and bay scallops (Thayer and Stuart 1974, Pohle et al. 1991, Ambrose and Irlandi 1992). Historically, eelgrass beds covered over 40% of the bottom in some New York estuaries (Dennison et al 1989); however, today they are greatly reduced. Declines in eelgrass have occurred along much of the east coast of the United States (Dennison et al. 1989, Valiela et al. 1992, Orth et al. 2006). Potential causes include eelgrass wasting disease, *Labyrinthula zosterae* (Tutin 1938, Muehlstein et al. 1988), brown tides (*Aureococcus anophagefferens*) that caused prolonged shading and subsequent mortality (Dennison et al. 1989), anthropogenic nutrient inputs that have similarly led to light reduction (Hauxwell et al. 2001), loss of filter feeders (Cerrato et al. 2004, Carroll et al. 2008, Wall et al. 2008), and fishing gear/practices that have directly removed eelgrass biomass (Peterson et al. 1987, Boese 2002, Bishop et al. 2005b). A combination of these factors has resulted in the current patchy distribution of eelgrass beds in Long Island, NY, estuaries.

Eelgrass is generally regarded as the preferred habitat of bay scallops (Belding 1910, Gutsell 1930, Thayer and Stuart 1974). Thus, declines in seagrasses and bay scallops in New York estuaries and along the east coast might be coupled. Bay scallop populations have declined dramatically along much of the US Atlantic and Gulf coasts in the last 30 years, even to the point of extinction in some areas (Summerson and Peterson 1990, Peterson and Summerson 1992, Tettelbach and Wenczel 1993, Arnold et al. 1998, Marelli et al. 1999). Several factors are believed to have contributed to these trends, including recruitment failures associated with the same brown tides that decimated seagrass (Tettelbach & Wenczel 1993) and red tide algal

blooms (Summerson & Peterson 1990), seagrass habitat loss associated with nutrient loading (Serveiss et al. 2004), and potential trophic cascading effects (Myers et al. 2007). In areas where disturbances such as brown tides have stopped occurring, scallops have not naturally recovered. Numerous attempts have been made to restore bay scallops in areas where they were formerly abundant; these have met with mixed success (Peterson et al. 1996, Goldberg et al. 2000, Arnold et al. 2005), although efforts in New York have been considerably more successful than other areas (Tettelbach and Smith 2009).

In New York, scallop populations crashed in 1985 after the occurrence of the first brown tide in the Peconic Bays, an estuarine system in eastern Long Island, NY. Subsequent blooms pushed scallops to the brink of extinction (Figure 1). Reseeding efforts commenced after the initial blooms with some success (Tettelbach and Wenczel 1993). Survival of free-planted seeds was relatively low, $\leq 12\%$, with extensive mortalities in the winter of 1990 due to a boring polychaete (Tettelbach and Wenczel 1993). These impacts, along with brown tides in 1991 and 1995, caused large scale reseeded efforts to be abandoned. A brown tide has not occurred in the Peconic estuary since 1995; however, scallops have failed to naturally recover and numbers of adult scallops in areas of the Peconic estuary have rarely been above 0.5 individuals/m² over the last 10 years (Lewis and Rivara 1998). The main hypothesis for the lack of a full bay scallop population recovery is the low density and abundances of spawning adults, as numbers of adult scallops in areas of the Peconic estuary have rarely been above 0.5 animals/m² over the last 10 years (Tettelbach and Smith 2009), which could lead to recruitment limitation by decreasing the rate of successful fertilization (Liermann and Hilborn 2001). This idea led to the creation of large scale spawner sanctuaries in the Peconic estuary as a method to boost the natural spawning stock,

and results have been overwhelmingly successful (Figure 2) (Tettelbach and Smith 2009, Tettelbach et al. in rev).

However, as spawning stock and larval supply increase in the Peconics due to the restoration efforts, other biological interactions are likely to become important for bay scallop population recovery. Predation on many benthic invertebrate species is prey density-dependent (Lipcius and Hines 1986, Eggleston 1990), and therefore, low population levels can serve as a predation refuge. As populations increase, predation becomes increasingly important – it is among the major sources of post-settlement mortality that can structure populations of many benthic invertebrate species (Gosselin and Qian 1997, Hunt and Scheibling 1997). Predation is a major source of mortality in juvenile bay scallops (Ordzie and Garofalo 1980, Tettelbach 1986, Prescott 1990, Bishop et al. 2005a), and numerous studies have demonstrated that survival of scallops is enhanced by the presence of vegetative structure (Carroll et al. 2010, Hernandez Cordero et al. 2012), and, in particular, seagrass (Prescott 1990, Pohle et al. 1991, Ambrose and Irlandi 1992, Bologna and Heck 1999, Irlandi et al. 1999).

Therefore, the current state of reduced eelgrass meadows in New York may limit the continued expansion of bay scallop populations. Eelgrass is a favored substrate for larval scallop attachment (Eckman 1987) and provides a spatial refuge for byssally attached juvenile scallops from predatory crabs (Pohle et al. 1991, Garcia-Esquivel and Bricelj 1993). Survival of bay scallops is generally higher in vegetation when compared to barren substrates (Prescott 1990, Irlandi et al. 1995, Streib et al. 1995, Weinstock 2010), although not always (Bologna and Heck 1999). Additionally, this survival enhancement typically comes at a cost – growth is typically reduced within seagrass habitats (Ambrose and Irlandi 1992, Irlandi et al. 1995, Bologna and Heck 1999, Irlandi et al. 1999). Thus, scallops exhibit an ‘ecological trade-off’ for associating

with highly structured seagrass habitats. This apparent ‘food-risk trade-off’ is common in many seagrass associated species, although typically noted in fish species (Sogard 1992, Harter and Heck 2006, Grol et al. 2008, Hammerschlag et al. 2010, Grol et al. 2011). Reduced growth can affect the scallops ability to obtain a partial refuge from predation at 25-30mm, which is also the size at which the swimming is most common (Garcia-Esquivel and Bricelj 1993) and a full size refuge from most crustacean predators at ~40mm (Tettelbach 1986).

Changes in overall seagrass landscape (e.g. reduction in eelgrass density and patch size) may have deleterious impacts on bay scallop populations (Irlandi et al. 1995, Irlandi et al. 1999). However, as eelgrass is disappearing and meadow morphologies are changing, alternative habitats may become increasingly important. While macroalgae do not provide all of the same ecosystem services as seagrass and can actually lead to loss of seagrass (Hauxwell et al. 2001, McGlathery 2001), they may serve as potential replacement substrates for a number of estuarine species. A number of macroalgal species have been documented as suitable habitat for invertebrates (Marx and Herrnkind 1985, Wilson et al. 1990, Sogard and Able 1991, Begin et al. 2004, Powers et al. 2007, Falls 2008), including bay scallops. Macroalgae are known to serve as substrates to which juvenile bay scallops attach (Kelley 1981, Tettelbach 1991), but it is unknown whether these macroalgal species provide a refuge comparable to that offered by eelgrass – although some literature suggests it might (Carroll et al. 2010, Hernandez Cordero et al. 2012).

Included in potentially useful macroalgal habitats are a number of invasive species that have enhanced the settlement success of native species including clams, mussels, epiphytes, and crustaceans, resulting in increases in abundance and diversity (Viejo 1999, Gribben and Wright 2006b, Rodriguez 2006, Schmidt and Scheibling 2006, Vazquez-Luis et al. 2009, Gestoso et al.

2010, Jones and Thornber 2010). Thus, it is possible that the upright, branching macroalga, *Codium fragile* spp. *tomentosoides*, introduced to the Peconic Bay system in the late 1950's (Carlton and Scanlon 1985), serves as a suitable alternative habitat to eelgrass. *Codium* is the dominant, canopy forming algal species that now occupies substrates where *Zostera* was formerly found (Cashin and Associates 1996). Despite being an invasive species, previous research has demonstrated similar or enhanced diversity and abundance of native fauna (Schmidt and Scheibling 2007), as well as enhanced recruitment and survival of a native mussel, *Mytilus galloprovincialis*, in *C. fragile* habitats (Bulleri et al. 2006).

Thus, bay scallops represent a unique model organism to examine the impacts of habitat and predation. They have a strong habitat association with seagrass as semi-mobile epifaunal species, and exhibit an ecological trade-off as a result of that association. Additionally, scallops can associate with macroalgae, including invasive species. Finally, scallops are the subject of intense restoration efforts, so there is considerable interest in examining the effects that habitat and predation might have on their populations. Specifically, this dissertation will address three major themes: 1) the impacts of landscape on scallop life history, 2) the potential of an invasive species to act as a suitable habitat, and 3) the impacts of predation on benthic recruitment.

Impacts of seagrass landscape on scallop life history

Seagrass habitats form productive and highly diverse ecosystems throughout the world and have been studied extensively (Hemminga and Duarte 2000) and typically exist as a fragmented mosaic of vegetated and unvegetated patches (Robbins and Bell 1994, Irlandi et al. 1995). Seagrass patches provide physical, complex habitat structure in uniform, unstructured soft substrates. Thus, seagrass patches serve a variety of ecosystem functions including being critical refuge habitat and foraging areas for a number of marine species.

However, there is currently a 'global crisis' in seagrass ecosystems, as seagrass loss is accelerating worldwide (Orth et al. 2006). While a combination of nutrient loading, suspended sediments and concomitant shading are most frequently blamed for large scale decline is (Short and Burdick 1996, Fonseca et al. 1998, Orth et al. 2010), at smaller spatial scales, variation in landscape structure (size, shape, distribution of patches) is driven by both natural and anthropogenic, abiotic and biotic disturbance factors. Wave energy (Fonseca and Bell 1998) and bioturbation (Townsend and Fonseca 1998) are both natural mechanisms that regulate seagrass patches. Continuous seagrass meadows are fragmented into discrete patches by a suite of human activities. These include anchoring, propeller scarring (Bell et al. 2002, Uhrin and Holmquist 2003), and destructive fishing practices (Peterson et al. 1987, Boese 2002, Bishop et al. 2005b). The confluence of natural and human-induced disturbances leads to a seagrass landscape that is an analog to many fragmented terrestrial landscapes, and, in turn, application of terrestrial landscape ecology concepts have been attempted in the marine setting (Robbins and Bell 1994, Bostrom et al. 2006, Hinchey et al. 2008).

For species which rely on seagrass habitats, such as bay scallops, fragmented seagrass landscapes can impact survival and growth. Many species of fish, crabs, gastropods, and bivalves, including scallops, exhibit poor survival in patchy habitats when compared to continuous seagrass meadows. Further, survival along patch edges is also reduced for a number of associated fauna (Bologna and Heck 1999, Warry et al. 2009, Macreadie et al. 2010, Moore and Hovel 2010) and as fragmentation increases, the amount of edge habitat also increases. However, effects of fragmentation on growth are more complicated. For filter feeding species, growth may be enhanced in patchy vs. continuous meadows (Bologna and Heck 1999), while

more mobile species may also locate prey more easily in patchy seagrass habitats (Smith et al. 2008, Smith et al. 2011).

Thus, changing seagrass landscapes can have serious impacts on scallop populations. A few studies have examined the impacts of seagrass landscapes on bay scallop demographics, focusing on seagrass patchiness (Irlandi et al. 1995, Irlandi et al. 1999) or within patch location (Bologna and Heck 1999) on survival and growth. These studies suggest that there may be a food/risk trade-off in seagrass landscapes, i.e., scallops in patchy seagrass and along seagrass edges exhibit faster growth but lower survival than scallops in the centers of more continuous patches or meadows. However, Bologna and Heck (1999) observed high densities along seagrass edges despite the high mortality risk, and studies have also suggested that larval settlement is highest along patch edges (Orth 1992). Thus, it is possible that patchy seagrass, and/or seagrass patches with edge habitat might be beneficial for scallop populations, even if there is greater risk at the individual level.

A downside to the aforementioned studies, however, is that they utilize natural seagrass patches. There are a number of potentially confounding variables in natural patches including area, shoot density, canopy height, and leaf number, that can make determining which factor is impacting survival and growth difficult. Artificial seagrass has been used in a number of studies (Bell et al. 1985, Virnstein and Curran 1986, Sogard and Able 1994, Eggleston et al. 1999) to mimic natural patches and allows landscape-level questions to be answered by controlling other potentially confounding variables. By controlling size and shape of patches, shoot densities, and other factors, the effects of size, shape, and within patch location can more easily be investigated.

The potential for an invasive species to act as a suitable habitat

With the loss of seagrass, other structured habitats are likely to become important for fauna that typically associate with seagrass. A number of other ecosystem engineering species (including some invasive species – see Crooks 2002) create structurally complex biogenic habitats. While historically, invasive species have been considered negatively (Elton 1958, Carlton 1989, Mack et al. 2000), there is some recent research which suggests that, at least in the case of marine plants, invaders may be beneficial to native species (Crooks 2002, Rodriguez 2006). A number of invasive plant species seem to enhance settlement/recruitment (Bulleri et al. 2006, Gribben and Wright 2006b, Gribben et al. 2009b), abundance and diversity (Viejo 1999, Rodriguez 2006, Schmidt and Scheibling 2006, Vazquez-Luis et al. 2009, Gestoso et al. 2010, Jones and Thornber 2010), and survival (Carroll et al. 2010, Martin and Valentine 2011) of native species.

The downfall of many of these studies is that they often ignore impacts on individual-level fitness (Wright and Gribben 2008), and those which examine impacts on survival tend to be short-term (Carroll et al. 2010) or performed in the laboratory (Martin and Valentine 2011). Long-term studies of an invasive algae on a native bivalve exhibited sub-lethal impacts on condition and fitness (Gribben and Wright 2006a, Gribben et al. 2009a), which ultimately led to reduced survival (Wright et al. 2007), particularly after episodic environmental perturbations (Wright and Gribben 2008). Few other studies have attempted to quantify the effects of invasive species on the life-history and fitness of native species; while invasive species may have positive short-term impacts on native species, they may also have negative long-term effects on associated fauna (Wright and Gribben 2008).

In the northern extent of their range, bay scallops have been found in association with an invasive, canopy-forming macroalgae, *Codium fragile* (Kelley 1981; Bricelj et al. 1987; Carroll

et al. 2010), which was introduced in the mid-1950s (Carlton and Scanlon 1985). Literature suggests *Codium fragile* has a positive effect on a number of native fauna where it has been introduced (Bulleri et al. 2006, Schmidt and Scheibling 2006, 2007, Sauchyn and Scheibling 2009, Jones and Thornber 2010, Drouin et al. 2011) including bay scallops (Carroll et al. 2010). Since engineering species can help facilitate native species and *Codium fragile* has been demonstrated to be beneficial to native species where it is introduced, it is likely that *Codium* may act as a suitable habitat for scallops.

The impacts of predation on benthic recruitment

Marine organisms are constantly at risk of predation. Predation is especially important in post-settlement individuals, whose small size makes them accessible to a suite of predators (Gosselin and Qian 1997, Hunt and Scheibling 1997). While impacts on prey may be direct, via consumption, or indirect, via changes in growth, behavior and/or habitat selection, predation has been considered the most important biotic factor affecting benthic communities (Connell 1975, Menge 1983, Polyakov et al. 2007). A whole suite of predators are capable of affecting benthic populations, including demersal fish and decapods (Virnstein 1977, Heck and Thoman 1981, Peterson 1982, Summerson and Peterson 1984, Whetstone and Eversole 1991, Barbeau and Scheibling 1994, van der Veer et al. 1998), as well as birds (Prescott 1990). As such, predicting patterns in predation and how predators influence benthic populations is increasingly important for management, conservation and restoration efforts.

There are many factors which can influence predation on benthic populations, including predator identity, predator and prey size and density, and habitat complexity. Multiple species are implicated as important predators of early post-settlement individuals; however, decapod crustaceans are considered among the most important (Nelson 1981, Menge 1983, Hunt and

Scheibling 1997). Decapods are capable of consuming very small invertebrate prey (Juanes 1992), although their ability to consume prey is determined by their claw size and the prey size (Juanes and Hartwick 1990, Whetstone and Eversole 1991, Seed and Hughes 1995, Ray-Culp et al. 1999, Aronhime and Brown 2009). Further, both predator and prey density can affect consumption either via predator-predator interactions (Sih et al. 1998, Griffen 2006) or predator response to changes in prey density (Holling 1959, Taylor 1984). Many decapod predators change their rates of consumption with differing prey densities (Lipcius and Hines 1986, Eggleston 1990, Wong and Barbeau 2005, Nadeau et al. 2009, Rindone and Eggleston 2011).

Habitat complexity also can have important effects on prey consumption (Heck and Orth 1980, Ray-Culp et al. 1999, Grabowski 2004, Warfe and Barmuta 2004, Grabowski et al. 2008, Mislan and Babcock 2008, Stoner 2009). Seagrass meadows in particular have often been considered as nursery habitats and predation refuges (Heck and Wetstone 1977, Orth et al. 1984, Heck et al. 1995, Heck and Orth 2006). The current ‘nursery role’ paradigm for seagrasses is that fauna experience lower predation within seagrass meadows, albeit with some exceptions (Mattila et al. 2008, Canion and Heck 2009). Regardless, many species, including bay scallops, exhibit higher survival in seagrass relative to unvegetated sediments. One down-side of many of these studies is that they examine habitat vs. no habitat even though the relationship between predation intensity and habitat complexity is not necessarily linear and predators are impacted differently (Heck and Orth 2006), suggesting that further investigation into the impacts of increasing habitat complexity are necessary.

Objectives and Hypothesis

Survival and/or persistence of scallop populations in New York estuaries is likely to be strongly influenced by habitat and predation, as these biotic interactions become more important

with increasing population density. Therefore, the objectives of the proposed study are to experimentally assess the effects that various habitats and predators on bay scallop population demographics – recruitment, survival and growth. Specifically, the objectives are to investigate the role of changing habitat landscape, to assess the effects of a potentially beneficial introduced species, *Codium fragile*, and to determine the potential predator impact on bay scallop populations.

Specifically, this project will address the following hypotheses:

1. Seagrass edges will positively affect scallop recruitment via enhanced settlement along edges
2. Scallops will exhibit a growth-survival trade-off as a consequence of their seagrass association, specifically:
 - a. Scallop growth will be reduced within seagrass patches
 - b. Scallop survival will be enhanced within seagrass patches
3. The introduced alga, *Codium fragile*, can serve as predation refuge for juvenile bay scallops
4. The introduced alga, *Codium fraile*, will not negatively affect scallop growth, condition or reproductive potential
5. Predation can control scallop recruitment in Shinnecock Bay

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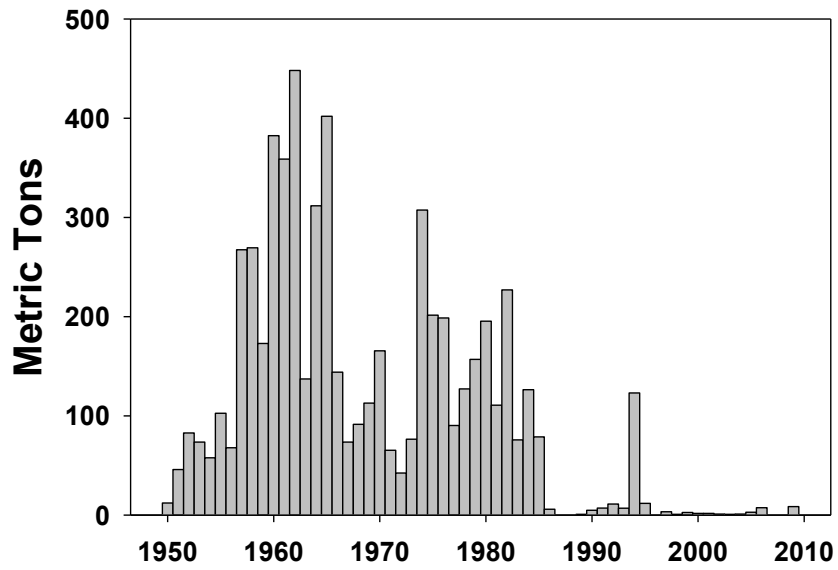


Figure 1: Commercial landings of bay scallops in New York from 1950 to 2009 illustrating the collapse in the mid 1980s due to the brown tide bloom and subsequent very low harvest to present.

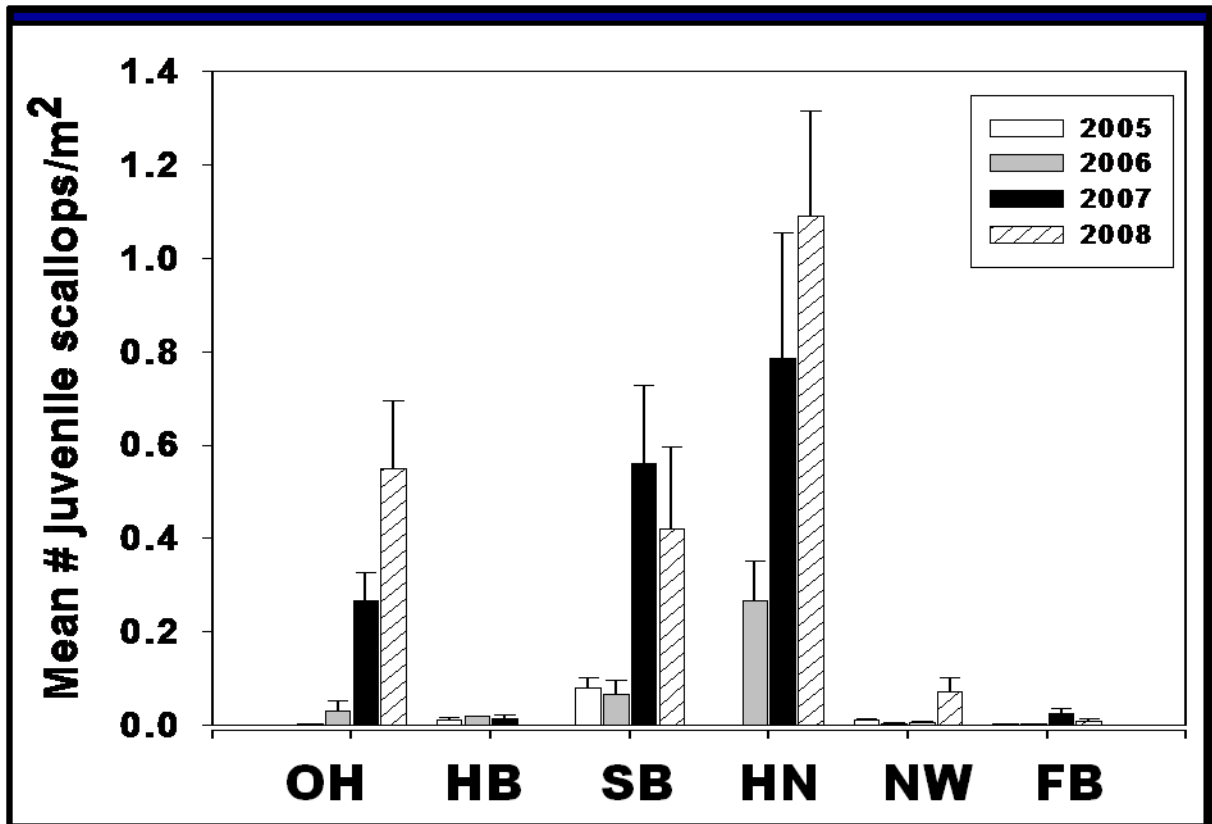


Figure 2: Density of juvenile scallops on the bottom in two years before (2005-2006) and two years immediately following (2007-2008) intense restoration efforts in Orient Harbor, one of the basins of the Peconic estuary, New York, from Tettelbach and Smith (2009). OH = Orient Harbor, HB = Hallock Bay, SB = Southold Bay, HN = Hog Neck, NW = Northwest Harbor and FB = Flanders Bay.

Chapter Two

Balancing the edge effects budget: bay scallop settlement and loss along a seagrass edge

Abstract:

Edge effects are a dominant subject in landscape ecology literature, yet are highly variable and poorly understood. Often, the literature suggests simple models for edge effects – positive (enhancement at the edge), negative (enhancement at the interior) or no effect (neutral) – on a variety of metrics, including abundance, diversity, mortality, etc. In the marine realm, much of this work has focused on fragmented seagrass habitats due to their importance for a variety of commercially important species. In this study, the settlement, recruitment, and survival of bay scallops was investigated across a variety of seagrass patch treatments. By simultaneously collecting settlers (those viable larvae available to settle and metamorphose) and recruits (those settlers which survive some period of time, in this case, 6 weeks) on the same collectors, we were able to demonstrate a ‘balance’ between positive and negative edge effects, resulting in a net neutral effect. Scallop settlement was significantly enhanced along seagrass edges, regardless of patch type while survival was elevated within patch interiors. However, recruitment – the net result of settlement and post settlement loss – did not vary significantly from edge to center, representing a neutral effect. Further, results suggest that post-settlement loss, most likely due to predation, appears to be the dominant mechanism structuring scallop abundance, not patterns in settlement. These data illustrate the complexity of edge effects, and suggest the metric used to investigate the effect (be it abundance, survival, etc) can often influence the magnitude and direction of the perceived effect. Traditionally, high predation along a habitat edge would have indicated an ‘ecological trap’ for the species in question; however, this study demonstrates that at the population level, an ‘ecological trap’ may not exist.

Introduction:

Understanding the impact of landscape characteristics (e.g., patch size, shape, corridors, etc) on ecological processes such as recruitment success is increasingly important as anthropogenic habitat fragmentation accelerates. Traditionally, the precepts of landscape ecology have been applied to terrestrial systems despite their clear importance to both aquatic and marine realms (Hinchey et al. 2008). Notable exceptions to this research trend have occurred in the area of seagrass community ecology, where investigators have begun to look at the effects of spatial pattern and configuration on ecosystem function (Robbins and Bell 1994, Irlandi et al. 1995, Eggleston et al. 1998, Hovel and Lipcius 2001, Darcy and Eggleston 2005). Seagrasses are important nearshore habitats which typically support high abundance and diversity of associated organisms (Heck and Orth 1980, Jackson et al. 2001). However, the total areal cover of seagrasses has declined worldwide due to anthropogenic influences (Orth et al. 2006), and at more local scales, a variety of impacts have created landscape patterns similar to those found in fragmented terrestrial habitats; i.e., mosaics of seagrass patches that vary in size, shape and degree of isolation (Robbins and Bell 1994), highlighting the importance of examining seagrass landscape characteristics on ecological processes.

The early consensus in landscape ecology was that ecotonal habitats, i.e., transitional zones between two distinct habitats, led to higher species abundances and increased species diversity; however, the modern perception has been that edges are undesirable features, associated with increased predation, decreased habitat quality, and are frequently sites for species invasion (Ries et al. 2004). Understanding the effects of habitat edges have on ecological processes become an integral part of recent landscape studies. In terrestrial studies, the direction (i.e., positive, negative, neutral) and magnitude of edge effects are often species-specific, and depend on

differences in resources/quality between adjacent habitats and interactions between species along habitat edges (Ries et al. 2004, Ries and Sisk 2004). A review by Ries et al (2004) offered three possible, predictable outcomes for a species response to a habitat edge: positive, where the response variable is highest at the edge and decreases with distance from edge; negative, where the response variable is lowest at the edge and increases with distance from edge; and neutral, where the response variable remains constant.

Similar edge effect predictions have also been made for marine seagrass systems, albeit without a potential neutral response (Macreadie et al. 2010a). In a review of seagrass landscape studies, Bostrom et al. (2006) found that species response was not consistent across landscape variables (i.e. size, shape, edge, etc) and postulated that seagrass fragmentation might not be detrimental to associated fauna if (1) there are abundant patches with high connectivity, (2) edge effects are not central to the species being studied, and (3) there is unrestricted movement between suitable patches. However, edge effects have been shown to be an important process for many seagrass associated fauna (Eggleston et al. 1998, Bell et al. 2001, Bologna and Heck 2002, Macreadie et al. 2010a, Macreadie et al. 2010b, Moore and Hovel 2010, Smith et al. 2011).

As emergent structures, seagrasses dampen water currents, leading to higher deposition of particles along the leading edges of seagrass patches (Peterson et al. 2004). Since bivalve larvae are weak swimmers and can be considered passive particles (Butman 1989, Jonsson et al. 1991), larvae should be expected to settle with higher frequency along seagrass edges. The resulting reduction of recruits into the patch with increasing distance from the edge has been termed a 'settlement shadow' (Orth 1992). However, seagrass edges can also have increased predator-prey interactions, leading to mortality (Irlandi et al. 1995, Smith et al. 2008). For individual species, the seagrass edge may create a trade-off of the aforementioned ecological processes

(Bologna and Heck 1999). These ecological trade-offs may result in observed net neutral effects across seagrass edges.

Bay scallops, *Argopecten irradians*, are a seagrass associated bivalve found along the east coast of the US (Thayer and Stuart 1974). As passive particles, larval bay scallop settlement is strongly influenced by eelgrass structure and hydrodynamics (Eckman 1987). Similar effects of seagrass structure are observed throughout the literature on a variety of species, including jingle shells, *Anomia simplex* (Eckman 1987), clams (Peterson 1986), various mussel species (Bologna and Heck 2000), and other bivalves (Bostrom and Bonsdorff 2000). Bologna and Heck (2000) investigated bivalve settlement to artificial seagrass and found enhanced settlement along the edge, with a relationship between total abundance and the perimeter of the patches, providing evidence of a 'settlement shadow' (Orth 1992). Assuming that scallop larvae are passive particles affected by hydrodynamics and emergent structure, we can predict a similar settlement pattern – higher abundance at the edge of patches, decreasing toward the center of the largest patches, or a 'positive' edge effect (Figure 1a).

Seagrass edges, however, also alter species interactions, and in particular, predator-prey dynamics. There is evidence to suggest that multiple fauna experience higher predator induced mortality along seagrass edges than within the patch (Bologna and Heck 1999, Gorman et al. 2009, Smith et al. 2011). Predation is considered a major mechanism structuring scallop abundance (Tettelbach 1986) and predation can be impacted by habitat change or loss (Prescott 1990, Carroll et al. 2010). Additionally, studies have demonstrated decreased scallop survival in both fragmented seagrass landscapes (Irlandi et al. 1995, Irlandi et al. 1999) and along habitat edges (Bologna and Heck 1999). Based on the available predation data, we can make a second prediction for scallop abundances with lowest numbers along seagrass edges, where predation

should be highest, and highest numbers within the seagrass habitat, yielding a ‘negative’ edge effect (Figure 1b).

Therefore, bay scallops may be considered model invertebrate fauna for landscape ecological studies in the marine environment and, as such, we can predict the outcomes of scallop settlement (where the scallops are settling in the seagrass environment) and recruitment (settling scallops that survive post-settlement processes over a given time period, for this study 6 weeks) against landscape variables such as shape and edge. In this study, we investigate the impacts of landscape parameters (shape, size, within patch location) on settlement and post settlement loss of scallops simultaneously, providing empirical evidence that apparent “neutral” responses to habitat edges represent a ‘balance’ between opposing edge effects, and show that predation is the dominant mechanism structuring scallop abundance and is itself not influenced by fragmentation.

Methods

Study site

Hallock Bay (HB) is one of the easternmost, enclosed basins in the Peconic Estuary (PE) system. HB is located on the eastern tip of the North Fork of Long Island, New York. It is characterized as a relatively shallow (<2 m mean depth) enclosed basin with seawater exchange through a narrow inlet and, as with other PE basins, the dominant freshwater contribution is through groundwater discharge. It is bracketed to the south and east by Orient Beach State Park, and to the north and west by low-density residential units.

Since the winter of 2007, a scallop restoration site has been established (41°07'41.28"N, 072°16'27.72"W), approximately 1.5 km from the experimental site (41°08'17.23"N, 072°15'47.96"W). Over the course of three consecutive winters (2007, 2008, and 2009)

approximately 500,000 scallops have been planted in the spawner sanctuary (~70,000, 169,000 and 240,000, respectively).

Artificial Seagrass Units

Artificial seagrass units (ASUs) have been used successfully in many studies to examine the impacts of seagrass structure on resident species (Virnstein and Curran 1986, Sogard and Able 1994, Bologna and Heck 2000). In addition, *Argopecten irradians* larvae readily settle on a variety of artificial substrates (Figure 2), with settlement apparently controlled by the availability of surface area (Ambrose and Lin 1991).

Two treatment sizes, ‘small’ (8.5 m²) and ‘large’ (17 m²), and two shapes, ‘circular’ and a four-pointed star or ‘stellate’ were replicated three times for small shapes, but due to logistical reasons, only twice for large shapes (Table 1). The shapes were selected with the assumption that linear patches may demonstrate more significant effects than circular ones (Lindenmayer and Fischer 2006) and to maximize differences in the amount of edge and perimeter-to-area ratios (Bologna and Heck 2000). Sizes were chosen so that patches were large enough to have both distinct edge and center habitats (>1m from the edge, Peterson et al 2004), as a shortcoming of many previous ASU studies has been that the size of ASUs was too small to have had discernable edge and center habitats. That is, in previous studies, ASUs were almost entirely edge habitat. Even at this scale of investigation, the 8.5 m² stellate shape had only 0.16 m² of center, or core, habitat. We selected the sizes and shapes in order to examine both impacts at the patch scale as well as impacts of within patch location.

ASUs were constructed by cutting VexarTM mesh into the desired shapes as a backing for the artificial shoots. Shoots were created by using green polypropylene ribbon tied to the mesh. Blade width, blade number and canopy height (500 shoots/m², blade width=5 mm, blade number

= 4, canopy height = 35 mm) were within the ranges reported for natural *Zostera* beds within eastern Long Island (Eckman 1987, Pohle et al. 1991). Each ASU was placed onto unvegetated sediment, anchored using screw anchors at the center of each mat and with a series of rebar stakes along the edges. The experimental units were randomly assigned a position within a 5x2 evenly interspersed matrix with a minimum separation distance of 5 m.

Recruitment collector construction and sampling

A series of smaller artificial eelgrass units (10 cm x 20 cm) were created in the same manner as the experimental patches, with a total of 10 artificial shoots. In this case, however, the eelgrass units served to collect scallop recruits. Five of the shoots were enclosed within an 800- μ m mesh bag secured to the collector with a tie wrap to prevent entry by potential predators, yet allow colonization by scallop larvae. The other five shoots were left exposed to quantify post-settlement loss (i.e., predation or emigration). The collectors were randomly assigned to either the edge or center of each ASU, and were attached to the Vexar via tie wrap so that the leaves of the ASU were under the collectors and were exposed once the collectors were removed. This prevented changes in shoot density on the ASUs from influencing predation, emigration/immigration, and settlement processes.

This design allowed for a predicted recruitment value equivalent to observed 'settlement' (individuals within the mesh bag) for comparison with short-term 'recruitment' (individuals outside of the mesh bag). For this study, recruitment is defined as those scallops surviving up to 6 weeks post-settlement. Additionally, survival for this study was calculated as the number of recruits divided by the number of settlers for each collector, with the assumption that the loss is due to mortality. While it is possible that scallops can move, several factors indicate the major loss component is due to mortality and emigration can be assumed to be negligible. Typical

behavior of post-set scallops (byssal attachment) and ontogenetic changes in behavior where swimming activity increases at intermediate sizes (15-30 mm) as scallop juveniles transition to the bottom (Tettelbach 1991, Garcia-Esquivel and Bricelj 1993) suggest that actively swimming does not readily occur at the sizes encountered. Additionally, it has been shown for other scallop species that swimming is difficult at sizes less than 12 mm due to hydrodynamic drag and high energy costs (Manuel and Dadswell 1993). Finally, strong tidal currents have been shown to be important for influencing bay scallop movement (Winter and Hamilton 1985, Tettelbach 1986, Powers and Peterson 2000), which do not occur in the study area.

A second series of collectors were designed in the same method described above; however, holes were cut into the mesh bags for a partial bag treatment. This treatment allowed predators to access the bags while maintaining the potential baffling effects of the fine mesh to estimate whether or not the bags artificially inflated settlement above some level of biotic control. There was no difference between inside and outside of the control bags ($p=0.310$), indicating that the mesh bags did not artificially inflate settlement. Because there was no difference, raw values for scallops inside the bags were used for statistical analysis with no correction.

Sets of recruitment collectors were deployed and collected every 6 weeks, offset by 3 week intervals, for a total of 4 sets of collectors spanning a period of 15 weeks in each of two years. After 6 weeks in the field, each set of collectors was returned to the lab for processing. Deployment of recruitment collectors coincided with scallop peak spat settlement, which begins in late May (Tettelbach et al. 1999). Collections were made the second week of July (15 July both years), the first week of August (3 Aug 2009 and 5 Aug 2010), the fourth week of August (26 Aug both years) and the second week of September (17 Sept 2009 and 16 Sept 2010). Collectors were separated into exposed and enclosed, and rinsed into an 800- μm sieve with a

high-power water hose. Because we could not discern which of the enclosed scallops were attached to the artificial seagrass vs. the mesh bag due to dislodgement during processing, any scallops attached to the outside of the mesh bags were included with those from the ‘exposed’ collectors. All scallop spat >1 mm shell height were enumerated and measured, as were all mud crabs, *Dyspanopeus sayi* found on or within the collectors. In addition, in 2010, all other fauna on the collectors were quantified.

Data analysis

A series of three-way ANOVA tests were used to compare differences in scallop settlement, recruitment and survival, as well as abundance of mud crabs.

For scallop settlement, ‘treatment’ (T), location (L) and collection (C) were fixed factors; the factor ‘treatment’ was constructed differently depending on the statistical comparison being considered. When comparing across patch area, ‘treatment’ had 2 levels, small and large. When comparing across patch shape, ‘treatment’ had 4 levels, large circle (LC), large star (LS), small circle (SC) and small star (SS). Comparisons across perimeter and P:A ratios had 3 levels, low, intermediate and high. Location and collection did not vary depending on the test. Location had 2 levels, either center or edge. Collection had 4 levels, collections 1, 2, 3 and 4. Analysis of scallop recruitment and abundance of mud crabs were conducted in the same manner. For scallop survival, treatment and location were the same as above; however, collection only had 3 timepoints as there were rarely new settlers in the 4th collection. When a significant effect of the response variable occurred, a multiple comparisons test (Holm-Sidak test) was used to determine statistically significant differences between treatments. Results were considered statistically significant at an alpha of 0.05.

Point counts of scallop settler and recruit abundances were scaled up to the whole patch for further tests of patch-scale effects. The amount of core habitat was calculated as the area of the ASU >1m from the edge of the patch. Edge area was calculated as the total ASU area minus the calculated core area (see Figure 3). The mean scallop settler abundance for the whole patch was calculated using the following equation:

$$(\overline{X}_{SE} \times A_E) + (\overline{X}_{SC} \times A_C)$$

where \overline{X}_{SE} is the mean density of settlers (as determined per collector) along the edge, A_E is amount of edge area, \overline{X}_{SC} is the mean number of settlers per collector at the center, and A_C is the amount of center area. This was repeated for recruits, and extrapolated patch survival was calculated as the number of recruits for the each patch divided by the number of settlers.

Finally, a matrix of Pearson's correlations was computed for all measures of patch morphology and both scallop abundance at the collector level and extrapolated patch-scale abundances.

Results

When predators were excluded, there was no difference in the mean abundance of scallops between patches of different size ($p=0.288$), perimeter ($p=0.560$), P:A ($p=0.280$), or shape ($p=0.489$). There were significantly higher mean scallop abundances along the edges of ASUs (6.78 ± 1.17 individuals per collector \pm SE) compared to the interior (4.81 ± 0.86 ; $p=0.05$, Figure 4a). There were significant differences for within-patch location (Figure 4a) and for collection ($p<0.001$). Mean peak settlement was observed on the second collection during the first week of August, with 17.25 ± 1.88 scallops per collector, when compared to other collections ($p<0.001$ for all comparisons, see Figure 5a).

On the exposed portion of collectors, where predators were allowed access, patch size ($p=0.287$) or shape ($p=0.074$) did not have an effect. However, both patch perimeter and P:A ratio had significant impacts on numbers of recruits. Patches with the lowest amount of perimeter ($p=0.035$) or intermediate P:A ($p=0.027$) ratios had the highest number of recruits. The small circle patches had both the lowest perimeter and the intermediate P:A ratio. Mean abundances of scallop recruits did not vary from edge to interior ($p=0.690$, Figure 4b). Similar to settlement, there was a significant temporal difference among collections ($p<0.001$), however, unlike patterns in settlement, the peak recruit abundance occurred in July, during the first collection (Figure 5b).

Scallop survival, estimated as the ratio of recruitment to settlement, did not vary between patches of different size ($p=0.810$), perimeter ($p=0.240$), P:A ratio ($p=0.145$), or shape ($p=0.169$). Survival was significantly enhanced at the middle of patches, 0.229 ± 0.043 , when compared to ASU edges 0.121 ± 0.027 ($p=0.015$, Figure 4c). Survival also varied over time; it was significantly higher in the first collection (0.332 ± 0.059) than the second (0.053 ± 0.011 , $p<0.001$) and third collections (0.153 ± 0.043 , $p=0.002$; for full statistical analysis see Table 2). No ratio was determined for the fourth collection, as there was generally no scallop settlement (Figure 5a). The within-patch location effect was strongest when examined with P:A ratio than other patch treatments.

Mud crabs were the most dominant predator recorded by the collectors. Crab abundance per collector did not differ among treatments ($p=0.128$) or within patch location ($p=0.746$, Figure 6a). Crab abundance did vary significantly among collections ($p=0.001$), increasing with time (Figure 6b).

Core area varied among treatments, being the least on the stellate shapes (0.16 m² and 0.5 m² for SS and LS, respectively) and the most on circular shapes (1.2 m² and 5.5 m² for SC and LC, respectively). The series of One-Way ANOVAs at this scale of observation yielded only 1 significant result (Table 3). Extrapolated recruits were significantly higher on large patches (676 ± 125 total recruits per ASU) than small patches (390 ± 72 recruits per ASU, p=0.037) across both years and all collection periods. There was no significant effect of any patch morphometric on total settlers or patch-scale survival. Likewise, the Pearson's correlations yielded only 1 significant result (Table 4). The total amount of settlers per patch was significantly related to the amount of perimeter (r=0.959, p=0.041).

Discussion

A standard interpretation of these results would be as a clear demonstration of a neutral edge effect. Though, in the past, many investigators have suggested such findings to be indicative of experimental error or lack statistical power in discerning true effects (Ries and Sisk 2004). However, using our collection methods, we are able to separate recruitment into its two component processes, namely settlement and post-settlement loss (mainly through mortality) and show for the first time that net neutral edge effects result from a balance of otherwise traditional positive and negative edge effect mechanisms (Figure 7). To our knowledge, this is the only study to simultaneously investigate “settlement” and “recruitment” on the same cohort of individuals within a landscape context and we did so by creating a collector that both protected individuals from predation and allowed natural post-settlement losses to occur. Unfortunately, assessing the generality of these findings is confounded by the difficulty in publishing neutral effects and their misinterpretation as specious.

Recent literature searches suggest that artificial seagrasses should have exhibited either a positive or negative edge effect on scallop recruitment (Macreadie et al 2010a), depending on which force was more important, supply or predation, making a neutral effect essentially a null result. Had this study only investigated scallop abundance, and not also quantified patterns in settlement, the conclusion would have been that there was no effect. Our results suggest that neutral effects are a real phenomenon and should contribute to the understanding of edge effects or at least highlight our incomplete understanding of edge effect budgets.

In this study, the seagrass edge had significant impacts on scallop settlement and survival, affecting the budget of new individuals recruiting to seagrass habitats. Settlement was highest at the patch edges when compared to the interior, regardless of size or shape, and this significant positive effect supports the argument of a settlement shadow, as predicted by Orth (1992) and Bologna and Heck (2000). This settlement enhancement at patch edges adds to the potential pool of recruits to a seagrass meadow. However, survival was lowest at patch edges, a pattern confirmed in other studies (Bologna and Heck 1999, Smith et al. 2011), removing individuals from the potential pool of recruits at the seagrass edge. This created a “balanced budget” of sorts, the addition of scallops via settlement was neutralized by loss via mortality.

While edge effects on settlement and survival were strong across all treatments, the overall effects of patch morphometrics on response variables were less clear. When examining patch morphology at the collector scale, there was no apparent effect of ASU size, perimeter, P:A or shape on scallop settlement or survival. However, there was a patch effect at the collector scale of scallop recruitment with significantly higher numbers of recruits per collector on patches with the lowest amount of perimeter and intermediate P:A (SC). Past investigators have suggested that patches with the lowest perimeter should have the lowest densities of bivalves (Bologna and

Heck 2000). A similar effect was observed in this study on settlers, not recruits, though our results do highlight the confounding influence of perimeter and P:A.

Fletcher et. al (2007) found that edge effects were either more common in nature than patch scale effects, easier to detect, or some combination of both. Since the overall amount of edge and core area varied between patches of different sizes and shapes, detecting differences driven by patch morphometrics would have required a sampling method different from our point estimates. We attempted to use our collector counts to scale up to the level of patch. Yet, of 24 statistical tests (12 One-Way ANOVAs and 12 Pearson Correlations) only 2 were significant. At the patch level, there were larger total scallop populations on larger patches than smaller patches, despite similar densities throughout. The significant positive relationship between calculated total settlers and perimeter mirrored the positive edge effects we observed on settlement, suggesting that edge effects may have driven patterns in patch morphology (Fletcher Jr et al. 2007).

There was a significantly more scallop settlers at the edges of patches than the interiors, and a strong positive correlation between settlement and perimeter for calculated settlers on the patch-scale. However, there were no significant effect of within-patch location on recruitment, or significant relationships between patch-scale recruit abundance and perimeter or P:A, suggesting that scallop population abundance across ASUs is not structured by patterns in settlement. Post-settlement processes, such as predatory mortality, are likely the dominant forces structuring scallop abundance on the mats, common for many benthic organisms (Hunt and Scheibling 1997, Scheibling and Robinson 2008, Prado et al. 2009). Numbers of scallops were reduced by 1-2 orders of magnitude from settling densities to actual recruits over a 6 week period. The pattern of settlement within seagrass patches disappeared when exposed to post-settlement loss.

The likely culprit is the xanthid crab, *Dyspanopeus sayi*, the dominant predator within our lagoonal system and an important predator on juvenile bay scallops (Streib et al. 1995). This relatively small species is not likely to be impeded by seagrass structure; they are patch residents (Irlandi et al. 1999) and exhibit enhanced foraging success with increasing seagrass complexity. In this study they were ubiquitous and homogeneously distributed throughout our ASU treatments, demonstrating that densities of these mesopredators (mud crabs) were not impacted by patch area, shape or within-patch location. It has been shown that small predators can be important consumers of post-set mollusks (Ray-Culp et al. 1999), and given their remarkably high abundance and seagrass climbing abilities (Pohle et al. 1991), these crabs likely frequently encountered by byssally-attached scallops within the canopy.

We must concede, however, that spatial pattern alone cannot inform estimates of predator activity or predation success (scallop survival). Since mud crabs did not exhibit an edge effect, it is possible that other predators foraging along patch edges may have contributed to the observed scallop loss. Potential scallop predators were occasionally recorded in or around the ASUs, including blue crabs, *Callinectes sapidus*, spider crabs, *Libinia dubia* and juvenile tautog, *Tautoga onitis*. Given the size and motility of these species, it remains possible that collector bias may have under-sampled both their abundance and perceived importance, though the small size of the post-set scallops (<10 mm) and the high densities of mud crabs across all treatments (262 ± 12 crabs per square meter) supports the notion that mud crabs played a pivotal role in post-settlement mortality.

The difference in survival between collection dates and within-patch location demonstrates a predator response to changes in prey density. There are typically two response categories of predators to changes in prey numbers – an aggregative response or a functional response (Taylor

1984). The lack of spatial patterning attributable to predators in this study was consistent with a functional response (Figure 8), though as mentioned, our approach to quantifying the predator field inhibits our ability to definitively rule out an aggregative response. Regardless, increasing consumption with increasing scallop supply demonstrates that these predators may not be satiated at current levels of restoration enhanced scallop settlement, at least for the basin studied.

While conditions appear favorable to settlement along seagrass edges, scallops survived poorly at these locations. The balancing of positive and negative edge effects on post-set scallops demonstrates a potential ecological trade-off for scallops at seagrass edges, as shown by others (Bologna and Heck 1999). In addition to being a potential trade-off, it is possible that the competing forces structuring scallop recruitment at seagrass edges represents an ‘ecological trap’ for scallops. Terrestrial literature suggests that habitat edges often act as ‘ecological traps’ (Ries and Fagan 2003), where fauna preferentially settle in a habitat where fitness is reduced (Robertson and Hutto 2006). Robertson and Hutto (2006) asserted that in order to demonstrate the existence of an ecological trap, three criteria must be met: 1) individuals should exhibit preference of one habitat over another, or at least, equal preference, 2) some measure of fitness must be different between habitats and 3) the fitness outcome for individuals settling in the preferred or equally preferred habitat must be reduced.

Our data appear to fit the criteria laid out by Robertson and Hutto (2006): larvae ‘prefer’ to settle along the edges and survival – a measure of individual fitness – is reduced in edge zones. However, this principle might not be so easily transferred to the marine environment. At the level of the individual, seagrass edges pose a potential trap for settlement-stage bay scallops, yet recruitment data suggests that there is no difference in densities between the seagrass edge and interior. Further, scallop growth is enhanced at seagrass edges relative to patch interiors

(Bologna and Heck 1999). Therefore, when considered at the population level, there does not appear to be a detrimental effect of edge-centric settlement.

‘Ecological traps’ in the terrestrial realm are often driven by incomplete resource mapping or predator spillover from adjacent habitats (Ries et al. 2004), resulting in reduced numbers in those habitats (Ries and Fagan 2003). Although positive behavioral cues are presented to scallops settling in edge habitats, at larger spatial scales this pattern is regulated by passive processes (local hydrology, Eckman 1987), a complication without a direct terrestrial analogue. In this system, the rate of delivery appeared sufficient to offset a strong negative edge effect. Given that realized recruitment densities did not differ from edge to interior, and the high levels of fragmentation exhibited by local seagrass meadows, we can infer that a large portion of the scallop population may in fact occur within edge habitats. That this takes place despite higher individual mortality, clearly illustrates the need for investigators to more closely examine the implications of ecological traps. Specifically, ‘ecological traps’ identified at the level of the individual may need to be revisited and reviewed at the population level, as we have demonstrated that population level effects may differ greatly from those recorded at smaller scales.

Likewise, a “soft” or a “hard” edge is likely to affect the degree and strength of both edge effects and ‘ecological traps.’ In this study a distinct contrast between the seagrass habitat and the surrounding barren substrate was used to detect edge effects. While this hard edge feature is common in eastern Long Island, in other seagrass systems, edges may exhibit reduced shoot densities, lower canopy height or other measure of complexity, yielding a soft edge or a gradual transition between habitats, which would increase predator efficiency. We therefore interpret our results as a conservative estimate of post-set scallop mortality. Further, since increasing habitat

complexity negatively effects seagrass predators, patches with soft transition zones are more likely to produce ‘ecological traps’ in seagrass environments, a direct contrast to the terrestrial environment, where studies have demonstrated nest predation to be stronger along edges with sharp contrasts than those with weaker contrasts between the two habitats (Lindenmayer and Fischer 2006 and references therein).

Conclusions

Studies of edge effects, and their driving mechanisms, are abundant in the terrestrial literature, although broad geographic patterns have not emerged (Lindenmayer and Fischer 2006). The composition and configuration of habitats can impact the magnitude and strength of the edge effect, leading to observed variability at local and regional scales. Many factors may contribute to the observed effect – temporal variability, contrast between adjacent habitats, mechanism for settlement, etc, and the metric used to investigate (abundance, diversity, survival, etc) the edge effect is just as likely to play a role in whether or not an effect is found as the habitat edge itself. In this study, the examined processes (settlement and survival) showed opposite edge effects, yielding a net neutral effect on recruits, suggesting that broad patterns of edge effects may remain similarly elusive in marine ‘seascapes.’

This is the first study to demonstrate a “balanced budget” between settlement and post settlement mortality simultaneously on the same cohort of naturally recruiting individuals, allowing components of the neutral edge response to be teased apart. However, the temporal variability in settlement, recruitment, and survival suggests that at any point in time, there may be an overall positive, negative or neutral result, indicating that perhaps the best indicator of an edge effect should be examined at longer temporal scales. In addition, the results indicate that while there is an ecological trade-off between settling along a habitat edge and survival at the

individual level, there does not appear to be a net negative affect at the population level. Thus, although the terrestrial literature posits that habitat edges in increasingly fragmented landscapes may act as ecological traps, it is possible that habitat fragmentation may not be detrimental to seagrass associated fauna, as concluded by Bostrom et al (2006). Rather, the strong positive effect of more individuals along seagrass edges due to typically passive processes of particle (and larval) settlement is likely to be enhanced in fragmented landscapes with more edge habitats. Although survival is lower along the edge, this study suggests that the density of recruits is similar at the edge and interior, and that there might not be a net negative effect of habitat fragmentation on scallop populations.

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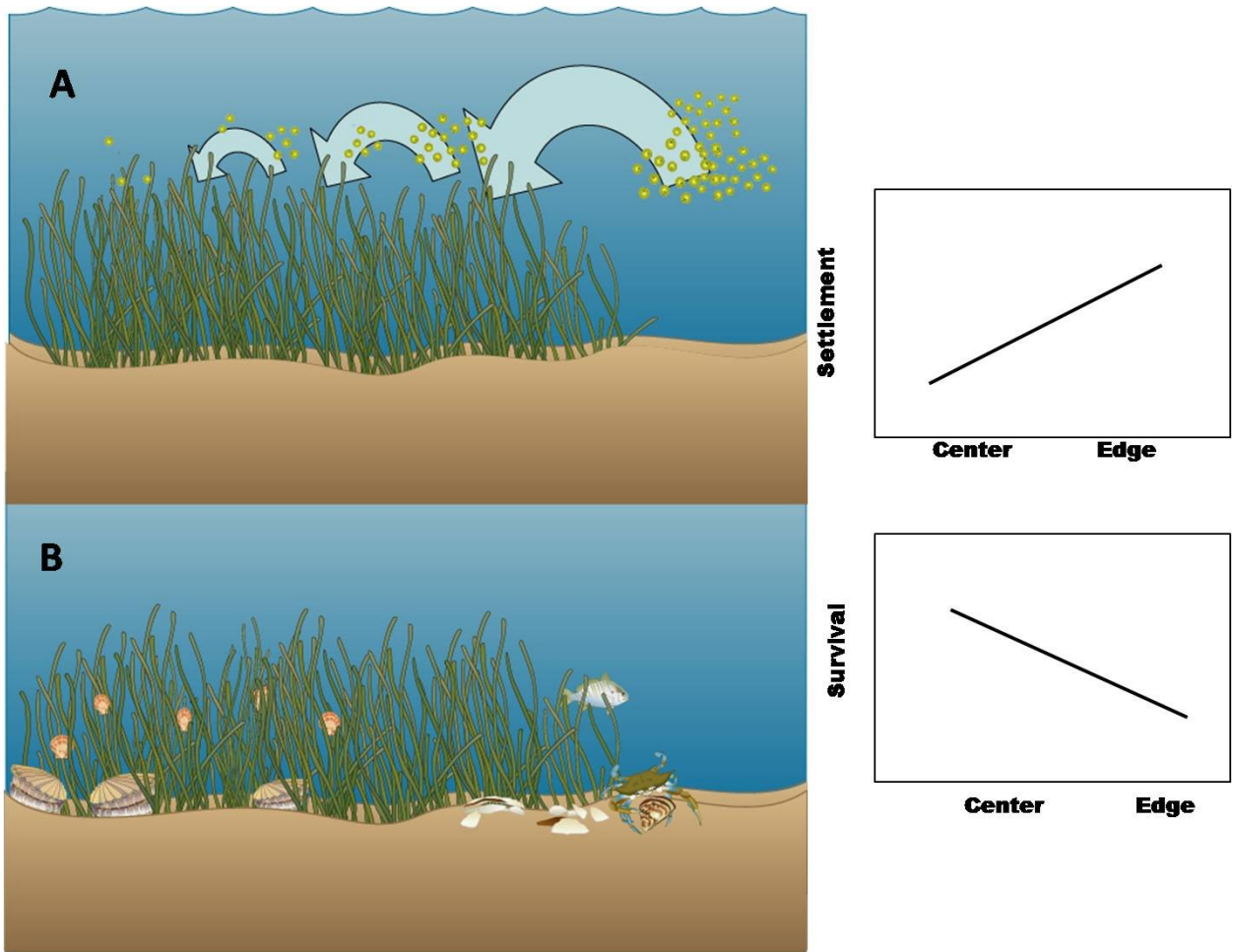


Figure 1: Conceptual diagram showing (A) the larval shadow, adapted from Orth 1992, and (B) predation across the edge of a seagrass patch to the interior, displaying both positive and negative edge effects.



Figure 2: Photograph of a bay scallop settler byssally attached to artificial seagrass from the experimental site. The width of the ribbon is 5mm.

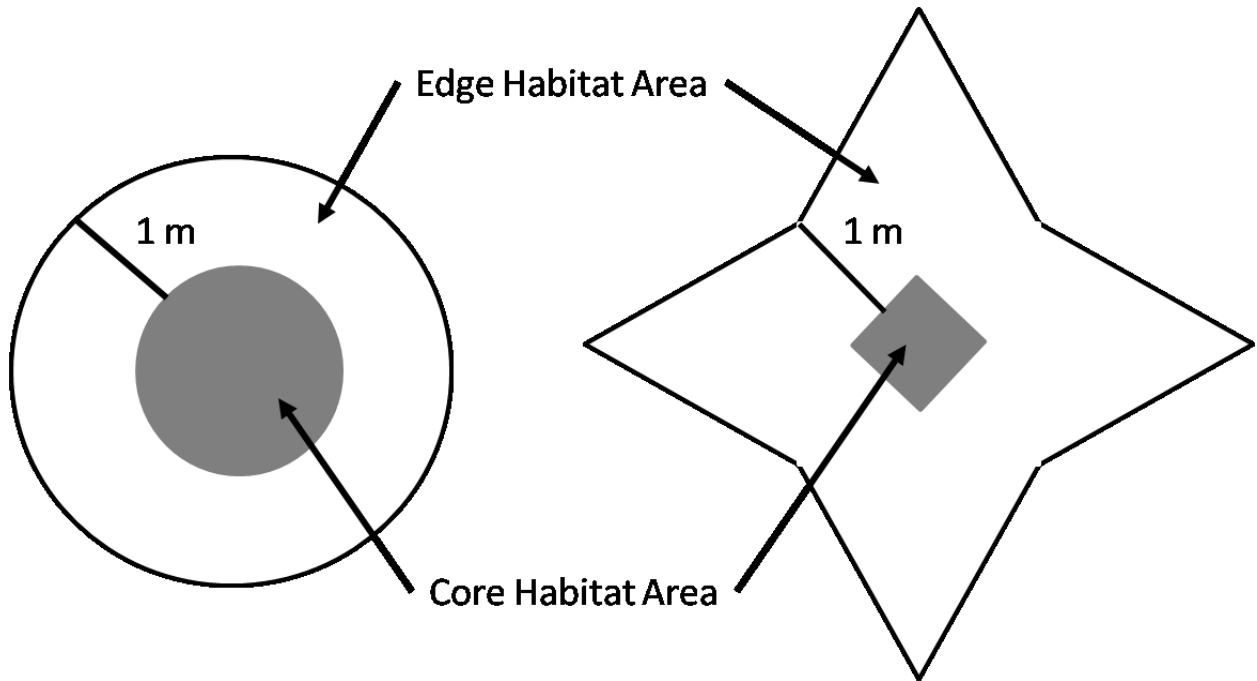


Figure 3: Model patches showing the edge (white) and core or center (gray) habitat areas. Core habitat was calculated as the total area $>1\text{m}$ from the edge of the patch.

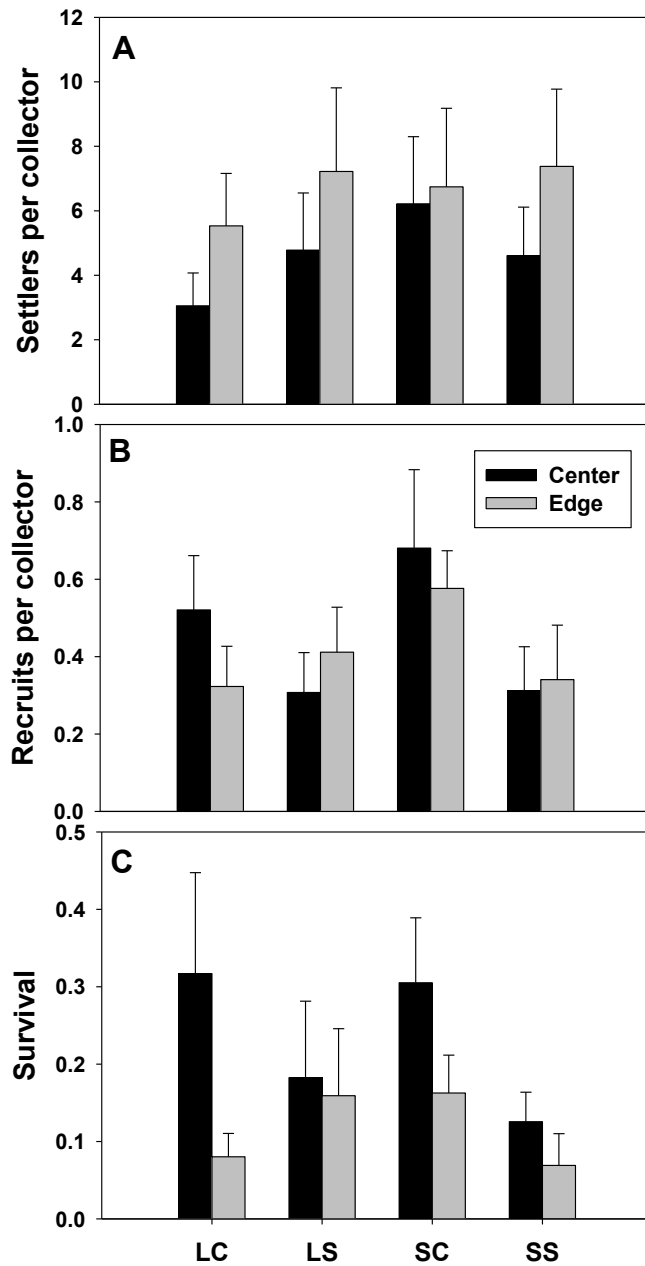


Figure 4: Mean densities (\pm SE) of (A) scallop settlers, (B) actual recruits and (C) survival – the ratio of recruits to settlers – per collector as a function of ASU treatment. Black bars represent collectors from the center, gray bars represent collectors from the edge. LC= Large Circle, LS= Large Star, SC= Small Circle and SS= Small Star. All collections from both years pooled for one center and one edge value for each ASU.

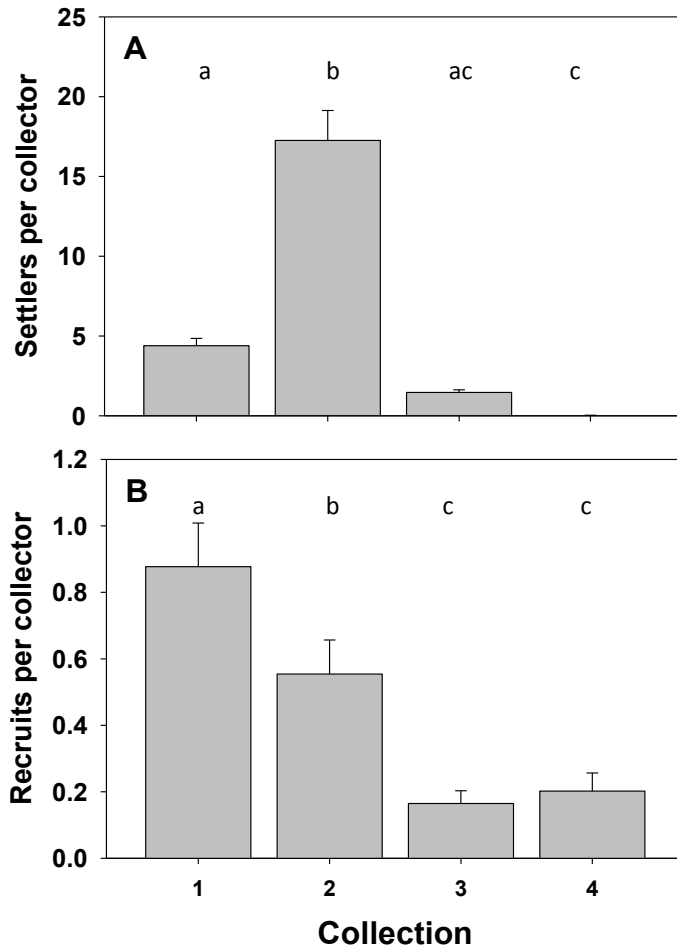


Figure 5: (A) Mean settlers per collector (+SE) and (B) mean recruits per collector (+SE) across both years and all treatments for each collection. Collection 1 was 15 July for both years, collection 2 was 3 August 2009 and 5 August 2010, collection 3 was 26 August for both years, and collection 4 was 17 September 2009 and 16 September 2010. Letters denote statistically significant differences as determined by multiple comparisons tests.

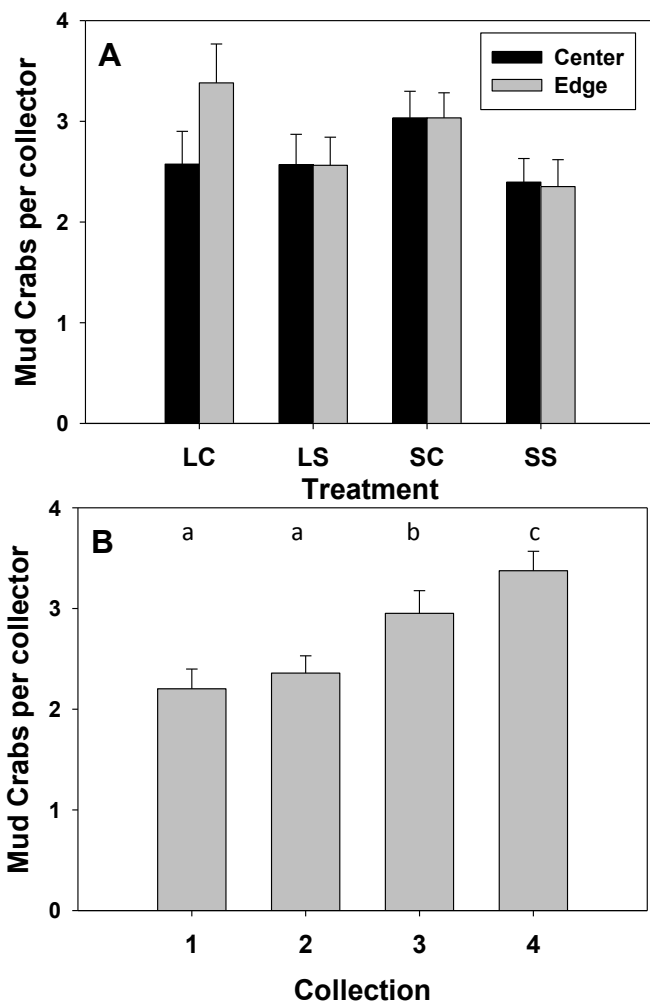


Figure 6: Mean densities (\pm SE) of mud crabs per collector (A) at the edge and center of each ASU and (B) across collection periods. For (A), black bars represent center collectors and gray bars represent edge collectors. Crab densities were pooled across all collections in both years to get one center and one edge value for each ASU. For (B), crabs were pooled across ASU treatments in both years for one crab density value for each collection. Collection 1 was 15 July for both years, collection 2 was 3 August 2009 and 5 August 2010, collection 3 was 26 August for both years, and collection 4 was 17 September 2009 and 16 September 2010. Letters note significant differences from multiple comparisons tests.

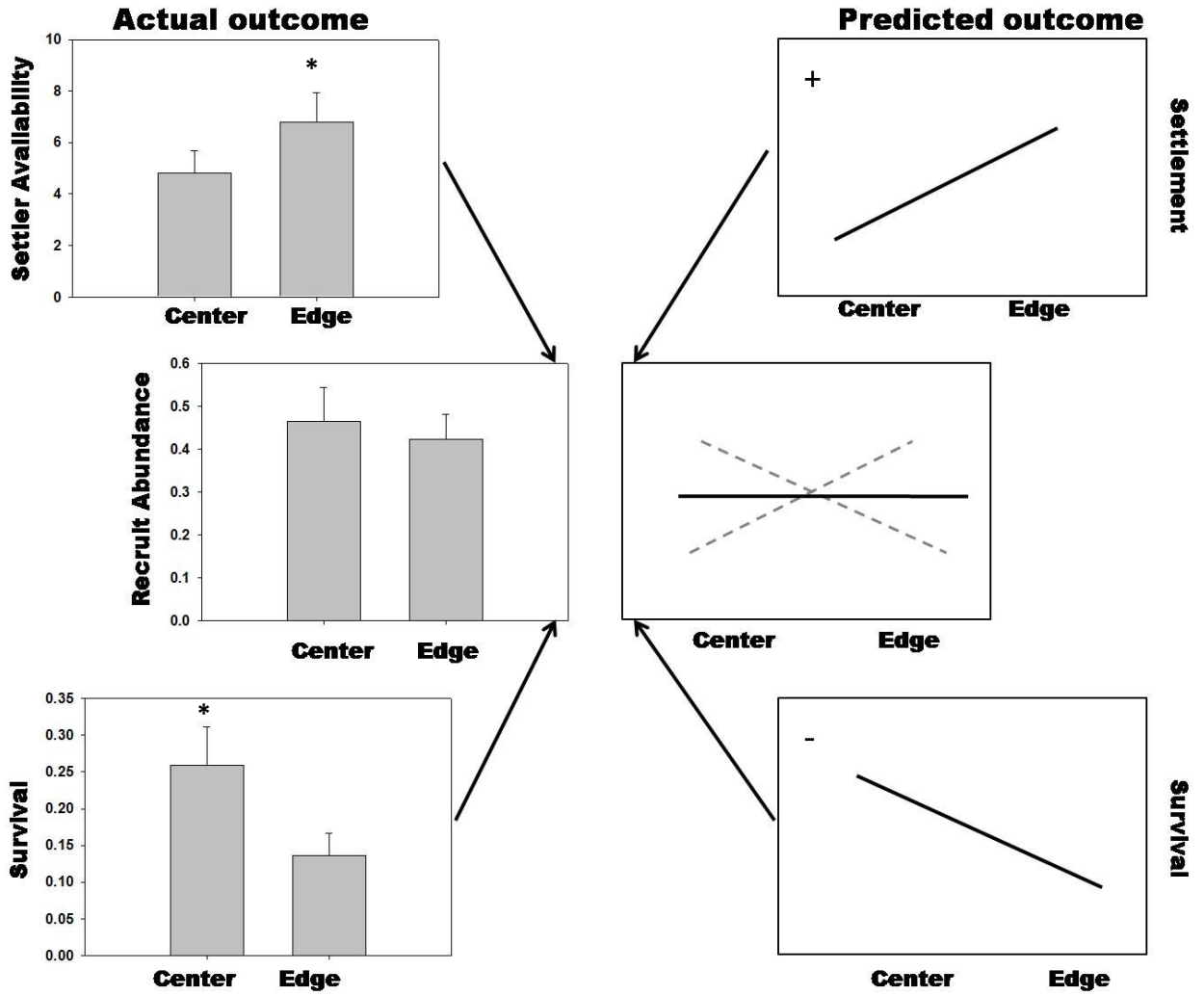


Figure 7: Actual versus predicted outcomes for settlement and survival. Settlement (positive edge effect predicted and observed) and survival (negative edge effect predicted and observed) balance each other out, leaving a net neutral edge effect on scallop abundance (not predicted).

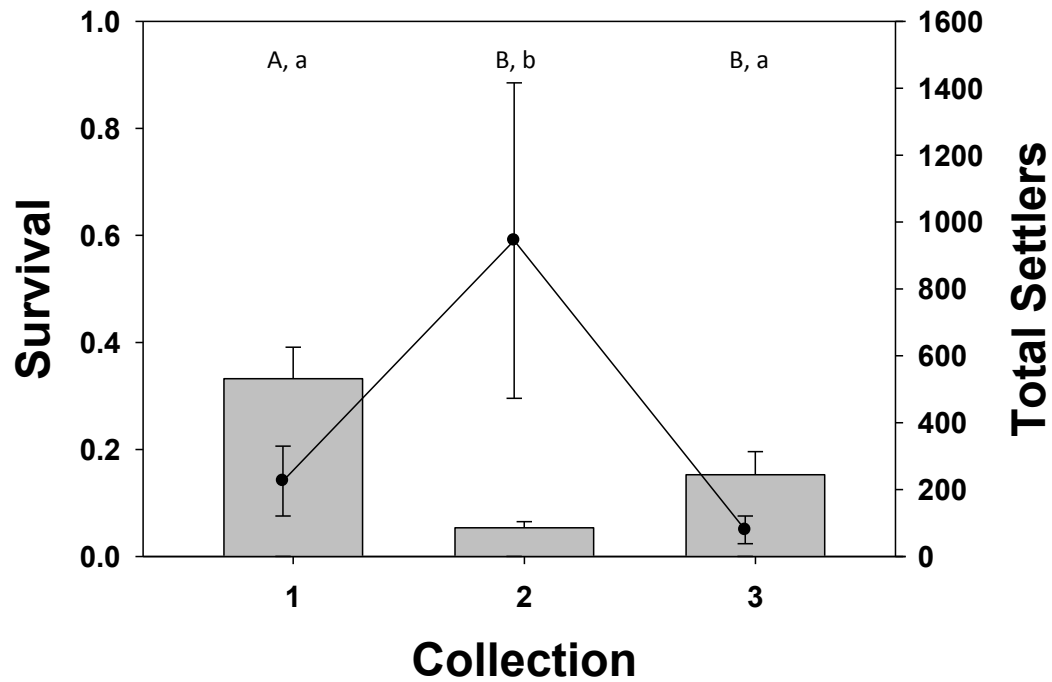


Figure 8: Survival of bay scallops as estimated by the ratio of actual recruits to settlers (bars, left axis) and mean total settlers for both years (line, right axis) against collection period. Survival estimates were pooled across all collectors for both years to arrive at a single value for each collection \pm SE. The total settlers are the mean number of settlers (only those collected in bags) for all collectors for both years \pm SE. Capital letters denote significant differences for survival, while lower case letters denote significant differences for settlers as determined by multiple comparisons tests.

Table 1: Dimensions of artificial seagrass units (ASUs). P:A ratio is the perimeter to area ratio of individual ASUs.

	Small		Large	
	Circular	Stellate	Circular	Stellate
Area (m ²)	8.5	8.5	17	17
Perimeter (m)	10.3	14.5	14.5	29
P:A ratio	1.21	1.7	0.85	1.7

Table 2: Table of results from Three-Way ANOVA tests comparing scallop settlement, recruitment, survival among patch treatments (T), within patch location (L) and collections (C).

Settlers per collector	df	SS	MS	F	P
Shape	3	97.311	32.437	0.813	0.489
Location	1	156.815	156.815	3.929	0.05
Collection	3	6792.669	2264.223	56.733	<0.001
Shape x Location	3	34.481	11.494	0.288	0.834
Shape x Collection	9	236.435	26.271	0.658	0.745
Location x Collection	3	195.632	65.211	1.634	0.185
Shape x Location x Collection	9	103.623	11.514	0.288	0.977
Residual	126	5028.694	39.91		
Total	157	13269.019	84.516		
Area	1	42.794	42.794	1.136	0.288
Location	1	157.181	157.181	4.173	0.043
Collection	3	6795.142	2265.047	60.132	<0.001
Area x Location	1	6.905	6.905	0.183	0.669
Area x Collection	3	95.249	31.75	0.843	0.473
Location x Collection	3	195.624	65.208	1.731	0.163
Area x Location x Collection	3	7.623	2.541	0.0675	0.977
Residual	142	5348.868	37.668		
Total	157	13269.019	84.516		
Perimeter	2	44.982	22.491	0.583	0.56
Location	1	120.266	120.266	3.116	0.08
Collection	3	6872.195	2290.732	59.355	<0.001
Perimeter x Location	2	35.004	17.502	0.453	0.636
Perimeter x Collection	6	160.245	26.707	0.692	0.656
Location x Collection	3	127.761	42.587	1.103	0.35
PerimeterxLocationxCollection	6	88.115	14.686	0.381	0.89
Residual	134	5171.537	38.594		

Total	157	13269.019	84.516		
P/A	2	97.126	48.563	1.284	0.28
Location	1	121.644	121.644	3.215	0.075
Collection	3	6023.127	2007.709	53.068	<0.001
P/A x Location	2	35.089	17.545	0.464	0.63
P/A x Collection	6	233.982	38.997	1.031	0.408
Location x Collection	3	154.239	51.413	1.359	0.258
P/A x Location x Collection	6	65.768	10.961	0.29	0.941
Residual	134	5069.584	37.833		
Total	157	13269.019	84.516		

Recruits per Collector

Shape	3	2.36	0.787	2.369	0.074
Location	1	0.053	0.053	0.16	0.69
Collection	3	12.176	4.059	12.223	<0.001
Shape x Location	3	0.504	0.168	0.506	0.679
Shape x Collection	9	0.833	0.0925	0.279	0.979
Location x Collection	3	0.0636	0.0212	0.0639	0.979
Shape x Location x Collection	9	1.928	0.214	0.645	0.757
Residual	126	41.839	0.332		
Total	157	60.631	0.386		

Area	1	0.375	0.375	1.14	0.287
Location	1	0.0653	0.0653	0.199	0.657
Collection	3	12.526	4.175	12.692	<0.001
Area x Location	1	0.00113	0.00113	0.00343	0.953
Area x Collection	3	0.0384	0.0128	0.0389	0.99
Location x Collection	3	0.0488	0.0163	0.0495	0.985
Area x Location x Collection	3	0.274	0.0913	0.277	0.842
Residual	142	46.715	0.329		
Total	157	60.631	0.386		

Perimeter	2	2.221	1.111	3.439	0.035
Location	1	0.0142	0.0142	0.0438	0.834
Collection	3	11.077	3.692	11.431	<0.001
Perimeter x Location	2	0.224	0.112	0.347	0.708
Perimeter x Collection	6	0.575	0.0958	0.297	0.938
Location x Collection	3	0.0496	0.0165	0.0511	0.985
PerimeterxLocationxCollection	6	1.102	0.184	0.569	0.755
Residual	134	43.283	0.323		
Total	157	60.631	0.386		
P/A	2	2.354	1.177	3.699	0.027
Location	1	0.211	0.211	0.663	0.417
Collection	3	12.952	4.317	13.57	<0.001
P/A x Location	2	0.476	0.238	0.748	0.475
P/A x Collection	6	0.794	0.132	0.416	0.868
Location x Collection	3	0.0409	0.0136	0.0429	0.988
P/A x Location x Collection	6	1.201	0.2	0.629	0.707
Residual	134	42.633	0.318		
Total	157	60.631	0.386		
Survival					
Shape	3	0.303	0.101	1.718	0.169
Location	1	0.365	0.365	6.202	0.015
Collection	2	1.486	0.743	12.627	<0.001
Shape x Location	3	0.182	0.0608	1.033	0.382
Shape x Collection	6	0.389	0.0648	1.101	0.368
Location x Collection	2	0.268	0.134	2.276	0.109
Shape x Location x Collection	6	0.668	0.111	1.892	0.091
Residual	90	5.297	0.0589		
Total	113	8.833	0.0782		

Area	1	0.00348	0.00348	0.0584	0.81
Location	1	0.343	0.343	5.748	0.018
Collection	2	1.58	0.79	13.241	<0.001
Area x Location	1	0.00976	0.00976	0.164	0.687
Area x Collection	2	0.163	0.0815	1.367	0.26
Location x Collection	2	0.276	0.138	2.31	0.104
Area x Location x Collection	2	0.524	0.262	4.39	0.015
Residual	102	6.085	0.0597		
Total	113	8.833	0.0782		
Perimeter	2	0.183	0.0917	1.45	0.24
Location	1	0.267	0.267	4.218	0.043
Collection	2	1.367	0.684	10.811	<0.001
Perimeter x Location	2	0.0664	0.0332	0.525	0.593
Perimeter x Collection	4	0.131	0.0327	0.517	0.723
Location x Collection	2	0.197	0.0985	1.558	0.216
PerimeterxLocationxCollection	4	0.39	0.0975	1.542	0.196
Residual	96	6.071	0.0632		
Total	113	8.833	0.0782		
P/A	2	0.23	0.115	1.972	0.145
Location	1	0.507	0.507	8.692	0.004
Collection	2	1.585	0.793	13.59	<0.001
P/A x Location	2	0.184	0.0919	1.575	0.212
P/A x Collection	4	0.319	0.0797	1.367	0.251
Location x Collection	2	0.273	0.137	2.341	0.102
P/A x Location x Collection	4	0.506	0.126	2.168	0.078
Residual	96	5.599	0.0583		
Total	113	8.833	0.0782		

Table 3: Table of results from One-Way ANOVA tests for the extrapolated, whole patch numbers of settlers, recruits and survival to investigate effects at the patch scale.

Extrapolated Settlers	df	SS	MS	<i>F</i>	p
Shape	3	487987636.2	162662545.4	1.215	0.31
Residual	76	10173090822	133856458.2		
Total	79	10661078458			
Area	1	351716382.8	351716382.8	2.661	0.107
Residual	78	10309362076	132171308.7		
Total	79	10661078458			
Perimeter	2	446733095.9	223366547.9	1.684	0.192
Residual	77	10214345363	132653835.9		
Total	79	10661078458			
P/A	2	120932727.9	60466363.96	0.442	0.645
Residual	77	10540145731	136885009.5		
Total	79	10661078458			
Extrapolated Recruits					
Shape	3	2194569.669	731523.223	2.085	0.109
Residual	76	26670495.55	350927.573		
Total	79	28865065.22			
Area	1	1568389.44	1568389.44	4.482	0.037
Residual	78	27296675.78	349957.382		
Total	79	28865065.22			
Perimeter	2	802300.766	401150.383	1.101	0.338

Residual	77	28062764.45	364451.486		
Total	79	28865065.22			
P/A	2	523001.771	261500.885	0.71	0.495
Residual	77	28342063.45	368078.746		
Total	79	28865065.22			
Survival					
Shape	3	0.0969	0.0323	0.781	0.51
Residual	56	2.316	0.0414		
Total	59	2.413			
Area	1	0.000173	0.000173	0.0041 7	0.949
Residual	58	2.413	0.0416		
Total	59	2.413			
Perimeter	2	0.0917	0.0459	1.126	0.331
Residual	57	2.321	0.0407		
Total	59	2.413			
P/A	2	4.523	2.261	0.436	0.649
Residual	57	295.886	5.191		
Total	59	300.409			

Table 4: Table of results from Pearson’s correlations for the mean number of settlers or recruits per collector for each ASU treatment (LC,LS,SC,SS, n=4) and survival per collector versus the various patch morphometrics; and the mean total calculated number of settlers, recruits and survival for the whole ASU vs patch morphometrics (P/A, perimeter, area).

	Settlers per Collector			Recruits per Collector			Survival per Collector		
	P/A	Perimeter	Area	P/A	Perimeter	Area	P/A	Perimeter	Area
R	0.582	-0.169	-0.809	-0.147	-0.171	-0.269	-0.495	-0.317	-0.110
P	0.418	0.831	0.191	0.853	0.829	0.731	0.505	0.683	0.890
N	4	4	4	4	4	4	4	4	4

	Settlers per Patch			Recruits per Patch			Survival per Patch		
	P/A	Perimeter	Area	P/A	Perimeter	Area	P/A	Perimeter	Area
R	0.283	0.959	0.826	-0.388	0.528	0.870	-0.851	-0.510	0.051
P	0.717	0.041	0.174	0.612	0.472	0.130	0.149	0.490	0.949
N	4	4	4	4	4	4	4	4	4

Chapter Three

Revisiting seascape ecology: Ecological trade-offs across a seagrass landscape

Abstract:

With some exceptions, the general findings from landscape ecological studies conducted in terrestrial systems is that increasing habitat fragmentation and patch isolation results in negative consequences on associated fauna. Among these negative consequences are increased amounts of edge habitats which are associated with increased predation and disease, decreased habitat quality, and sites for species invasions. In marine systems, seagrass meadows, which serve as essential nursery and adult habitat for numerous species, experiences both natural and anthropogenic fragmentation resulting in patches. Results from studies involving seagrass patch size and edge effects on associated fauna have been equivocal – studies suggest that patchy seagrass habitats may be both beneficial and/or detrimental. One reason for the variable results might be the existence of ecological trade-offs for species which associate with seagrass habitats. Bay scallops, *Argopecten irradians*, are useful model organisms for studying the response of a semi-mobile bilvale to changes in seagrass landscapes – they exhibit a strong habitat association and seagrass offers both a settlement substrate and a predation refuge, but they also experience reduced growth in seagrass. This study investigated the potential ecological survival-growth trade-off for bay scallops living within a seagrass landscape. By placing caged scallops at the centers and edges of 2 different sizes and shapes (varying perimeter:area ratio) of patches, and tethering scallops in the same locations, this study demonstrated a significant survival-growth trade-off for scallops. Scallops consistently grew fastest in bare sand and slowest at patch centers, while survival showed the opposite trend. Using modified minimize mortality (μ) to foraging (f) ratio models, seagrass edge habitat was identified as the best location for scallops. Further, investigations of core-area index (CAI) suggest that small, complex patches might offer scallops a balance between predation risk and maximized growth. Taken in sum, these results

suggest that edge habitats may not have negative impacts on populations of associated fauna, and that patchy seagrass habitats might even benefit organisms like bay scallops by maximizing risk vs. reward.

Introduction

As anthropogenic habitat fragmentation and loss accelerates, it is increasingly important to understand the impacts of changing spatial structure on the ecology of an ecosystem. The burgeoning field of landscape ecology has begun to answer questions about fragmented and patchy habitat (Turner 2005); however, until recently, field studies have been limited to terrestrial habitats. The inclusion of marine settings in landscape ecology (Hinchey et al. 2008) has given rise to a sub-discipline coined ‘seascape ecology’ (sensu Pittman et al. 2011). While a number of marine habitats have since been investigated, seagrass habitats remain well suited for such study (Robbins and Bell 1994) and so have received considerable attention (Irlandi et al. 1995, Hovel et al. 2002, Bostrom et al. 2006, Jelbart et al. 2006, Bostrom et al. 2011).

With some exceptions, the general findings from landscape ecological studies conducted in terrestrial systems is that increasing habitat fragmentation and patch isolation results in negative consequences on associated fauna (Ries et al. 2004, Lindenmayer and Fischer 2006). Among these are increased amount of edge or transition habitat, often associated with increased predation and disease, decreased habitat quality, and sites for species invasions (Ries et al. 2004). In terrestrial studies, habitat edges have often been considered ‘ecological traps’, where individuals preferentially settle in a habitat within which they do poorly (Ries and Fagan 2003, Ries et al. 2004, Robertson and Hutto 2006). However, these patch size and edge effects have proven to be highly variable across seagrass landscapes.

Studies involving the impacts of seagrass patch size and degree of patchiness have yielded positive (Irlandi et al. 1995, Irlandi 1997, Eggleston et al. 1998, Irlandi et al. 1999), negative (Hovel and Lipcius 2001, Hovel 2003, Hovel and Fonseca 2005) or both positive and negative (Gorman et al. 2009) relationships with survival and patch size. Likewise, seagrass edge studies

have yielded highly variable survival and growth results (Bologna and Heck 1999, 2002, Macreadie et al. 2010a, Macreadie et al. 2010b, Carroll et al. 2012). Patch shape has received less attention, typically focusing on perimeter to area (P:A) ratios and faunal abundance (Bologna and Heck 2000, Tanner 2003). A review of seagrass landscape studies found that species responses were not consistent across landscape variables (i.e. size, shape, edge) and postulated that seagrass fragmentation might not be detrimental to associated fauna (Bostrom et al. 2006).

Among the reasons for variable results in the seascape literature and the possibility that fragmentation might not be detrimental in seagrass habitats is that a number of species experience ecological trade-offs in seagrass habitats. A number of fish species experience a ‘food-risk trade-off’ when associating with vegetative habitats (Sogard 1992, Dahlgren and Eggleston 2000, Harter and Heck 2006, Grol et al. 2008, Hammerschlag et al. 2010, Grol et al. 2011) as individuals try to balance the threat of mortality and foraging efficiency (Gilliam and Fraser 1987, Gotceitas 1990). Bivalves also exhibit potential food-risk trade-offs, growing more slowly in seagrass habitats within which they have higher survival (Bologna and Heck 1999, Irlandi et al. 1999, Frandsen and Dolmer 2002, Johnson and Heck 2007). To understand what drives the observed variability in responses of mobile organisms to seagrass fragmentation, potential ecological trade-offs need to be more fully explored.

Bay scallops, *Argopecten irradians* are useful model organisms for studying seagrass landscapes. They exhibit a strong association with seagrass habitats (Belding 1910, Thayer and Stuart 1974); seagrass, a favored substrate for settlement (Eckman 1987), and offers a spatial refuge from benthic predators (Pohle et al. 1991). Historical studies suggest that seagrass landscape configuration can have significant impacts on scallop survival and growth (Irlandi et

al. 1995, Irlandi et al. 1999), and two previous studies suggest scallops exhibit a food-risk type trade-off in association with seagrass habitats (Ambrose and Irlandi 1992, Bologna and Heck 1999). Bay scallops are the target of numerous restoration efforts (Peterson et al. 1996, Arnold et al. 2005, Tettelbach and Smith 2009), so there is considerable interest in having a better understanding of scallop-habitat interactions in anthropogenically influenced environments.

This study aimed to quantify the impacts of seagrass patch size and shape and within patch location on the growth and survival of bay scallops in an experimental field setting. Specifically, we investigated the potential ecological survival-growth trade-off for bay scallops living in seagrass habitats. This was accomplished by placing hatchery-reared scallops in experimental artificial seagrass units (ASUs) and comparing growth and survival values to rates based on size and abundance of naturally recruiting scallops.

Methods

Study Site

Hallock Bay (HB) is a small, shallow embayment located at the eastern end of the north fork of Long Island, New York. One of the eastern-most basins of the Peconic Estuary (PE) system, HB is an enclosed, lagoonal-type estuary, with a narrow inlet for tidal exchange. Subterranean groundwater seepage provides the major freshwater input.

HB was chosen, in part, because it formerly had lush eelgrass meadows (Streib et al. 1995), supported a large scallop population and is currently the site of restoration and monitoring efforts (Tettelbach et al, *in review*). The site of the field experiments (41°08'17.23"N, 072°15'47.96"W) was located approximately 1.5km from an on-bottom 'spawner sanctuary' established as part of recent restoration efforts (Tettelbach and Smith 2009). The study site was characterized as

having muddy sand sediments and relatively little submerged vegetation in the form of macroalgae.

Artificial Seagrass Units

To assess the impacts of seagrass patch morphology on bay scallop survival and growth, a series of artificial seagrass units (ASUs) was constructed. This technique has been successfully employed in numerous studies of seagrass associated species (Virnstein and Curran 1986, Eggleston et al. 1998, 199, Bologna and Heck 2000, Healey and Hovel 2004, Macreadie et al. 2009). The advantage of using ASUs is that they control for variables that are typically confounding in natural seagrass beds, such as differences in canopy height, shoot density, and area.

Two treatment sizes, small (8.5m²) and large (17m²), and two shapes, a circle and a four-pointed star, were replicated: 3 each for the small shapes, but due to logistical reasons, only 2 each for the large shapes. The shapes were selected to manipulate edge and perimeter to area ratios (Bologna and Heck 2000). Sizes were chosen to allow discernable edge and center (>1m from the edge) habitats. ASUs of this relatively large size have not typically been used previously. Details of ASU construction are given in Carroll et al. (2012). In 2007, only small patches were deployed; all size patches were used in 2008 and 2009. Due to the 2x2 shape x size combination, 4 different values for core area index (CAI, Figure 1) were calculated and used for analysis.

Scallop growth

Hatchery-reared scallops, spawned at the Cornell Cooperative Extension of Suffolk County shellfish hatchery in Southold, NY and grown-out to appropriate size in Goose Creek, Southold, NY, were placed within 38 x 46 cm, 1mm mesh predator exclusion devices inside the ASUs.

Scallops were marked using numbered white wire tags secured with super glue. Sets of 10 uniquely tagged scallops were measured for shell height, defined as the distance from the umbo to the farthest point from the hinge, to the nearest 0.1mm, and placed into exclusion devices. Replicate sets of scallops were placed along the edge and within the interior (>1m from edge) of all ASUs, another set was placed on barren (unvegetated, muddy sand with some shell hash) substrate within 5 meters of the ASU array. Scallops were placed in the field for 12 weeks – from 25 July to 17 October in 2007, starting size ~11.5mm, from 20 August to 12 November in 2008, starting size ~20mm, and from 29 July to 20 October 2009, starting size ~15mm. In 2007 and 2008, scallops were measured every 2 weeks. Since shell height did not deviate among treatments until the end of the 12-week experiment in 2007 and 2008, only initial and final shell heights were measured in 2009. At the end of the 12-week period in all years, all scallops were collected, re-measured to the nearest 0.1mm and dissected for condition analysis.

Condition indices were computed using the following dry weight condition indices (CI):

$$CI = (\textit{tissue dry weight} / \textit{shell height}) \times 100 \text{ (Rheault and Rice 1996)} \quad (1)$$

$$CI = (\textit{tissue dry weight} / \textit{shell weight}) \times 100 \text{ (Shriver et al. 2002)} \quad (2)$$

In 2007, CI was only calculated using Eq. 1, both indices were used in 2008 and 2009. Low CI values indicate that energy reserves have been depleted for maintenance under poor environmental conditions (Martinez and Mettifugo 1998). A ratio of shell height/shell weight was also computed as a proxy for shell strength, as differences in shell weight are indicative of differences in shell thickness and ultimately strength (Freeman 2007).

Chlorophyll and water flow

Since phytoplankton biomass and composition are likely to influence scallop growth, in 2008 water samples were taken from within the canopy at the center of a large circle ASU, along the

edge, and ~ 10 cm off the bottom above unvegetated sediments as a proxy of food availability. Sets of 60-mL syringes were collected used by divers to draw water by placing the syringe opening within the canopy. Total chlorophyll a (Chl a) was measured by filtering replicate water samples onto GF/F filters, freezing and extracting in acetone, and measuring fluorescence with a Turner fluorometer (Parsons et al., 1984). Samples were collected 4 times in 2008 during the scallop deployment, from the middle of August to the end of September, from each ASU.

Standard plaster dissolution methods were used as a proxy for differences in flow (Komatsu and Kawai 1992). Plaster of Paris was formed in an ice-cube tray, dried to constant mass, and then sanded so that the mass of each cube was approximately the same. Cubes were weighed, glued onto a plastic card, and fastened to bricks. Sets of bricks were placed in the field outside of ASUs and along the edge and center of a large circle. Cubes were recovered after 24 hrs, dried to constant mass and weighed. Percent loss was calculated for each location.

Scallop Survival

In 2008, scallop survival was investigated by tethering juvenile scallops within ASUs, along ASU edges and in barren substrate, as described above. Since scallop size has been demonstrated as the most important factor affecting survival in the field, only small (18-25mm) hatchery-reared scallops, below the ~40mm predation threshold (Tettelbach 1986) were used. A slipknot of monofilament fishing line was tied around the ‘ears’ of individual scallops and glued in place. Sets of 10 scallops were then tethered to a 4m nylon sink line, spaced ~40cm apart (Talman et al. 2004), and placed at the edge and center of each ASU. Tethers were checked for prey survival at 24-hr intervals for a period of 3 consecutive days. Since microfracture damage of shells from failed predation attempts could compromise shell strength, all scallops were replaced daily. This experiment was conducted in August and November of 2008, when predator activities were

expected to be different (Carroll et al. 2010). Since no tethers detached from scallops after 72hr in the lab, missing individuals were interpreted as consumed. When found, damaged shells were examined to determine what type of predator was likely responsible for the observed mortality (Tettelbach 1986, Prescott 1990). For example, crabs typically leave chipped, cracked or crushed shells, whereas large gastropods like whelks leave clean, articulated or disarticulated shells with no visible damage.

Percent mortality was calculated using the following equation:

$$\mu = 1 - \frac{N_t}{N_0} \quad (3)$$

where μ is the calculated rate of mortality, N_t is the number of scallops surviving after one day and N_0 is the number of scallops deployed.

Natural settlement

Natural settlement was monitored during 2009 and 2010 as part of a study to examine recruitment and natural mortality to different locations within the ASUs (Carroll et al. 2012). All scallops from collectors were counted and measured to the nearest mm. Because the date of settlement was not known, growth rates could not be calculated. Differences in the distribution of sizes of naturally settled scallops were used as a proxy to estimate differences in growth, with the assumption that the scallops settled around the same time. Additionally, the unique collector design, which monitored both settlement (those larvae available to settle on the collectors) and recruitment (post-set individuals which survived to 6 weeks), allowed for estimation of survival. Survival was calculated as the number of recruits divided by the number of settled for each collector, with the assumption that loss was due to mortality. Patterns in growth and survival of naturally setting scallops were used to compare to those naïve, hatchery reared scallops placed within the ASU array.

Mortality to growth rate

Species commonly choose among habitats that differ in the net energy received and the risk of death due to predation, leading to a choice model where organisms attempt to minimize the ratio of mortality rate (μ) to gross foraging rate (f) (Gilliam and Fraser 1987). While typically applied to highly mobile species and species which show ontogenetic changes in habitat (e.g., Dahlgren and Eggleston 2000), Bologna and Heck (1999) adapted it for use with scallops by estimating changes in scallop biomass as a proxy for foraging rate. For scallops placed in the ASUs in 2008 (the only year scallops were tethered), μ/f ratios were calculated using equation 3 above and the following equation:

$$f = \text{Growth rate (mm d}^{-1}\text{)} \times \frac{\text{Scallop Tissue dry weight (g)}}{\text{Shell Height (mm)}} \times 1000\text{mg/g} \quad (4)$$

Where f is the calculated average increase in biomass, the growth rate is the difference between the final and initial shell height, and the condition index is the relationship between tissue dry weight and shell height (equation 1).

The “minimize μ/f ” model only applies if the refuge is safe from any predatory mortality, and there are no differences in metabolic costs in each habitat (Gilliam and Fraser 1987). Since there are only 2 ways to minimize this equation, making μ very small or making f very big, two correction factors can be used to account for nonzero mortality of the refuge or significant differences in growth. If the mortality rate in the refuge is nonzero, this can be corrected to “minimize $(\mu-c)/f$,” where c is the nonzero mortality rate of the refuge, in this case patch centers, thus reducing the “risk” in the non-refuge habitats, i.e., patch edges and bare sand. If the costs of associated with the refuge habitat is significantly different, the model becomes “minimize $\mu/(f+k)$,” where k is the difference between the metabolic costs within the seagrass habitats

(either patch centers or edges) and bare sand. Since growth is greater in the unvegetated treatments, k is negative and therefore penalizing the refuge habitats for the cost of growth.

Statistical Analysis

A three-way ANOVA was used to compare growth and condition among small patches across all 3 years because only small patches were used in the first year of the study with year, patch type (circle or star) and location (center and edge) as the explanatory factors. Because of differences in number of patch treatments among years (2 in 2007, 4 in 2008 and 2009) and since growth and condition may have been confounded by slightly different starting dates and scallop sizes, within year differences were analyzed separately using two-way ANOVAs with patch type (small circle, SC; small star, SS; large circle, LC; and large star, LS) and within patch location (center and edge) as explanatory factors.

Since scallops in unvegetated sediments did not fit into either a patch shape or location factor, they were analyzed differently. Circle patches had greater impact on scallop growth than star patches (see below), so a series of one-way ANOVAs was used to compare scallop growth in circular patches compared to sandy habitats for each year. To test for patterns across all years, a two-way ANOVA was used to test for differences in scallop growth and condition using shell height with year and location (center, edge, sand) as factors. When ANOVAs yielded significant results, a Holm-Sidak test was used for multiple comparisons within each factor. Additionally, Pearson correlations were used to test the relationship between CAI and scallop growth for mean values in each year and across all years.

For tethered scallop survival, a three-way ANOVA was used with date (August or November), patch type and within patch location as fixed factors. Since within patch location was found to have a significant effect, survival of scallops tethered in bare sand were compared

to patch centers and edges using a one-way ANOVA. As with growth, Holm-Sidak tests were used for multiple comparisons within and between factors. The relationship between CAI and survival was tested using both a Pearson correlation and a non-linear regression.

Differences in growth rates for natural set scallops were approximated by testing size distributions of scallops between the center and edges across all patches using a two-sample Kolmogorov-Smirnov test for each date of collection. If $D_{\max} > D_{0.05}$, then the two samples were considered to come from separate distributions. For survival of natural set scallops, two-way ANOVAs were used with patch type and location as fixed factors described above with data pooled across all collections and years. Finally, as above, the relationship between survival at the centers of patches and CAI were tested using a Pearson correlation.

For the “minimize μ/f ” model, randomly assigned μ and f values calculated from raw field values of mortality (μ) and cage-mean growth rates (f) were used in simulations to determine habitat-specific (center, edge, sand) μ/f values, which were used for comparison between habitats. The randomization procedure was repeated 2000 times for scallops in each habitat. A one-way ANOVA was then used to determine whether differences were significant and a Tukey HSD test was used for multiple comparisons.

For the correction factor c , randomly assigned values from field measurements of mortality for scallops at patch centers were subtracted from randomly assigned field values of μ for scallops at patch edges or in sand, and were divided by randomly assigned field growth rate values (f) for scallops at the edge or in sand, respectively, to 2000 permutations. Since $(\mu - c)$ should reward habitats with mortality values similar to or lower than the ‘refuge’ habitat, negative values were accepted. The resulting $(\mu - c)/f$ for scallops at patch edges or in sand were tested using a T-test. For the correction factor k , which is the difference between growth at patch

centers or edges and sand, randomly assigned field measurements of f for scallops in sand were subtracted from randomly assigned field measurements of f for scallops in either patch centers or edges to generate k values. Next, $(f+k)$ was calculated using generated k with the same value f value used to calculate k . Randomly generated values from field measurements of μ for scallops at patch centers or edges were then divided by the resulting $(f+k)$ for centers or edges, respectively, to 2000 permutations. Since values for k are always negative, in instances where k is larger than f the resulting $\mu/(f+k)$ is negative, rewarding scallops experiencing high cost of growth; because k is supposed to penalize the cost of growth, the absolute value of $\mu/(f+k)$ was used. The randomly generated $\mu/(f+k)$ values were compared between centers and edges using a T-test.

Results

Scallop growth

Scallop growth and condition were variable between years. In 2007, when only small patches were used, both growth and condition were significantly affected by within patch location, but not by patch type. Scallops located at the edge grew 31.1 ± 0.4 mm in SH (mean \pm SE) over the course of 12 weeks, significantly more than scallops in the center of patches, which grew 28.6 ± 0.4 mm SH (two-way ANOVA, $df=1$, $F=20.550$, $p<0.001$). Likewise, the mean condition index (CI) for scallops at patch edges (1.86 ± 0.04) was significantly enhanced relative to scallops in patch centers (1.60 ± 0.04 , $df=1$, $F=22.828$, $p<0.001$). Scallop growth between sand and the centers and edges of circle patches was significant (one-way ANOVA, $df=2$, $F=18.474$, $p<0.001$); growth in sand (34.5 ± 0.5 mm) and at the edge of circle patches (31.9 ± 0.7 mm) were both higher than for scallops growing in the center of circle patches ($28.4 \pm$

0.4mm, $p < 0.001$ for both). Core area index (CAI) growth relationships were not calculated since there were only 2 treatments.

In 2008, there was a significant effect of both patch type (two-way ANOVA, $df=3$, $F=4.249$, $p=0.009$) and within patch location ($df=1$, $F=4.333$, $p=0.042$) on scallop growth. However, neither metric of CI, nor shell height to shell weight (SH/SW) ratio showed significant differences between patch type or location. When scallops on circle patches were compared to those on sand, there was a significant effect of location with scallops on sand being the largest (sand - 29.7 ± 1.3 mm; edges - 27.4 ± 0.8 mm; centers - 24.5 ± 1.1 mm; one-way ANOVA, $df=2$, $F=3.491$, $p=0.045$). Likewise, a significant effect of location on condition using shell height was observed (sand - 2.43 ± 0.13 ; edges - 1.99 ± 0.05 ; centers - 1.77 ± 0.08 ; $df=2$, $F=5.234$, $p=0.012$) with scallops on sand having the highest condition. However, neither condition using shell weight ($p=0.465$) or SH/SW ratios ($p=0.110$) were significantly different among locations. CAI was not significantly related to scallop growth ($r=-0.466$, $p=0.534$) or condition ($r=-0.660$, $p=0.340$).

Growth in 2009 was generally lower than the previous two years (Figure 2); however, unlike 2007 and 2008, growth was not significantly affected by patch type or location (two-way ANOVA, $df=3$, $F=2.705$, $p=0.055$; $df=1$, $F=0.0590$, $p=0.809$, respectively). Neither condition index showed significant differences among patch type ($p=0.153$ and $p=0.158$ for CI by shell height and CI by shell weight, respectively) or location ($p=0.079$ and $p=0.603$, respectively). The SH/SW ratio was affected by patch type (two-way ANOVA, $df=3$, $F=3.995$, $p=0.012$), with scallops located on large circles (16.0 ± 0.5 mm g^{-1}) having higher SH/SW than those in small stars (14.0 ± 0.4 mm g^{-1} ; $p=0.001$), but no other patch treatments differed from one another. When testing for location within the circle patches and bare sand, there was no difference in

scallop growth (one-way ANOVA, $df=2$, $F=1.330$, $p=0.280$). However, location between circle patches and sand did significantly affect condition index using shell height (equation 1, $df=2$, $F=6.325$, $p=0.005$), with scallops in sand having greater condition (0.923 ± 0.03) than those in circle centers (0.718 ± 0.02 , $p=0.001$) and at circle edges (0.765 ± 0.03 , $p=0.010$). There was no difference in condition index using shell weight (equation 2, $df=2$, $F=1.629$, $p=0.213$). However, scallops in sand ($13.0 \pm 0.4 \text{ mm g}^{-1}$) also had lower SH/SW than those in patch centers ($15.5 \pm 0.4 \text{ mm g}^{-1}$; $p=0.005$) and patch edges ($15.0 \pm 0.4 \text{ mm/g}$; $p=0.020$), which were not different from each other ($p=0.391$, see Tables 1 and 2 for full statistical results). CAI was not significantly correlated with either scallop growth ($r=-0.850$, $p=0.150$) or condition using shell height ($r=-0.798$, $p=0.202$).

When investigating scallop growth in small patches across years, the pattern of differences between center and edge were maintained. Despite significantly different growth rates between all years (two-way ANOVA, $df=2$, $F=87.007$, $p<0.001$), growth significantly varied between locations ($df=2$, $F=8.889$, $p<0.001$). Scallop growth in 2007 ($31.5 \pm 0.8\text{mm}$) was significantly higher than 2008 ($26.6 \pm 0.7\text{mm}$, $p<0.001$) and 2009 ($19.4 \pm 0.6\text{mm}$, $p<0.001$, Figure 2a); scallop growth rates in the latter two years were also different from each other ($p<0.001$). Similarly, scallops on sand grew $28.1 \pm 1.1\text{mm}$, while scallops located at patch edges grew only $25.4 \pm 0.3\text{mm}$ ($p=0.022$). Scallops at patch centers grew significantly less than both sand and edge scallops ($23.9 \pm 0.3\text{mm}$, $p<0.001$ for sand, $p=0.004$ for edges, Figure 2b). Similarly, scallop condition using equation 1 was significantly different between years and locations ($df=2$, $F=145.754$, $p<0.001$; $df=2$, $F=17.113$, $p<0.001$, respectively). CI in 2007 (1.97 ± 0.07) and 2008 (2.07 ± 0.07) were significantly higher than CI in 2009 (0.85 ± 0.5 , $p<0.001$ for both), but were not different from each other ($p=0.329$, Figure 2c). Scallops at patch edges had

significantly higher CI than those in patch centers (1.54 ± 0.03 and 1.38 ± 0.03 , respectively; $p < 0.001$), although both were significantly lower than scallops on sand (1.93 ± 0.10 ; $p < 0.001$ for both; Figure 2d). Across all years mean growth was not significantly correlated with CAI ($r = -0.833$, $p = 0.167$).

Chlorophyll and flow

Chlorophyll concentrations varied between sample dates. Chlorophyll was highest in patch centers on 21 August 2008 ($p = 0.002$), on patch edges on 3 September ($p = 0.042$), and over bare sand on 19 September ($p = 0.007$). On the remaining sample date, 30 September, no location was significantly different ($p = 0.092$). Plaster dissolution was greatest in unvegetated habitats, losing $12.6 \pm 0.2\%$ of mass in 24 hours, significantly higher than both edge and center habitats ($7.9 \pm 0.6\%$ and $8.0 \pm 0.2\%$, respectively, $p < 0.001$ for both). Dissolution did not differ from the patch edge to the patch center ($p = 0.956$).

Scallop Survival

Survival of tethered scallops over 3 days was significantly affected by patch type (three-way ANOVA, $df = 3$, $F = 4.011$, $p = 0.011$) and location ($df = 1$, $F = 7.669$, $p = 0.007$), but not between August and October ($df = 1$, $F = 3.686$, $p = 0.059$). Scallops tethered within small stars had significantly higher mortality (0.630 ± 0.048) than those tethered in large circles (0.374 ± 0.058 , $p = 0.001$), however, there were no other differences between patch treatments. Scallops tethered along patch edges had higher mortality (0.586 ± 0.054) than those in the centers of patches (0.356 ± 0.040 , $p = 0.007$). Mortality of scallops in sand was 0.833 ± 0.085 , significantly higher than both seagrass patch centers ($p < 0.001$) and patch edges ($p = 0.036$, Figure 3). Despite not being significantly different, scallops tethered in November exhibited higher mortality ($0.564 \pm$

0.037) than those tethered in August (0.463 ± 0.029). The relationship between CAI and survival was non significant ($r=0.889$, $p=0.111$).

Natural set

The series of Kolmogorov-Smirnov two sample tests showed that scallops from the center and edges of all patches were from the same distribution. D_{\max} was closest to D_{α} during periods of peak settlement in both 2009 and 2010, however, these differences were not significant ($D_{\max} = 0.101$, $D_{\alpha} = 0.122$ for 2009, $D_{\max} = 0.043$, $D_{\alpha} = 0.074$ for 2010, see Table 3). Survival of natural set was enhanced in the center of patches (0.23 ± 0.04) relative to patch edges (0.12 ± 0.04 , $p=0.030$). For survival in 2010, the relationship between CAI and survival was significant ($r=0.950$, $p=0.049$). When both years were pooled, the relationship between CAI and survival also significant and non-linear ($y=0.061*\ln(x) + 0.382$, $r^2=0.919$, $p=0.026$, Figure 4).

Mortality to growth rate

Scallops in the center of a seagrass patch or in patches with relatively low perimeter to area minimized the ratio of mortality to growth rate. In terms of growth, scallops in the centers of all patches had a shell growth rate of 0.29 mm d^{-1} and an estimated increase in dry tissue weight (dtw) of $5.2 \pm 0.2 \text{ mg d}^{-1}$. Scallops located along patch edges grew 0.31 mm d^{-1} and increased tissue biomass at a rate of $6.0 \pm 0.2 \text{ mg dtw d}^{-1}$. Shell growth rate for scallops on sand was 0.35 mm d^{-1} , and their tissue biomass increased by an estimated $8.6 \pm 0.5 \text{ mg dtw d}^{-1}$. When doing 2000 permutations using field measurements, the calculated values of μ/f were significantly different ($p<0.001$). Scallops at patch centers experienced a significantly lower μ/f (0.093 ± 0.001) than both patch edges (0.106 ± 0.001 , $p<0.001$) and sand (0.106 ± 0.000 , $p<0.001$), which were not different from each other ($p=0.999$).

When correcting for the nonzero mortality and the cost of growth for living in seagrass patch centers, the resulting μ/f values change. Using the modified “minimize $(\mu-c)/f$ ” model, where $c =$ the nonzero mortality risk across centers of all patches, $(\mu-c)/f$ for scallops at the edge becomes 0.028 ± 0.001 , whereas the $(\mu-c)/f$ for scallops in sand becomes 0.053 ± 0.001 ($p < 0.001$; Figure 5B). In the modified “minimize $\mu/(f+k)$ ” model, the new value for scallops at patch edges becomes 0.191 ± 0.003 , while the value at patch centers becomes 0.311 ± 0.011 ($p < 0.001$; Figure 5C).

Discussion

For bay scallops, living within seagrass meadows represents a potential ecological trade-off (Figure 6) between growth and survival. In this study, seagrass landscape impacted both the growth and mortality of juvenile bay scallops. Across all 3 years of the growth study, there was a significant pattern of fastest growth in unvegetated habitats, intermediate growth at habitat edges, and slowest growth at patch centers, although total growth varied interannually. This opposed survival trends for tethered scallops which were highest at the centers of patches and lowest in unvegetated sediments. Such trade-offs can have implications for recovering scallop populations, as seagrass has long been considered the preferred scallop habitat and is frequently used to assess habitat suitability in the field (Belding 1910).

Seagrasses have long been demonstrated to reduce foraging efficiency of predators (Heck and Orth 1980, Heck and Thoman 1981, Orth et al. 1984, Heck and Orth 2006), and artificial seagrass habitat proved effective for enhancing survival of both tethered and naturally set scallops in this study. Scallops located at the center demonstrated the highest survival, and although scallop survival located along patch edges was reduced relative to the center, it was still higher compared that on unvegetated substrate outside patches. This is in contrast to the findings

of Bologna and Heck (1999), who observed the highest predation along patch edges. Further, our pattern was consistent with other scallop studies, which showed higher survival in large, continuous patches of natural seagrass (Irlandi et al. 1995, Irlandi et al. 1999).

Bologna and Heck (1999) proposed that more scallops might be located along the edge than at patch interiors despite high predation due to a food-risk trade-off. Numerous species that associate with complex or vegetated habitats exhibit similar trade-offs (Gilliam and Fraser 1987, Gotceitas 1990, Sogard 1992, Halpin 2000, Harter and Heck 2006, Grol et al. 2008, Hammerschlag et al. 2010, Grol et al. 2011). While most of the studies have focused on fish, studies with scallops and other bivalves have shown slower growth within continuous seagrass meadows relative to more patchy meadows or unvegetated sediments (Irlandi et al. 1999, Frandsen and Dolmer 2002, Johnson and Heck 2007). Additionally, scallops tend to accumulate along patch edges via settlement processes (Carroll et al. 2012) and/or active movement (Hamilton and Koch 1996, Bologna and Heck 1999). That scallops ‘choose’ to live in a zone with higher predation indicates that conditions might be favorable for maximizing growth.

In this study, scallops within seagrass patches showed higher survival than those in sand; however, growth was significantly reduced in seagrass patches relative to scallops in unvegetated habitats. While it has been suggested that statistically significant differences in shell growth might not be biologically relevant (Irlandi et al. 1999), we argue the differences observed in this study were likely to have been biologically important. The 0.11 mm/day difference in growth rate between the scallops in the centers of patches versus unvegetated habitats was up to ~9mm over 12 weeks. To obtain a partial predation refuge at ~31mm (Garcia-Esquivel and Bricelj 1993), it would thus take scallops located at patch centers over 40 d longer to reach this size compared to scallops on bare sand. Likewise, while the difference in growth between center and

edge habitats were smaller (2-3mm), scallops in patch centers would take 7-10 d longer to obtain the 31mm parital refuge than those at edges. These differences are likely to have biological ramifications despite the reduction in predatory mortality within the seagrass patches.

Further, examining other metrics of individual fitness also indicated that scallop growth and condition are negatively affected by residing within a seagrass meadow, reinforcing the idea that differences in growth were biologically significant. Scallop condition, calculated by dividing the somatic tissue growth by the length of the scallop shell, demonstrated significant differences due to location within the seagrass landscape across all three years, with the pattern that scallop condition on sand was greater than on edges which was better than within centers. While condition index using shell weight showed no differences between habitat and patch location treatments, it can be argued that condition index using shell height is more meaningful, given shell growth and tissue weight growth in bivalves can be uncoupled -- especially in rapidly growing bivalves (Lewis and Cerrato 1997) -- and the fact that scallops exhibit compensatory growth (Auster and Stewart 1984). Differences in condition can have serious implications on long-term growth and survival, particularly into the first winter (Sekino 1992). Many studies have failed to examine individual fitness (other than simple growth rates); however, terrestrial studies indicate that individuals at habitat edges should exhibit lower fitness due to higher rates of parasitism or lower reproductive output, among others (Ries and Fagan 2003, Robertson and Hutto 2006). In this study, individuals at patch edges were in better condition than those within patches. This pattern was consistent across 3 years with very different growth rates.

While natural set scallops in different habitats did not exhibit different growth rates, as estimated by comparing cumulative size-frequency distributions between scallops at patch edges vs. centers, these results do not disagree with our caged scallop findings. Natural set scallops

had a maximum of 6 weeks to grow, and our bi-weekly field measurements from 2007 and 2008 both indicated that deviations in growth rate did not become apparent until the end of the 12-week experimental period. It is likely that the consequences of reduced condition observed in the caged scallops may take longer than 6 weeks to manifest in shell growth, leading to the lack of differences observed over shorter timescales. Unfortunately, condition was not measured on the small, naturally setting scallops. In terms of survival, natural set scallops supported differential survival between edge and center habitats, and survival within patch centers showed a significant relationship with CAI. It has been suggested that higher mortality at seagrass edges only serves to ‘balance’ the enhanced settlement from the larval stage (Carroll et al. 2012).

Our results point to an ecological trade-off which has also been demonstrated previously for scallops, where the proposed mechanism was a food-risk trade-off (Bologna and Heck 1999). Gilliam and Fraser (1987) first introduced a model where individuals seek to minimize the ratio of mortality rate (μ) to foraging rate (f), although this model was developed for fish, which can more actively choose habitats and exhibit ontogenetic habitat shifts (Dahlgren and Eggleston 2000); thus, fauna are predicted to live in a habitat within which μ/f is the lowest. For this study, changes in scallop biomass were used as a proxy for foraging rate values (sensu Bologna and Heck 1999). In the present model, scallops would seek to minimize mortality to biomass growth ratios. This study found the μ/f ratio to be lowest within the center of seagrass patches due, in most part, to lower predation.

However, the μ/f of scallops at patch edges and bare sand treatments were also relatively low and similar to each other. This is in sharp contrast with results from Bologna and Heck (1999) where μ/f was 2-3xs higher at patch edges than bare sand and patch centers, mainly attributable to the 6x to 70x higher mortality in this edge zone. In the present study, mortality was highest in

sand and intermediate along patch edges. One possible reason for the difference between the two studies, other than location (Bologna and Heck 1999 conducted their study in Florida), is the respective predators responsible for scallop mortality. Shell damage (cracked, broken shells) in this study was indicative of crab predators, while the major predator in the Bologna and Heck study was a large gastropod. Direct contact by gastropod predators prompts bay scallop swimming behavior and thus potential escape (Ordzie and Garofalo 1980, Peterson et al. 1982, Winter and Hamilton 1985), so the inability of large tethered scallops to evade important predators such as whelks may have artificially inflated their predation values. Similarly, Barbeau and Scheibling (1994) found that tethering sea scallops, *Placopecten magellanicus*, artificially inflated predation rates by sea stars, whose predation success was determined by capture rates, but not for crabs, whose predation success was determined by encounter rates. Therefore, it is possible that scallops in the Bologna and Heck (1999) study were more easily to captured by the gastropods, which were twice as likely to encounter scallops along seagrass edges due to diurnal movement into and out of the seagrass patches.

In this study, decapod crustaceans were likely most responsible for mortality of scallops. While large crabs were occasionally observed in the study area, the small mud crab, *Dyspanopeus sayi*, was extremely abundant (100s per square meter) and ubiquitous throughout the study site (Carroll et al. *in press*). Since crab predation rates on scallops was not likely to be affected by tethering (Barbeau and Scheibling 1994), these values were expected to represent field mortality rates. Scallop mortality within artificial seagrass habitat was significantly lower than those in bare sand, which has been evident in other studies in natural seagrass with bay scallops (Prescott 1990, Irlandi et al. 1995, Irlandi et al. 1999), other bivalves (Peterson 1982, Peterson et al. 1984, Irlandi 1994, 1996), and other fauna (Peterson et al. 2001, Hovel and

Fonseca 2005, Jelbart et al. 2006). However, scallops on bare sand gained significantly more tissue biomass per day than scallops located within seagrass, which likely led to the similar μ/f ratios observed between edges and sand.

In the μ/f literature, it is generally hypothesized that individuals will choose habitats that balance risk of predation and food resources, especially for fish (Gilliam and Fraser 1987, Gotceitas 1990). Additionally, as the reward for growth increases (i.e., as food availability becomes greater in the riskier habitat), multiple species have been shown to move into the riskier habitat (Gilliam and Fraser 1987, Macreadie et al. 2010b). Bologna and Heck (1999) arrived at the conclusion that the μ/f ratio does not explain why individual density is highest at seagrass edges. While our results show why scallops prefer the center of seagrass beds to barren sediments, we can also show why scallops may prefer seagrass edges over interiors and sand by modifying μ/f ratios. The standard “minimize μ/f ” model assumes that mortality within the refuge habitat is zero and that metabolic costs within the refuge habitat are not decidedly different (Gilliam and Fraser 1987).

In this study, predation risk was variable but present in all habitats, and there was a significant metabolic cost of living within the refuge (seagrass) habitat. Correcting for this nonzero mortality, the new model, “minimize $(\mu-c)/f$,” where c is the mortality rate in the refuge (Gilliam and Fraser 1987), shows significantly lower values for scallops along the edge when compared to those on sandy substrate. In order to ascertain why scallops might be more abundant at patch edges (Bologna and Heck 1999), the model needs to be modified to reflect the biological cost of seagrass association. Using the corrected model to “minimize $\mu/(f+k)$ ” where k is the difference between growth in and out of the refuge habitat (Gilliam and Fraser 1987), the new model shows significantly lower values for scallops at patch edges when compared to patch

centers (see Figure 5). Thus, when accounting for both nonzero mortality and the cost to growth in seagrass habitats, scallops seem to do the best at patch edges. Although these simplified models were originally designed for highly mobile species, which can more freely make habitat decisions, they can be used to partially explain why less mobile species, such as scallops, may remain in settlement habitats even in the face of high predation.

The “minimize μ/f ” model was also designed as an explanation for species that exhibit ontogenetic habitat shifts (Dahlgren and Eggleston 2000). Bay scallops utilize the seagrass canopy as an above bottom refuge from predation, despite slower growth there (Ambrose and Irlandi 1992, Garcia-Esquivel and Bricelj 1993). However, as scallops grow, they shift habitat from utilizing seagrass to the bottom – between 98 and 100% of scallops less than 12mm were found attached to the seagrass canopy during field surveys in New York in 1990. Scallops then undergo a transitional period, where growth rate and swimming ability increase between 12 and 29mm, a period where they move to the bottom. Once they reached 31mm, all scallops were located on the bottom and attain a partial size refuge from predation (Garcia-Esquivel and Bricelj 1993). Since neither specific growth rates of post-set scallops nor biomass were measured, μ/f values for post set could not be calculated. However, assuming that separation in growth rates does not occur until after 10-12 weeks, back of the envelope calculations of μ/f for post-set using growth rates from Garcia-Esquivel and Bricelj (1993) of $\sim 2\text{mg d}^{-1}$ and mortality of post-set from spat collectors from this study (0.88 for patch edges, 0.77 for patch centers), suggest that μ/f at patch centers (0.40) is minimized for small, post-set scallops relative to patch edges (0.46). Even if only μ/f values are considered without correction factors, these values suggest that μ/f changes with ontogeny; values of μ/f were 4x greater for natural setting scallops in the first 6 weeks than larger scallops monitored for growth during this experiment, and the difference between the

center and edge habitats was 6x greater at post-set size than at the larger, caged and tethered scallop size. It is likely, then, that scallops experience ontogenetic shifts in the risk of associating with certain habitats.

The results of this study also suggest two important shifts from previously established habitat landscape paradigms. First, patchy habitats and/or smaller seagrass patches with higher amounts of edge might actually be beneficial for certain populations since scallops seem to balance growth and survival at patch edges. While it has been suggested by others that fragmented seagrass meadows may not adversely affect a number of species (Healey and Hovel 2004, Bostrom et al. 2006, Hirst and Attrill 2008), these studies look only at abundances and suggest that for opportunistic species that do not show density-area relationships, any seagrass patch, no matter how small, is better than no seagrass. However, studies rarely examine the processes leading to these relationships. For scallops, patchy seagrasses may be better for two reasons. First, having more edge habitat enhances scallop settlement, and despite higher mortality along the edge, numbers of recruits are the same (Carroll et al. 2012) or greater (Bologna and Heck 1999) at patch edges. Second, scallop growth and condition is enhanced at patch edges relative to interiors, and growth and condition of individuals at the center of patches increases as CAI decreases (this study). These results show that both low threshold values for CAI are needed to enhance survival at patch centers, and that survival and growth intercept each other at low CAI values, suggesting that in smaller and/or more complex patches where edge area is greater than core area, the growth and survival trade-off may be maximized. Thus, small, isolated patches should not be assumed to be less valuable than larger, continuous patches (Healey and Hovel 2004).

Second, these results suggest the terrestrial precepts of patchy landscapes and edge habitats as ‘ecological traps’ (Ries and Fagan 2003, Robertson and Hutto 2006) might not generally apply to marine habitats. Ecological traps occur when a species preferentially settles in a habitat within which it does poorly, and from a survival standpoint, data from this and other studies (Bologna and Heck 1999, Smith et al. 2011) might suggest that seagrass patch edges are ecological traps – fauna choose this habitat but survival is reduced. However, when examining metrics of fitness (growth, condition), individuals at seagrass edges actually exhibit greater fitness than their counterparts in patch interiors. Further, despite high mortality, scallop density is the same or greater along seagrass patch edges than interiors, so at the population level, edges are not likely to have an overall negative impact (Carroll et al. 2012). This suggests that ecological traps should be examined at the population level and across multiple ecological processes, and might explain the lack of ‘ecological traps’ in the marine literature.

In summary, this study demonstrated an ecological trade-off for bay scallops within a seagrass habitat landscape. While initial patterns of scallop abundance within a seagrass habitat were determined by settlement, their unique ability among bivalves to move suggests that as ontogenetic changes in scallop behavior occurs – as scallops grow, they leave the refuge of the seagrass canopy and relocated to the bottom where their swimming activity increases until they reach a size over 40mm – larger juveniles and adults can choose more suitable habitats. The “minimize μ/f ” model suggests that such mobile species would choose a habitat that reduces predation risk relative to foraging success. By using modified μ/f equations, the data suggests that scallops along seagrass edges minimize mortality to growth ratios relative to both seagrass interiors and unvegetated sediments. Finally, it is likely that edge habitats may not have net

negative impacts on populations of associated fauna, and that patchy seagrass habitats might even benefit organisms like bay scallops.

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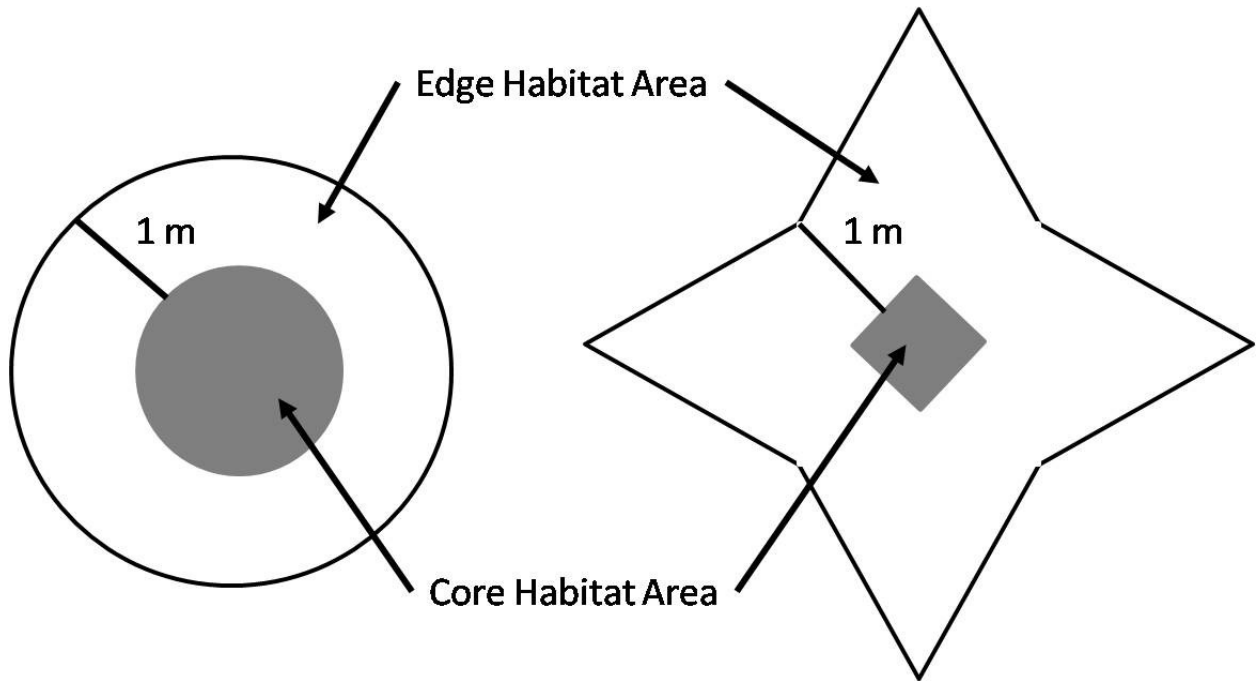


Figure 1: Conceptual diagram illustrating the calculation of the core area index (CAI) for the two shapes of artificial seagrass units (ASUs) utilized in this study.

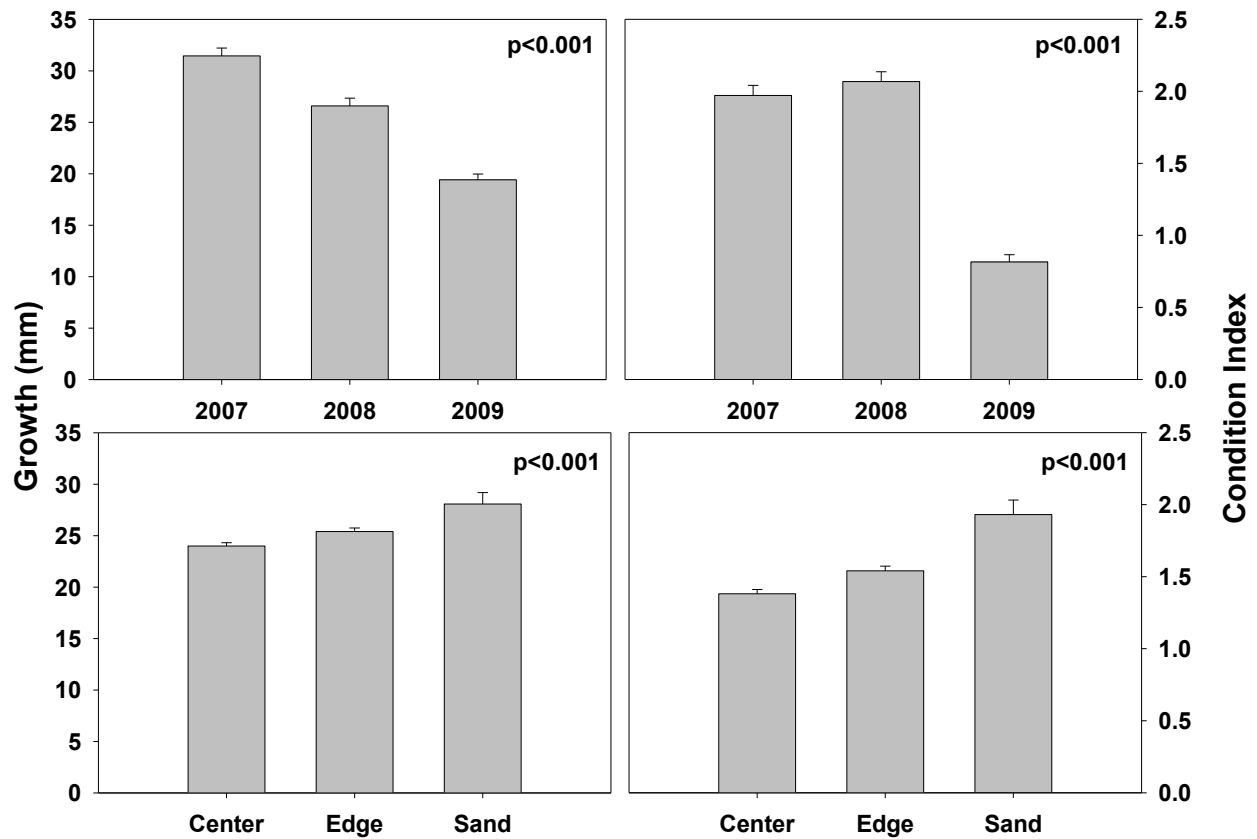


Figure 2: Mean shell growth (mm) of scallops during each year of the study (A) and placed within each location across all three years (B), and condition index (scallop tissue dry weight/shell height) during each year (C) and within each location across all three years (D). Error bars represent standard error.

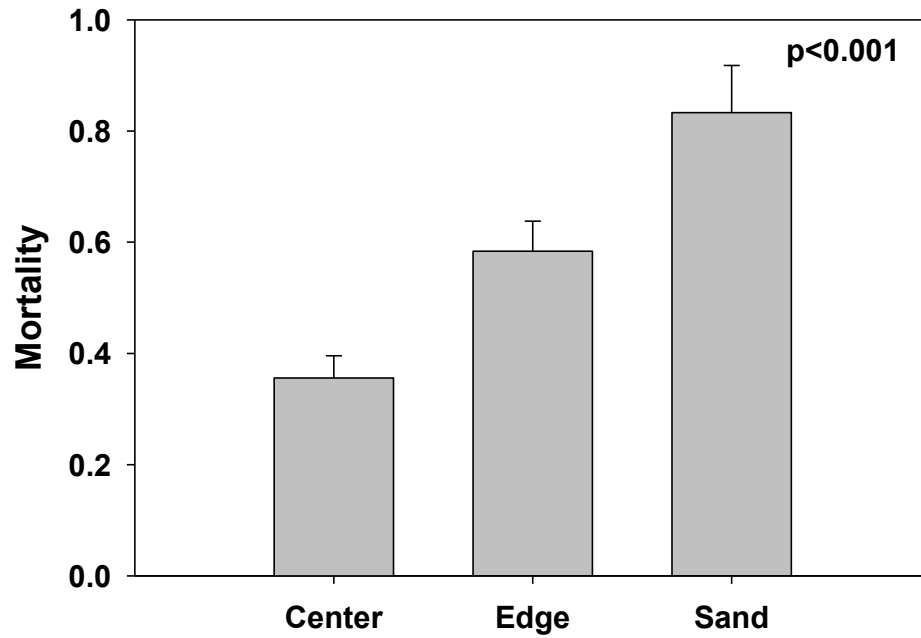


Figure 3: Mean mortality in both August and October of 2008 of scallops tethered across seagrass patch locations. Error bars represent standard error.

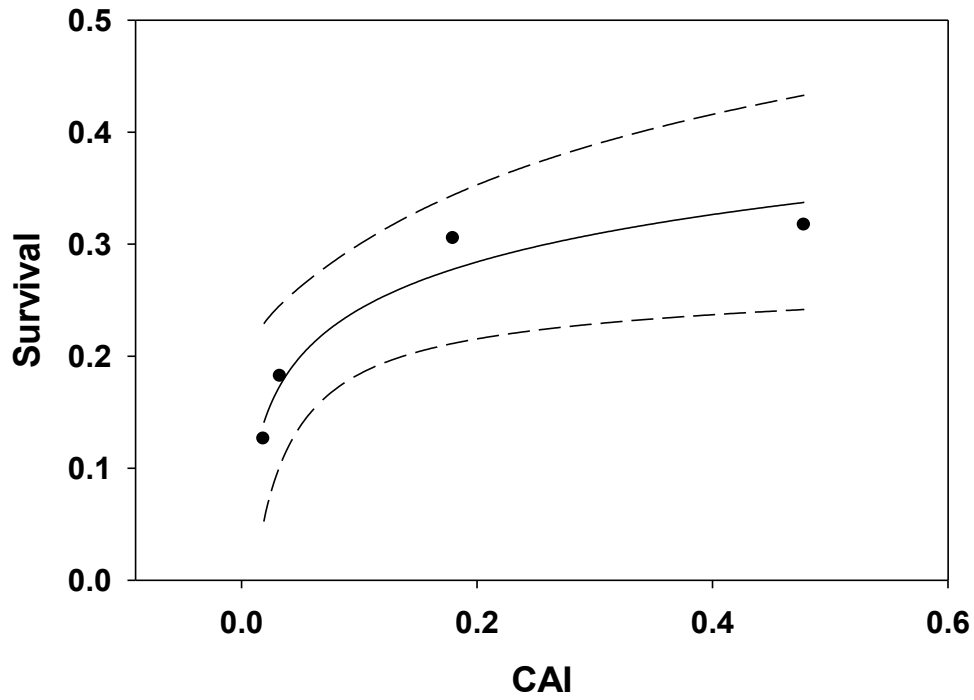


Figure 4: Survival as a function of core area index (CAI) illustrating a non-linear relationship with increasing patch interior habitat. Solid line is the line of best fit ($y=0.061 \cdot \ln(x) + 0.382$, $r^2=0.919$, $p=0.026$). Dashed lines represent 95% confidence intervals.

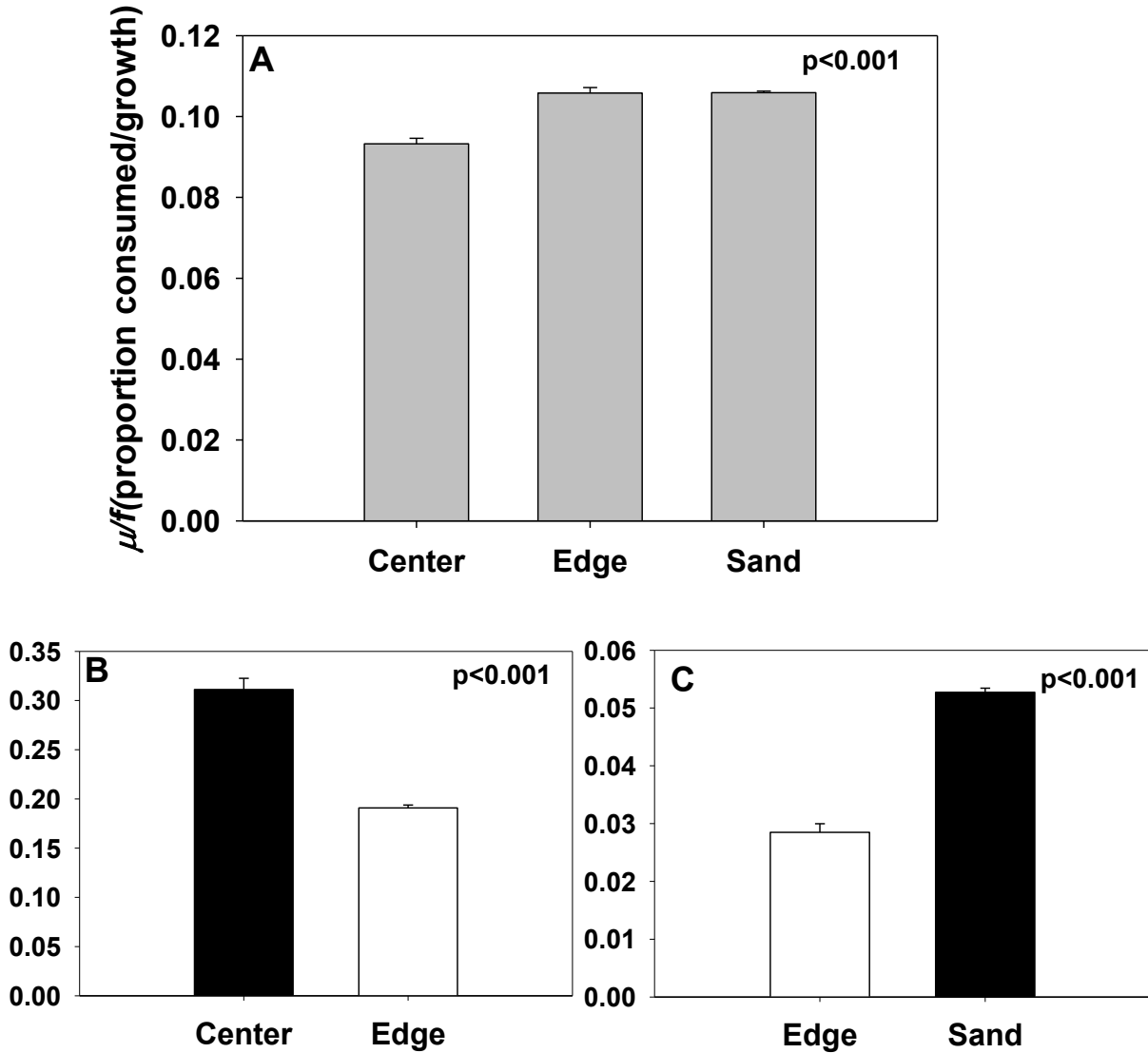


Figure 5: Mean μ/f (mortality rate/growth rate) of scallops placed in each seagrass patch location (A). Error bars represent standard error. μ/f values are corrected for different metabolic costs of associating with seagrass, $\mu/(f+k)$, where k is the difference in growth between sand and each seagrass habitat (B), and corrected for nonzero refuge mortality, $(\mu-c)/f$, where c is the mortality in the patch centers (C). All values are calculated from a randomization procedure by generating 2000 random permutations from field measurements of mortality and growth rates within each habitat.

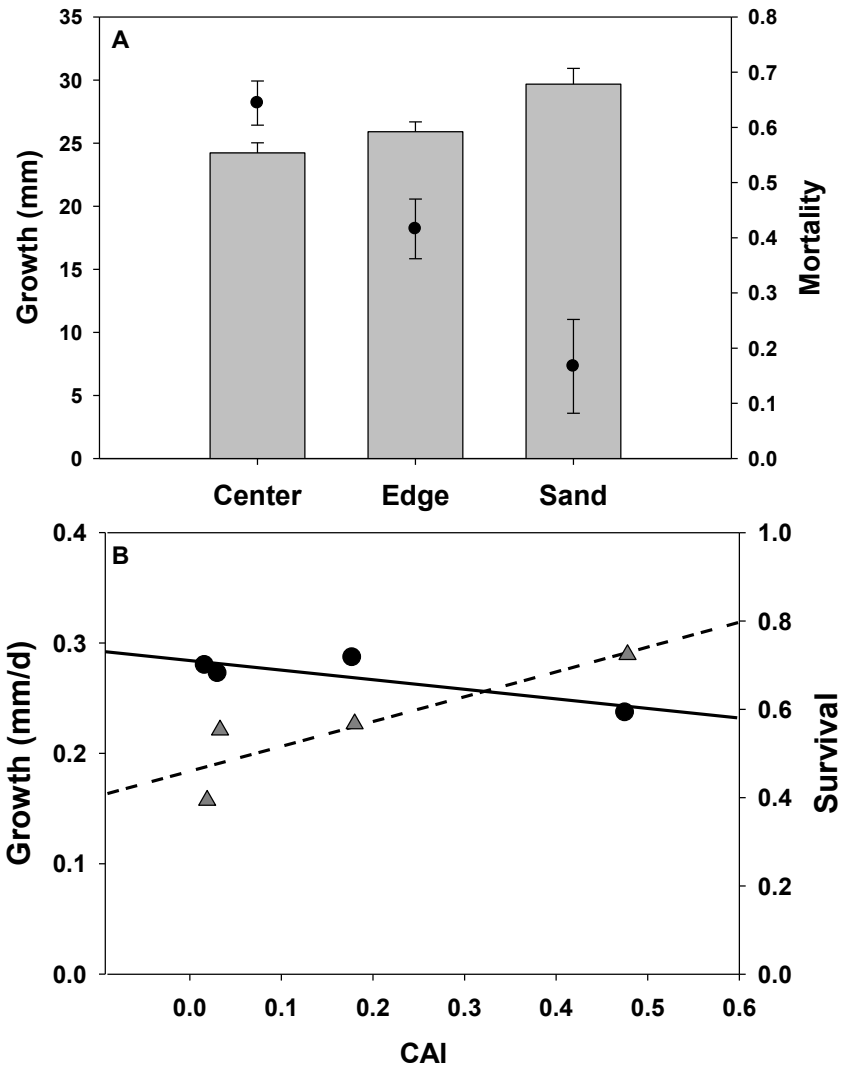


Figure 6: Mean growth (mm) (gray bars) and survival (scatter points) of scallops in 2008 in the different locations, showing the growth-risk trade-off (A). Error bars represent standard error. (B) The relationship between growth rate (mm/d, black circles, solid line, $Growth = 23.87 - (7.29 \times CAI, r^2 = 0.542, p = 0.167)$) and survival (gray triangles, dashed line, $Survival = 0.46 + 0.56 \times CAI, r^2 = 0.684, p = 0.111$) with core area index (CAI) for scallops in patch centers across all years.

Table 1: Table of two-way ANOVA (Mat x Location) results for each measured metric and each year. Mat was the type of ASU (Large Circle, Large Star, Small Circle, Small Star), and Location was either center or edge. CI is the condition index, calculated as the Tissue Dry Weight/ Shell Height (TDW/SW). CI 2 is the condition index calculated using shell weight (TDW/SW).

2007

<i>Growth</i>	DF	SS	MS	F	P
Mat	1	2.667	2.667	0.887	0.353
Location	1	61.794	61.794	20.55	<0.001
Mat x Location	1	10.197	10.197	3.391	0.074
Residual	36	108.253	3.007		
Total	39	183.489	4.705		

CI (TDW/SH)

Mat	1	0.029	0.029	0.91	0.347
Location	1	0.727	0.727	22.828	<0.001
Mat x Location	1	0.0758	0.0758	2.381	0.132
Residual	36	1.146	0.0318		
Total	39	1.985	0.0509		

2008

Growth

Mat	3	207.513	69.171	4.249	0.009
Location	1	70.526	70.526	4.333	0.042
Mat x Location	3	44.1	14.7	0.903	0.446
Residual	52	846.46	16.278		
Total	59	1127.824	19.116		

CI (TDW/SH)

Mat	3	0.188	0.0628	0.37	0.775
Location	1	0.412	0.412	2.432	0.125
Mat x Location	3	0.328	0.109	0.645	0.59
Residual	52	8.81	0.169		
Total	59	9.601	0.163		

CI 2 (TDW/SW)

Mat	3	2.735	0.912	0.395	0.757
Location	1	1.19	1.19	0.516	0.476
Mat x Location	3	5.566	1.855	0.804	0.498
Residual	52	120.061	2.309		
Total	59	129.411	2.193		

SH/SW

Mat	3	7.253	2.418	0.506	0.68
Location	1	7.442	7.442	1.557	0.218
Mat x Location	3	10.474	3.491	0.73	0.539
Residual	52	248.557	4.78		
Total	59	272.352	4.616		

2009

Growth

Mat	3	22.51	7.503	2.705	0.055
Location	1	0.164	0.164	0.059	0.809
Mat x Location	3	9.066	3.022	1.09	0.362
Residual	51	141.459	2.774		
Total	58	174.068	3.001		

CI (TDW/SH)

Mat	3	0.101	0.0337	1.831	0.153
Location	1	0.0593	0.0593	3.22	0.079
Mat x Location	3	0.0124	0.00413	0.225	0.879
Residual	51	0.938	0.0184		
Total	58	1.119	0.0193		

CI 2 (TDW/SW)

Mat	3	5.268	1.756	1.919	0.138
Location	1	0.25	0.25	0.273	0.603
Mat x Location	3	6.018	2.006	2.192	0.1
Residual	51	46.673	0.915		
Total	58	58	1		

SH/SW

Mat	3	28.459	9.486	3.995	0.012
Location	1	9.231	9.231	3.887	0.054
Mat x Location	3	4.459	1.486	0.626	0.602
Residual	51	121.106	2.375		
Total	58	166.528	2.871		

Table 2: Table of one-way ANOVA results for center, edge and sand, using only circle patches. Mat was the type of ASU (LC, LS, SC,SS), and Location was either edge or interior. CI is the condition index, calculated as the Tissue Dry Weight/ Shell Height (TDW/SW). CI 2 is the condition index calculated using shell weight (TDW/SW).

2007					
<i>Growth</i>	DF	SS	MS	F	P
Between Groups	2	100.509	50.254	18.474	<0.001
Residual	19	51.686	2.72		
Total	21	152.195			
<i>CI (TDW/SH)</i>					
Between Groups	2	1.637	0.818	49.238	<0.001
Residual	19	0.316	0.0166		
Total	21	1.953			
2008					
<i>Growth</i>					
Between Groups	2	84.725	42.362	3.491	0.045
Residual	27	327.652	12.135		
Total	29	412.377			
<i>CI (TDW/SH)</i>					
Between Groups	2	0.894	0.447	5.234	0.012
Residual	27	2.305	0.0854		
Total	29	3.199			
<i>CI 2 (TDW/SW)</i>					
Between Groups	2	1.879	0.939	0.789	0.465
Residual	27	32.151	1.191		

Total	29	34.03			
<i>SH/SW</i>					
Between Groups	2	9.383	4.692	2.395	0.11
Residual	27	52.881	1.959		
Total	29	62.264			

2009

Growth

Between Groups	2	7.917	3.958	1.33	0.28
Residual	30	89.268	2.976		
Total	32	97.185			

CI (TDW/SH)

Between Groups	2	0.131	0.0656	6.325	0.005
Residual	30	0.311	0.0104		
Total	32	0.442			

CI 2 (TDW/SW)

Between Groups	2	3.287	1.644	1.629	0.213
Residual	30	30.271	1.009		
Total	32	33.559			

SH/SW

Between Groups	2	20.281	10.141	4.512	0.019
Residual	30	67.426	2.248		
Total	32	87.707			

Table 3: Table of the values for the Kolmogorov-Smirnov tests. N_1 was the number of scallops across all collectors at the center. N_2 was the number of scallops across all collectors at the edge. D_α is the calculated difference between samples for an α of 0.05, and D_{\max} is the absolute value of the maximum difference between the two samples.

Date	N1	N2	Dα	Dmax
7.15.09	70	104	0.209	0.110
8.03.09	226	273	0.122	0.101
8.26.09	24	19	0.417	0.329
7.15.10	151	230	0.142	0.049
8.5.10	559	851	0.074	0.043
8.26.10	57	79	0.236	0.115

Chapter Four

Comparative Survival of Bay Scallops in Eelgrass and the Introduced Alga, *Codium fragile*, in a New York estuary

Abstract

Eelgrass, *Zostera marina*, is generally regarded as the preferred habitat of bay scallops, but in some cases scallop populations have persisted or increased in areas lacking eelgrass. This suggests that some other substrate(s) may serve important ecological functions for bay scallops. One candidate is *Codium fragile*, a macroalgal species with which bay scallops are known to associate and in which we commonly find juvenile and adult bay scallops in eastern Long Island, New York. In this study, we examined whether survival of planted bay scallops differed in *Codium*, eelgrass, and *Codium* + eelgrass substrates at two sites during August and October of two years. Survival of tethered scallops and recoveries of live free-planted individuals varied with scallop size, planting season and year, but no differences were observed between the three substrates for a given scallop size and planting date. Crab (particularly *Dyspanopeus sayi*) and whelk predation were implicated as important causes of tethered scallop mortalities while emigration and removal by predators likely contributed to scallop losses. Densities of naturally recruited 0+ yr scallops recovered by visual and suction dredge sampling were similar in the eelgrass and *Codium* substrates. While our results suggest that *Codium* may offer some degree of predation refuge for bay scallops, further work needs to weigh the potential disadvantages of this substrate (such as low DO levels, potential attachment and transport of scallops, and differences in current flow, food availability and sedimentation relative to eelgrass) to determine if *Codium* may serve as a valuable habitat for bay scallops throughout their lifespan.

Introduction

Populations of bay scallops, *Argopecten irradians* (Lamarck, 1819), have declined dramatically along much of the US Atlantic and Gulf coasts in the last 30 years, even to the point of extinction in some areas (Peterson and Summerson 1992; Tettelbach and Wenczel 1993; Arnold et al. 1998; Marelli et al. 1999; Bologna et al. 2001). Several factors are believed to have contributed to these trends, including recruitment failures associated with brown tide (Tettelbach and Wenczel 1993) and red tide algal blooms (Summerson and Peterson 1990), habitat loss associated with nutrient loading (Serveiss et al. 2004), and potential trophic cascading effects (Myers et al. 2007). Numerous attempts have been made to restore bay scallops in areas where they were formerly abundant; these have met with mixed success (Tettelbach and Wenczel 1993; Wenczel et al. 1994; Peterson et al. 1996; Arnold 2001; Tettelbach and Smith 2009).

Declines in bay scallop populations and their inability to recover to prior levels may be linked to outright disappearance or reduction in density and patch size of eelgrass, *Zostera marina* L, 1753, over much of the historical range of bay scallops (Dennison et al. 1989; Valiela et al. 1992; Pickerell and Schott 2004). Eelgrass is generally regarded as the preferred habitat of bay scallops (Belding 1910; Gutsell 1930; Thayer and Stuart 1974). It is a favored substrate for larval scallop attachment (Eckman 1987) and juvenile scallops that byssally attach in the eelgrass canopy may attain spatial refuge from some predators (Pohle et al. 1991; Ambrose and Irlandi 1992; Garcia-Esquivel and Bricelj 1993; Streib et al. 1995). Bay scallop survival is poorer on unvegetated versus vegetated substrates (Prescott 1990) and changes in eelgrass patch size, configuration and density can have deleterious impacts on bay scallop survival (Irlandi et al. 1995; 1999).

In some cases, bay scallop populations have increased following declines in eelgrass coverage (Marshall 1947) or have remained abundant even when eelgrass is absent. For example, Flanders Bay, at the western end of the Peconic Bays, Long Island, New York, USA, supported one of the three most important commercial bay scallop fisheries in New York through the 1970's and early 1980's (NYSDEC 2008) despite a complete absence of eelgrass (Cashin Associates 1996). In this case, it is logical to suggest that some other substrate may serve a comparable ecological function as eelgrass for bay scallops, as Marshall (1960) first noted in the Niantic River, Connecticut, where an unidentified branching alga had such a dense set of scallops that fishermen referred to it as "scallop weed".

Macroalgae such as *Ulva*, *Gracilaria*, *Aghardhiella*, *Chondrus*, and *Codium* are known to serve as substrates to which juvenile bay scallops attach (Kelley 1981; Tettelbach 1991) and Tettelbach (1986) found equal or significantly higher densities of juvenile and adult bay scallops in macroalgal substrates compared to eelgrass; however, it is unknown whether these macroalgae provide spatial refuge from predation comparable to that offered by eelgrass. The upright, branching macroalga, *Codium fragile* spp. *tomentosoides* (van Goor) P.C. Silva 1955, introduced to the Peconic Bay system in the late 1950's (Carlton and Scanlon 1985), is of particular interest because it is a dominant, canopy forming algal species that now occupies substrates where *Zostera marina* was formerly found (Cashin and Associates 1996). In surveys of scallop populations in the Peconic Bays from 2005-2008 we have consistently found juvenile and adult bay scallops at 12 different sites where *C. fragile* is the dominant vegetation (S. Tettelbach, unpubl. data). Similar observations have been made in other regional estuaries (M. Chintala, pers comm. USEPA, Atlantic Ecology Division, Narragansett, RI). *C. fragile* also has been documented as suitable habitat for other species. Schmidt and Scheibling (2007) found similar or

higher diversity and abundance of native benthic fauna (e.g. gastropods, crustaceans) in *Codium* compared to other substrates while Bulleri et al. (2006) observed enhanced recruitment and survival of native mussels, *Mytilus galloprovincialis* (Lamarck, 1819), in *Codium*, relative to unvegetated habitats.

The purpose of the present study was to examine survival of northern bay scallops, *Argopecten irradians irradians* (Lamarck, 1819), in different vegetated substrates in the field. Specifically, we compared scallop survival in *Codium fragile*, hereafter referred to as *Codium*, relative to *Zostera marina*, hereafter referred to as eelgrass, and a combined treatment of eelgrass and *Codium*, hereafter referred to as mixed, during four different timepoints over two years.

Materials and Methods

Study Site Characterization

Three different habitat types within the same embayment were chosen for our field experiments: eelgrass only, *Codium* only, and mixed eelgrass + *Codium*. In 2006, eelgrass and *Codium* substrates were located within an eelgrass meadow off Barcelona Neck, East Hampton, NY (N 41°00.797' W 72°15.555') (Fig. 1). Eelgrass did not reappear at this site in 2007; therefore, we chose to work in the nearest eelgrass meadow - located ~1.7 km to the west in Sag Harbor, New York (N 41°01.108' W 72°16.913') (Fig. 1). The mean water depth at both sites in both years was ~2m MLW.

Vegetation was dominated by the target species – eelgrass and *Codium* but some drift macroalgae, such as *Spyridia* sp., were also present. Sediments at both sites were dominated by low organic (<0.4%) medium and fine sands. Because of the inherent differences in the structure of eelgrass and *Codium*, we quantified the nature of the two substrates in as much detail as possible. For eelgrass, we measured shoot densities, wet weight biomass, canopy height, and

percent cover, while for *Codium* we quantified percent cover, wet weight biomass and canopy height . The observed eelgrass densities were representative of those seen in Peconic Bay eelgrass meadows (Cashin and Associates 1996) while the bottom cover of *Codium* which we used in this study, usually between 80-100%, was representative of one endpoint for *Codium* substrates in which we find natural populations of bay scallops.

Experimental Design

Scallop survival in the eelgrass and *Codium* substrates was determined via two approaches: (1) releases of scallops directly to the bottom (free planting) and (2) tethering. The experimental design considered 3 factors: vegetation type (3 levels), time (2 levels), and scallop size (2 levels in year 1, 1 level in year 2). For each combination of the factorial design, we employed 4 replicate free-plantings of 25 scallops each, and 10 tethers. Thus, for each scallop size group on each date, a total of 300 ($n=3$ substrates \times 4 replicates \times 25) scallops were free-planted while a total of 30 tethered scallops ($n=3$ substrates \times 10) were deployed. Experiments were conducted in both summer and fall in order to examine how survival rates might vary in response to potential temporal changes in submerged aquatic vegetation (SAV) characteristics or different assemblages of predatory species (Tettelbach 1986); the dates of scallop deployment were 22-29 August and 20-27 October 2006 and 23-30 August and 19-26 October 2007.

Two size classes of scallops were selected for experiments on the basis of their relative susceptibility to crustacean predators, with “small” (14-21 mm shell height) and “large” (49-64 mm shell height) sizes being above and below the size of ~40 mm shell height at which bay scallops reach a size refuge from most species/sizes of crabs found in northeast United States estuarine waters (Tettelbach 1986). In 2006, both small and large scallops were used for experiments, but in 2007 only the smaller size class was available.

Field and Laboratory Methods

Scallops were obtained from the Town of East Hampton, NY shellfish hatchery and marked in the laboratory prior to field deployment. After removing fouling organisms, a small plastic Dymo® label was attached to each shell with super glue; each replicate group was marked with a unique number or letter. For tethering experiments, scallop tags were glued over one end of a 25 cm piece of clear monofilament line while the other end of the line was tied to a 25 cm long piece of bent galvanized steel wire marked with flagging tape. Tags used for small and large scallops, respectively, represented additional mean wet weights of up to 4.3 % and 0.2 %. Control groups of 25 small and large tagged scallops were kept in running seawater tables at the Suffolk County Marine Environmental Learning Center in Southold, New York for the respective 1-week field experimental periods in order to monitor mortality possibly associated with tagging and/or tethering. In all study periods there was 100% tag retention and survival of control scallops.

Prior to field deployments, four replicate 1m diameter release circles for each of the three substrates were chosen and marked using nylon line and flagging tape and anchored in place with curved rebar stakes. Release circles were located ≥ 2 m apart. On the dates when field experiments began, tethered scallops were staked into the bottom >50 cm apart in each of the respective substrates and respective groups of scallops were free-planted directly into the release circles.

Seven days after respective deployments, tethered scallops were recovered, then free-planted individuals were recovered via both visual searches and suction dredging. Visual searches for a given release circle started in the center and continued outside the circle in a concentric fashion for ~10 minutes. Suction dredging was conducted first within the release circle, then within the

perimeter of a 2 m circle encompassing the original release circle, to recover any live scallops, empty shells with intact hinges, and loose tags not found during visual searches, and to collect predators. Efficiency of suction dredge sampling was tested with small and large marked scallops and proved to have 96-100% retention efficiency. Suction dredge samples were placed into separate plastic garbage bags on the boat and refrigerated or frozen within a few hours after returning from the field.

Sample processing in the laboratory was completed within 24 hrs of collection; this entailed counting all live and dead scallops (tethered or free-planted), and assessing damage to shells of dead scallops (e.g. chipping, drill holes) to gain insight into predators (e.g. crabs, drills, whelks) that may have been responsible for mortality (Tettelbach 1986; Prescott 1990). Potential predators of the respective size groups of scallops used in the experiment were either identified and measured immediately or frozen for subsequent analysis; carapace width, shell length, and total length were measured for crabs, gastropods, and fish, respectively. For large scallops, potential predators were considered to include the gastropod mollusks *Busycon*, *Busycotypus*, *Eupleura*, and *Urosalpinx* and crabs of the genera *Callinectes*, *Cancer*, *Carcinus*, *Libinia*, and *Ovalipes*. For small scallops, all of the above genera were considered potential predators, as well as Asian shore crabs (*Hemigrapsus* sp.), hermit crabs (*Pagurus pollicaris* (Say, 1817)), and mud crabs (*Dyspanopeus sayi* (S.I Smith, 1869)) with carapace widths ≥ 12 mm. The characterization of the above gastropods as potential predators is based on the accounts of Belding (1910), Gutsell (1930), and our personal observations. For crabs, considerations were based on laboratory predation rates derived for all of the above crab species (except *Hemigrapsus*) feeding on various sizes of bay scallops (Tettelbach 1986), as well as predation rates derived for *D. sayi* feeding on bay scallops in the field and the laboratory (Streib et al. 1995).

Statistical analysis

For free-planted scallops, missing individuals could not be assumed to be dead because the propensity of bay scallop movement is well documented (Belding 1910; Moore and Marshall 1967; Tettelbach 1986). Therefore, analyses focused on the percentage of live scallops recovered from the initial number released in each circle. Data were also analyzed separately using a one-way ANOVA to test for differences between habitat type, and a two-way ANOVA to test for differences between substrate type and time. When a significant effect of the response variable occurred, a multiple comparisons test (Tukey's Studentized Range Test) was used to determine statistically significant differences between treatments. Prior to ANOVA analysis, data was arcsine transformed to meet assumption of equal variance and normality. For tethered scallops, survival was calculated directly from counts of live animals; missing scallops were considered to be dead as there was no incidental tag loss seen in control groups. Tethering data (presence/absence) were analyzed using the Pearson Chi-Squared test (3x2 contingency table) and Fisher's Exact test (2x2 contingency table) where appropriate to determine statistically significant differences between substrate and month. Results were considered significantly different if $p < 0.05$.

Results

Study Site Characterization

Zostera shoot densities at Barcelona (2006) and Sag Harbor (2007) were similar in August ($p=0.448$) and October ($p=0.119$), but because shoot lengths were greater at Sag Harbor than at Barcelona average wet weight biomass differed at the two sites (Table 1). At both sites, respective shoot densities decreased significantly ($p \leq 0.001$ for both years), as did other metrics, from August to October in both years (Table 1).

Codium substrates consistently had the highest wet weight biomass ($p \leq 0.004$; Table 1); but, as with eelgrass, characteristics of *Codium* varied between sites and seasons. Wet weight biomass of *Codium* only substrates was significantly higher ($p < 0.001$) at Sag Harbor in August 2007 than at Barcelona in August 2006, but were not statistically different ($p = 1.00$) in October of the two years. At Sag Harbor, wet weight biomass of *Codium* substrates significantly declined from August to October ($p = 0.008$); this pattern was not observed at Barcelona ($p = 0.552$). Similar patterns were observed in the mixed substrate (Table 1). Median water temperatures were comparable ($p = 0.08$) for the August study periods during the two years: 23.3°C and 22.8°C , respectively for 2006 and 2007; however, median water temperature in late October 2006 (13.0°C) was significantly cooler ($p < 0.001$) than in late October 2007 (17.9°C).

Free planted scallops

Rates and patterns of live scallop recovery differed depending on scallop size and season, but were statistically the same in the eelgrass, mixed, and *Codium* only substrates for a given scallop size group and date. In August 2006, percent recovery of large live scallops ($83.7 \pm 3.6\%$) was significantly higher ($p < 0.001$) than for small scallops ($25.7 \pm 3.3\%$) (Fig. 2); percent recoveries of live large and small scallops did not vary between substrates in August ($p = 0.972$ and 0.764 , respectively) (Fig 2). In October 2006, percent recovery of live scallops was significantly lower than in August 2006, for both large ($12.0 \pm 6.2\%$, $p < 0.001$) and small scallops ($6.2 \pm 2.7\%$, $p < 0.001$). However, there was no significant difference ($p = 0.387$) in percent live recoveries of the two size classes in October and there were no differences between substrates for either large ($p = 0.770$) or small scallops ($p = 0.238$; Fig. 2).

Additional recoveries of live scallops which had been counted as missing from the August 2006 releases were made in October 2006: one large scallop from mixed, and three small

scallops (one from eelgrass and two from mixed). These additions did not alter the conclusions of the statistical analyses.

In 2007, when only small juvenile scallops were used, the patterns of seasonal recovery of live scallops were opposite to those seen in 2006, i.e. live recovery in August ($3.3 \pm 1.4\%$) was significantly lower ($p=0.002$) than in October ($21.3 \pm 4.6\%$). There were no significant differences in recovery of live scallops between substrates for either August ($p=0.953$) or October 2007 ($p=0.793$) (Fig. 2). No missing tagged scallops from the August experiments were recovered in October 2007.

Tethered scallops

Survival of tethered scallops (Fig. 3) differed depending on scallop size, substrate, and season. Large scallop survival in 2006 was generally higher than that of small scallops for both seasons. In August 2006, large scallop survival ranged from 30-90% and varied significantly ($p=0.02$) between substrates, with the highest survival in *Codium*. In October 2006, overall large scallop survival was lower (0-80%) and differed significantly ($p=0.001$) between substrates, with 0% survival in the mixed. Small scallop survival in August 2006 (50-60%) was higher than in October 2006 (10-30%; $p=0.016$; Fig. 3), but there were no respective differences ($p=0.875$ for August; $p=0.605$ for October) in survival in the three substrates for either month. In 2007, survival of small, tethered scallops in August was very low (0-10%; Fig. 3) and did not differ between habitats ($p=0.355$). Survival of tethered small scallops in October (10-60%) was higher than in August 2007 (0-10%; $p=0.002$); October survival was marginally different between substrates ($p=0.054$) with survival enhanced in mixed (50%) and *Codium* (60%) substrates relative to eelgrass only (10%).

Damage to shells of dead scallops that remained attached to tethers was used to determine the responsible predators. Scallop mortality was assumed if scallops were recovered as empty shells (with or without damage), as tags only (shells gone) and as tags and shells missing completely. Missing shells comprised a majority of the dead small scallops in both 2006 and 2007. Shells of dead large scallops were generally recovered (Table 2).

Potential Predators

Predators recovered from suction dredge samples were mostly crabs, with mud crabs *Dyspanopeus sayi* clearly the most abundant (Fig. 4). Other species of potential predators, recovered at much lower numbers, included six crabs, four gastropods, and one fish, *Tautoga onitis* (Linnaeus, 1758) (Fig. 4). Three rock crabs, *Cancer irroratus* Say 1817, were also sighted at Barcelona in October 2006 while small schools (≤ 15) of scup, *Stenotomus chrysops* (Linnaeus, 1766), from ~ 6-25 cm TL, were observed unsuccessfully attempting to prey on small scallops during both years. *Busycotypus canaliculatum* (Linnaeus, 1758) and *Libinia* spp. were directly observed preying on large marked scallops in the field after scallops were planted in October 2006.

Predator abundance varied significantly between habitats, timepoints and years. While the highest mean densities of predators of small scallops retained in suction dredge samples were noted in eelgrass only ($3.34 \pm 0.83 \text{ m}^{-2}$) and *Codium* substrates ($3.18 \pm 2.09 \text{ m}^{-2}$) there were no statistical differences in numbers of predators between substrates for either juvenile or adult scallop release circles in August 2006 (Fig. 5). In October 2006, numbers of potential predators of small scallops varied significantly between vegetative substrates ($p=0.024$), with *Codium* ($5.26 \pm 1.09 \text{ m}^{-2}$) and mixed ($5.31 \pm 0.56 \text{ m}^{-2}$) having higher numbers of predators than eelgrass ($1.43 \pm 0.83 \text{ m}^{-2}$; $p=0.015$, $p=0.02$, respectively).

In August 2007, densities of sampled predators did not differ between substrates ($p=0.373$); in October 2007, predator densities were highest in *Codium* ($3.98 \pm 2.08 \text{ m}^{-2}$; Fig. 5) but there were no statistical differences between the three vegetative substrates ($p=0.230$).

Natural recruits

In addition to tagged individuals, a total of 75 naturally recruited, juvenile (0+ yr) scallops were recovered during visual/suction dredge surveys from 2-m diameter circles centered around the free-plant release sites during the 2006 and 2007 sampling periods (Fig. 6). In August 2006, a total of 14 natural recruits were recovered from the three substrates, while only three seed scallops were found in October 2006. In 2007, more than double the number of naturally recruited scallops were observed (August 2007: $n=24$; October 2007: $n=34$; Fig. 6). The highest densities of natural recruits were consistently found in eelgrass, but these were not statistically different from the *Codium* and mixed vegetative substrates.

Discussion

Our study has demonstrated that patterns of bay scallop survival and recovery in eelgrass, *Codium*, and mixed substrates were similar for scallops of a given size in different areas, times and years – even though the basic nature of eelgrass and *Codium* is different. Numerous studies have attempted to quantify habitats of varying structural complexity. Bulleri et al. (2005, 2006) and Schmidt and Scheibling (2007) examined the potential effects of *Codium fragile* on benthic invertebrates and characterized *Codium* habitats on the basis of plant density, plant wet weight, thallus length and circumference, and canopy cover. Powers et al (2007) examined the habitat value of submerged vegetation versus the community of fouling organisms on aquaculture cages and compared the two substrates on the basis of biomass. Similarly, Kraufvelin and Salovius (2004) compared structurally different macroalgal habitats by obtaining biomass and

standardizing over a unit of bottom area. None of the above metrics can exactly compare the structure of eelgrass and *Codium*, or other macroalgae, but as in these other studies, we have attempted to characterize these substrates extensively and we chose eelgrass and *Codium* substrates that were representative of benthic habitats in eastern Long Island where we commonly encounter bay scallops. While we can't infer that scallop survival and recovery will be the same in other eelgrass and *Codium* substrates with different physical characteristics, or in other areas, the similar survival of bay scallops in the three substrate types used in this study suggests that *Codium* may provide a predation refuge comparable to eelgrass for juvenile and adult scallops even though *Codium* had equal or greater predator densities than eelgrass.

Percent live recoveries (83-85%) of large free-planted scallops in the three different substrates at Barcelona, 1 week after planting in August 2006, were similar to those (69-78%) documented by Tettelbach (1986) for 1 week releases of comparable sizes of scallops in sparse eelgrass, during August, September and October 1984. Percent live recoveries (6-17%) of large free-planted scallops in October 2006, however, were much lower than expected. This difference was likely due to disturbance of the Barcelona site by a 46-65 km hr⁻¹ gale which blew through the area a few hours after scallops were planted on 20 October (Weather Underground 2006) – as evidenced by burial of some release circles by up to 3 cm of sand. The low recoveries of free-planted scallops and lower survival of tethered scallops in October 2006 thus probably reflect transport and/or burial of scallops (Tettelbach et al. 1990) in addition to predation.

Live percent recoveries of free-planted small juvenile scallops in the present study were low (average = 3-30%), particularly in August 2007 (average = 3-5%), but were comparable to those reported in the literature. Tettelbach (1986) determined that predation rates on 8 and 25 mm scallops in Connecticut eelgrass beds after 1 week releases in August and September were 70%

and 47%, respectively. Bishop et al. (2005) suggested that summer predation rates on small (10.1-17.0mm) and medium (17.1-24.0mm) scallop recruits in North Carolina was greater than 80% at 13 days after release. Darcy & Eggleston (2005) documented losses of ~60% for scallops ≥ 30 mm, 4 days after release, in artificial seagrass patches deployed in North Carolina.

While we can't be certain of the fate of missing free-planted scallops in our study, evaluation of survival rates of tethered scallops and damage to shells of dead scallops permit inferences on the extent of mortality of free-planted scallops due to predation (Peterson et al. 2001). In the present study, higher overall live recoveries of large free-planted scallops (80-85%) compared to survival of groups of tethered scallops (30, 60, 90%) in August 2006 suggests that large tethered scallops were more heavily predated. Four of 11 (~36 %) dead large tethered shells showed evidence of crab predation while ~64 % showed no shell damage at all. The latter is likely indicative of whelk predation (Tettelbach, 1986; Prescott, 1990) since no sea stars were present in the area. Direct contact by gastropod predators cues bay scallop swimming behavior and thus potential escape (Ordzie and Garofalo 1980; Peterson et al. 1982; Winter and Hamilton 1985) so the inability of large tethered scallops to evade important predators such as whelks (Belding 1910; Gutsell 1930; Peterson et al. 1982; Prescott 1990; Powers and Kittinger 2002) may have artificially inflated observed predation rates on large scallops in our study. By contrast, only 4/19 (21%) of dead small tethered scallops lacked shell damage, suggesting that whelk predation on this size class was less important. Crabs were implicated in the mortality of 15/19 (= 79%) of small tethered scallops for which shells (broken or chipped) were recovered. Given the high density of mud crabs, *Dyspanopeus sayi*, that we observed and their known ability to consume bay scallops (Tettelbach 1986; Streib et al. 1995) they probably were the most important predators of small scallops in this study.

Barbeau and Scheibling (1994) demonstrated that tethering sea scallops, *Placopecten magellanicus*, artificially inflated predation rates by sea stars, whose predation success was determined by capture rates, but not crabs, whose predation success was determined by encounter rates. If predation rates by crabs on tethered bay scallops are not inflated, a conclusion also drawn by Bologna and Heck (1999), then lower recovery of live free-planted scallops compared to survival of tethered scallops can be attributed to emigration (Moore and Marshall 1967; Winter and Hamilton 1985; Tettelbach 1986; Hamilton and Koch 1996; Bologna and Heck 1999). This was probably the case for small scallops in all periods during our study except August 2007, when tethered survival and live recovery of free-planted scallops was the same. The high percentages of missing small tethered scallops (where the tethering wire was located, but with no scallop) in the eelgrass (20 missing/40 recovered = 50%), *Codium* (23 missing/38 recovered = 61%), and mixed (21 missing/39 recovered = 54%) substrates suggests that removal by predators was an important process in the present study. Tettelbach (1986) found that shells of scallops predated by crabs were usually found within 1-3 m of circles where scallops were free-planted; i.e. crabs ate their prey where they found them. If crabs had been responsible for removing the missing scallops from their tethers in our study we should have recovered more loose tags (none) or empty shells (two). This suggests that the missing tethered scallops were removed by predators which consumed the small scallops whole – probably finfish (Peterson et al. 2001).

While we have documented similar survival rates of bay scallops in eelgrass and *Codium* substrates in this study, further work is required to determine if the apparent spatial refuge from predation offered by *Codium* is similar to that offered by the eelgrass canopy (Pohle et al. 1991, Ambrose and Irlandi 1992, Garcia-Esquivel and Bricelj 1993, Streib et al. 1995) (Figure 7) and

whether *Codium* is valuable as a habitat for bay scallops throughout their lifespan. Clearly, there are several adverse characteristics of *Codium*, relative to eelgrass, that may make *Codium* detrimental to bay scallops, including the occurrence of low DO levels (Valiela et al. 1997; Tyler 2007). *Codium* may also attach to the shells of living scallops, which in turn may be transported to intertidal areas and die (Malinowski and Ramus 1973; Prescott 1990). Water flow through *Codium* may also be different than through eelgrass and thus may affect food availability, sedimentation rates or predator-prey interactions (Ferner et al. 2009).

Nevertheless, the association of juvenile and adult bay scallops with *Codium* has been documented in Connecticut (Tettelbach 1986, 1991), Rhode Island (M. Chintala, pers. comm.) and Massachusetts (Kelley 1981) and, in this study, we recovered comparable densities of naturally recruited bay scallops from *Codium* and eelgrass in suction dredge samples from Barcelona in 2006 and Sag Harbor in 2007. In addition, we have recorded similar densities (up to 0.7 ind m⁻²) of live, naturally recruited scallops in substrates with 50-80% canopy cover of *Codium* (similar to stands used in this study) at other sites in eastern Long Island, New York during October of 2007 and 2008 (S. Tettelbach, unpubl. data). Furthermore, while eelgrass continues to decline in Long Island estuaries (Pickerell and Schott 2004) we have documented order of magnitude increases in bay scallop populations in 2007 and 2008 due to our recent restoration efforts in a nearby embayment, Orient Harbor (Tettelbach and Smith 2009). These population increases have been seen in areas devoid of and far removed (>3 km) from eelgrass meadows and reinforce the hypothesis that substrates other than eelgrass, including *Codium*, may serve as important habitats for bay scallops. Future work should examine a spectrum of different *Codium* densities and characteristics to determine the relative ecological value of this substrate to bay scallops.

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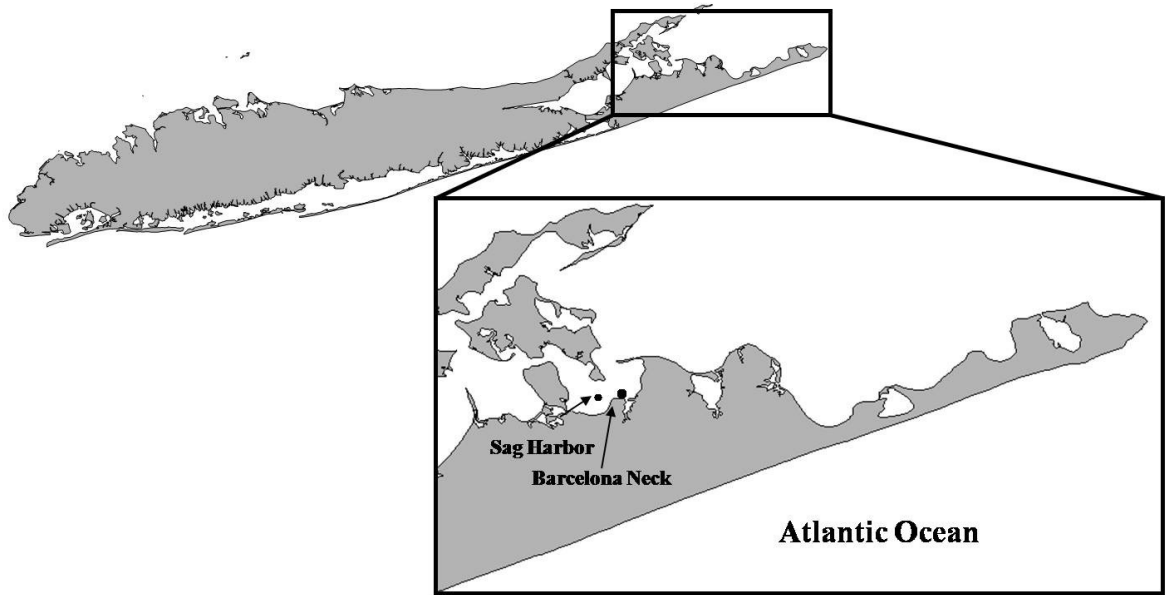


Figure 1: Map of the study sites on Long Island, New York, US. Inset is the study area, showing the location of Barcelona Neck in Northwest Harbor, East Hampton, NY and Sag Harbor, NY, at the eastern end of the Peconic estuary. Circles indicate the study sites, Barcelona Neck was used in year 1, Sag Harbor in year 2.

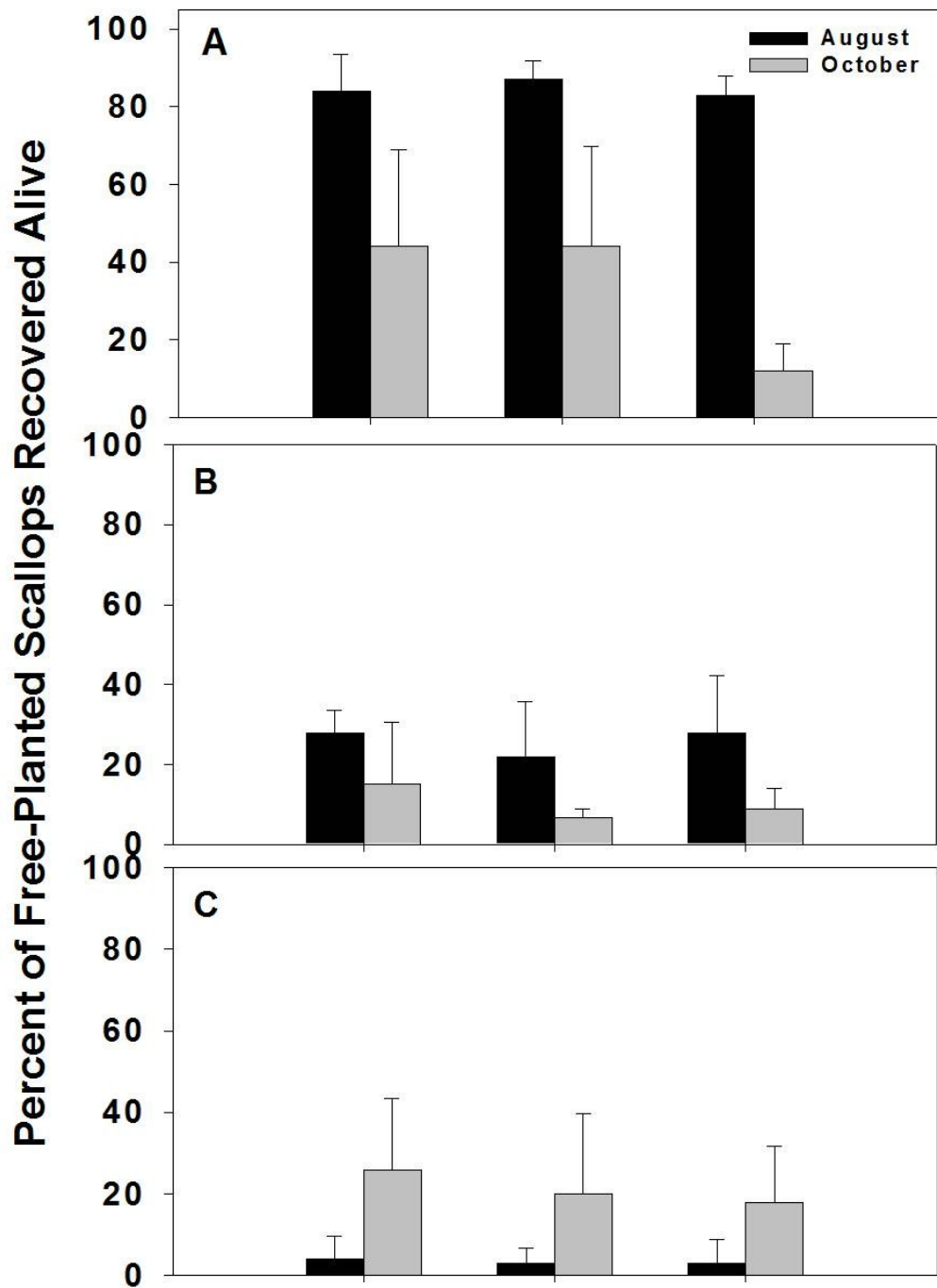


Figure 2: Percent recovery of free-planted tagged after 7 days in the 3 different substrates: eelgrass only, mix – eelgrass + *Codium fragile* combined, and *Codium* - *Codium fragile* only. (A): large (50-64mm) scallops, 2006; (B): small (14-21 mm) scallops, 2006; (C): small (14-21 mm) scallops, 2007. Bars = mean + 1 SE; black bars = August; gray bars = October.

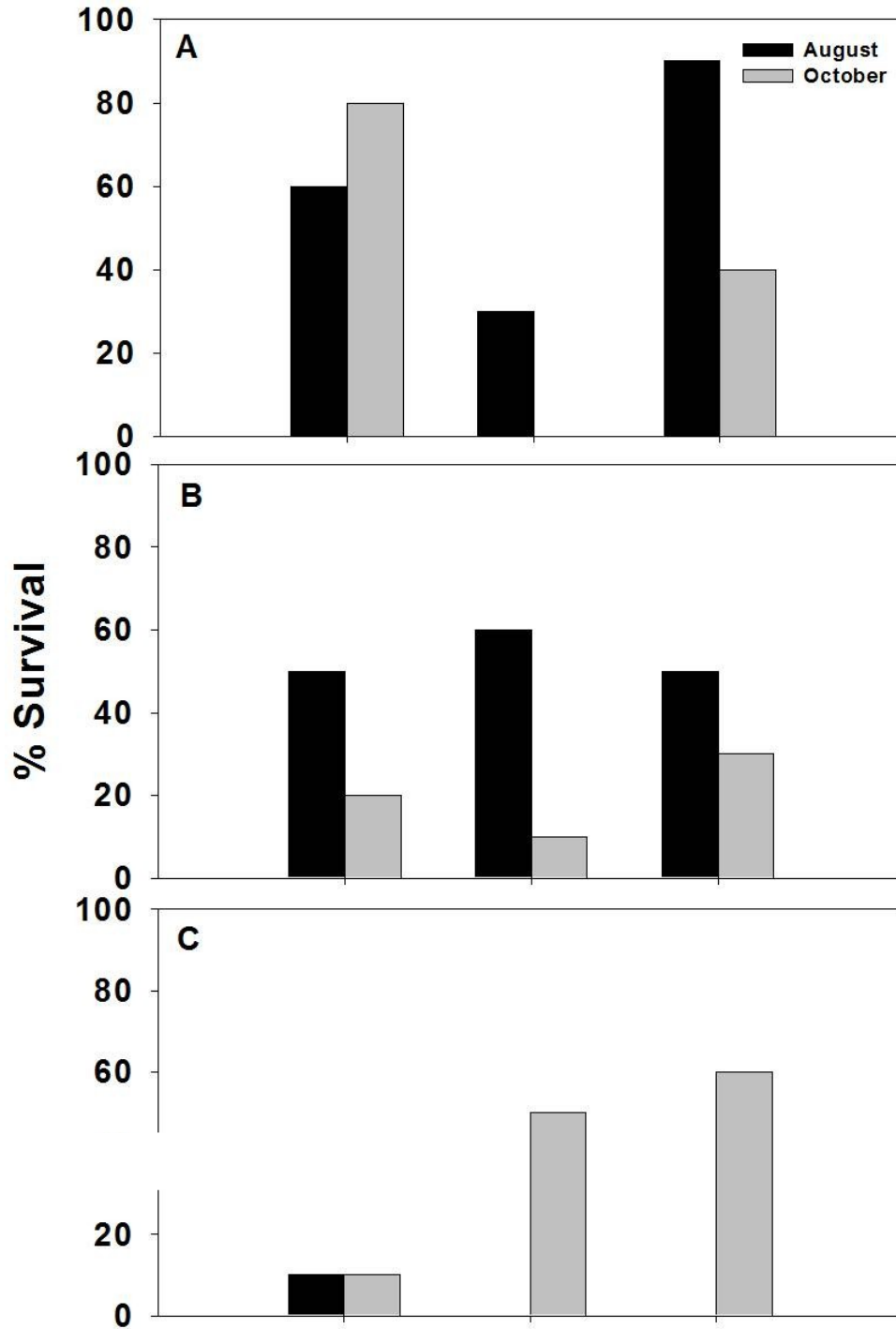


Figure 3: Mean percent survival of tethered scallops in the 3 substrates: eelgrass only, mix – eelgrass + *Codium fragile* combined, and *Codium* - *Codium fragile* only. (A): large (50-64mm) scallops, 2006; (B): small (14-21 mm) scallops, 2006; (C): small (14-21 mm) scallops, 2007. Black bars = August; gray bars = October.

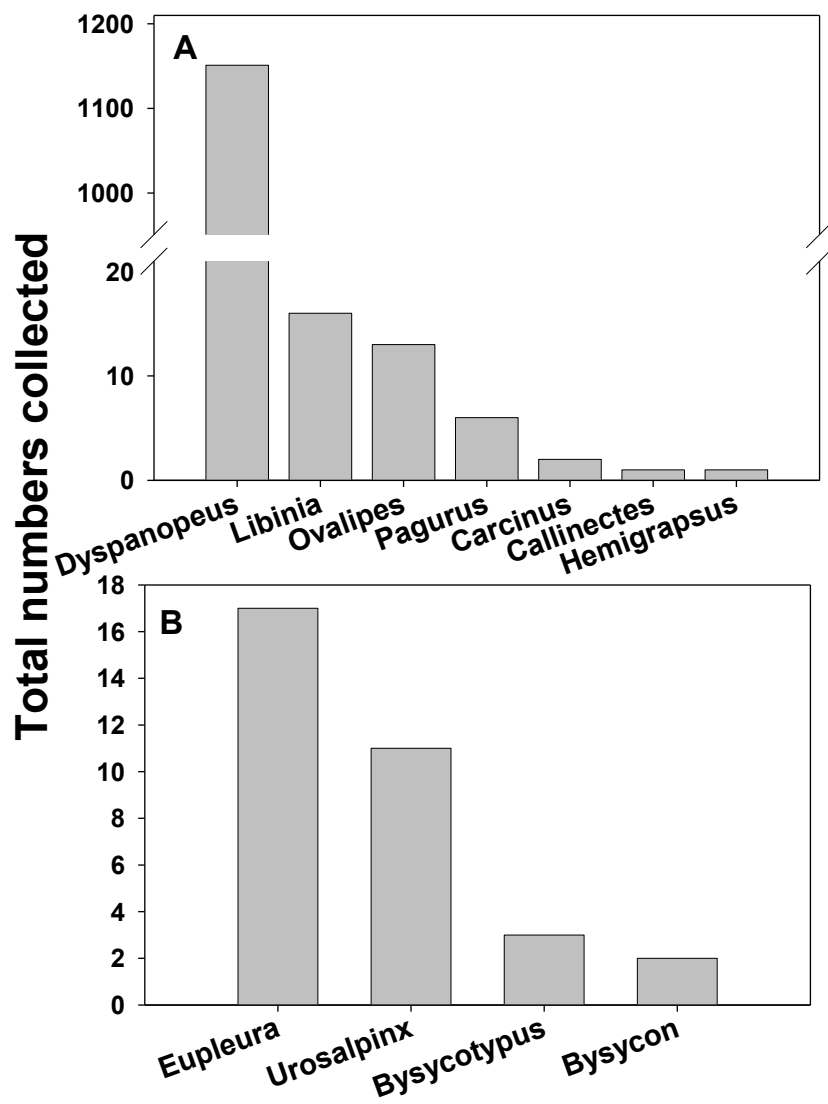


Figure 4: Total numbers of potential predators of small scallops collected via suction dredging. A) Decapod crustacean predators >12mm carapace width. B) Gastropod molluscs.

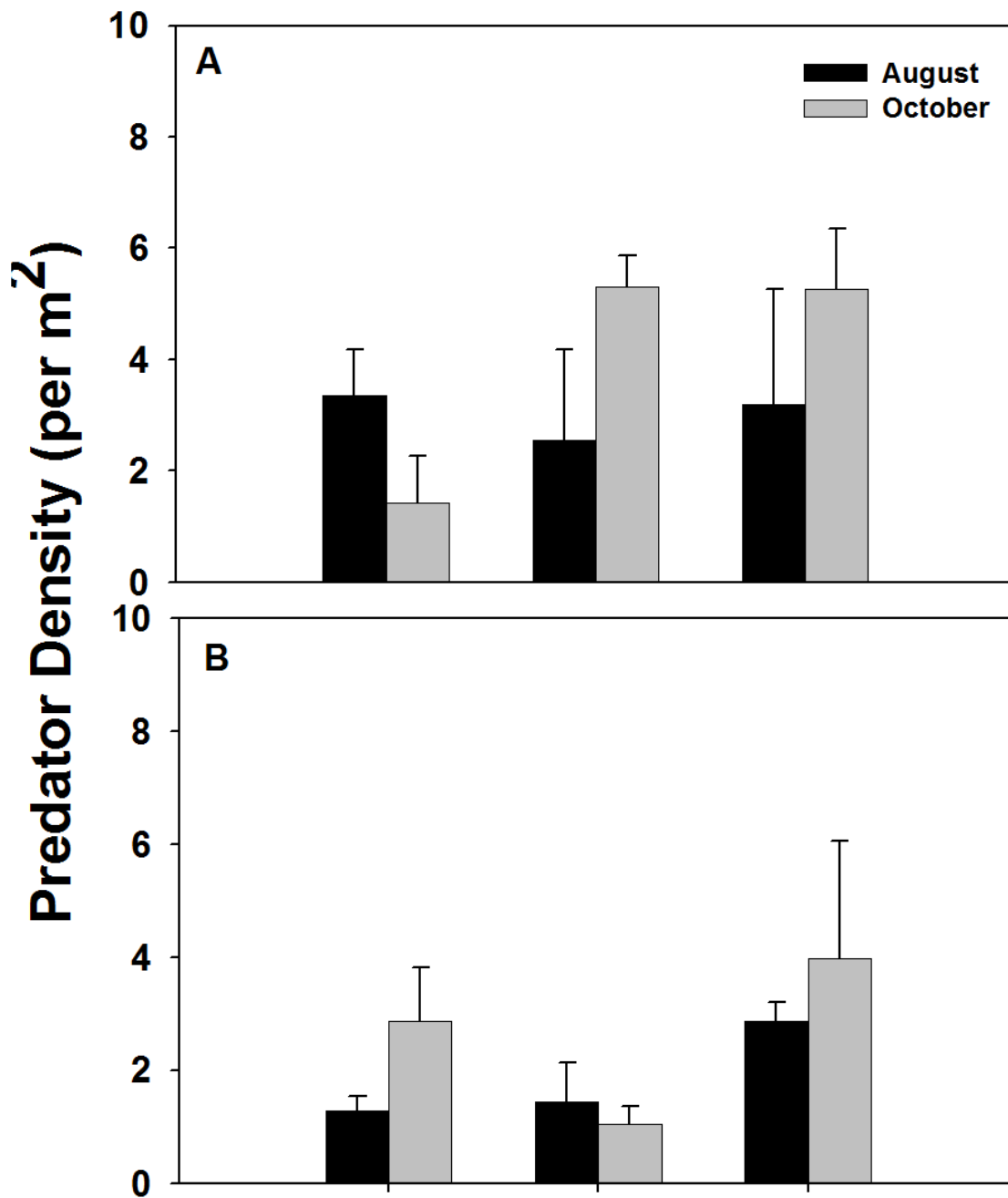


Figure 5: Bay scallop predator density in the 3 substrates: eelgrass only, mix – eelgrass + *Codium fragile* combined, and *Codium* - *Codium fragile* only. (A): 2006; (B): 2007. Bars = mean + 1 SE; black bars = August; gray bars = October.

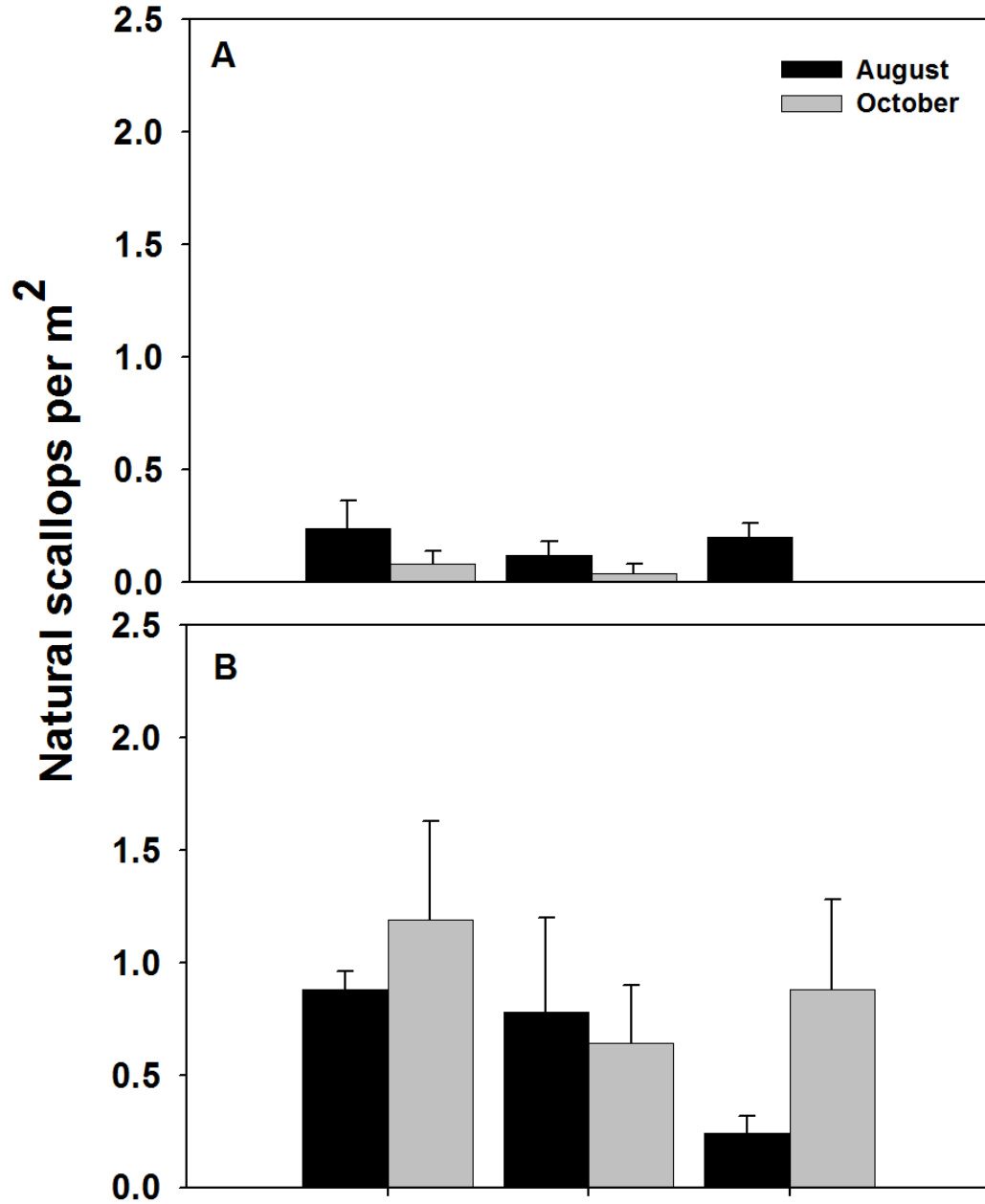


Figure 6: Naturally recruited juvenile (0+ yr) scallops collected in the free-planted circles, at the end of the 1-week experimental periods, within the 3 substrates: eelgrass only, mix – eelgrass + *Codium fragile* combined, and *Codium* - *Codium fragile* only. (A): 2006; (B): 2007. Bars = mean + 1 SE; black bars = August; gray bars = October.

Scallop seed on eelgrass blade



2 scallop seeds on Codium branches

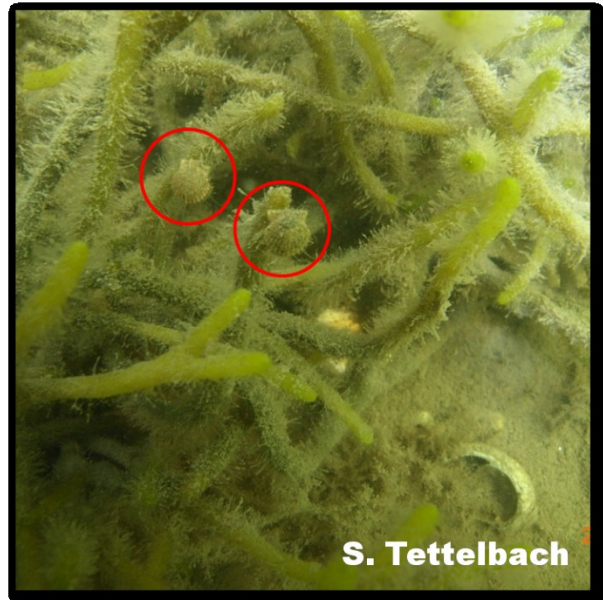


Figure 7: Underwater of photographs of seed scallops attached to eelgrass, *Zostera marina*, and Codium, *Codium fragile*, in the field. Red circles highlight the scallops in the photographs. The scallops were ~8mm.

Table 1. Percent cover, shoot counts, canopy height and wet biomass of the three substrates into which tagged bay scallops were free-planted in late August and late October of 2006 and 2007. Percent cover (mean \pm SE) of SAV's; SC = shoot count density of eelgrass (mean # m⁻² \pm SE); CH = canopy height for the eelgrass or *Codium*; and wet weight biomass (g). Eelgrass and *Codium* substrates were examined at Barcelona Neck in 2006 and at Sag Harbor in 2007.

Substrate	August 2006	October 2006	August 2007	October 2007
Eelgrass only	92.5 \pm 0.9%	62.9 \pm 1.8%	97.8 \pm 1.0%	82.5 \pm 1.4 %
	SC: 330.7 \pm 20.1	SC: 158.5 \pm 40.7	SC: 356.0 \pm 23.5	SC: 181.3 \pm 14.9
	CH: 20cm	CH: 15cm	CH: 37cm	CH: 37cm
	1177 \pm 365g	363 \pm 122g	3799 \pm 802g	2357 \pm 127g
Eelgrass+ <i>Codium</i>	92.5 \pm 0.9%	80.0 \pm 3.8%	92.5 \pm 1.4%	87.5 \pm 4.3%
	SC: 328.0 \pm 25.6	SC: 124.8 \pm 25.6	SC: 268.8 \pm 41.6	SC: 174.4 \pm 20.8
	CH: 20cm	CH: 20cm	CH: 37cm	CH: 30cm
	1240 \pm 185g	2194 \pm 351g	8178 \pm 916g	4009 \pm 930g
<i>Codium</i> only	77.0 \pm 3.9%	82.5 \pm 3.3%	97.5 \pm 1.4%	98.8 \pm 1.3%
	CH: 20cm	CH: 20cm	CH: 30cm	CH: 30cm
	5539 \pm 854g	7554 \pm 1721g	23889 \pm 2814g	7090 \pm 3219g

Table 2. Survival and shell damage results for scallops tethered in eelgrass, *Codium*, and eelgrass + *Codium* substrates at Barcelona (2006) and Sag Harbor (2007) New York. N = 10 tethers for each scallop size group in each substrate on each date. For dead scallops, recovered scallops either had articulated shell valves with no damage or had chipped or cracked shells. Missing scallops = tether recovered with no scallop shell(s) attached. *, ** = 1 or 2 tethers not recovered.

	Eelgrass				Eelgrass+Codium				Codium				
	Live		Dead		Live		Dead		Live		Dead		
	No	Damage	Chip/Crack	Missing	No	Damage	Chip/Crack	Missing	No	Damage	Chip/Crack	Missing	
August 2006	Large	6	1	1	1*	3	4	3	0	9	1	0	0
	Small	5	0	2	3	6	0	2	2	5	0	1	4
October 2006	Large	8	0	0	2	0	1	9	0	4	0	2	3*
	Small	2	0	1	7	1	0	3	5*	3	0	1	6
August 2007	Small	1	0	2	7	0	1	0	9	0	1	2	7
October 2007	Small	1	1	0	6**	5	0	0	5	6	1	0	3

Chapter Five

Can the introduced *Codium fragile* act as an eelgrass surrogate for the native bay scallop, *Argopecten irradians*? Comparisons of fitness between multiple habitats

Abstract:

Biological invasions have accelerated due to anthropogenic activities and are considered one of the greatest threats to biodiversity across the globe. Most studies have focused on the negative impacts of non-indigenous species, however, the impacts of introductions in the marine environment are less understood and more variable. In some instances, it has been suggested that invaders may actually facilitate native species. *Codium fragile* is a notoriously invasive macroalga in marine systems, however, recent studies have suggested that *Codium fragile* may actually enhance abundance of native fauna. While it has been suggested that invasive macroalgae negatively affects growth and condition of associated fauna, prior studies only make comparisons to bare sediments. Since many native species exhibit food-risk trade-offs when associating with native habitats, including the bay scallop, *Argopecten irradians*, comparison of demographic rates for species that use a given habitat type should be made between invasive and native habitats. This study sought to compare long term survival, growth and condition of bay scallops between the native eelgrass, *Zostera marina* and the invasive *Codium fragile*. After 12 week experiments, long term survival was not different between habitats. Further, in 3 of 4 experiments, scallops in both habitats exhibited the same final growth and condition in the two habitats. While scallops in the 4th experiment performed poorly in *Codium* habitats, investigations of a natural set of scallops across the habitat suggests those results may be an experimental artifact due to being in cages under the canopy. While the present results do suggest that there is likely to be site- and species-specific impacts of invaders on local habitat function, this study support the hypothesis that *Codium fragile* may be a suitable habitat for scallops in the absence of eelgrass.

Introduction

Biological invasions, despite being a fundamentally natural process, have accelerated due to human activities and are considered one of the greatest threats to biodiversity on the global scale (Elton 1958; Carlton 1989; Mack et al. 2000). Most invasion studies focus on negative impacts of non-indigenous species. Among these impacts are competition, predation, biodiversity loss, changes in ecosystem processes and disease (Vitousek et al. 1996; Mack et al. 2000; Crooks 2002; Grosholz 2002). However, impacts of introductions in the marine and estuarine environments are less understood and more variable (Grosholz 2002; Williams and Grosholz 2008); furthermore, there is disagreement about the overall impacts of invasive ecosystem engineers (Crooks 2002) to the point that some invaders may act as facilitators for native species (Rodriguez 2006).

A number of invasive plant species seem to enhance settlement/recruitment (Bulleri et al. 2006; Gribben and Wright 2006b; Gribben et al. 2009b), abundance and diversity (Viejo 1999; Rodriguez 2006; Schmidt and Scheibling 2006; Vazquez-Luis et al. 2009; Gestoso et al. 2010; Jones and Thornber 2010), as well as survival (Carroll et al. 2010; Martin and Valentine 2011) of native species. These invasive plant species may be considered ‘ecosystem engineers,’ since the creation of biogenic habitat and the modification of physical resources (structure, water flow, light, particulate matter) are the most common mechanisms leading to such enhancements (Crooks 2002; Rodriguez 2006).

Many native species that are positively affected by an invader associate with naturally vegetated habitats, thus, in areas where native vegetation has been previously lost the invader is providing a limiting resource (i.e. habitat)(Rodriguez 2006; Carroll et al. 2010). Invasive structural engineers therefore represent ‘novel’ habitats in areas devoid of alternative structure,

leading to ecological enhancement. Further, non-indigenous submerged aquatic vegetation (SAV) can be more structurally complex than native species (Schmidt and Scheibling 2006; Martin and Valentine 2011). Since species abundance and diversity are often tightly linked to habitat complexity, the added structural elements can enhance local diversity.

Presently, the literature focuses on the abundance and diversity of native species in association with a non-indigenous macroalgal species (NIMS), overlooking consequences to individual-level fitness (Wright and Gribben 2008), and studies that do examine impacts on survival tend to be short-term (Carroll et al. 2010) and/or laboratory experiments (Martin and Valentine 2011). Long-term studies of an invasive algae on a native bivalve exhibited sublethal impacts on condition and fitness (Gribben and Wright 2006a; Gribben et al. 2009a) that ultimately led to reduced survival (Wright et al. 2007), particularly after episodic environmental perturbation (Wright and Gribben 2008). Few other studies have attempted to quantify the effects of an invasive species on the life-history and fitness of a native species, and while invasive species may have positive short-term impacts on native species, the possibility for negative long-term effects on associated fauna remains (Wright and Gribben 2008).

In many instances, species associated with SAV experience ‘ecological trade-offs’ – when one ecological process is negatively affected while another is positively affected – for living in highly structured habitat. Some species that associate with structurally complex vegetation grow faster in other habitats and utilize the complex SAV habitats because it enhances their survival, leading to a ‘food-risk trade-off,’ where an organism trades growth for survival. This has been observed for many fish (Sogard 1992; Harter and Heck 2006; Grol et al. 2008; Hammerschlag et al. 2010; Grol et al. 2011), as well as bivalve species (Irlandi et al. 1999; Frandsen and Dolmer 2002; Johnson and Heck 2007). However, the few studies that have examined individual fitness

of a native species in association with an invasive engineer have done so only in comparison to unvegetated, unstructured habitats (Gribben and Wright 2006a; Wright and Gribben 2008; Gribben et al. 2009a). This ignores the potential ecological trade-offs of a species within a native complex habitat. Since ecological trade-offs occur between native species in natural, unimpacted habitats, the effects of an invader on individual fitness of a native species should be compared to complex habitats in addition to barren substrates.

The bay scallop, *Argopecten irradians*, represents a useful model organism for investigating the impacts of invasive ecosystem engineers. This species historically supported vibrant fisheries in many US Atlantic and Gulf coast states before population collapses, and many scallop restoration efforts have been attempted throughout their geographic range, from Massachusetts to Florida, with varying degrees of success (Peterson et al. 1996; Goldberg et al. 2000; Arnold et al. 2005; Tettelbach and Smith 2009). Bay scallops exhibit a strong habitat association with seagrass (Belding 1910; Gutsell 1930; Thayer and Stuart 1974) which has recently declined throughout much of the bay scallops' range (Orth et al. 2006). Further, many studies have demonstrated an ecological trade-off (reduced growth but higher survival) with scallops in seagrass, suggesting that these habitats lead to slower growth but higher survival for post-set juveniles, as well as adults (Garcia-Esquivel and Bricelj 1993; Irlandi et al. 1995; Bologna and Heck 1999).

In the northern extent of their range, bay scallops have been observed among the invasive, canopy-forming macroalgae, *Codium fragile* (Kelley 1981; Bricelj et al. 1987; Carroll et al. 2010); a species introduced to the northwest Atlantic from Japan in the mid-1950s (Carlton and Scanlon 1985). Literature suggests *Codium fragile* has had a positive effect on a number of native fauna (Bulleri et al. 2006; Schmidt and Scheibling 2006; Schmidt and Scheibling 2007;

Sauchyn and Scheibling 2009; Jones and Thornber 2010; Drouin et al. 2011) including bay scallops (Carroll et al. 2010). However, long term survival or individual fitness of fauna associated with *Codium fragile* assemblages has not been previously investigated. Since scallop growth is impacted by structural complexity within seagrass meadows (Bologna and Heck 1999), it is possible that the dense, branching canopy formed by *Codium fragile* may also influence scallop growth, condition or reproductive output, as well as life-history traits linked to food quantity/quality (Kirby-Smith 1972; Cahalan et al. 1989; Rheault and Rice 1996).

Since bay scallops are focal species for numerous restoration efforts and have high commercial value, understanding the positive and negative effects of *Codium fragile* on scallop populations, especially in comparison to native habitats, has become increasingly important. The objective of this study was to examine the impacts of the invasive macroalga, *Codium fragile*, on the northern bay scallop, *Argopecten irradians irradians*. Specifically, we compared long term (>11 weeks) survival, growth and condition of juvenile scallops in *C. fragile*, eelgrass, and unvegetated habitats at two sites during two years, with reproductive condition also investigated at one of the sites in one of the years.

Methods

Study Sites

Shinnecock Bay is a small, shallow, lagoon estuary located on the South Shore of Long Island, New York. It is characterized by sandy sediments and, currently, has some of the most extensive eelgrass meadows in New York. Experimental sites for habitat-specific growth were located along the northeastern shore of the bay. ‘Eelgrass’ (41°01.030’N, 072°16.986’W), ‘Sand’ (01.030’N, 16.978’W) and ‘*Codium*’ (01.027’N, 16.994’W) habitats were within 1000m along the same exposed shoreline, and at similar depths (~1 to 1.5m MLW). The eelgrass site was sandy,

with 373 ± 81 shoots per m^2 , and areal cover ranging from 67% to 85%. The sand site contained little vegetative cover (less than 5%), although drift macroalgae was present. The *C. fragile* site had between 58% to 100% percent cover. To sample a wider range of local hydrographical conditions, a second site, Sag Harbor ($41^{\circ}01.108'N$, $072^{\circ}16.913'W$; Figure 1) was chosen. This embayment is deeper (site depth 2-3m MLW), connected to a different watershed, has a different set of fetch distances and experiences stronger tidal currents (see Carroll et al. 2010 for a full site description).

Juvenile growth and condition

Groups of wild-set scallops, collected via spat bags during monitoring for the large scale restoration efforts in the Peconics (see Tettelbach et al. *in review*) were placed within predator exclusion devices (35x17x8 cm) constructed from 8-gauge, coated wire and enclosed in a 1-mm mesh bag. Sets of 10 scallops were marked by gluing numbered white wire tags to the dorsal valve, then measured to the nearest 0.1mm before deployment, and placed into the cages. Five replicate cages were uniquely labeled and placed into each of the three habitats at the two study sites, for a total of 50 scallops per habitat per site. Cages were deployed 12 weeks in 2009 and 11 weeks in 2010. At the end of the development period, cages were retrieved, and all living scallops were identified (if possible) and measured to the nearest 0.1mm. Growth rates were calculated using the following equation:

$$\text{Growth rate} = (\text{Final shell height} - \text{initial shell height}) / \text{number of days deployed} \quad (1)$$

Since shell and tissue growth may be uncoupled for bivalves (Lewis and Cerrato 1997), scallop tissues were then removed into pre-weighed aluminum boats and dried to constant mass at 70C for at least 48 hr. Condition indices were computed using the following 2 methods:

$$CI = (\text{tissue dry weight} / \text{shell height}) \times 100 \quad (\text{Rheault and Rice 1996}) \quad (2)$$

$$CI = (tissue\ dry\ weight/shell\ weight) \times 100 \text{ (Shriver et al. 2002)} \quad (3)$$

Low values indicate that energy reserves have been depleted for maintenance under poor environmental conditions (Martinez and Mettifugo 1998). Additionally, a ratio of shell height to shell weight was computed as a proxy for shell strength, higher values (i.e., longer, lighter shells) denote lower strength.

Since food supply was the hypothesized factor contributing to differential growth in the various habitats, water samples were collected from within vegetated canopies using 60 mL syringes and from near-bottom (~10cm) in un-vegetated habitats using sample bottles by SCUBA divers, with 6 collections per habitat. Syringes were filtered onto replicated GF/F filters and 5 µm polycarbonate filters, frozen, extracted in acetone, and measured for fluorescence with a Turner fluorometer (Parsons et al., 1984). Differential filtration allowed the amount of chlorophyll in the > 5 and < 5 µm size fractions to be determined. Both total chlorophyll a (Chl_a) and size fractionated (<5µm Chl_a) were measured since scallops filter different sizes of phytoplankton with varied efficiency.

Reproductive output

In year 1 of the study, sets of adult scallops were placed into the three habitats in Shinnecock Bay to investigate the impacts of food availability on gonad development (Sastry 1968). Year-old scallops were obtained from hatchery stock and overwintered on long-lines in Orient Harbor as part of a bay scallop restoration effort in New York (Tettelbach and Smith 2009). Sets of six, year-old scallops were placed into the cages described above, and covered with 10mm mesh to prevent access by large predators. Initially, a subset of 30 randomly selected scallops was sacrificed for initial shell heights, condition and gonad indices on 11 June 2009. At subsequent 2-week intervals starting 25 June 2009, for a period of 10 weeks, two cages containing scallops

were removed from each habitat. Scallops were measured for shell height and dissected. Gonads were removed and placed into a set of pre-weighed aluminum boats; the remaining tissues were placed into another set of corresponding tins. Condition indices were computed as described above. The gonad condition index (GI) was computed using the following equation:

$$GI = (\text{gonad dry weight} / \text{total tissue dry weight}) \times 100 \text{ (Barber and Blake 1991)} \quad (4)$$

Scallops were placed into the various habitats in June of 2009 and tracked for 10 weeks through the end of August, encompassing a period of time when gonad development was expected to peak, and spawning was expected to have occurred (Taylor and Capuzzo 1983; Tettelbach and Weinstock 2008).

Natural Set Scallops

In addition to experimental scallops, a total of 10-12 haphazardly placed 0.25-m² quadrats were used at the conclusion of the growth studies to determine densities of natural set and adult scallops in the various habitats in year 2. All seed scallops in the quadrats were collected for processing (Sag Harbor site only). This site was selected because the Peconic Estuary was the site of intense restoration efforts and increased natural populations of scallops (Tettelbach and Smith 2009). Additional scallops were haphazardly selected until a total of 20 seed scallops from each habitat were collected. Shell heights and condition indices were obtained using the methods previously described. Collection occurred in November of 2011, at the conclusion of the growth study, during a period of time when fall surveys of juvenile scallops, which settled during the summer, are monitored for the restoration effort (Tettelbach and Smith 2009).

Statistics

Due to a significant site x habitat interaction while conducting a three-way ANOVA, each site was analyzed using a two-way ANOVA (cages as the replicates) with year and habitat as the

explanatory factors and either survival, growth rate, condition, or shell height/shell weight as the response variables. For reproductive output and chlorophyll *a* data, a series of one-way ANOVAs was run due to a significant date x habitat interaction during analysis using two-way ANOVAs. For natural set scallops, density, size, condition and shell height/ shell weight were the response variables in a series of one-way ANOVA comparing habitats. Where appropriate, group differences were assessed using the Holm-Sidak multiple comparisons test.

Results

Juvenile scallop growth and condition

Differences in scallop survival, growth and condition between habitats varied between sites (site x habitat interaction, $p < 0.001$, $p = 0.008$, $p < 0.001$, respectively) so sites were analyzed separately.

Shinnecock Bay – Survival across all three habitats was significantly higher in 2009 ($92.4 \pm 2.4\%$) than 2010 ($72.2 \pm 2.6\%$, two-way ANOVA, $df = 1$, $F = 32.653$, $p < 0.001$). Scallops survival was also affected by habitat (two-way ANOVA, $df = 2$, $F = 10.329$, $p < 0.001$) across both years; survival in both *Codium fragile* ($91.0 \pm 2.9\%$) and eelgrass ($84.6 \pm 3.0\%$) was higher than survival on sand ($71.3 \pm 3.3\%$, $p < 0.001$ and $p = 0.006$, respectively), but not different from each other ($p = 0.139$). Growth rate did not vary by year (two-way ANOVA, $df = 1$, $F = 1.501$, $p = 0.234$), but did vary by habitat ($df = 2$, $F = 9.146$, $p = 0.001$). Similar to survival, growth in both eelgrass ($0.335 \pm 0.005 \text{ mm d}^{-1}$) and *C. fragile* ($0.331 \pm 0.005 \text{ mm d}^{-1}$) was significantly faster than on sand ($0.306 \pm 0.005 \text{ mm d}^{-1}$; $p < 0.001$ and $p = 0.002$, respectively), but were not different than each other ($p = 0.561$, Figure 2).

Condition index using eq. 2 did not significantly differ between years (two-way ANOVA, $df = 1$, $F = 2.519$, $p = 0.127$) but did significantly vary among habitats ($df = 2$, $F = 19.084$, $p < 0.001$),

although that difference depended on the year (year x habitat interaction, $df=2$, $F=5.226$, $p=0.014$). In 2009, differences in condition among habitats were not significant, while in 2010, scallops on both eelgrass (2.25 ± 0.09) and *C. fragile* (2.09 ± 0.08) were in significantly better condition than those on sand (1.45 ± 0.09 ; $p<0.001$ for both), but were not different from one another ($p=0.199$; see Figure 2). Condition using eq. 3 showed similar patterns, with the significant difference among habitats ($p<0.001$) depended on the year (year x habitat interaction, $p<0.001$). The shell height to shell weight ratio differed by both year (two-way ANOVA, $df=1$, $F=7.793$, $p=0.011$) and habitat ($df=2$, $F=6.327$, $p=0.007$).

Sag Harbor – Survival across all three habitats was significantly higher in 2009 ($92.2 \pm 3.0\%$) than 2010 ($69.8 \pm 3.1\%$, two-way ANOVA, $df=1$, $F=26.945$, $p<0.001$), but not amongst habitats ($df=2$, $F=2.065$, $p=0.152$) although there was a significant year x habitat interaction ($df=2$, $F=6.014$, $p=0.009$). While there was no difference in survival among habitats in 2009 ($p=0.604$), in 2010 survival was higher in both eelgrass ($82.0 \pm 4.9\%$) and on sand ($74.0 \pm 4.9\%$) than in *C. fragile* ($53.3 \pm 6.4\%$, $p=0.002$ and $p=0.018$, respectively), but was not different between eelgrass and sand ($p=0.263$). Growth rate did not vary by year (two-way ANOVA, $df=1$, $F=0.159$, $p=0.694$), but did vary by habitat ($df=2$, $F=3.778$, $p=0.040$). Across both years, growth rates were faster in eelgrass (0.364 ± 0.010 mm d⁻¹) than *C. fragile* (0.324 ± 0.011 mm d⁻¹; $p=0.013$). Growth in sand (0.353 ± 0.011 mm d⁻¹) was not different than either *C. fragile* ($p=0.075$) or eelgrass ($p=0.417$, Figure 3).

Condition index using eq. 2 differed between years (two-way ANOVA, $df=1$, $F=9.450$, $p=0.006$) and among habitats ($df=2$, $F=8.998$, $p=0.002$). Condition was higher in 2010 (1.93 ± 0.09) than 2009 (1.56 ± 0.08). Condition of scallops in both eelgrass (1.94 ± 0.10) and sand (1.92 ± 0.10) was significantly better than those in *C. fragile* (1.37 ± 0.11 ; $p<0.001$ and $p=0.002$,

respectively), but were not different from one another ($p=0.862$; see Figure 3). Condition using eq. 3 was not significantly different between years (two-way ANOVA, $df=1$, $F=1.995$, $p=0.172$), but differed by habitat ($df=2$, $F=16.907$, $p<0.001$), although this difference between habitats was affected by year (year x habitat interaction, $df=2$, $F=4.391$, $p=0.027$). Shell height to shell weight ratio was significantly different between years ($df=1$, $F=6.404$, $p=0.019$), but not among habitats ($df=2$, $F=2.831$, $p=0.082$).

Chlorophyll

Due to significant date x habitat interactions, each date was analyzed at each site using a series of one-way ANOVA. Both total chlorophyll *a* and >5- μm size fractionated Chl *a* were highly variable over time and between habitat treatments with no habitat having consistently greater Chl *a* concentrations (Figure 4, Table 1).

Reproductive output

Scallops significantly increased their shell height over the course of the experiment ($p<0.001$) but this did not differ by habitat ($p=0.106$). Due to a date x habitat interaction ($p=0.040$) for gonad index (GI), a series of one-way ANOVAs was conducted. GI was not significantly different among habitat treatments on 25 June 2009 ($p=0.751$). On 9 July, GI was significantly higher in *Codium fragile* (0.32 ± 0.01) and sand (0.28 ± 0.02) treatments than eelgrass treatments (0.20 ± 0.02 , $p<0.001$ and $p=0.006$, respectively). Scallops in sand had significantly higher GI (0.29 ± 0.02) than both *C. fragile* (0.21 ± 0.02 , $p=0.003$) and eelgrass (0.20 ± 0.01 , $p=0.002$) on 23 July. There were no differences among habitats during collections on either 7 August ($p=0.909$) or 20 August ($p=0.486$; Figure 5).

Natural scallops

In Shinnecock Bay, only one scallop was found and occurred in the *Codium fragile* habitat. In Sag Harbor, scallop abundances were higher in both eelgrass and *C. fragile* than sand, although due to high variability within samples, these differences were not significant ($p=0.178$). Scallop shell height was not different across the three habitats in Sag Harbor ($p=0.380$; Figure 6), nor was either metric of CI ($p=0.669$ for shell height, $p=0.947$ for shell weight). The shell height to weight ratio was also the same between the three habitats ($p=0.433$).

Discussion

Bay scallops exhibited variable responses to *Codium fragile* habitats in comparison to native eelgrass in the 2 years and at the two sites of this study; however, the results generally support the hypothesis that *Codium fragile* may act as a suitable alternative habitat. In a previous study, short-term (7 d) predatory mortality did not differ between eelgrass and *Codium* (Carroll et al. 2010), and in this study, long-term survival across both sites and both years were similar, $85.5 \pm 3.3\%$ in eelgrass and $85.0 \pm 4.1\%$ in *Codium*. The results also suggest a highly complex relationship between native bay scallops and the invasive species.

Codium fragile has historically been considered detrimental to native species (Fralick and Mathieson 1973; Trowbridge 1998), yet more recent studies have shown a net positive influence. Several recent studies have documented the same or enhanced diversity and abundance of organisms in *Codium fragile* habitats relative to other macroalgae (Schmidt and Scheibling 2006; Schmidt and Scheibling 2007), barren substrates (Bulleri et al. 2006), and seagrass (Drouin et al. 2011). Even with the potential negative impacts of *C. fragile* that manifested at Sag Harbor during the 2010 study, high abundances of scallops have been observed associating with *C. fragile* in the Peconic Estuary, NY (this study; Carroll et al. 2010), Nantucket, Massachusetts (Kelley 1981), and Rhose Island (M. Chintala, USEPA, *pers. comm.*) These studies all suggest

that an invasive species, particularly one that creates habitat like *C. fragile*, may have an overall positive impact on native communities of vegetation-associated fauna.

A recent trend in invasive literature suggests non-native ecosystem engineers may not have negative impacts on native species (Rodriguez 2006); however, the majority of studies focus on community-level metrics of abundance and diversity, or survival of individuals, to demonstrate that invasive species can facilitate or enhance native species (Gestoso et al. 2010; Martin and Valentine 2011; Valinoti et al. 2011). Few studies have focused on other individual metrics such as condition (Posey et al, 1993; Wright and Gribben 2008), but those studies that examined individual-level fitness have shown overwhelmingly negative results. The invasive alga *Caulerpa taxifolia* has been shown to negatively impact long term survival, growth and tissue condition of the native, infaunal clam, *Anadara trapezia* (Wright et al. 2007; Wright and Gribben 2008; Gribben et al. 2009a). Results from Shinnecock Bay during this study suggest that for epifaunal bay scallops there might not be long term, negative consequences for associating with an invader. However, the variable results between years at Sag Harbor suggest negative consequences may result on an annual or site-specific basis.

This study sought to compare the impacts of *Codium fragile* on bay scallops with the effects of eelgrass since a number of native species exhibit reduced growth and/or fitness in native, structurally complex habitats compared to barren substrates. Comparisons of these trade-offs to the ‘negative’ effects of invasive habitat formers on native species have been conspicuously absent in the literature. It is possible that conclusions of the few other studies which investigate individual measures of fitness of native species associating with invasive algal habitats may have been different if comparisons were made to native vegetated habitats. Across 2 years at one study site and in 1 of 2 years at the other site, scallop survival, growth and/or condition were not

different between *C. fragile* and eelgrass. Additionally, naturally set scallops in these habitats did not exhibit differences in size or condition. Thus, in order to ascertain whether a true negative effect of a non-indigenous submerged aquatic vegetation (SAV) on individual level fitness metrics exists, studies must start to consider invaders within the context of naturally occurring ecological trade-offs.

There were site-specific responses in demographic rates of scallops between eelgrass and *Codium fragile*. In Shinnecock Bay, scallops displayed high survival, growth and condition in both vegetated habitats relative to scallops placed on bare sand, although they were not different from each other. This is in contrast to the reported literature, as previous studies have established a food-risk trade-off for scallops between sand and seagrass (Ambrose and Irlandi 1992; Irlandi et al. 1995; Bologna and Heck 1999; Chapter 3). It is likely that both SAV served to buffer wind-wave activity in the shallower Shinnecock Bay sites, where partial cage burial was frequently observed at the ‘Sand’ site. This can have implications for scallop populations, as burial has been shown to be a significant source of overwinter mortality in scallops (Tettelbach et al. 1990). Further, reproductive output did not seem to differ in *Codium fragile* and eelgrass habitats, which can have implications for population persistence and growth. Reproduction in scallops has been shown to vary as a function of food availability (Sastry and Blake 1971; Barber and Blake 1983; Bricelj et al. 1987). The lack of variation chl *a*, a proxy for food availability, between the 3 habitats types can be interpreted as the most likely explanation for the observed similarities in reproductive output.

Response variables differed markedly between Sag Harbor and Shinnecock Bay. Both growth rate and condition showed significant consequences for a *Codium fragile* association. Survival showed significant annual differences, although those differences depended on habitat.

Growth rates showed marginally significant differences among habitats across both years, although it has been posited by Irlandi et al. (1999) that statistical difference in growth rates may not be biologically significant. Across both years, scallops in eelgrass attained a mean final shell height of 41.7mm, while those in *C. fragile* attained a final shell height of 38.5mm, suggesting that over the same time period, scallops in both habitats attained a documented size-refuge from most predators of ~31mm (Garcia-Esquivel and Bricelj 1993), suggesting that the statistical differences in growth during this study also might not have been biologically significant.

A number of factors may have contribute to statistical differences in growth rate that might not be biologically significant. First, shell and somatic growth in bivalves may become uncoupled in rapidly growing species (Lewis and Cerrato 1997); and, second, scallops exhibit compensatory growth to obtain a determinate final size (Auster and Stewart 1984). Condition of scallops using eq 2 suggested highly significant differences between years and among habitats. Testing condition using eq. 3 also resulted in significant differences among habitats, although those differences depended on the year. These differences in condition suggest that the previously reported differences in growth rates are biologically significant. Associating with *Codium fragile* in Sag Harbor resulted in significantly reduced growth and condition; there appears to be long-term consequences for scallops living in *C. fragile*, especially for scallops heading into the first winter when energy storage is most important (Epp et al. 1988). These long-term impacts on condition have been observed in other bivalve-invasive macroalgal associations (Wright and Gribben 2008; Gribben et al. 2009a).

Natural-set scallops in Sag Harbor, collected in November of 2010, did not exhibit any differences in density, size or condition between eelgrass and *Codium* habitat types and similar densities have also been reported previously (Carroll et al. 2010). This was in sharp contrast to

the results of caged scallops in the second year of the study at Sag Harbor, although the reason for differences in condition of scallops between habitats and between caged and natural scallops remains unclear. There are two possible explanations for the difference in growth and condition between caged and natural scallops within the *Codium fragile* canopy. First, the results may have been due to the use of naïve (transplanted) scallops being placed in ‘novel’ habitats, i.e., scallops collected as spat and placed into various habitats. However, comparable studies examining the impacts of an invasive alga on an infaunal bivalve showed deleterious effects on both transplanted as well as naturally setting individuals (Wright and Gribben 2008; Gribben et al. 2009a), and naïve scallops in Shinnecock Bay did not exhibit differences between *C. fragile* and eelgrass, so the results in Sag Harbor were likely not due to the use of transplanted individuals.

A second possible explanation may be linked to scallop behavior. Small, juvenile scallops attach to structures above the sediment surface as a predation refuge (Pohle et al. 1991), and in the benthic surveys, many natural scallops were located within and on top of the *Codium fragile* canopy, while scallops in the cages were under the canopy. It has been suggested that for the infaunal bivalve *Anadara trapezia*, behavioral modifications (“popping-up”) in the presence of the invasive *Caulerpa taxifolia* mitigate its negative impacts (Wright et al. 2010), so it is possible that the attachment behavior of scallops affords them the ability to escape potentially poor conditions they may have otherwise experienced under the *Codium* canopy, leading to both higher densities and greater relative condition.

Such patterns typically indicate differences in food availability (Tettelbach et al. 2010), as reduced food is most often implicated in the trade-off facing scallops associating with seagrass (Bologna and Heck 1999). Unfortunately, chlorophyll monitoring was not conducted in 2010,

but when measured in 2009, both total chlorophyll *a* and >5 μ m chlorophyll *a* values did not show a pattern by habitat. However, water column food quantity alone may not explain differences in growth. There are three alternative explanations for this: (1) the available food was of different quality (Milke et al. 2006); (2) there were differences in benthic chlorophyll which scallops have been demonstrated to utilize (Davis and Marshall 1961); or (3) there were differences in flow between the habitats, impacting food delivery (Cahalan et al. 1989).

While food quality was not measured directly, when chlorophyll was monitored, concentration of chlorophyll >5 μ m was used as a proxy for optimal food since scallop particle retention decreases significantly below this threshold (Riisgard 1988). Unfortunately, neither benthic chlorophyll nor flow was measured during this study, though we argue that flow may have been the explanatory factor. The Sag Harbor study site is bowl-shaped, and likely due to its buoyant and mobile nature, the *Codium* habitat in year 2 was denser, deeper and farther from the leading edge of the tidal channel. Combined with the complex canopy formed by the invasive alga, it is likely that flow and ultimately food delivery to scallops may have been reduced in cages under the canopy, an issue demonstrated in other bivalve-SAV associations (Reusch 1998; Allen and Williams 2003; Brusati and Grosholz 2007; Tsai et al. 2010).

While there remains an incomplete understanding of the overall impacts of invasive species on native marine species (Williams and Grosholz 2008), there is a growing body of evidence suggesting that invasive SAV may be beneficial for native species (Gribben and Wright 2006b; Rodriguez 2006; Schmidt and Scheibling 2007; Polte and Buschbaum 2008; Gestoso et al. 2010; Martin and Valentine 2011). The few studies that have examined impacts of an SAV invader on the individual-level fitness of native species suggests a negative effect (Posey et al. 1993; Wright and Gribben 2008; Gribben et al. 2009a; Byers et al. 2010). Two recent studies indicate fitness

might not be different between native and invasive habitats – urchins may receive higher quality food in invaded habitats than native kelp habitats (Sauchyn and Scheibling 2009) and blue crabs have been demonstrated to grow as well in salt marshes invaded by *Phragmites australis* in other native habitats (Long et al. 2011), and even in the Posey et al. (1993) study, a second bivalve species demonstrated no negative effects of an invader association. Further, since a number of species exhibit ecological trade-offs between somatic condition and predatory mortality in complex habitats formed by native species, ‘negative’ impacts of invasive engineers on fitness may be overstated.

Originally, it was proposed that in the absence of eelgrass, *Codium fragile* might be a viable replacement habitat in northwest Atlantic estuaries based on survival data (Carroll et al. 2010); the results of this study support such a hypothesis, albeit with some caveats. In Shinnecock Bay, there were no differences in any measured metrics for scallops placed in eelgrass or *C. fragile*. However, results in Sag Harbor suggest both interannual and spatial variability in the impact of *Codium* – caged scallops exhibited long-term consequences on individual fitness. Yet, these differences were not manifested in naturally settling scallops in Sag Harbor, perhaps due to scallop behavior. Further, the ‘reduced’ growth rates in *C. fragile* in this study (0.32 mm d^{-1}) and resulting calculated tissue growth rates (4.4 mg d^{-1}) were as high or higher than other literature values reported for scallops in Connecticut (Tettelbach 1986), Florida (Irlandi et al. 1995; 1999), Massachusetts (Shriver et al 1998), and New York (Eckman 1987; Bricelj et al. 1987; Garcia-Esquivel and Bricelj 1993).. Taken in aggregate, these findings support the call for more inter annual and site-specific comparisons to native habitats when examining the impacts of an invasive species on individual fitness of fauna with known food-risk trade-offs, but suggest *Codium fragile* may be a viable habitat alternative to seagrass for bay scallops.

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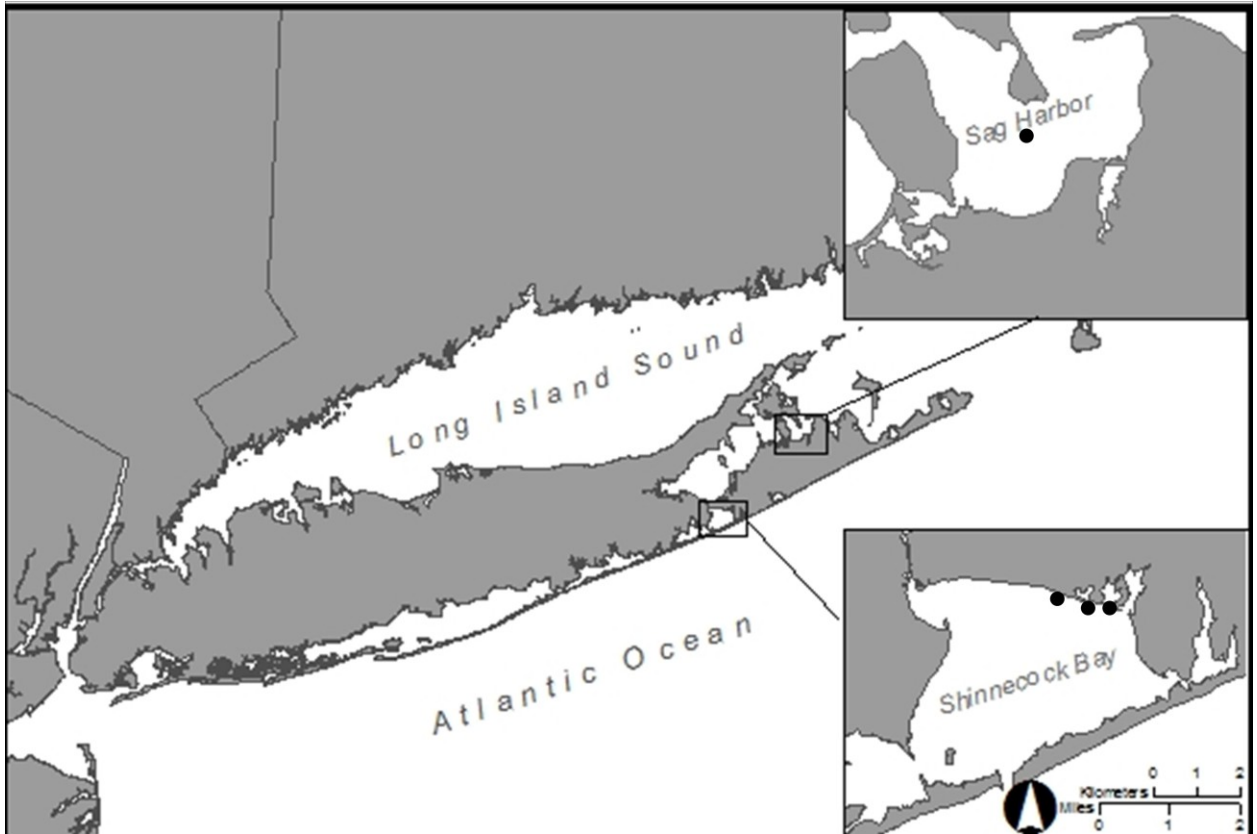


Figure 1: Map of the study sites on Long Island, New York, US. Insets show the study areas, indicating the locations of Sag Harbor, NY, and Shinnecock Bay, NY. Circles indicate the study sites.

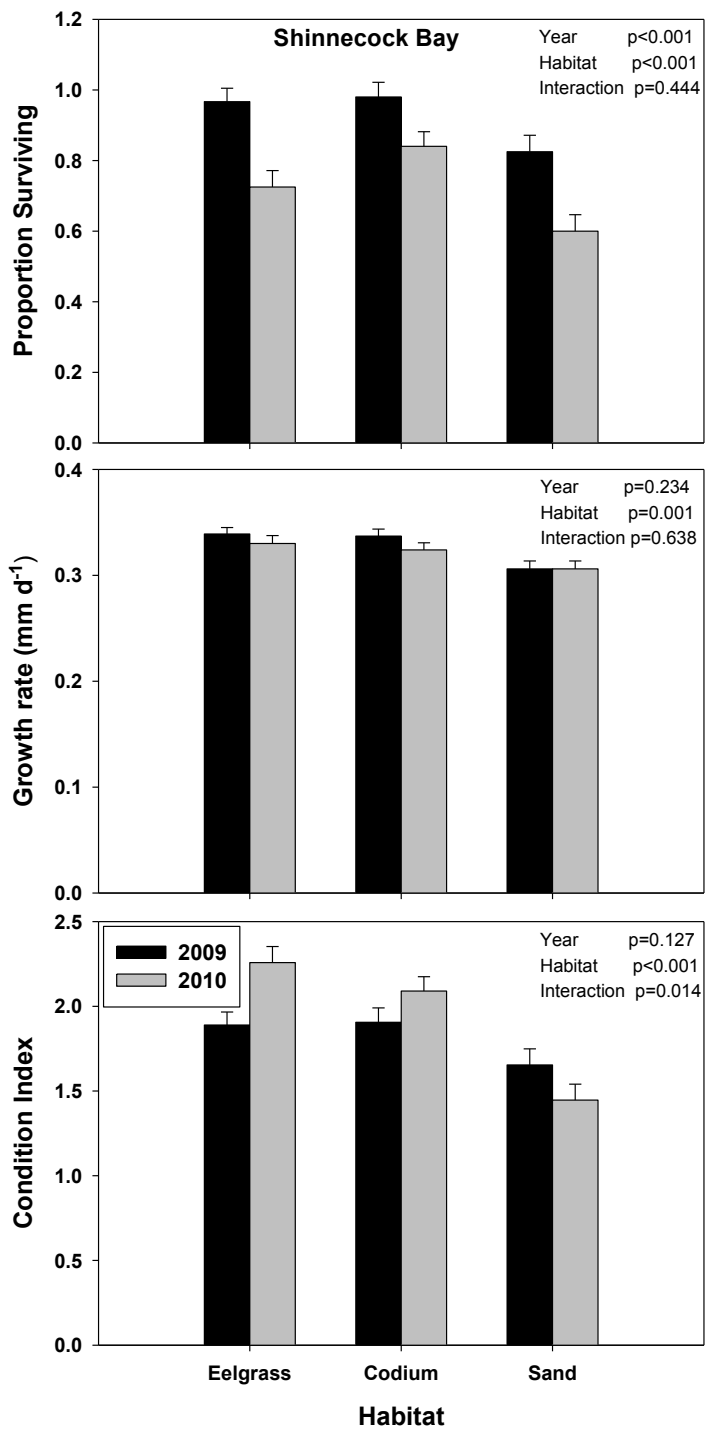


Figure 2: Survival (proportion surviving), growth (mm d⁻¹) and condition index (CI = (tissue dry weight/shell height) x 100) of juvenile scallops placed in three habitats in Shinnecock Bay, New York for 10 weeks in 2009 and 11 weeks in 2010, illustrating the results of two-way ANOVA.

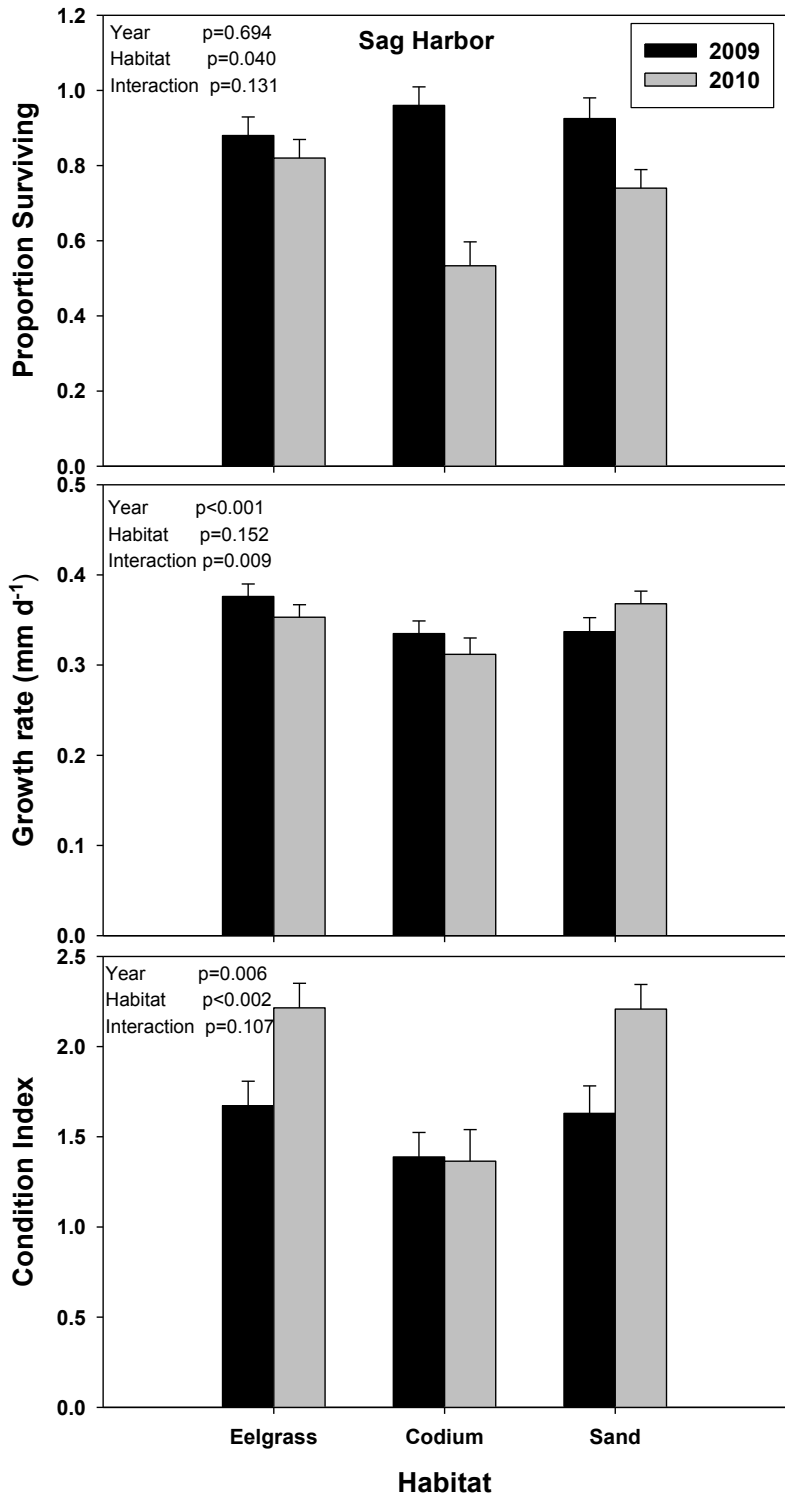


Figure 3: Survival (proportion surviving), growth (mm d⁻¹) and condition index (CI = (tissue dry weight/shell height) x 100) of juvenile scallops placed in three habitats in Sag Harbor, New York, for 10 weeks in 2009 and 11 weeks in 2010.

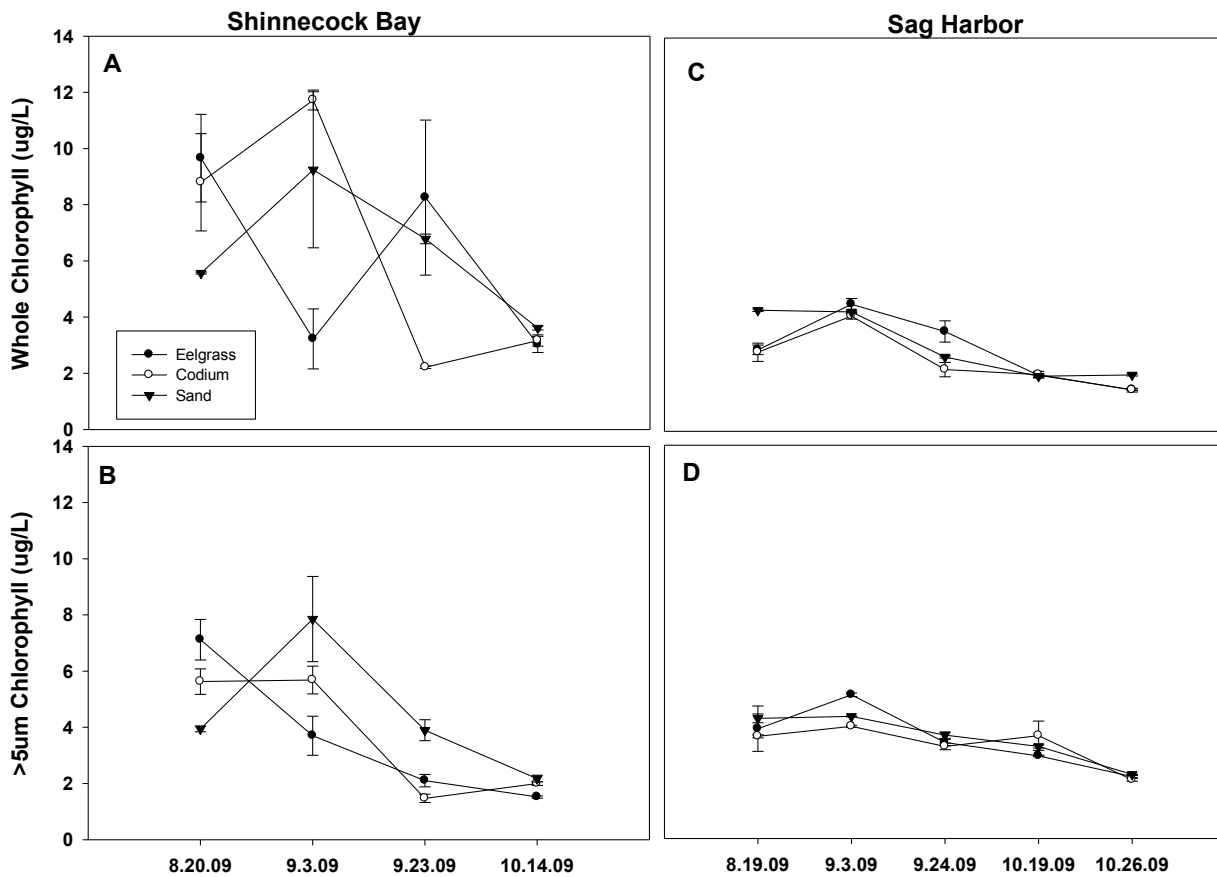


Figure 4: Chlorophyll a measurements for 2009 at Shinnecock Bay (A and B) and Sag Harbor (C and D). Total chlorophyll is on the top two panels (A and C) and 5 µm size-fractionated chlorophyll is represented in the bottom panels (B and D). Closed and open circles, and closed triangles represent measurements recorded in eelgrass, in *Codium fragile*, and on sand, respectively.

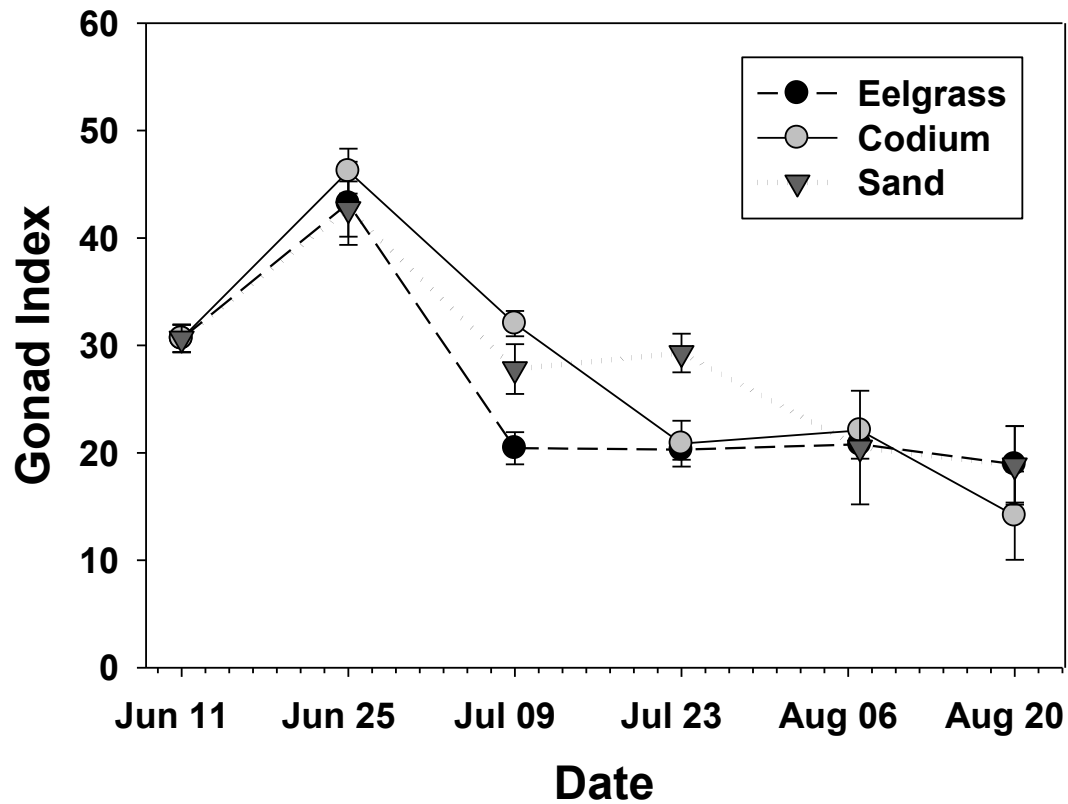


Figure 5: Gonad indices for scallops placed in the 3 different habitat types in Shinnecock Bay in 2009. Gonad Index (GI) = (gonad dry weight/total tissue dry weight) x 100, and is a proxy for reproductive output (Barber and Blake 1991). Dashed line with black circles represents scallops in eelgrass, gray circles with solid line is for scallops placed in *Codium fragile* and gray triangles with dotted lines is for scallops on barren substrates.

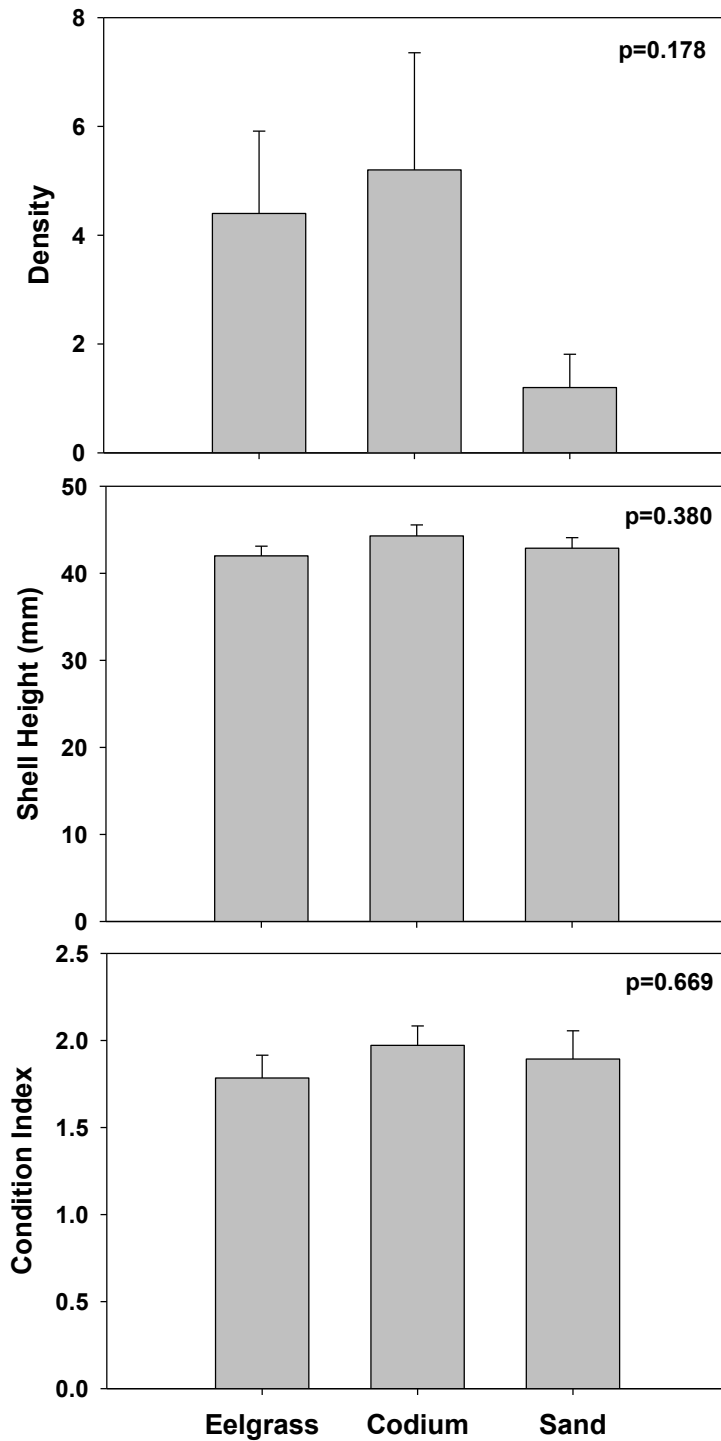


Figure 6: Density (scallops m⁻²), shell height (mm) and condition index using shell height for natural set scallops collected in the 3 habitats in Sag Harbor, NY, collected in November of 2010, at the same time the field experiments were ended.

Table 1: Table of whole chlorophyll *a* (Chl *a*) and >5µm Chl *a* collected using diver operated 60ml syringes into the canopy of eelgrass and *Codium* habitats or ~10 cm above the bottom in unvegetated habitats at each site on each sample date. Analysis indicates the results of one-way ANOVA on each date at each site for each habitat, where alpha of <0.05 was considered significant, and the direction of the multiple comparisons results.

Date	Shinnecock Bay						Sag Harbor						Analysis for Whole Chl <i>a</i>			
	Eelgrass		<i>Codium</i>		Sand		Eelgrass		<i>Codium</i>		Sand		α	eel v. cod	eel v. sand	cod v. sand
8/20/2009	Whole	>5µm	Whole	>5µm	Whole	>5µm	Whole	>5µm	Whole	>5µm	Whole	>5µm	0.022	=	>	=
9/3/2009	9.66 ± 1.56	7.12 ± 5.63	8.80 ± 1.73	5.63 ± 0.45	5.57 ± 0.03	3.94 ± 0.10	3.22 ± 1.07	3.70 ± 0.70	11.73 ± 0.35	5.68 ± 0.49	9.24 ± 2.78	7.85 ± 1.51	0.002	<	=	>
9/23/2009	8.25 ± 2.76	2.10 ± 0.22	2.22 ± 0.04	1.47 ± 0.14	6.78 ± 0.17	3.90 ± 0.37	3.03 ± 0.29	1.52 ± 0.04	3.17 ± 0.20	2.00 ± 0.07	3.61 ± 0.07	2.17 ± 0.12	0.009	>	=	<
10/14/2009	3.03 ± 0.29	1.52 ± 0.04	3.17 ± 0.20	2.00 ± 0.07	3.61 ± 0.07	2.17 ± 0.12	3.03 ± 0.29	1.52 ± 0.04	3.17 ± 0.20	2.00 ± 0.07	3.61 ± 0.07	2.17 ± 0.12	0.031	=	<	=
Date	Eelgrass		<i>Codium</i>		Sand		Eelgrass		<i>Codium</i>		Sand		Analysis for Whole Chl <i>a</i>			
8/19/2009	Whole	>5µm	Whole	>5µm	Whole	>5µm	Whole	>5µm	Whole	>5µm	Whole	>5µm	α	eel v. cod	eel v. sand	cod v. sand
9/3/2009	2.90 ± 0.17	2.61 ± 0.91	2.81 ± 0.33	2.30 ± 0.06	4.31 ± 0.04	3.03 ± 0.18	4.52 ± 0.20	3.97 ± 0.07	4.10 ± 0.11	2.70 ± 0.04	4.25 ± 0.02	3.10 ± 0.02	<0.001	=	<	<
9/24/2009	3.55 ± 0.38	2.06 ± 0.13	2.20 ± 0.25	1.90 ± 0.13	2.64 ± 0.04	2.35 ± 0.13	1.99 ± 0.05	1.52 ± 0.02	2.02 ± 0.11	2.33 ± 0.59	1.96 ± 0.06	1.90 ± 0.07	0.022	>	=	=
10/19/2009	1.99 ± 0.05	1.52 ± 0.02	2.02 ± 0.11	2.33 ± 0.59	1.96 ± 0.06	1.90 ± 0.07	1.48 ± 0.03	0.69 ± 0.04	1.47 ± 0.07	0.56 ± 0.06	2.00 ± 0.03	0.77 ± 0.01	0.730	>	>	<
10/26/2009	1.48 ± 0.03	0.69 ± 0.04	1.47 ± 0.07	0.56 ± 0.06	2.00 ± 0.03	0.77 ± 0.01	1.48 ± 0.03	0.69 ± 0.04	1.47 ± 0.07	0.56 ± 0.06	2.00 ± 0.03	0.77 ± 0.01	<0.001	=	<	<

Chapter Six

Basin-scale variability in habitat and predation intensity and its potential effects on recruitment of an epifaunal bivalve

Abstract:

Predation is among the most important factors contributing to benthic community structure, and as such, predicting patterns in predation is increasingly important for management and restoration efforts. Habitat complexity can have a strong influence on predation rates, however, both predator and prey densities tend to be highest in complex habitats, and so understanding the degree to which increasing complexity impacts a suite of common predators is a key step in predicting field predation. This study sought to examine consumption rates of 4 major scallop predators across a series of seagrass shoot densities and apply these rates to a predator impact (PI) model (sensu Menge 1983) that incorporated field habitat complexity, predator density and scallop settlement. Despite limitations, the PI model correctly predicted that scallop density would be highest at Cormorant Point, Shinnecock Bay, since the PI value was lowest there. A combination of model factors likely contributed to high densities at this site – high density, continuous seagrass, lowest predator densities and highest scallop settlement. While there were several limitations to the study that reduce the predictive power of the PI model, it was useful in identifying sites where impact is high vs. low, as well as identified mud crabs, *Dyspanopeus sayi*, as the most important scallop consumer in the basin. This model is a useful rudimentary tool to incorporate the impact of predators into management and restoration planning.

Introduction:

Predation has been considered to be the most important factor affecting marine communities (Connell 1975, Menge 1983). Post-settlement mortality, attributable to predation has been shown to be a major factor determining recruitment in many benthic populations (Gosselin and Qian 1997, Hunt and Scheibling 1997, Carroll et al. 2012). Prey impacts may be direct (i.e., consumption) or indirect, as a number of species exhibit altered behavior, growth and/or morphology in the presence of predator cues (Lima 1998, Nakaoka 2000). In response, numerous marine species, including fish and bivalves, exhibit what has been called a ‘food-risk trade-off’ (Gilliam and Fraser 1987, Dahlgren and Eggleston 2000). Predicting patterns in predation and how they influence benthic populations is increasingly important for management, conservation and restoration efforts.

A number of factors influence the overall impact of predation on benthic populations, including predator identity, predator and prey density, and habitat complexity. While many species are implicated in predatory mortality of post-settlement benthic invertebrates, decapod crustaceans are among the most important (Nelson 1981, Menge 1983, Hunt and Scheibling 1997). Predatory decapods are responsible for consuming very small invertebrate prey (Juanes 1992), although their ability to consume prey is determined by claw and prey size (Juanes and Hartwick 1990, Whetstone and Eversole 1991, Seed and Hughes 1995, Ray-Culp et al. 1999, Aronhime and Brown 2009).

Complex habitats, such as seagrass beds or oyster reefs often provide post-settlement individuals a refuge from predation (Heck and Orth 1980, Ray-Culp et al. 1999, Grabowski 2004, Warfe and Barmuta 2004, Grabowski et al. 2008, Mislán and Babcock 2008, Stoner 2009). Although recent studies suggest some exceptions to the ‘nursery’ role of seagrasses (Mattila et

al. 2008, Canion and Heck 2009), it is still widely accepted that many fauna experience lower predation within seagrass meadows, an effect that varies inversely with complexity (Leber 1985, Ray-Culp et al. 1999, Heck and Orth 2006).

Paradoxically, many predatory decapods appear to exhibit positive relationships with habitat complexity (Eggleston et al. 1998, Hovel 2003) in the same seagrass habitats thought to simultaneously enhance recruitment success of bivalves (Peterson 1986, Orth 1992, Bologna and Heck 2000), including bay scallops, *Argopecten irradians* (Eckman 1987, Carroll et al. 2012). Scallops have a strong association with seagrass habitats (Belding 1910, Gutsell 1930), which they utilize as a refuge from predation (Prescott 1990, Pohle et al. 1991, Garcia-Esquivel and Bricelj 1993, Irlandi et al. 1995, Irlandi et al. 1999), despite potentially high densities of predators in these habitats. Thus, the bay scallop is a useful model organism to study the relationship between predator identity, density and habitat complexity.

There are multiple decapod crab species present in the estuaries of Long Island, New York that are voracious predators of juvenile bivalves, including green (*Carcinus maenas*), blue (*Callinectes sapidus*), spider (*Libinia* spp.) and mud crabs (*Dyspanopeus sayi*) (Ropes 1989). The invasive green crab is considered a major consumer of small bivalves (Ropes 1968, Mascaro and Seed 2000, Miron et al. 2005). Likewise, the blue crab is also considered an important predators capable of structuring bivalve populations (Eggleston 1990, Eggleston et al. 1992, Seitz et al. 2001, Dittel et al. 2006). While spider crabs, *Libinia* spp., are omnivorous, mollusks comprise the highest proportion of animals in their diets (Ropes 1989). Finally, despite their relatively small size, mud crabs (Xanthidae) are also capable of consuming large quantities of small, post-settlement bivalves (Whetstone and Eversole 1991, Streib et al. 1995, Silliman et al. 2004, Grabowski et al. 2008, Kulp et al. 2011).

Typically, studies have examined predation within versus outside of structured habitat (Peterson 1986, Bologna and Heck 1999), between completely different habitats (Barshaw and Lavalli 1988, Dittel et al. 1996, Carroll et al. 2010), or using a single predator species across a range of measured complexity (Heck and Thoman 1981, Peterson 1982, Gotceitas and Colgan 1989, Ray-Culp et al. 1999, Mattila et al. 2008). The prevailing synthesis has been that the effects of habitat on predation are non-linear (Heck and Orth 2006). With the exception of mud crabs, little is known about the effects of seagrass shoot density on decapods foraging for scallops, although foraging by crabs should be impacted by three-dimensional structure (Hovel and Lipcius 2002, Grabowski and Powers 2004). No study has sought to quantify the effects of a range of habitat complexity on the predation rates for a suite of common Northwest Atlantic predators. Calculating individual daily consumption as a function of habitat for each of these species and quantifying field densities are important steps toward determining site- and species-specific impacts on scallop recruitment.

Since predicting predation is important for restoration efforts, this study aimed to quantify consumption rates of four major decapod predators on bay scallops as a function of habitat complexity. These values were then combined with field data on habitat, predator density and scallop settlement, in an attempt to create a site-specific predictive predator impact index (Menge 1983) as well as to identify the most important consumers of post-set bay scallops. Finally, the predator impact index was compared to actual field densities of scallop recruits to assess its feasibility.

Methods:

Study site:

Shinnecock Bay is a relatively shallow, lagoonal estuary located along the south shore of Long Island. It has major oceanic exchange from the south through the Shinnecock Inlet (40.8425 N, -72.4761 W) and receives periodic water pulses from the Peconic Estuary to the north when the tide gates in the Shinnecock Canal (40.8875 N, -72.5014W) are opened. The major source of freshwater input is via rain- and groundwater. Six sites were selected in the eastern basin of the Shinnecock Bay system (Figure 1, Table 1) for this study.

Field surveys

Field sampling for predator and scallop abundance was conducted via suction dredging, an effective *in situ* method for sampling decapod crustaceans (Orth and van Montfrans 1987, Johnson and Heck 2006, Carroll et al. 2010). A 1-m² metal frame with a meter high 1mm mesh curtain was haphazardly thrown into the water from a boat and immediately suction dredged into a 750- μ m mesh bag. The samples were then placed on ice, returned to the lab and sorted. Sample processing usually took ~3 days, with the samples kept near-freezing until they had been processed. Individuals were identified to the lowest possible taxon and counted. Crabs were identified to species, sexed and measured for carapace width. Shrimp were identified and enumerated, as were other bivalves and non-predatory gastropods. Predatory gastropods were measured for total length.

Habitat complexity was conducted by haphazardly tossing gridded 1-m² quadrats and assessing presence/absence of habitat within each cell. For the purposes of this study, ‘shell hash’ was defined as non-living, broken shells – typically *Mytilus edulis* mussels – that formed a three dimensional structure above the bottom. Other habitat characteristics included ‘Crepidula’ which was living *Crepidula fornicata*, ‘Eelgrass’, *Zostera marina*, ‘Ulva’, *Ulva lactuca*,

‘Codium’, *Codium fragile*, and ‘red macroalgae’ (*Gracilaria* sp., *Aghardhiella* sp., and *Spyridia* sp.) which were grouped together due to the difficulty of discerning species under water.

Predation experiments:

A series of mesocosm experiments were conducted at the Stony Brook-Southampton Marine Station, using 378.5 L Rubbermaid® tubs, with an approximate bottom area of 0.78m². The tubs were lined with 7.5 cm of sand, and received one of 4 levels of habitat complexity using seagrass mimics of 0, 200, 400 and 800 shoots m⁻². Seagrass mimics were constructed using 5mm wide curling ribbon. Each shoot consisted of 4 leaves and a canopy height of 35cm. Tub s were plumbed with constantly flowing raw seawater from Old Fort Pond, a part of Shinnecock Bay, to allow conditions within the mesocosms (temperature, salinity, dissolved oxygen) to be similar and remain as close as possible to ambient conditions. In addition, air diffusers were placed within each tub to ensure mesocosms remained at oxygen saturation levels.

Mesocosm experiments were run using 4 different species of crab found in varying abundances throughout the region – 1) mud crabs, *Dyspanopeus sayi*, 2) spider crabs, *Libinia emarginata*, 3) green crabs, *Carcinus maenas*, and 4) blue crabs, *Callinectes sapidus*. Mud crabs were hand-collected via SCUBA from Shinnecock Bay. Spider crabs and green crabs were collected using modified lobster cages deployed near the Shinnecock Inlet. Blue crabs were collected by a commercial fisherman in Great South Bay, Long Island, NY.

Sets of 25 similar size scallops were free-released into mesocosms; scallop sizes were determined by predator and trial – between 10-18mm SH for mud crabs, 15-25mm for green crabs, 18-22mm for spider crabs and 20-25mm for blue crabs (see Table 2 for size ranges for each experiment). After a prior 48 hour starvation period, appropriate predators were added (either groups of 5 mud crabs due to their small size and high abundances in the field or a single

individual of other crab species). Only male crabs were used to control for any variability in feeding between sexes. Crabs were measured for carapace width (CW) and major chela height. CW ranged from 17-24mm for mud crabs, 63-81mm for green crabs, 84-103mm for spider crabs, and 118-139mm for blue crabs. Trials were allowed to run for 20 hours (Tettelbach 1986), after which time, predators were removed, and surviving scallops were enumerated. Artificial seagrass was then removed and rinsed onto a sieve to ensure retrieval of all scallops from the tubs. Broken shells were also removed. Any scallops whose shells were crushed but still had remaining tissues were considered consumed. Temperature and salinity were recorded at the beginning and end of each trial. Temperature ranged from 16-26°C across all experiments, although it did not vary more than 0.5°C within any one trial. Salinity ranged from 25-29 PSU across all experiments (see Table 2).

Due to availability of scallops and crabs, differing numbers of replicate trials were conducted for each crab species. Mud crabs were used in 4 trials with 3 replicates of each habitat complexity (n=12 per habitat treatment). Spider crabs, due to the low availability of the larger sizes required, were only used in 2 trials (n=6 per habitat). Green crabs were the most easily obtainable species and were used in 5 trials (n=14 per habitat, one trial only had 2 replicate sets). Blue crabs were used in 3 trials (n=9 per habitat).

Scallop larval settlement:

Scallop larval settlement was monitored at the 6 sites using spat collectors modified after Ambrose and Lin (1991). These consisted of a 750µm mesh spat bag (Atlantic Aquaculture), stuffed with a standardized piece of blue Netron® plastic mesh (38 x 46 cm) to keep the bag from collapsing, and a small Styrofoam float attached to each spat bag to extend it vertically. Sets of two spat bags were attached to a cinder block which was marked at the surface with a

lobster buoy. In 2010, 38 x 46 cm sized spat bags were used. In 2011, 38 x 78 cm bags were used because the smaller bags were no longer available; however, the same size of Netron mesh was maintained in 2011. Three cinder blocks were deployed at each timepoint for a total of 6 collectors per site per sampling period.

In 2010, spat collectors were deployed during all months when bay scallop larvae might have been present in the water column (Tettelbach and Weinstock 2008). Initial deployments of sets of 3 blocks took place in the beginning of June. A second set of collectors was deployed 3 weeks later. On a 3 week basis, new sets of spat collectors replaced those which had been in the water for 6 weeks until the beginning of October, resulting in a mid-November final retrieval and a total of 6 sampling dates (see Tettelbach et al, *in review*). Since 15% of the scallop spat collected in 2010 occurred in the first collection (deployed in June and collected in July), spat bags were deployed in early May in 2011 to ensure we did not miss an early peak. However, since less than 1% of the total scallops occurred in the final 2 samples of 2010, we deployed 6 sets of collectors in 2011, ending with a mid-October retrieval.

During retrieval, spat bags were placed into individually labeled plastic garbage bags and returned to the lab where juvenile scallops were washed from the bags and retained on an 800- μ m mesh screen. Scallops were then sorted, enumerated and measured to the nearest mm.

Predator Impact

The predator impact model was adapted from Menge (1983) as follows:

$$PI_n = \frac{\sum_{i=1}^4 C_i(SS_n) \times \rho_{i,n} \times t_{v,i}}{Sp_n}$$

where PI_n is the predator impact at site n , $C_i(SS_n)$ is the consumption of species i as a function of the shoot density (SS) at site n , $\rho_{i,n}$ is the density of species i at site n , $t_{v,i}$ is the number days a scallop is vulnerable to predation by species i based on size, and Sp_n is the total calculated spat

settlement across the whole season at site n . *Codium fragile* offers a similar predation refuge to scallops as eelgrass (Carroll et al. 2010), so for Heady Creek, shoot density was estimated as the number of shoots required for the equivalent percent cover of *Codium*. Since scallops reach size refuges from certain predators, $t_{v,i}$ was computed using maximum predator size from this field survey and maximum scallop size consumed by a predator of that size from Tettelbach (1986; Table 3) and 2 growth rates – 2.5 and 3mm wk⁻¹ typical for bay scallops in the northwest Atlantic (Tettelbach 1986, Eckman 1987).

Values for consumption C were obtained from mesocosm data. Per capita consumption was calculated by using mesocosm predation data across a range of habitats and determining a best fit regression using Aikaike's Information Criterion (AIC) from 3 typical predation models (see Data analysis section). Field values for shoot density (SS) at site n were input into the regression equation to determine the per capita consumption at site n as a function of its seagrass habitat.

The density of each species at each site ($\rho_{i,n}$) was determined by the field suction survey data and was the mean density of each species across all four sampling periods. Finally, Sp_n is the scallop spat settlement as determined by the spat collectors placed at each site. To approximate settling densities, the mean number of spat per bag for a collection was divided by the area of substrate available for scallops to attach (38cm x 46cm Netron plastic mesh; 0.1748m²). Then, total settlement was calculated as the sum of the settlement densities across each collection.

Data analysis

For potential predator and scallop densities, predators were grouped into decapods and gastropods. All decapods sampled were considered as potential predators except for the shrimp *Hippolyte zostericola* which is an epiphyte grazer. Both *Crangon* and *Palaemonetes* shrimps were considered potential predators for post-set bay scallop spat (van der Veer et al. 1998), and

all crabs were considered potential predators. Differences between sites were determined using a one-way ANOVA on the mean abundances across all seasons. Differences in gastropod predators were similarly examined.

A two-way ANOVA was run with predators and habitat as the explanatory factors for the proportion of scallops consumed. However, in order to determine the predictive value of consumption as a function of habitat complexity, regression models were fit to mesocosm consumption data using the nls2 package in R and determining best fit by using Aikake's Information Criterion (AIC) and model weights (W_i). Three typical predation models for crabs were used, based on functional response models for consumption with prey density. These models were chosen since differences in prey density can affect a crabs ability to locate and capture food (Seitz et al. 2000), and with the expectation that habitat complexity, in this case seagrass shoot density, would also affect the predators ability to locate food. The three models for this study, linear, logarithmic and logistic, were chosen to mimic the shapes of Type I, Type II, and Type III functional response models.

A two-way ANOVA with year and site as the factors was conducted to discern differences in spat settlement between sites and years. Since there were significant differences by site but a significant year x site interaction, and because there was a distinct seasonal pattern in settlement one-way ANOVAs were run to test for differences between sites within each year during peak settlement. In 2010, this was collections 1 and 2, and for 2011, this was collections 2-4. Data were $\log(x+1)$ transformed to fit the assumptions of normality.

Results

Field surveys

Eelgrass occurred at 4 of the 6 study sites, with the maximum cover 99% at Cormorant Point (CP). Far Pond (FP) had 76% eelgrass cover, while East Shinnecock Bay (ESB) and Warner's Island (WI) were patchy, with 46 and 41% eelgrass cover, respectively. Other vegetation included red macroalgae which was present at all 6 study locations, *Ulva*, which occurred at 4 of the 6 sites, and *Codium*, which occurred only at the Heady Creek (HC) site. The dominant structure at the Bridge site (B) was shell hash covering 60% of the bottom and consisting mainly of mussel shells, while in HC, *Crepidula* covered 85% of the bottom surveyed (Table 4).

Mud crabs, *Dyspanopeus sayi*, were the dominant decapods encountered during the suction surveys. Over 3,900 mud crabs were collected in 48 suction samples across all 6 sites and 4 time points, composing 69% of the decapod crustation catch and 47% of total individuals collected. A total of 187 blue crabs were collected (see Table 5 for all species). Across all sampling periods, there was a significant difference in potential predatory decapod distribution between the study sites ($p < 0.001$). HC had the highest densities of decapods with 243 ± 59 (hereafter, mean \pm SE) individuals per m^2 , significantly higher than all other sites ($p < 0.001$ for all, Figure 3a). No other sites were statistically significantly different from each other. The only other site which was dominated by shells was B, which also had the next highest decapods densities (99.7 ± 37.8 decapods per m^2). Sites with seagrass varied in decapod predator density (WI: 80.0 ± 18.4 decapods per m^2 ; ESB: 53.1 ± 22.5 ; CP: 74.3 ± 8.2 ; FP: 60.6 ± 8.6 ; Table 6).

The mud snail, *Ilyanassa obsoleta*, was the dominant gastropod collected during dredge surveys, with 1,542 collected, composing 87% of the gastropod catch and 19% of the total individuals collected, despite only being collected at CP. Drills comprised the next two most common gastropods, with *Urosalpinx cinerea* and *Eupleura caudata* making up 6 and 3% of the gastropods collected, respectively (see Table 5). Again, HC had the highest densities of

gastropods (16.9 ± 8.7 gastropods per m^2 , $p=0.012$), significantly more than all other sites. The other five sites were not different from each other (Figure 3b).

On the bottom, there was a significant difference in scallop density across the sites ($p=0.016$). Two sites, B and ESB, did not have any scallops collected across the whole sampling season. The highest abundance occurred at CP, with 6.6 ± 3.6 individuals per m^2 for all collections. This comprised 88% of all scallops collected via dredging in 2011. Likewise, FP was the next highest mean abundance, 0.5 ± 0.3 individuals per m^2 , making of 7% of all scallops on the bottom. HC and WI yielded 3 and 2% of the total scallops, respectively (Figure 3c).

Predation experiments:

Both habitat (two-way ANOVA, $df=3$, $F=8.407$, $p<0.001$) and predator identity ($df=3$, $F=13.046$, $p<0.001$) significantly affected scallop mortality, although there was no interaction ($df=9$, $F=1.048$, $p=0.405$), suggesting the direction of the change across habitats was the same across predator species (Figure 4a). Scallops in mesocosms with no shoots had significantly lower survival than in tanks with 400 or 800 shoots per m^2 ($p<0.001$ for both). Additionally, scallops in tanks which contained 200 shoots exhibited significantly lower survival than tanks with 400 ($p=0.004$) and 800 shoots ($p<0.001$).

Green crab consumption was significantly greater than groups of 5 mud crabs ($p<0.001$) as well as individual blue crabs ($p=0.004$). Likewise spider crabs also exhibited higher consumption than groups of mud crabs ($p=0.005$). Spider crab consumption was not different than blue crabs ($p=0.107$) or green crabs ($p=0.393$), while individual blue crab consumption was not different than groups of mud crabs ($p=0.203$, Figure 4b). Across all habitats, mud crabs consumed 0.84 ± 0.12 scallops per individual. Green crabs had the highest per capita consumption rate of 9.57 ± 0.80 scallops over the 20 hour experiment. Spider crabs exhibited a

high but variable predation rate, consuming 8.79 ± 1.51 scallops per crab. Of the large crabs examined, blue crabs consumed the least amount of scallops over the 20 hour experiment, with a 6.00 ± 1.03 scallops per crab.

Using a regression approach, predictive models were generated for the consumption of scallops by each predator as a function of habitat complexity. For mud crabs, the logarithmic regression was the best fit; scallops consumed = $-0.1123 \cdot \log(SS) + 1.5126$, $n = 48$, residual sum of squares (RSS) = 1543, AIC = 308.7943, $W_i = 0.6274$ (Figure 4, Table 7). A linear regression fit best for green crabs (scallops consumed = $-0.0103 \cdot SS + 16.625$, $n = 56$, RSS = 2834, AIC = 384.6683, $W_i = 0.6777$) and spider crabs (scallops consumed = $-0.01337 \cdot SS + 16.244$, $n = 24$, RSS = 1961, AIC = 179.7842, $W_i = 0.5433$). A logarithmic regression also fit best for blue crabs (scallops consumed = $-0.686 \cdot \log(SS) + 9.9073$, $n = 36$, RSS = 1520, AIC = 231.6936, $W_i = 0.5691$, Figure 4, Table 7). These best fit regressions were used for the predator impact model (Table 8).

Scallop larval settlement

There was a distinct seasonal pattern in scallop settlement in both 2010 and 2011. Peak scallop settlement occurred in August of 2010 with 77% of the total scallops collected during 2010 on this time-point (Figure 5a). Like 2010, peak settlement occurred on 8 August, yielding 58% of scallops collected (Figure 5b), although collectors retrieved on 19 July and 30 August, just before and after the peak settlement, consisted of 22% and 14% of the total scallops collected. Little recruitment occurred in other collections.

There was a significant effect of year (two-way ANOVA, $df=5$, $F=269.991$, $p<0.001$) and site ($df=5$, $F=340.701$, $p<0.001$) on scallop settlement, however the site differences depended on year (site x year interaction; $df=25$, $F=181.278$, $p<0.001$). More spat per bag were collected in

2010 across all sites (53.2 ± 6.2 , mean \pm SE) than in 2011 (11.9 ± 3.9 spat per bag). Because of the site by year interaction and the strong seasonal pattern, site differences were further examined within each year using one-way ANOVA only during peak settlement.

During peak settlement in 2010, which occurred in collections 1 and 2, scallop settlement was highest at 2 sites nearest the inlet – ESB (217 ± 63 spat per bag) and WI (193 ± 39 spat per bag) – as well as in HC (144 ± 63 spat per bag) (Figure 6). Maximum spat per bag at sites ESB, WI, HC and CP all experienced significantly higher spat settlement than B ($p < 0.001$ for all), however, no other sites were different from each other. 30% of scallops were collected at ESB, followed by 27% at WI, 20% at HC and 15% at CP (Figure 6).

Patterns in scallop settlement in 2011 were different than during 2010 (see Figure 6). During peak settlement, maximum spat per bag occurred at the CP site (93 ± 19), and settlement at CP was significantly higher than all other sites ($p < 0.001$ for all). FP experienced the next highest settlement (17 ± 1 spat per bag) which was significantly more than sites B ($p < 0.001$), FP ($p < 0.001$) and HC ($p < 0.001$). Like 2010, all sites experienced higher settlement than site B (Figure 6, Table 7).

Predator Impact Model

Potential scallop consumption for each predator at each site was calculated by multiplying the daily rate of consumption as a function of habitat (Table 8), the field densities of each predator (Table 6) and the time to vulnerability for each predator (Table 3). The impact of each species varied across the sites. While the model predicts that blue crabs could potentially consume the most scallops at FP and CP, mud crabs were the most important consumers at the other 4 sites. Across all the sites, mud crabs at present densities could potentially consume over 27,000 scallops across the 6 study sites before they attain size a refuge (Figure 7).

Predator impact was calculated using the ratio of the above value and the by the total number of scallop settlers at each site across the whole monitoring season (Table 7). Values lower than 1 would indicate that settlement is higher than potential consumption. PI varied by site ($p < 0.001$); it was lowest at CP (3.03 ± 0.20 , Table 9). Habitat complexity had a significant effect on PI; a piecewise regression on means showed 2 distinct regions, indicative of a threshold habitat value ($r^2 = 0.991$, $p = 0.0056$, Figure 8). Values for PI (all greater than 1) suggested that there should be no scallop recruitment in the system, which was true for most sites (densities ≤ 0.5 per meter squared). The site with lowest PI had the highest scallop densities (CP), likewise, the site with the highest PI had zero scallops (B; Figure 9).

Discussion

Scallops, like many estuarine bivalves throughout the United States, have historically supported vibrant fisheries which subsequently collapsed, and are the target of many restoration efforts. For bay scallops, the threat of predation is immense – they can obtain a partial size refuge from most predators after just a few months, but can never escape predation from large gastropods (Bologna and Heck 1999), adult blue crabs (Tettelbach 1986), gulls (Prescott 1990), or rays (Myers et al. 2007). Thus, it is important to consider predation for restoration efforts. The general results from this study suggest that low scallop populations in Shinnecock Bay, New York, may be attributable to high predation pressure.

Predator densities were relatively high throughout Shinnecock Bay. Decapod crustaceans were extremely abundant, ranging from ~ 50 to over 200 decapods m^{-2} , depending on the study site. These densities were driven mainly by the mud crab, *Dyspanopeus sayi*, which were the numerically dominant predator in this system. Mud crabs were 3x to 100x more abundant than blue crabs, *Callinectes sapidus*, the next most abundant true crab predator, and 2 to 3 orders of

magnitude greater than other crab predators collected. Changes in abundance of mud crabs are difficult to ascertain, since long term data sets of mud crab abundance are rare. In Great South Bay, NY, mud crabs were also the dominant predator by density over 16 years of data (Polyakov et al. 2007), however, their abundances were 1-3 orders of magnitude lower than our surveys yielded. Studies from other Long Island bays from the mid 1990s (Streib et al. 1995) and more recently (Carroll et al. 2010) suggest mud crab populations were also lower than this study. Populations of mud crabs may be increased relative to prior studies, although differences in collection methods between studies and lack of any long term data renders any trends speculative at best.

There are some long term data which suggests that blue crabs may be increasing on Long Island. High blue crab abundance is a relatively new phenomenon in Long Island, New York, waters, where landings data (NYDEC) and long-term data sets (Polyakov et al. 2007) suggest high abundances only started within the past 15 years. If blue crab abundance continues to increase, they may become the dominant post-set bivalve consumer in this system. In embayments where blue crabs are abundant, they are implicated as the most important benthic predator (Eggleston et al. 1992, O'Connor et al. 2008). Further, blue crabs are a dominant predator of scallops in North Carolina (Bishop and Wear 2005, Bishop et al. 2005) and Virginia (R. Seitz, pers. comm.) and are capable of eating even adult scallops (Tettelbach 1986). Thus, if populations in New York continue to rise, blue crabs can have major impacts on scallop populations and restoration efforts.

Identification of the major scallop predator can have other implications for restoration efforts, such as scallop planting size and density. In order to determine the important scallop predators in the system, rates of consumption as a function of habitat complexity and field

densities need to be considered. This study answered both questions – field suction surveys for potential predator identification and densities and a series of mesocosm experiments across 4 levels of habitat complexity to determine per capita scallop consumption with changes in seagrass shoot density. Mesocosms results suggested that all four predators tested – the aforementioned mud and blue crabs, as well as green crabs, *Carcinus maenas*, and spider crabs, *Libinia emarginata* – exhibited a decrease in consumption with increasing habitat complexity. However, when fitting regressions to the data, Akaike's Information Criterion suggested that best-fit regressions varied between predators. Scallop consumption by mud and blue crabs exhibited a logarithmic relationship with seagrass shoot density, whereas consumption by green and spider crabs exhibited a linear relationship with seagrass.

The relationship between scallop consumption and seagrass shoot density was used in a modified predator impact (PI) index (Menge 1983). Despite the complicated relationships between consumption by the various crab predators and habitat, when PI was compared with field values of habitat complexity, a significant, two-segmented piecewise regression suggested that PI decreases with increasing habitat complexity to some threshold level of seagrass shoot density (between 200 and 300 shoots m^{-2}), above which, PI no longer declines. It has been suggested in the literature that the relationship between predation and habitat complexity is non-linear (Heck and Thoman 1981, Gotceitas and Colgan 1989, Heck and Orth 2006), and despite some of the mesocosm experiments showing linear relationships between consumption and habitat, the PI model generally supports the literature. Further, the linear relationships observed in mesocosm studies may be due to not having enough different levels of complexity (Gotceitas and Colgan 1989).

In addition to identifying a threshold habitat complexity level, the model identified mud crabs as the predator most likely responsible for the bulk of the scallop predation in Shinnecock Bay. Mud crabs have been implicated as major consumers of small bivalves (Whetstone and Eversole 1991, Streib et al. 1995, Ray-Culp et al. 1999, Silliman et al. 2004, Kulp et al. 2011), including scallops (Tettelbach 1986, Carroll et al. 2012), where they can access post-set scallops which bysally attach in the seagrass canopy (Pohle et al. 1991). At least one other study has found that the potential predatory impact of mud crabs was the highest among decapod crustaceans examined and attributed that impact to their two order of magnitude higher densities in the field (Rindone and Eggleston 2011). As previously mentioned, mud crabs were 1 to 3 orders of magnitude more abundant than other crabs, contributing to the high predator impact value for mud crabs. While the larger crabs were capable of higher rates of per capita consumption, in simulated predator extinctions, it has been suggested that when biomass and densities of smaller mud crabs increases to the same level of biomass as the larger decapods, they are capable of the same level of consumption (O'Connor et al. 2008).

The model also correctly predicted the site of highest scallop densities. Cormorant Point (CP), with scallop densities exceeding 6 individuals m^{-2} , had the lowest calculated PI (3.00). A combination of factors – high habitat complexity, low relative predator density, highest scallop settlement – likely led to the highest on-bottom scallop densities at CP. However, PI values >1 indicate that more scallops can be consumed than are available to settle so the high PI calculated from this study suggests some limitations to the model. Despite limitations, the PI model suggests that scallops should not be found at the other study sites. Indeed, in over 40 one-meter squared suction samples at sites other than Cormorant Point (the only site with considerable scallop density), only 7 scallops were recorded (0.175 scallops m^{-2}). Regardless, PI values at all

sites being >1 suggest that predation may be slightly overestimated, but this model is still useful conservative estimate of predator impact.

Differences between the values of PI and the presence of scallops suggest there are limitations within this model, and those should be considered in future studies. One issue is with the predicted values for scallop settlement. For the purpose of this study, the numbers of spat per bag were extrapolated to a per m² value by taking the cross-section of the Netron mesh used in spat collectors, and a cumulative value was derived by adding the projected scallop settlers across all collection dates. This value is likely an underestimate; it is not known how settlement to the bag translates to settlement on the bottom, and there were scallops on the bottom at 4 of the study sites which according to the PI equation suggests more should be settling than predicted. A second major issue is using mesocosm predation rates and translating them to the field. A number of issues arise in mesocosms: (1) the inability of predators and prey to move into new areas, (2) predator and prey densities, (3) the sizes of animals used and (4) varied conditions between the lab and field (Ray-Culp et al. 1999).

It is possible that values of consumption could be overestimates, as exclusively adult, male crabs were used and scallop prey abundances were high (32 m⁻²), relative to values observed in the field (up to 22m⁻² in this study). While settlement may occur at much higher densities (hundreds; Eckmen 1987, Carroll et al., 2012), having high densities of scallops in mesocosms could influence the predation by crabs, many of which exhibit density-dependent predation (Eggleston et al. 1992, Seitz et al. 2001). Despite the scallop's ability to swim as an escape response, crab consumption of scallops is determined largely by encounter rates (Barbeau and Scheibling 1994), and thus mesocosm densities being higher than field densities of scallop prey could have increased encounter rates. In addition, the mesocosm experiments also did not

address alternative prey, as the presence of alternative prey may have reduced consumption of scallops in the field.

While it is likely that predation from mesocosms is an overestimate based on PI values, the possibility exists that predation could also be an underestimate for field consumption. During field surveys, 7 other decapod species were collected that may consume post-settlement scallops (see results). Further, two other decapods that were not observed in the suction surveys, the flat claw hermit, *Pagurus pollicarus*, and the Asian shore crab, *Hemigrapsus sanguineus*, also occur in this system. Five species of molluscivorous gastropods collected during surveys, as well as Forbes' sea stars, *Asterias forbesi*. Also, while little is known about finfish predators on scallops, at least 5 fish regularly encountered in Shinnecock Bay are capable of consuming scallops, including blackfish (*Tautog onitis*), cunner (*Tautoglabrus adspersus*), porgies (*Stenotomus chrysops*), toadfish (*Opsanus tau*) and northern puffers (*Spheroides maculaus*). It is possible that all of these predators might contribute to the extremely high predation potential for scallops.

Despite the limitations, the PI model is still a valuable tool. Menge (1983) also found limitations in the PI but suggested the results were promising. In Menge's rocky shore system, he investigated mussels which set and persist at much higher densities than scallops, and so the PI values from his study were <1 (Menge 1983). Regardless, Menge (1983) was unable to find any significant relationship between predator impact and prey density. While there are limitations with how I modified the index, it can be considered an improvement over Menge's PI for 2 reasons. First, despite overestimates in the overall PI values, the current index successfully predicted the site with the highest scallop densities. Second, the current index also indicates a

threshold level of habitat complexity below which PI increases, which is supported by the literature (Heck and Orth 2006).

There are three areas where the model can be improved in order to become a better predictor of prey density. A first improvement would be to more accurately assess scallop settlement to the bottom. It is likely that densities of scallops in this study were being underestimated; Tettelbach (1986) reached a similar conclusion in his predation study. The second improvement would be to incorporate the predator's relationship with shoot complexity into the model. Currently, this index only uses the relationship between scallop consumption and habitat complexity. More information should be incorporated, such as both search and handling time for various predators at different complexities, more levels of habitat complexity, and the relationship between predator density and habitat complexity in the field. Finally, size is a major factor that affects scallop predation (Tettelbach 1986, Bishop et al. 2005, Carroll et al. 2010). In a similar attempt at a predation index, Tettelbach (1986) was able to show strong effects of scallop size on its potential predation by a similar suite of predators to those tested here. Given the scallops ability to grow quickly, this issue of size should be better incorporated into future attempts at the PI.

In spite of limitations, this study supports the theory that scallop populations in New York are recruitment-limited (Tettelbach and Smith 2009), although it appears that, at least in Shinnecock Bay, this limitation could be due to both intense predation and low larval supply. While low adult population densities have been implicated as the major contributing factor to lack of a natural recovery over the last 15 years (Tettelbach and Smith 2009, Tettelbach et al. 2010), and major restoration efforts have led to enhanced larval settlement in the Peconic estuary (Tettelbach and Smith 2009), no such restoration has been undertaken in the Long

Island's South Shore estuaries. At some sites in this study, however, spat settlement was as high as some restoration basins in the Peconics (Tettelbach et al., *in review*). Thus, recruitment-limitation in Shinnecock Bay may not be solely a result of low larval supply, but may also be due to intense post-settlement mortality from predation.

Conclusions

A combination of high habitat complexity, low predator density – including the lowest densities of mud crabs across all study sites – and high scallop settlement contributed to ‘high’ on-bottom scallop densities at Cormorant Point. Seagrass coverage averaged 99% throughout the CP study site, approximately 610 shoots per square meter, and mesocosm experiments suggested that all predators tested were impacted at this level of complexity. Even though the density of the four target predator species combined was 45 ± 6 individuals m^{-2} , this was the lowest among the six sites examined, and scallop settlement at CP was highest, with an average around 50 scallops per collector across the whole season, and a peak settlement of 200 individuals per collector. All other sites had lower or no seagrass, higher numbers of predators, and lower settlement, which combined for essentially zero scallops across the other study sites. While imperfect, the predator impact model may be valuable, especially as a rudimentary tool for informing restoration efforts, especially as it suggests that predator field should be considered when planning for restoration (Tettelbach et al. 1987, 2003).

While there are limitations to the scope of this study, as well as other potential factors that might affect successful scallop recruitment, these results suggest predation may be limiting recruitment and that predation is likely being driven primarily by mud crabs. However, it is impossible to determine whether the dominant predators are capable of driving scallop abundance to zero without investigating the functional response, especially as a function of

habitat. Other environmental variables can also contribute to low abundances, including currents, temperature and food availability, although they were not examined here. Still, in the absence of other variables, this study suggests that predation is structuring the scallop population in Shinnecock Bay, the predation is impacted by habitat at a low threshold value, and the dominant predator is small. Therefore, in addition to normal criteria for restoration site selection, such as habitat presence and historical data, the predator field – the players and densities – should be considered an important factor for restoration efforts.

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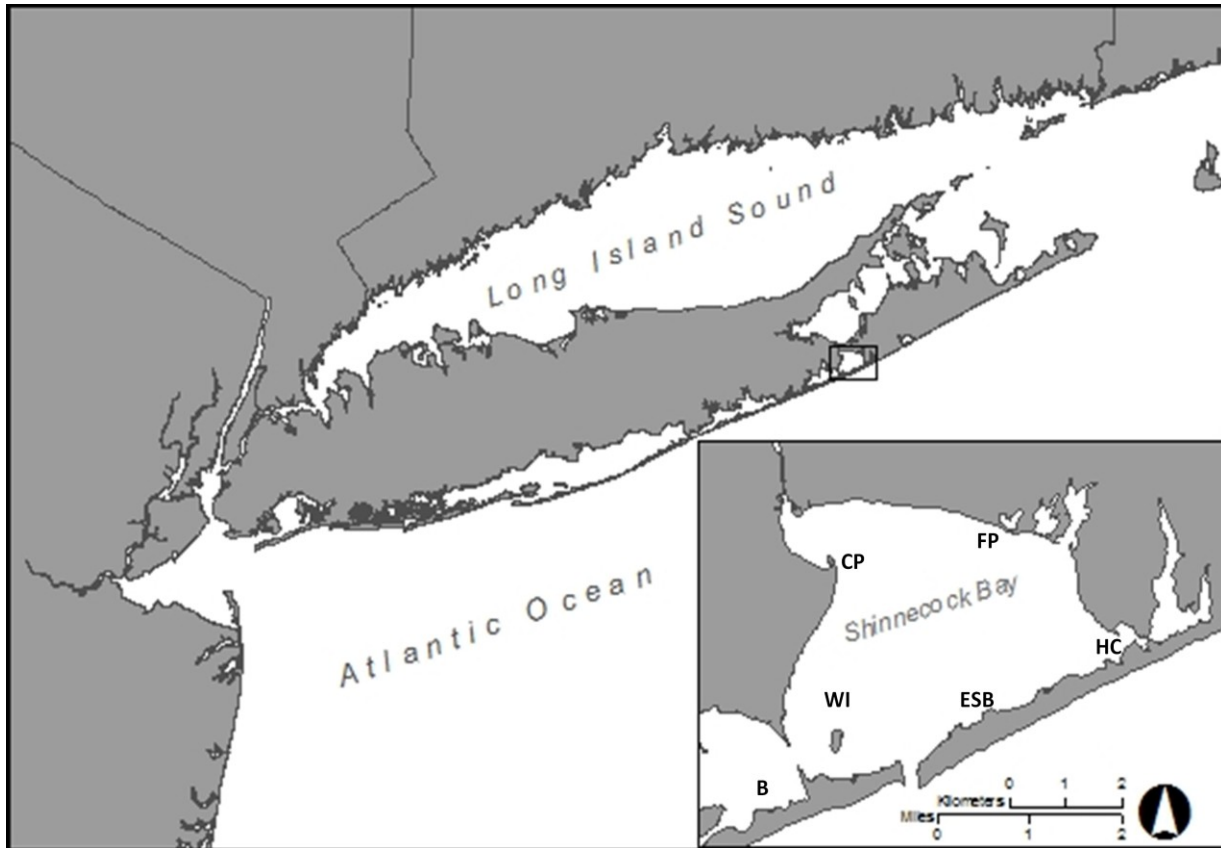


Figure 1: Map of the study location, Shinnecock Bay, located on the east end of Long Island, New York, with the 6 study sites. CP is Cormorant Point, WI is Warner's Island, B is the Bridge, ESB is East Shinnecock Bay, HC is Heady Creek and FP is Far Pond.

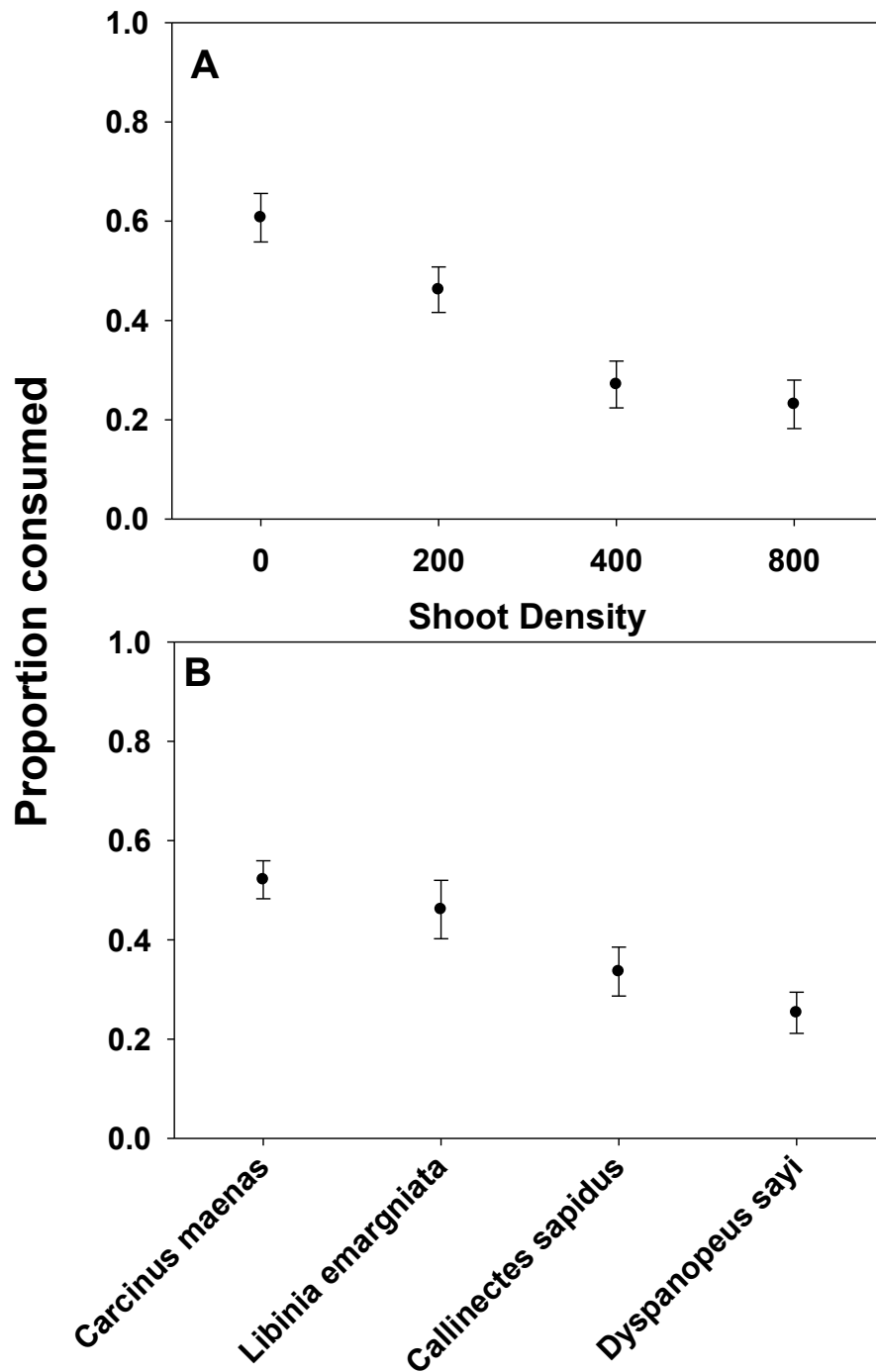


Figure 2: Proportion of scallops consumed at each shoot density across all predators tested (A) and proportion consumed per crab across all habitat treatments (B). Error bars are \pm SE.

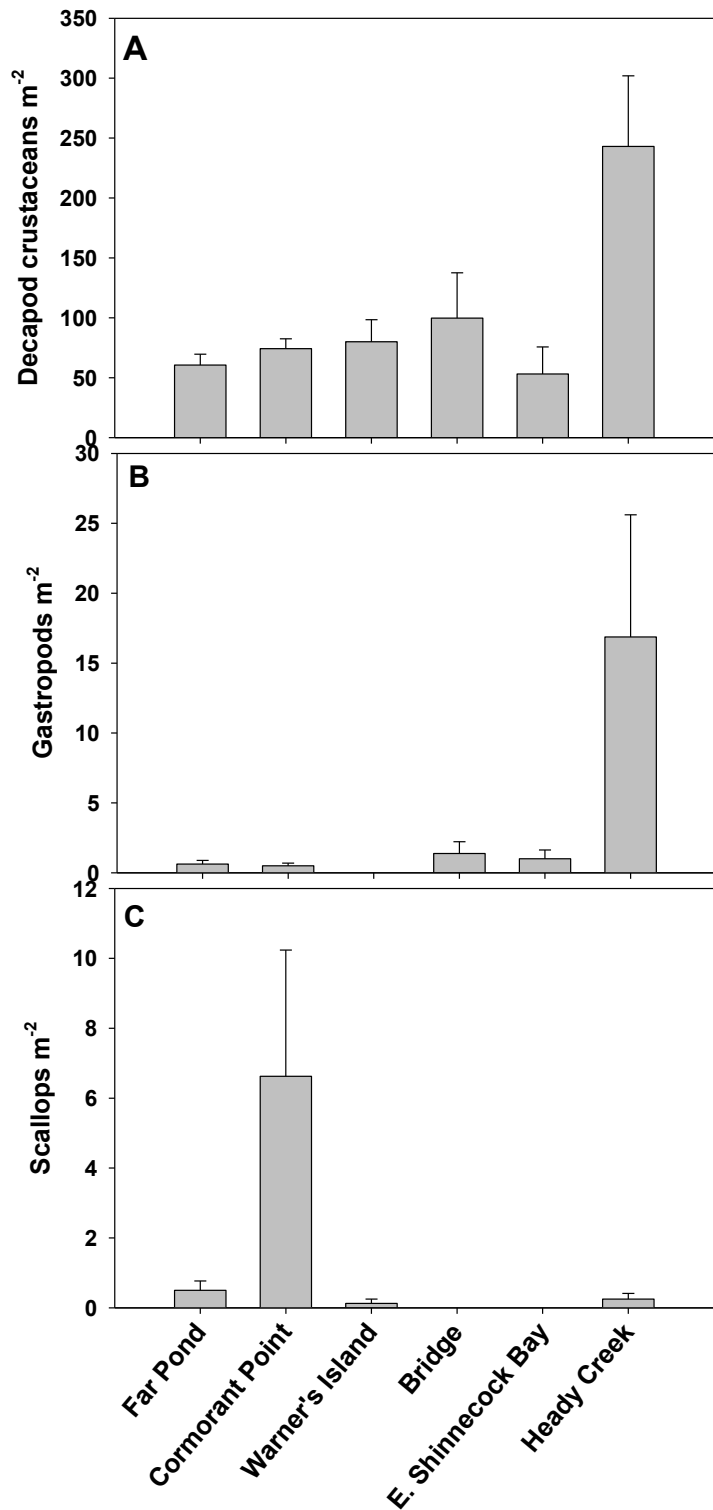


Figure 3: Mean density (+SE) of decapod crustaceans (A), gastropod mollusks (B), and bay scallops (C) at each of the 6 field survey sites across all 4 suction survey collections.

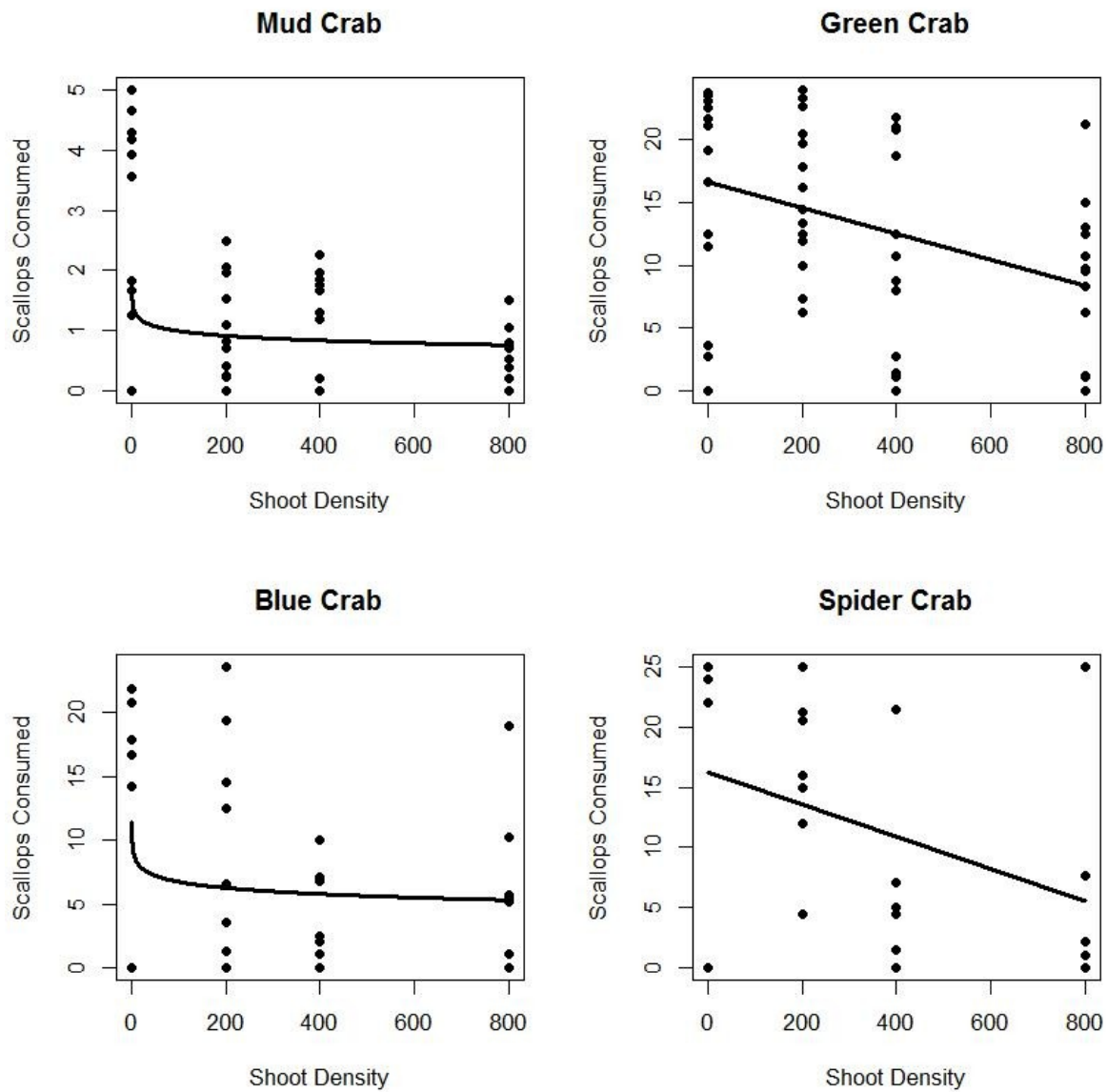


Figure 4: Total scallops consumed for each crab species at each habitat complexity. Closed circles represent individual replicates. The regression lines indicate the best fit regressions using Aikake’s Information Criterion (AIC) and model weights (W_i) values. Mud crabs: scallops consumed = $-0.1123 \cdot \log(SS) + 1.5126$, $n = 48$, residual sum of squares (RSS) = 1543, AIC = 308.7943, $W_i = 0.6274$. Green crabs: scallops consumed = $-0.0103 \cdot SS + 16.625$, $n = 56$, RSS = 2834, AIC = 384.6683, $W_i = 0.6777$. Blue crabs: scallops consumed = $-0.686 \cdot \log(SS) + 9.9073$, $n = 36$, RSS = 1520, AIC = 231.6936, $W_i = 0.5691$. Spider crabs: scallops consumed = $-0.01337 \cdot SS + 16.244$, $n = 24$, RSS = 1961, AIC = 179.7842, $W_i = 0.5433$.

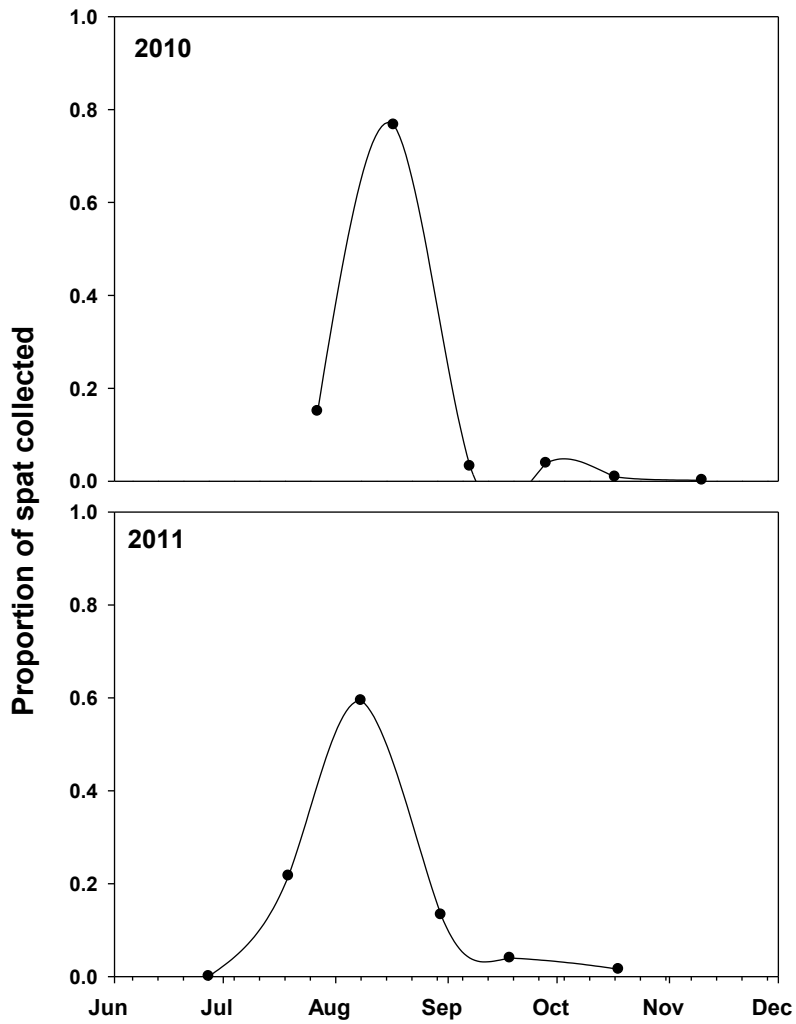


Figure 5: The proportion of total scallop spat collected at each sampling date across all sampling sites for the entire sampling season in 2010 (top) and 2011 (bottom). Scallop spat were collected via spat collection bags, sampled every 3 weeks at 6 study sites within Shinnecock Bay, NY.

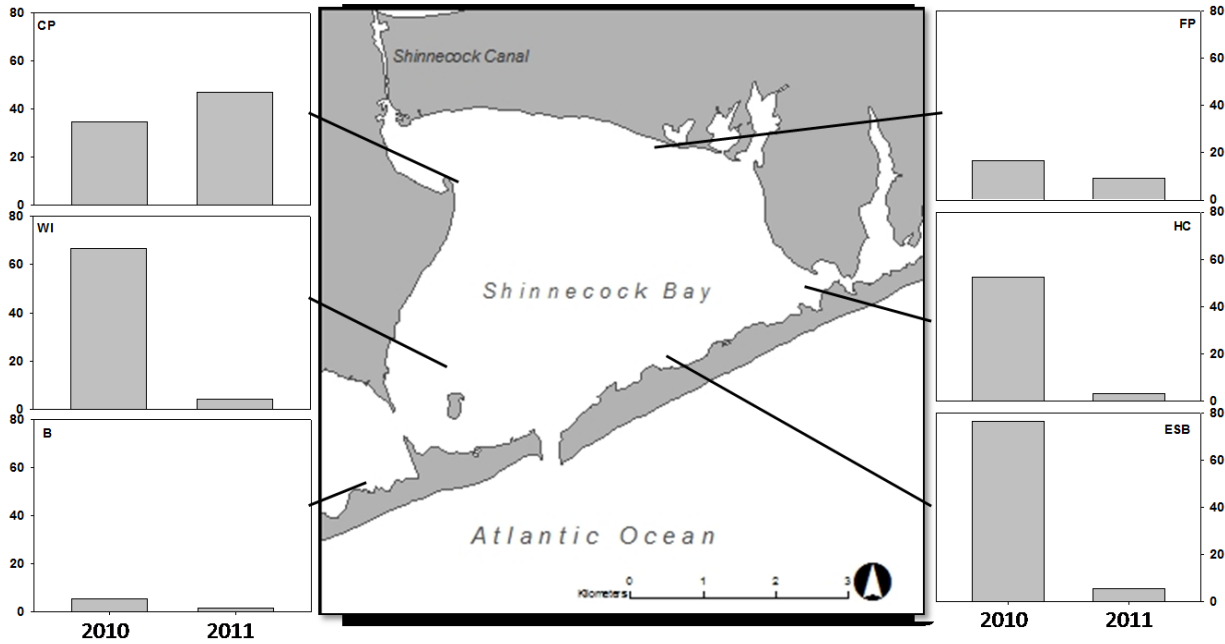


Figure 6: Mean number of scallop spat per collection bag across the entire sampling season (May-October) for each of the 6 study sites in 2010 and 2011. CP is Cormorant Point, WI is Warner's Island, B is Bridge, FP is Far Pond, HC is Heady Creek, and ESB is East Shinnecock Bay. Error bars are not presented because across the season, settlement goes from zero, peaks and goes back to zero; the seasonal nature of settlement would make error bars so large as to make the data bars so small in the figures it would be difficult to see differences.

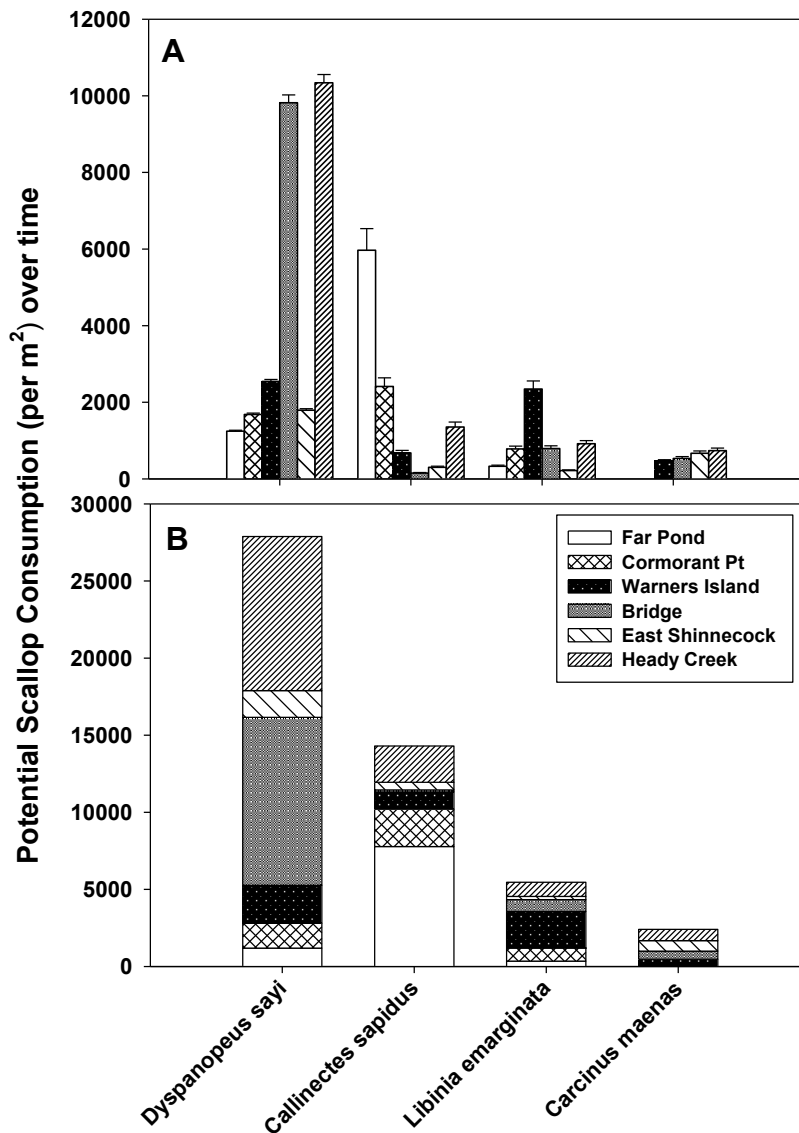


Figure 7: Potential scallop consumption per m^2 over the period of time scallops are susceptible to predation by each predator (47-49d for mud crabs, *Dyspanopeus sayi*, 72-87d for blue crabs, *Callinectes sapidus*, and 117-140 days for both spider crabs, *Libinia emarginata*, and green crabs, *Carcinus maenas*, based on regressions for per capita consumption from the mesocosm data and predator densities at each site. Consumption by each predator for each site (A) and a stacked bar plot illustrating the potential numbers of scallops consumed by each predator with the stacked bars representing each study site.

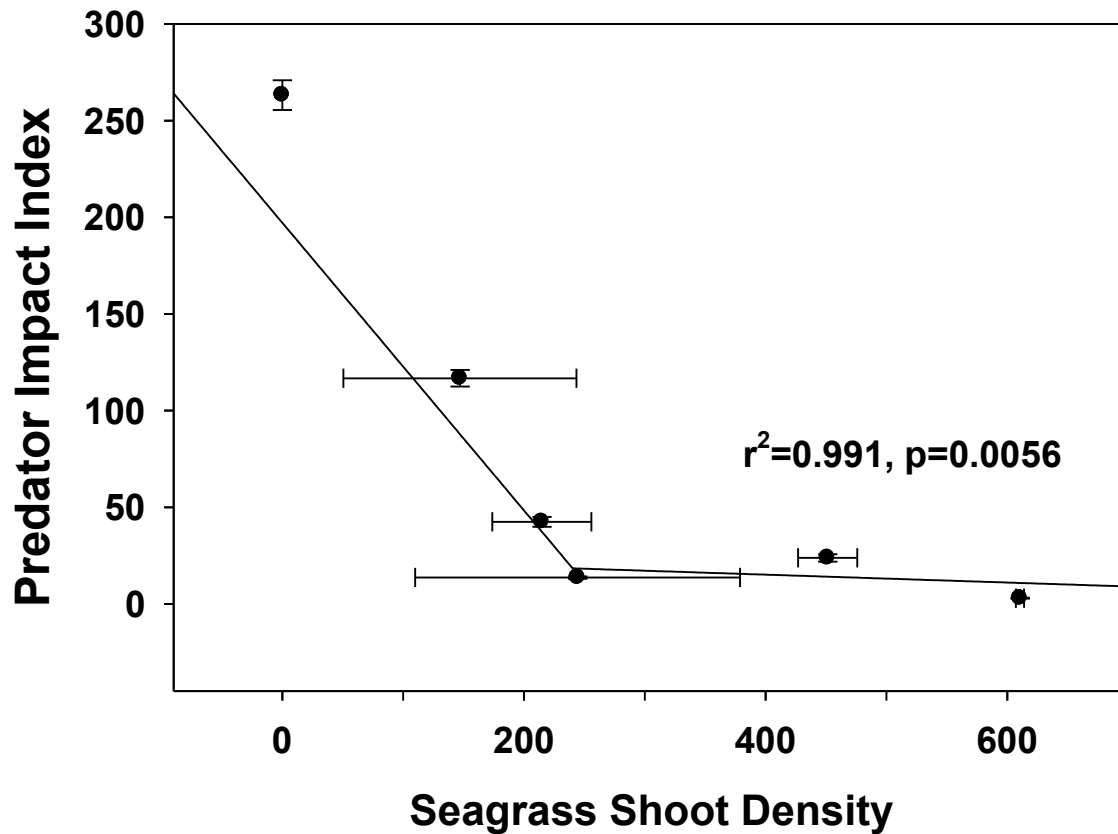


Figure 8: Significant piecewise, or segmented, regression showing the relationship between predator impact (PI) and habitat complexity in the field. Circles represent study sites, and error bars are \pm SE. Predator impact is the relationship between the per capita consumption of each predator as a function of the habitat complexity at each site, the density of predators at each site, the number of days scallops are vulnerable to each predator and an estimate of scallop settlement from spat collector data, and seagrass shoot density values were from bottom surveys at each of the 6 study locations, in shoots m⁻².

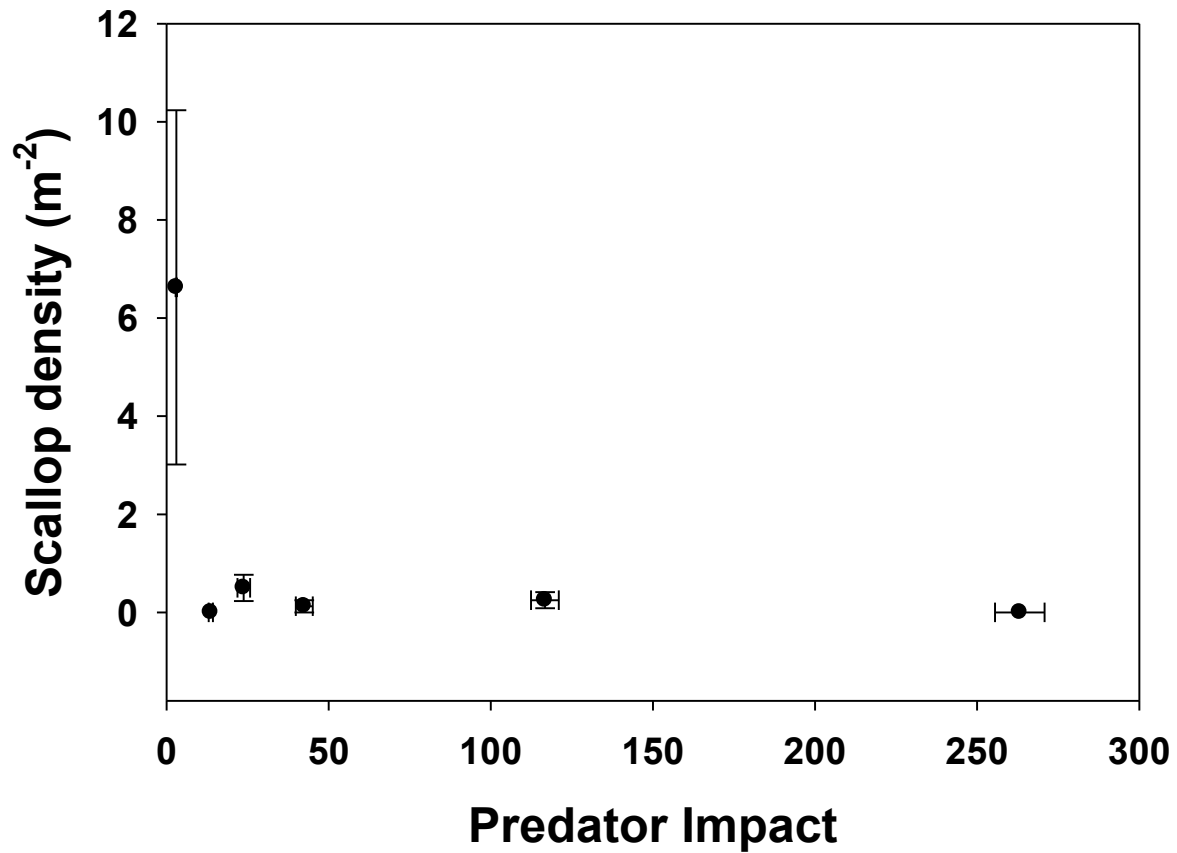


Figure 9: Relationship between mean on-bottom scallop density across the whole season and predator impact (PI), with circles representing values for study sites and error bars are \pm SE. Scallop densities were calculated from suction dredge samples and the predator impact is the relationship between the per capita consumption of each predator as a function of the habitat complexity at each site, the density of predators at each site, the number of days scallops are vulnerable to each predator and an estimate of scallop settlement from spat collector data.

Table 1: Coordinates for each study location in Shinnecock Bay, NY.

Site	Latitude	Longitude
Far Pond	40.87842	-72.4582
Cormorant Point	40.87385	-72.4904
Warner's Island	40.85149	-72.4911
Bridge	40.84188	-72.5048
East Shinnecock Bay	40.85655	-72.4553
Heady Creek	40.85946	-72.4343

Table 2: Predator identity, size, scallop size and environmental conditions for each trial of the mesocosm experiments.

Trial	Date	Predator	Predator Size (mm)	Scallop Size (mm)	Temperature (°C)	Salinity (PSU)
1	8/19/2011	<i>Dyspanopeus sayi</i>	17-22	14-18	24.0-24.6	29.1-29.2
2	8/20/2011	<i>Dyspanopeus sayi</i>	17-22	14-18	24.2-24.8	27.3-27.6
3	8/25/2011	<i>Dyspanopeus sayi</i>	17-23	10-15	25.9-26.4	25.4-25.6
4	9/1/2011	<i>Carcinus maenas</i>	69-81	15-18	24.8-25.4	28.1-28.3
5	9/2/2011	<i>Carcinus maenas</i>	65-70	15-18	25.2-25.4	28.5-28.6
6	9/12/2011	<i>Carcinus maenas</i>	63-73	17-20	23.8-24.3	28.4-28.7
7	9/13/2011	<i>Carcinus maenas</i>	66-76	18-21	25.2-26.0	26.5-26.7
8	9/14/2011	None	NA	17-21	24.9-25.6	26.7-27.0
9	9/20/2011	<i>Libinia dubia</i>	90-102	18-22	19.8-20.2	30.5-30.6
10	9/23/2011	<i>Libinia dubia</i>	84-103	18-22	21.4-21.5	25.9-26.2
11	9/26/2011	<i>Callinectes sapidus</i>	120-139	23-25	23.4-23.7	28.9-29.0
12	9/28/2011	<i>Carcinus maenas</i>	66-78	23-25	21.8-22.1	28.1-28.5
13	9/29/2011	<i>Callinectes sapidus</i>	118-133	20-25	21.7-22.2	25.7-26.1
14	10/3/2011	<i>Callinectes sapidus</i>	124-132	20-25	18.6-19.3	28.0-28.2
15	10/12/2011	<i>Dyspanopeus sayi</i>	18-24	13-16	18.3-18.6	29.6-29.7

Table 3: Days to vulnerability for scallops based on growth rates, maximum size of scallop consumption from Tettelbach (1986) and maximum carapace width of decapods from field surveys.

Predator	Max CW from surveys	Max size of scallop	Days vulnerable 2.5mm/wk	Days vulnerable 3 mm/wk
<i>Dyspanopeus sayi</i>	22	19	49	47
<i>Callinectes sapidus</i>	77	31	87	72
<i>Carcinus maenas</i>	59	50	140	116
<i>Libinia dubia</i>	67	50	140	116

Table 4: Percent cover of different habitat types at each site using gridded quadrat surveys for habitat. Shell hash was dead *Mytelus edulis* shells, Crepidula was living *Crepidula fornicate*, Eelgrass was *Zostera marina*, Red Macro was a mixture of red macroalgae, including *Agardhiella* sp., *Gracilaria* sp., and *Spyridia* sp., Ulva represented *Ulva lactuca*, Codium was *Codium fragile*, and red sponge was *Microciona prolifera*.

Site	Structured Habitat Type						
	Shell Hash	Crepidula	Eelgrass	Red Macro	Ulva	Codium	Red Sponge
Far Pond	0	0	76.0	13.3	0	0	0
Cormorant Pt	0	0	99.3	0.2	0	0	0
Warners	0	0	41.3	11.7	0.2	0	0
Bridge	60.2	0	0	0.2	0.2	0	0
E. Shinnecock Bay	0	0	45.7	1.7	0.2	0	0
Heady Creek	2.5	84.5	0	9.2	1.8	31.5	3.5

Table 5: Table of organisms counted from suction sampling at the 6 field survey sites, separated into taxonomic groups.

Group	Scientific name	Common name	Total	% of group	% of total
Decapods	<i>Dyspanopeus sayi</i>	Mud crab	3920	68.52	47.22
	<i>Hippolyte zostericola</i>	Zostera shrimp	835	14.60	10.06
	<i>Crangon semptemspinosa</i>	Sand shrimp	278	4.86	3.35
	<i>Pagurus longicarpus</i>	Long-clam hermit	272	4.75	3.28
	<i>Callinectes sapidus</i>	Blue crab	187	3.27	2.25
	<i>Palaemonetes sp.</i>	Grass shrimp	133	2.32	1.60
	<i>Cancer irrorata</i>	Rock crab	45	0.79	0.54
	<i>Libinia emarginata</i>	Spider crab	27	0.47	0.33
	<i>Carcinus maenas</i>	Green crab	10	0.17	0.12
	<i>Ovalipes ocellatus</i>	Lady crab	9	0.16	0.11
	<i>Portunus gibbesii</i>	Blue swimmer crab	3	0.05	0.04
	<i>Portunus spinimanus</i>	Blue swimmer crab	2	0.03	0.02
Gastropods	<i>Illyanasa obsoleta</i>	Mud snails	1542	87.22	18.58
	<i>Urosalpinx cinerea</i>	Oyster drill	107	6.05	1.29
	<i>Eupleura caudate</i>	Thick-lip drill	53	3.00	0.64
	<i>Anachis sp.</i>	Dove snails	41	2.32	0.49
	<i>Illyanasa trivittata</i>	3-lined mud	17	0.96	0.20
	<i>Litorina littorea</i>	Litorine	5	0.28	0.06
	<i>Busycotypis canaliculatus</i>	Knobbed Whelk	1	0.06	0.01
	<i>Busycon carica</i>	Channeled Whelk	1	0.06	0.01
	<i>Euspira heros</i>	Moon snail	1	0.06	0.01
Bivalves	<i>Argopecten irradians</i>	Bay Scallop	127	45.52	1.53
	<i>Mercenaria mercenaria</i>	Hard clam	92	32.97	1.11
	<i>Mya arenaria</i>	Softshell clam	60	21.51	0.72
Fish	<i>Gobiosoma bosc</i>	Naked goby	318	85.25	3.83
	<i>Syngnathus fuscus</i>	Northern Pipefish	22	5.90	0.27
	<i>Pseudopleuronectes americanus</i>	Winter flounder	14	3.75	0.17
	<i>Myoxocephalus aeneus</i>	Grubby	9	2.41	0.11
	<i>Gasterosteus aculeatus</i>	stickleback	8	2.14	0.10
	<i>Opsanus tau</i>	Toadfish	1	0.27	0.01
	<i>Tautoglabrus adspersus</i>	cunner	1	0.27	0.01
	Echinoderms	<i>Asterias sp.</i>	Sea star	153	95.63
<i>Sclerodactyla briareus</i>		Sea cucumber	7	4.38	0.08

Table 6: Mean predator density for the four target species at each site (\pm SE).

	Far Pond	Cormorant Pt	Warners Island	Bridge	East Shinnecock	Heady Creek
<i>Dyspanopeus sayi</i>	31.25 \pm 4.45	44.00 \pm 12.12	58.38 \pm 16.26	89.25 \pm 38.37	41.63 \pm 19.16	222.50 \pm 61.33
<i>Callinectes sapidus</i>	13.13 \pm 3.71	5.50 \pm 1.51	1.38 \pm 0.71	0.13 \pm 0.13	0.62 \pm 0.26	2.63 \pm 2.21
<i>Carcinus maenas</i>	0	0	0.25 \pm 0.16	0.25 \pm 0.16	0.37 \pm 0.26	0.38 \pm 0.26
<i>Libinia dubia</i>	0.25 \pm 0.16	0.75 \pm 0.52	1.38 \pm 0.82	0.38 \pm 0.18	0.13 \pm 0.13	0.50 \pm 0.26

Table 7: Regression types, number of parameters, number of samples (n), Akaike's Information Criterion (AIC), Δ AIC and model weights (W_i) for regressions run using the nls2 package in R for the total scallops consumed by each predator as a function of habitat complexity. Lowest AIC and Δ AIC, as well as highest W_i indicate the model of best fit.

		# parameters	n	AIC	Δ AIC	W_i
Mud crabs	Linear	2	48	158.9288	4.6406	0.061645
	Logarithmic	2	48	154.2883	0	0.627465
	Logistic	3	48	155.6928	1.4045	0.31089
Green crabs	Linear	2	56	384.6683	0	0.677651
	Logarithmic	2	56	390.6513	5.983	0.034026
	Logistic	3	56	386.3774	1.7091	0.288323
Blue crabs	Linear	2	36	235.7369	4.0433	0.075367
	Logarithmic	2	36	231.6936	0	0.569081
	Logistic	3	36	232.6343	0.9407	0.355552
Spider crabs	Linear	2	24	179.7842	0	0.543308
	Logarithmic	2	24	181.8584	2.0742	0.192592
	Logistic	3	24	181.2269	1.4427	0.2641

Table 8: Individual consumption rates (\pm SE) at each shoot density and a line of best fit regression, determined by Aikaike's Information Criterion (AIC) for consumption as a function of habitat.

Predator	Shoot density				Regression
	0	200	400	800	
<i>Dyspanopeus sayi</i>	2.53 \pm 0.56	1.03 \pm 0.23	0.98 \pm 0.28	0.43 \pm 0.17	# Eaten=-0.1123*ln(SS)+1.5126
<i>Callinectes sapidus</i>	16.05 \pm 2.86	9.07 \pm 2.94	3.29 \pm 1.25	5.18 \pm 2.09	# Eaten=-0.6857*ln(SS)+9.9073
<i>Carcinus maenas</i>	15.97 \pm 2.26	15.71 \pm 1.56	12.11 \pm 2.28	8.50 \pm 1.65	# Eaten=-0.0103*(SS)+16.625
<i>Libinia dubia</i>	16.00 \pm 5.08	16.78 \pm 3.06	6.47 \pm 3.15	7.17 \pm 4.24	# Eaten=-0.01337*(SS)+12.746

Table 9: Mean bottom densities (\pm SE) of scallops, cumulative settlement (scallops m^{-2}) across all collections, and calculated predator impact (PI) at each site.

	Density	Cumulative Settlement	Total PI
Far Pond	0.50 \pm 0.27	317	23.8
Cormorant Pt	6.62 \pm 3.61	1621	3.0
Warners Island	0.13 \pm 0.13	143	42.5
Bridge	0	47	263.2
East Shinnecock	0	218	13.7
Heady Creek	0.25 \pm 0.16	114	116.7

Chapter Seven

Conclusion

Conclusion

Seagrasses provide a variety of ecosystem services and contribute to the high productivity of many coastal systems. One of the most studied aspects of seagrass ecology is the creation of critical habitat formed by the complex 3D canopy. Typically, these studies have investigated how the structure provided by seagrass affects recruitment, growth and survival of a variety of fin and shellfish species of commercial, recreational or ecological importance, by comparing metrics between grass and unvegetated areas. Investigations of patterns in abundance and survival between vegetated and barren substrates demonstrated higher abundance and survival of a variety of species in the structured habitat, leading to seagrass being considered a “nursery” habitat (Heck and Orth 1980, Orth et al. 1984, Bell and Westoby 1986, Orth 1992, Heck et al. 1995, Irlandi et al. 1995, Irlandi 1997, Bell et al. 2001, Heck et al. 2003, Ford et al. 2010, Warren et al. 2010).

More recently, studies have begun to apply terrestrial landscape-scale principles to marine habitats, and seagrass, which tends to exist as a mosaic of patches due to both natural and anthropogenic forcing (Bostrom et al. 2006). In the terrestrial realm, patchy and fragmented habitats tend to be considered less desirable, and that general idea has been the basis of many marine seagrass seascape studies. It has been held that fragmentation of seagrass habitats would result in negative responses by associated fauna, although this is largely inherited from terrestrial literature. However, in many instances, fauna actually respond positively to patchy seagrass habitats (Eggleston et al. 1998, Hovel and Lipcius 2001, Bologna and Heck 2002, Jelbart et al. 2006, Macreadie et al. 2009, Macreadie et al. 2010a), suggesting the idea that large, continuous patches are better than small patches has little support in the scientific literature. In a recent review, Bostrom et al (2006) suggested that fragmentation was not likely to have overall

negative consequences if 1) there are abundant patches with high connectivity, 2) edge effects are not central to the species being studied, and 3) there is unrestricted movement between suitable patches.

Additionally, a number of seagrass associated species are often typically found in other structured habitats – salt marshes, mangroves, oyster reefs, macroalgae, etc. (Sogard 1992, Heck et al. 1995, Glancy et al. 2003, Hosack et al. 2006). As habitat fragments and declines, edge habitats provide opportunities for other species to move in, including invasive species (Fagan et al. 1999). When seagrass declines, it is sometimes replaced by other structured habitat, including invasive macroalgae, such as *Codium fragile* in New York. Many studies investigating the impacts of macroalgae, particularly invasive species, on fauna typically do so relative to unvegetated sediment (Gribben and Wright 2006a, Gribben et al. 2009), while few compare between multiple structurally complex habitats. This is especially the case in the invasive marine macrophyte literature. However, research which compares demographics between structurally complex native and invasive habitats, such as this research, suggests the habitat has similar value.

The general conclusions from this study suggest two major shifts from current paradigms in marine ecological literature. First, fragmented seagrass meadows may be beneficial for populations of associated fauna, such as bay scallops. Patchy seagrass leads to increased settlement of bivalve larvae (Chapter 2) and enhanced growth of individuals even in the face of high predation rates in this zone (Chapter 3). Further, the similar density of scallops across a seagrass landscape in addition to increased growth suggests that scallop population growth is reliant on these edge habitats. Second, invasive species may facilitate native species. In the absence of seagrass, this research has demonstrated that an invasive macroalgae may facilitate

survival of typically seagrass-associating fauna (Chapter 4). In addition, the prevailing literature which examines individual levels of fitness suggests that species, in particular bivalves, experience reduced fitness in non-native vegetation. The results from this dissertation, however, show opposite results; site-specific results for scallop survival, growth and condition were not different between seagrass, the preferred habitat, and *Codium fragile*, the invader (Chapter 5), and the shortcoming of previous studies are the failure to compare between complex habitats. These results, in sum, provide valuable information for management and restoration efforts.

Seagrass landscapes

Seagrasses form critical subtidal habitats for many marine species, and their ecological importance has been widely examined. Despite their ecological importance, seagrass habitats have been experiencing both fragmentation and loss (Orth et al. 2006)(Figure 1). Fragmentation can result from natural processes, such as growth and patch formation (Hemminga and Duarte 2000), hydrodynamic activity (Fonseca and Bell 1998, Fonseca et al. 2002), depth (Robbins and Bell 1994), and animal foraging (Orth 1975, Hovel and Lipcius 2002, Rivers and Short 2007, Lal et al. 2010). However, due to their existence in shallow, coastal systems, seagrass meadows are also threatened by numerous anthropogenic activities which physically remove and fragment seagrass including improper boating resulting in propeller scars (Bell et al. 2002, Uhrin and Holmquist 2003), destructive fishing practices (Peterson et al. 1987, Boese 2002, Bishop et al. 2005b), anchoring (Walker et al. 1989), and construction of docks (Burdick and Short 1999).

The value and vulnerability of seagrass, and its fragmented nature, lend well to the application of terrestrial landscape principles to the marine realm (Robbins and Bell 1994). One of the main concerns and most studied concepts in landscape ecology are edge effects. Habitat edges influence both species abundance and ecological processes (Harris 1988, Fagan et

al. 1999, Ries and Sisk 2004), and as the fragmentation increases, the proportion of edge also increases (Murcia 1995, Smith et al. 2008). The early consensus in landscape ecology is that ecotones – transition zones between two habitats – were favorable habitats, enhancing species abundance and diversity, but more recently, edges are considered to have detrimental consequences for species found there (Ries et al. 2004, Ries and Sisk 2004), even being considered ‘ecological traps’ (Ries and Fagan 2003, Robertson and Hutto 2006). Specifically, the literature suggests that habitat edges alter species interactions which lead to observed patterns; edges can differentially influence the movement of individuals, induce species mortality, facilitate cross-boundary subsidies, and create opportunities for novel interactions and invasions (Fagan et al. 1999).

While small patches, and patches with higher amounts of edge, have long been considered negative in the terrestrial realm, in seagrass systems, the single large or several small habitat patch debate has been considered for decades (McNeill and Fairweather 1993). In their study, McNeill and Fairweather (1993) suggested that there was higher abundance and diversity of organisms in two small patches of equal area to a single large patch. Despite these findings, the assumption is still that continuous meadows are better than small, isolated patches (Uhrin and Holmquist 2003, Tanner 2005, Horinouchi 2009, Macreadie et al. 2009). One reason is likely the strong, negative effect of predation. Predation risk may be elevated at patch edges because predators may focus foraging along edges, different predator types overlap at edges, and the habitat’s refuge value may be lower at edges (Chapter 2, 3; Smith et al. 2011b).

In over 50 seagrass edge effects studies, the most common negative effect is due to decreased survival at habitat edges (Chapter 2, 3; Bologna and Heck 1999, Selgrath et al. 2007, Gorman et al. 2009, Smith et al. 2011a) and in patchy habitats (Irlandi 1994, Irlandi et al. 1995, Irlandi

1997, Irlandi et al. 1999). However, the overall effects of edges and fragmented habitats in the seagrass literature has been variable across species investigated (Eggleston et al. 1998, Eggleston et al. 1999, Bell et al. 2001, Uhrin and Holmquist 2003, Healey and Hovel 2004, Tanner 2005, Macreadie et al. 2010a, Murphy et al. 2010). In reviews of seascape literature, both Connolly and Hindell (2006) and Bostrom et al. (2011) suggest that 70-77% of patch size studies showed no significant or inconsistent relationships and up to 85% of edge studies also showed no significant responses. My review of the literature agrees; responses to patch size and edge are variable, showing positive, negative and neutral responses (Table 1). A number of studies also demonstrated positive effects on faunal abundance and diversity (Bologna and Heck 2002, Tanner 2003, Jelbart et al. 2006, Smith et al. 2008, Warry et al. 2009, Bostrom et al. 2010, Moore and Hovel 2010, Smith et al. 2010, Arponen and Bostrom 2012), settlement (Bologna and Heck 2000, Bostrom et al. 2010, Macreadie et al. 2010a, Carroll et al. 2012), response to resources (Macreadie et al. 2010b), and growth (Chapter 3; Reusch 1998, Bologna and Heck 1999, Irlandi et al. 1999).

One potential reason for the variable responses to fragmented seagrass and edge effects may be in the different explanatory models for distribution within a seagrass landscape by Connolly and Hindell (2006), which I have matched to some papers from the literature to explain their observed response:

Disturbance – higher faunal densities in larger patches may be due to higher disturbance along seagrass edges and in small patches - (Uhrin and Holmquist 2003)

Encounter – rate of encounter with seagrass would lead to higher densities in smaller patches with greater P:A, either passive via larval dispersal (Chapter 3; Bologna and

Heck 2000, Macreadie et al. 2010a) or active via faunal movement (Eggleston et al. 1998, Eggleston et al. 1999, Macreadie et al. 2010a)

Food – higher food resources may lead to greater densities in larger patches and/or along seagrass edges (Bell et al. 2001, Macreadie et al. 2010b)

Predation – most common model, where predators are more prevalent along edges and/or have more access to the interior of small patches (Bologna and Heck 1999, Peterson et al. 2001, Selgrath et al. 2007)

Larval supply – higher densities in smaller patches and patch edges due to depositional processes (Orth 1992, Carroll et al. 2012)

Migration – mainly in larger, mobile fauna, explaining movements between habitats (Hammerschlag et al. 2010)

There are other reasons that might explain some of the variability in response to edge effects. First, some of the earlier studies which invoked edge effects based on the assumption that perimeter to area ratios increase as patch size decreases (Bell et al. 2001, Jelbart et al. 2006). While this is true if all the patches are similarly shaped, this is not always the case. Further, the earlier studies which invoked edge effects based on patch size were really investigating patch size effects and attributing differences to differing amounts of edge. In this way, patch size effects and edge effects were confounded (Ewers and Didham 2006). While some terrestrial literature suggests that patch size effects are just edge effects scaled up (Fletcher Jr et al. 2007), the degree to which patch size and edge are related is less understood. Certain studies have demonstrated that edge effects were not apparent unless patch size was taken into account, suggesting that small patches which are almost entirely edge to not show similar patterns as larger patches (Jelbart et al. 2006, Smith et al. 2010).

Further complicating the issue is the size of the edge. For this dissertation, a 1 meter distance from the hard edge was used to denote edge and core habitats, based on changes in hydrodynamics caused by the emergent structure (Peterson et al. 2004). Other studies use different edge scales based on the size of the organisms (Bologna and Heck 2002, Horinouchi 2009), although our understanding of how an organism perceived a habitat as homogenous is lacking (Bostrom et al. 2006). Differences in patch scale and edge scale likely also contribute to the equivocal edge effects results throughout the literature. Regardless, edge effects are best investigated by directly sampling edges and interiors (Bologna and Heck 2002, Hovel and Lipcius 2002, Jelbart et al. 2006), which is how I proceeded with this dissertation research (see Chapters 2, 3).

Another major reason for some of the variability is due to differences in investigating patterns versus processes (Chapter 2). Most edge effects studies have investigated patterns – patterns in faunal density, diversity, recruitment, etc. The problem with investigating patterns is that they also vary across sites and at regional scales, and on both diurnal and slightly longer temporal scales, which likely leads to the variable patterns. Predation is among the most commonly evoked mechanisms leading to observed patch scale and edge patterns. However, predation can also vary diurnally (Peterson et al. 2001) and seasonally, as well as across sites. Further, predation doesn't explain why densities might be highest along seagrass patch edges, since predation also tends to be highest along the edge, suggesting multiple processes as mechanisms driving observed patterns. Few studies have attempted to investigate multiple processes and potential trade-offs resulting from uneven distribution and abundance of organisms across and within patches.

Macreadie et al. (2010b), looked at the uneven distribution of pipefish across seagrass patches and were able to link pipefish abundance to resource distribution. The pattern in that study was that pipefish were more abundant along patch edges, despite significantly higher predation risk in this zone, attributable to differences in food supply – small, invertebrate food was more abundant at patch edges. When they added food to the interior of patches, pipefish distribution shifted; there was an even distribution of pipefish throughout the patch (Macreadie et al. 2010b). Bologna and Heck (1999) attempted to explain their observed pattern of high scallop density along seagrass patch edges to a trade-off between growth and survival. They observed that scallops placed in sand would swim towards seagrass, which has been shown in other studies as well (Hamilton and Koch 1996). By tethering scallops at different positions within a seagrass landscape, they investigated both survival and used survivors to estimate growth. Bologna and Heck (1999) then used these values in the context of a minimize risk to foraging efficiency (μ/f) model to determine why scallops would be more abundant along seagrass patch edges. While the results of Bologna and Heck (1999) did not show μ/f to be lowest at seagrass edges, their examination of an ecological trade-off within a landscape context was promising.

This dissertation research attempted to continue investigating the patterns and processes impacting bay scallops within a seagrass patch. First, the settlement, recruitment, and survival of bay scallops was investigated across a variety of seagrass patch treatments, with the expectation of observing significant edge effects (Chapter 2). By simultaneously collecting settlers and recruits on the same collectors, this dissertation demonstrated a ‘balance’ between positive and negative edge effects, resulting in a net neutral effect. However, this was only explained by breaking down the pattern in scallop recruitment into its 2 major processes – settlement and post-settlement loss. Scallop settlement was significantly enhanced along seagrass edges, regardless

of patch type, and likewise, survival was significantly enhanced within patch interiors. However, recruitment – the net result of settlement and post settlement loss – did not significantly vary from edge to center. The data suggest that edge effects are highly complex and result from many different processes. Another important aspect of this work suggests that seagrass edges may not represent ecological traps as habitat edges do in terrestrial studies (Chapter 2). Since no difference in recruitment was observed, and there is more edge than interior habitat, the bulk of the recruiting population occurred along the edge. Thus, at the population level, edges may enhance scallop populations, from a recruitment perspective.

While the recruitment study involved post-set scallops, this dissertation also investigated the ecological trade-off for scallops suggested by Bologna and Heck (1999). However, different from that study, I used artificial seagrass to control for confounding variables in natural patches – such as shoot density, leaf number, canopy height, size and shape – in order to examine differences in growth and survival of scallops placed across a seagrass landscape (Chapter 3). Despite different growth rates across the three years studied, the pattern in growth and condition remained the same – highest in unvegetated sediments, intermediate at patch edges and slowest in patch interiors, which suggests a biological cost for scallops associated with seagrass habitats (although growth rates for this study are among the highest reported in the literature, see Table 2). Survival of tethered scallops showed an opposite pattern, however, being highest in patch interiors and lowest over barren sediment, and thus showed a potential food-risk trade-off for the scallops in seagrass patches. Using the minimize μ/f model, and modified models to account for the non-zero refuge mortality and the biological cost for associating with the refuge habitat, I was able to demonstrate that scallops may be more abundant at habitat edges or remain in settlement habitats because the μ/f is minimized in this habitat (Chapter 3). Further, by looking

at the core area index (CAI), this dissertation also demonstrated low threshold values of CAI needed to enhance scallop survival, and that growth and survival intercept at a low CAI, suggesting that smaller and/or more complex shaped patches may maximize growth and survival.

Thus, small, isolated patches should not be assumed less valuable than larger, continuous patches. Patchy habitats and smaller patches might actually be beneficial for populations of some species. While it has been suggested by others that fragmented seagrass meadows may not adversely affect a number of species (Healey and Hovel 2004, Bostrom et al. 2006, Hirst and Attrill 2008), these studies look only at abundances and suggest that for opportunistic species that do not show density-area relationships, any seagrass patch, no matter how small, is better than no seagrass. However, as I have previously argued, studies rarely examine the processes leading to these relationships. In this dissertation, looking at both recruitment and a food-risk trade-off, the results demonstrated strong but opposing edge effects. Settlement and growth were higher along patch edges despite lower survival there. While the individual risk of predation is much greater along patch edges or in small patches, for scallop populations, patchy seagrasses may be better for two reasons; 1) having more edge habitat enhances scallop settlement, and despite higher mortality along the edge, numbers of recruits are the same (Chapter 2) or greater (Bologna and Heck 1999) at patch edges, and 2) scallop growth and condition is enhanced at patch edges relative to interiors, and growth and condition of individuals at the center of patches increases as CAI decreases (Chapter 3).

The results from this dissertation, taken in sum with equivocal results from the literature, suggest that seagrass edges and fragmented seagrass meadows are unlikely to have negative consequences for bay scallops. While this may be divergent from the prevailing paradigm that large, continuous seagrass meadows are better than smaller, isolated patches, this idea is more

driven by terrestrial studies than any of the marine literature. If fragmentation of seagrass meadows has negative consequences as assumed, results in the literature pertaining to seagrass edges and patch size should be overwhelmingly negative. However, these results simply do not exist. Many studies show no effect of size or edge, although that may be a result of competing processes affecting the overall observed pattern (Chapter 2). Further, many studies show positive edge effects and species responding to small patch sizes, and while studies showing significant negative results do exist, the variable and equivocal results throughout the seascape literature suggest that strong negative impacts are unlikely for most associated fauna. This does not suggest seagrass habitats are not important, but that small, isolated patches are likely as valuable or more valuable than larger, continuous patches.

This value, however, pertains to faunal use. Seagrasses provide a suite of ecosystem services – sediment stabilization, oxygen production, allochthonous transport of productivity, nutrient acquisition and sequestration, among others. Little is known about how small patches vs. large patches might affect these processes. Addition, questions pertaining to resistance to degradation, patch health and persistence relating to patch size still need to be answered. Preliminary work suggests that small patches are remarkably stable (B. Furman, pers. comm.) and produce more seeds per capita than larger patches (L. Jackson, pers. comm.), although how these things affect seagrass ecosystem services warrant further investigation.

Changing habitats: Invasive species

A commonly cited problem with increasing habitat edges from fragmentation and loss is that these are sites for species invasions (Fagan et al. 1999, Ries et al. 2004). Additionally, degraded ecosystems are also sites of invasion, although it is difficult to discern if the invader is the driver or passenger (Didham et al. 2005). Regardless the reason for invasion, non-indigenous species

are considered among the greatest threats to biodiversity on the global scale (Elton 1958, Carlton 1989, Mack et al. 2000). Among the negative impacts associated with species invasions are competition, predation, biodiversity loss, changes in ecosystem processes, and disease (Vitousek et al. 1996, Mack et al. 2000, Crooks 2002, Grosholz 2002). In fact, biological invasions are currently considered to be one of the major environmental issues of public concern, although it varies in potential impact between systems (Sala et al. 2000).

Invasive species can affect the availability or quality of resources, such as food, space and habitat, either directly or indirectly, via their presence (Crooks 2002) – a process coined ecosystem engineering (Jones et al. 1994). These organisms are capable of creating, destroying or otherwise modifying physical habitats which affects resources needed by other species within the system, including living space, light, nutrients, sediment, etc, either positively or negatively (Jones et al. 1997). Thus, a number of invasive species are ecosystem engineers, since one of the most dramatic effects of invasion is alteration of ecosystems (Crooks 2002). There are three main ways in which invasives can affect ecosystems: 1) invasive species can utilize resources differently than natives and affect their availability; 2) invasives can alter the flow of energy and biomass through food webs; and 3) invasive species can affect disturbance regimes (Vitousek 1990, Crooks 2002).

Some of the most notorious engineering marine invaders are macroalgae. It has been suggested that non-indigenous macroalgal species (NIMS) are of particular concern because of the growing ecological and economical impacts these species (Schaffelke et al. 2006, Schaffelke and Hewitt 2007, Williams and Smith 2007). There have been 277 documented macroalgal introductions worldwide, although ecological studies have been relegated to only 6% of the most conspicuous species (Williams and Smith 2007). Field experimental data has only been

produced for 6 of those 277 species, including *Codium fragile* ssp. *tomentosoides*, *Sargassum muticum*, *Caulerpa taxifolia* and *Caulerpa racemosa*, *Unidaria pinnatifida*, and *Womersleyella setacea* (Thomsen et al. 2009). While these are among the most intensively studied species, results of ecological impacts have been variable, and typically different with regards to macrophyte communities vs. faunal communities (Williams and Smith 2007, Thomsen et al. 2009).

As ecosystem engineers, it is possible that many of these species can have positive impacts. While most of the NIMS literature focuses on negative impacts on native macrophyte communities, when investigating faunal use, many studies show positive impacts. And though much of the literature investigating invasive facilitation focuses on multiple invasive species, coining the term “invasional meltdown (Simberloff and Von Holle 1999),” there is a growing body of evidence of invasive species facilitating native species (Bulleri et al. 2006, Rodriguez 2006, Martin and Valentine 2011, Rohr et al. 2011, Watling et al. 2011). Facilitation is found in terrestrial, aquatic and marine systems, with habitat modification by engineers the most frequently documented mechanism for facilitation (Rodriguez 2006). In marine systems, NIMS often create novel habitats which alter physical conditions and/or replaces existing or lost habitats. While the growth of invasive macroalgae may negatively affect growth of native algal species (Levin et al. 2002, Williams and Smith 2007, White and Shurin 2011), the structure it creates is quickly utilized by native fauna (Viejo 1999, Wallentinus and Nyberg 2007, Polte and Buschbaum 2008, Gestoso et al. 2010, Thomsen 2010, Gestoso et al. 2012).

Rodriguez (2006) gives 4 scenarios which invasive species might facilitate native species – 1) when they provide a limiting resource; 2) when they increase habitat complexity; 3) when they replace a native species and fulfill a role; and 4) when they provide significant release from

predators and competition; thus, there are multiple pathways for invasive species to facilitate native species (Figure 2). This is becoming a common pattern when in recent NIMS literature, even the most ‘notorious’ invaders. *Sargassum muticum* has been demonstrated to have similar or enhance diversity and abundance relative to native algal species (Viejo 1999, Buschbaum et al. 2006, Polte and Buschbaum 2008, Gestoso et al. 2010, 2012). Even invasive populations of *Caulerpa* sp. have recently been shown to host similar communities to native macrophytes, albeit less common (Prado and Thibaut 2008, Vazquez-Luis et al. 2008, Burfeind et al. 2009, Vazquez-Luis et al. 2009, Deudero et al. 2011). Thus, the invasive species may be facilitating native species via substitutive processes, as they are providing a potentially limiting resource (habitat) and increasing habitat complexity (Chapter 4, 5). However, most of these studies involved looking at patterns in species assemblages. Issues between patterns and processes have already been raised in this chapter, and apply here as well. One of the reasons for such variable results is a lack of process oriented studies.

Very few studies have investigated the impact of an invasive macroalga on the fitness and condition of native species, and understanding these relationships is important for understanding the patterns associated with invasives (Chapter 5). Only a handful of studies have examined this relationship, with most of the research in this regard examining the interaction between the native bivalve *Anadara trapezia* and the invasive alga *Caulerpa taxifolia* in Australia (Gribben and Wright 2006a, Wright et al. 2007, Wright and Gribben 2008, Gribben et al. 2009, Byers et al. 2010), although one study was conducted in the Chesapeake with the invasive plant *Hydrilla verticillata* and the native clam *Rangia cuneata* (Posey et al. 1993). The results were overwhelmingly negative – both *Anadara* and *Rangia* experience significantly reduced tissue growth in the presence of invasive SAV relative to unvegetated habitats. Poor condition had

long term impacts on survival and reproductive output in *Anadara* (Gribben and Wright 2006a, Wright et al. 2007, Gribben et al. 2009), although the study with *Rangia* was only over a few months and despite significantly reduced condition, no condition-related depressed survival was reported (Posey et al. 1993).

However, the presence of *Caulerpa* actually enhanced settlement and survival from predatory mortality of *Anadara trapezia* (Gribben and Wright 2006b), and survival was not different between *Hydrilla* and unvegetated sediments for *Rangia*, while *Corbicula fluminea* exhibited enhanced survival within *Hydrilla* patches (Posey et al. 1993). Additionally, numerous species experience survival-growth trade-offs when associated with native submerged aquatic vegetation (SAV) (Chapter 3; Sogard 1992, Irlandi 1997, Bologna and Heck 1999, Dahlgren and Eggleston 2000, Frandsen and Dolmer 2002, Harter and Heck 2006), although comparisons have not been made in population demographics between invasive and native habitat formers. Two other studies, while not examining condition directly, suggest that invasive vegetative species might not have adverse effects on native fauna. Blue crabs have been demonstrated to grow at similar rates in marshes invaded by *Phragmites australis* as in other habitats (Long et al. 2011), and urchins consuming *Codium fragile* obtain higher quality (lower C:N) food resources than native kelps (Sauchyn and Scheibling 2009). Taken in concert, it is likely that invasive SAV may be suitable alternative habitats, especially in the absence of native habitats.

For this dissertation, I investigated the role of *Codium fragile*, among the most notorious invasive species in the world (Trowbridge 1998), as an alternative habitat for bay scallops. Introduced to the Long Island Sound sometime in the 1950s (Bouck and Morgan 1957), *Codium* became a concern for shellfisheries due to its ability to attach to the shells of living bivalves, particularly oysters and scallops (Ramus 1971). This concern led to numerous studies of the

ecophysiology of the invader (Fralick and Mathieson 1973, Malinowski and Ramus 1973, Wassman and Ramus 1973, Trowbridge 1998). However, until recently, few studies had rigorously investigated the environmental impacts of *Codium* (Levin et al. 2002, Scheibling and Gagnon 2006, Schmidt and Scheibling 2007), and thus much of the negative perception of *Codium* may have to do with an early moniker, “oyster thief,” used to describe the alga (Ramus 1971).

Further, the effects of *Codium fragile* on native species are variable depending on the assemblage being studied (see Table 3). Introduced populations of *Codium fragile* do negatively affect native macrophytes, with the potential to displace kelps and other seaweeds (Trowbridge 2001, Levin et al. 2002, Sumi and Scheibling 2005, Scheibling and Gagnon 2006), as well as seagrass (Garbary et al. 2004, Drouin et al. 2012). Yet, a growing body of research suggests that *Codium* may functionally replace the native macrophytes and provide both habitat (Chapter 4) and food for native fauna. In addition to colonizing bare space after a disturbance (Kelly et al. 2011), *Codium* also readily colonizes man-made hard structures (Bulleri et al. 2005). When it moves in, *Codium* is colonized by a number of native fauna (Chapter 4; Levin et al. 2002, Bulleri et al. 2006, Schmidt and Scheibling 2006, 2007, Drouin et al. 2011, Kelly et al. 2011), provides a food resource for some (Trowbridge and Todd 2001, Harris and Jones 2005), and provides a predation refuge for others (Chapter 4; Bulleri et al. 2006, Carroll et al. 2010). Thus it is possible that *Codium* can serve as a replacement habitat in the absence of eelgrass for the commercially valuable bay scallop. Comparisons of survival, growth and condition of native fauna between invaded and natural vegetated habitats are rare, so this dissertation focused on comparisons between eelgrass and *Codium fragile* (Chapter 4, 5).

While eelgrass, *Zostera marina*, is generally regarded as the preferred habitat of bay scallops, scallop populations have persisted or increased in areas lacking eelgrass (Tettelbach and Smith 2009), and are frequently found in association with *Codium fragile*. *Codium* forms an upright, complex, branching canopy which seems to serve a similar function for scallops as eelgrass provides – a predation refuge. Juvenile and adult bay scallops in eastern Long Island, New York are commonly found in *Codium*, so recovery of free-released scallops and survival of tethered scallops was investigated first to examine the potential predation refuge role of *Codium* (Chapter 4). This study was conducted at 2 sites and 2 years across 3 different habitats: *Codium* only, eelgrass only, and *Codium*+eelgrass mix. Survival of tethered scallops and recoveries of live free-planted individuals varied with scallop size, planting season and year, but no differences were observed between the three substrates for a given scallop size and planting date. Further, densities of naturally recruited 0+ yr scallops recovered by visual and suction dredge sampling were similar in the eelgrass and *Codium* substrates, and predator densities, particularly of the numerically abundant mud crab, *Dyspanopeus sayi*, were also not different among habitats. These results suggest that *Codium* offers some degree of predation refuge for bay scallops, at least over short time periods (Chapter 4).

Despite similar survival over short-term periods, relatively little was known of the long term consequences of a *Codium* association for bay scallops. Since scallops exhibit food-risk trade-off when associating with eelgrass (Chapter 3), the same complex *Codium* canopy that offers a refuge from predation may also inhibit scallop growth and condition. This research sought to examine whether scallops placed in *Codium* would differ from those in eelgrass and on unvegetated surfaces by placing caged scallops within each of 3 habitats at 2 hydrodynamically different sites over 2 years (Chapter 5). Scallops were measured for long term (3 month)

survival, growth, and condition. In Shinnecock Bay, scallops in both vegetated habitats grew significantly faster and were in significantly better condition than scallops in unvegetated sediments in both years, likely due to shallow depths and wind-wave activity which the vegetation served to buffer. In Sag Harbor, results were mixed. There were significant differences in survival, growth and condition between habitats, although some of these depending on the year (Chapter 5) and, despite this, both shell and tissue growth values in *Codium* were high relative to scallops in other studies (see Table 2). Natural set scallops in Sag Harbor displayed no differences in shell height or condition between eelgrass and *Codium*, suggesting that the caged results may be an experimental artifact. Results of this study suggest *Codium* may be a viable replacement habitat for bay scallops, although it highlights the complex relationships between invasive engineers and native species (Chapter 5).

The results from this dissertation research are in sharp contrast to the only previously reported literature on bivalve condition in the presence of an invasive ecosystem engineer. One major difference between this study and previous studies is the comparison to a native ecosystem engineer. As mentioned previously, scallops, among many other species, experience a food-risk trade-off for its association with seagrass, and thus comparing growth and condition of a native species in an invasive engineer relative to barren sediment is missing a key component. Based on the available literature, growth and condition should be reduced in the invasive vegetation relative to unvegetated substrates; findings which suggest this is the case should not be alarming. The real issue is when the growth and condition differs from the native habitat, and in this study, interannual and site-specific differences occurred, suggesting that in some cases, the invader is beneficial for the native (Chapter 5).

There are other differences between this and other studies that make it stand out. First, scallops are epifaunal, are capable of swimming, and bysally attach to surfaces off the bottom. These behavioral adaptations (Figure 3) may make them more suitable to adapting to an invasive engineer than infaunal bivalves like those studies in Australia. Water quality conditions within a thick algal canopy can be poor (Valiela et al. 1997, Holmer et al. 2009), and so the ability of scallops to maintain a position within or on top of the *Codium* canopy likely helps them do well in the presence of the invader. In Australia, researchers have observed a change in behavior of *Anadara trapezia* within *Caulerpa* invaded meadows, where the clams “pop-up” out of the sediment in order to get to slightly better conditions (Wright et al. 2010). This behavioral response, where the *Anadara* are completely emerged from the sediments, allows similar survivorship to unvegetated areas. Similar observations have not been made with other species, but it seems likely that behavioral modifications can allow natives to persist in the presence of invasive engineers.

Another issue may be with lag time effects since invasion, as it may take time before a native species responds, either positively or negatively, after initial invasion (Goodenough 2010). While the impacts of a new invasive species on its new environment are well known, long term studies tend to show an increase in species richness following introduction of invasives, contrary to common thoughts (Bruno et al. 2005, Goodenough 2010). Since many studies occur when invasions are new, and possibly before the native species have been able to respond, results may prematurely conclude negative results as a result of the invasion. It has been shown recently that native species can evolve to adapt to the colonization of invaders (Carroll 2007), so it is likely that lag effects are real and should start to be considered more in the marine literature. *Codium* invaded Long Island waters in the 1950s and thus, native species have also had almost 60 years

to adapt, whereas *Caulerpa taxifolia* is a recent introduction to Australian bays studied, having only established since the early 2000s (Wright et al. 2010).

The results from this portion of my dissertation suggest that invasive species may be suitable alternative habitats, facilitating native species, especially in the absence of native ecosystem engineers. Invasive species carry a negative connotation, being blamed as one of the biggest threats to biodiversity, although many studies fail to separate the ecosystem effects from the invader and effects from other stressors. Many invasive species are passengers to ecological change, not drivers (Didham et al. 2005), and links between invasion and negative effects on native species, including extinction, are based on anecdotal and correlative evidence (Gurevitch and Padilla 2004, Goodenough 2010). While *Codium* can potentially negatively affect seagrass (Drouin et al. 2012), *Codium* did not become abundant in the Peconic estuary until after a series of stressors affected eelgrass there – wasting disease, shoreline hardening, nutrient additions from agriculture, and brown tide. Likewise, many invasive species move into an area after it has already been stressed, and thus these new species may be filling voids of already lost species (Rodriguez 2006). Without necessary lag time to allow for native species to adapt to invaders, it is impossible to predict potential ecological consequences, suggesting that more long-term studies on invasive-native interactions are needed in the marine environment.

This research and the literature indicate that the impacts of invaders on native communities are extremely complex, with many studies showing both positive and negative effects on native fauna. Making generalizations across species and sites is difficult; species may respond differently to the invader, and as this research suggests, even the same species may respond differently across study sites. This illustrates the importance of trying to tease out other environmental stressors that may be having an effect in concert with the invader. While it has

been suggested that assessing the impacts of non-indigenous species should be done on a species- and ecosystem-specific level (Martin and Valentine 2011), these results suggest that even species-specific generalizations should not be made. However, this research indicates that invasive species may provide valuable resources, including habitat, for native species. The paradigm of non-indigenous species all being bad, or that ‘invasive’ species have negative consequences on biodiversity should at least be modified. Many examples in the literature show similar or enhanced diversity and abundance in invaded habitats, and even when examining species-specific demographics, invasives can facilitate natives.

Habitat and Predation

Although habitats are changing throughout the bay scallops’ range, this dissertation illustrates that structured habitat is critical to enhance scallop populations. Marine organisms are constantly at risk of predation, and habitat complexity is extremely important for enhancing survival of many species (Heck and Orth 1980, Ray-Culp et al. 1999, Grabowski 2004, Warfe and Barmuta 2004, Grabowski et al. 2008, Mislan and Babcock 2008, Stoner 2009). In particular, post-settlement mortality is a major determining factor in recruitment to benthic populations and is often attributed to predation (Gosselin and Qian 1997, Hunt and Scheibling 1997), and predation is considered the most important factor affecting benthic communities (Connell 1975, Menge 1983).

As scallop spawning stock and larval supply increase in the Peconics due to the restoration efforts (Tettelbach et al. *in review*), other biological interactions are likely to become equally important for bay scallop population recovery. Predation on many benthic invertebrate species is prey density-dependent (Eggleston et al. 1992), and therefore, low population levels can be a predation refuge. As populations increase, predation becomes increasingly important, since it is

most frequently cited as the major source of mortality for juvenile scallops (Ordzie and Garofalo 1980, Tettelbach 1986, Prescott 1990, Bishop et al. 2005a). Scallops have been shown to have a strong association with seagrass habitats (Belding 1910, Gutsell 1930), which they utilize as a refuge from predation (Prescott 1990, Pohle et al. 1991, Garcia-Esquivel and Bricelj 1993, Irlandi et al. 1995, Irlandi et al. 1999). This dissertation research supports that seagrass is a valuable predation refuge for bay scallops, even at a cost for growth, and suggests an invasive macroalgae is a valuable alternative habitat.

While multiple species are implicated as important predators of early post-settlement invertebrates, decapods are considered among the most important (Nelson 1981, Menge 1983, Hunt and Scheibling 1997). Decapods are capable of consuming very small invertebrate prey (Juanes 1992), and their ability to consume prey is determined by their claw size and the prey size (Juanes and Hartwick 1990, Whetstone and Eversole 1991, Seed and Hughes 1995, Ray-Culp et al. 1999, Aronhime and Brown 2009). However, relatively little is known as to how a range of habitat complexity affects a suite of common decapod predators. In the scallop literature, mud crabs have received the only attention in regards to changes habitat complexity on predation of scallops (Bauer 1994, Streib et al. 1995), and results suggested that as shoot density increased, mud crabs had easier access to scallops in the canopy. There are many decapod predators common to New York waters, including green crabs, *Carcinus maenas*, blue crabs, *Callinectes sapidus*, and spider crabs, *Libinia* sp. (Tettelbach 1986) that have not received much attention with regards to habitat complexity.

Yet, habitat loss is occurring at an alarming rate, so attempting to understand the impacts of changing habitat complexity on predation of scallops is paramount. Results from this dissertation highlight the importance of habitat, but suggest that fragmented seagrass is not likely

to have a negative impact on scallop populations. In fact, the ‘nursery role’ paradigm of seagrasses has recently been called into question, with some literature suggesting that since both predator and prey density increase with habitat, prey survival is not actually enhanced when these densities are taken into account (Mattila et al. 2008, Canion and Heck 2009). Many predation studies examine habitat vs. no habitat even though the relationship between predation intensity and habitat complexity is not necessarily linear and predators are impacted differently (Heck and Orth 2006). And while I have suggested that seagrass patchiness is not detrimental for scallops, patch size and seagrass shoot density are often confounded in natural seagrass, with smaller patches tending to have lower density (Bologna and Heck 2000, Sirota and Hovel 2006).

Predicting patterns in predation and how they influence scallop recruitment and populations is increasingly important for successful management, conservation and restoration. Scallops are a commercially important species experiencing considerable restoration efforts, and predation needs to be considered for any restoration project since it is typically the major source of mortality. Predation is not static, however, and rates change based on many different factors – predator type, size and density, prey size and density, habitat complexity, among others – and it can become difficult to make predictions on the threats from predation. Menge (1983) developed a potentially useful tool to determine predator impact for mussels on a rocky shore. While the results were not significant in predicting the final amount of prey, they were encouraging. A good step further is incorporating changes in habitat complexity into such a model to increase the accuracy toward determining site- and species-specific impacts of predation on scallop recruitment. No previous studies have attempted to quantify how changing seagrass shoot densities affects the predation rates across a suite of common Northwest Atlantic

predators, or attempted to calculate a predator impact model which takes into account habitat (Chapter 6). Despite potential limitations in such a model, it is still valuable, at least as a rudimentary tool for informing restoration efforts.

Further, the premise behind scallop restoration efforts, at least in New York, is recruitment failure (Tettelbach and Smith 2009), although the assumption has been that recruitment failure was due to low larval supply resulting from low population densities. The low population densities of scallops observed would likely lead to reproductive failure (Levitan et al. 1992, Levitan and Petersen 1995), and populations of scallops had generally been lower than 0.5 scallops m⁻² in the Peconic Estuary for much of the decade following the population crash (Lewis and Rivara 1998). While boosting adult densities has ultimately led to enhanced larval settlement and ultimately increased on bottom densities in the Peconic Estuary (Tettelbach and Smith 2009), low larval supply is not the only reason for recruitment failure. Recruitment is an arbitrary term and has different meaning in different studies. However, if we consider recruitment to adult populations or to the fishery, then high post-settlement mortality, driven by predation, could also contribute to recruitment failure. Again, it is then important to consider predation for successful restoration.

For Chapter 6, I attempted to use a predator impact model (sensu Menge 1983), which takes into account habitat complexity, for bay scallops using mesocosm data and field densities for predators, habitat, and settlement. Consumption of four common scallop predators was examined across 4 levels of habitat complexity in mesocosm experiments, and regressions were run to estimate consumption per shoot density. Additionally, both scallop and predator density was calculated via suction dredge surveys over 4 collection dates throughout the summer, and scallop settlement was obtained using spat collectors. All predators tested were affected by increasing

habitat complexity, although each predator was significantly impacted at a different shoot density. Consumption rates based on mesocosms and predator density in the field suggests that mud crabs, *Dyspanopeus sayi*, are likely the most important scallop consumer in Shinnecock Bay (Chapter 6). Habitat complexity, predator identity and density, scallop settlement, and predator impact varied across the basin. A combination of factors likely contributed to the ‘high’ scallop recruitment at Cormorant Point (~6 per square meter) – it was the site of most continuous seagrass density, the highest scallop settlement, and the lowest density of the four predators tested. In the other 5 sites studied, the number of scallop recruits was also very low ($\leq 0.5 \text{ m}^{-2}$). Although there were many limitations to the model, it is still a useful tool. The model also suggests a threshold value of habitat, at a relatively low shoot density (between 200 and 400 shoots m^{-2}), needed to increase survival (Chapter 6).

Unfortunately, there were many limitations to this study. One limitation is that it is generally difficult to extrapolate mesocosm data to the field. In this case, I used only adult crabs, and larger juvenile scallops, did not provide alternative food sources, kept densities constant, and used only single predators. Any of those factors could contribute to overestimates of prey consumption, and lead to differences between mesocosms and the field. Conversely, predation rates for the field were calculated based on just 4 predators tested despite that there are almost 20 other potential scallop predators, for different parts of their life history, within this study system. It is possible that calculated consumption rates may be lower than those experienced by scallops in the field.

Two other issues that affected the reality of these mesocosm experiments was the lack of multiple predators and the lack of top predators. Multiple predators tend to interact with each other when foraging together, leading to predation that is rarely additive (Sih et al. 1998, Griffen

2006, Wong et al. 2010). Absent from these studies is habitat complexity, which strongly influences predation. The few studies which have examined multiple predators and habitat complexity, albeit in oyster reefs, suggest that as habitat complexity increases, interactions between predators decreases (Hughes and Grabowski 2006). Since multiple predators are present in the field, in complex habitats, their interactions likely decrease leading to potentially additive prey consumption. Preliminary research that arose in association with this dissertation indicated that, while the results were not significant, increasing seagrass habitat complexity may decrease the interaction between blue crabs and green crabs. At low shoot densities, there appeared to be a risk reduction for scallops in the presence of multiple predators, however at the highest shoot density, there did not seem to be a reduction (see Figure 4).

Interactions across multiple trophic levels are also missing from this study. In particular, a number of finfish are predators on benthic invertebrates, such as crabs, and thus their presence could impede crab predation on scallops. In multiple studies in the mid 1980s, toadfish were implicated in increasing hard clam survival, through either trait mediated interaction (Day 1987) or direct control of crab predators (Gibbons and Castagna 1985, Bisker and Castagna 1989). Bay scallop survival increased in treatments with crabs that also contained pinfish, *Lagodon rhomboides* (Bishop and Wear 2005), and puffers, *Spheroides maculatus* (Tanikawa-Oglesby 1996). It has been suggested that while habitat complexity influences predator-prey interactions, it does not affect the trophic cascade, i.e. that the top predator either directly or indirectly affected the intermediate predator's prey foraging rates regardless of habitat complexity (Grabowski 2004). However, still few studies incorporate habitat complexity and tri-trophic interactions. Preliminary results from my mesocosms suggest that the presence of toadfish reduced the mud crabs foraging on scallops at low and intermediate levels of habitat complexity,

but not at high complexity (see Figure 5), suggesting that habitat complexity may negate potentially positive effects of predator interactions.

Regardless of the limitations, an important aspect of this research is identifying the major consumers of juvenile bay scallops in this system – mud crabs. Mud crabs have been implicated as major consumers of small bivalves (Whetstone and Eversole 1991, Streib et al. 1995, Ray-Culp et al. 1999, Silliman et al. 2004, Kulp et al. 2011), and have been implicated as the most important predator compared to other decapods due their two order of magnitude higher densities in the field (Rindone and Eggleston 2011). Chapter 6 demonstrated densities of mud crabs were 3x to 100x greater than blue crabs, the next dominant predator, and 2 to 3 orders of magnitude greater than any other crab species collected, suggesting that despite lower per capita rates of consumption, mud crabs are the most important scallop consumer in this system. However, the literature suggests that where present, blue crabs should be the dominant benthic predator (Eggleston et al. 1992, O'Connor et al. 2008), and at certain sites where blue crab densities were high, I predicted higher consumption of scallops by blue crabs. Landings data (NYDEC, Figure 6) and long-term data sets (Polyakov et al. 2007) suggest high abundances of blue crabs only started within the past 15 years. If blue crab abundance continues to increase, they may become the dominant post-set bivalve consumer in this system.

The results from the Chapter 6 seem to contradict conclusions from earlier chapters suggesting patchy seagrass (Chapter 3) and alternative habitats (Chapter 5) are viable habitats for scallops. While it is true that the field data suggests the site with the most eelgrass was also the site with the highest on-bottom scallop abundances, multiple factors also contributed to the ‘high’ abundances there, including high larval settlement and low predator densities. The PI work suggests relatively low to intermediate seagrass shoot densities were necessary to decrease

predator impact and increase scallop survival (Chapter 6). Further, the preliminary multiple predator and tri-trophic studies suggest that at high shoot densities, predator interactions, which would otherwise increase prey survival, are likely reduced. The major predator for scallops in this system, mud crabs, are also not impeded by seagrass habitats – they are ubiquitous throughout seagrass patches (Carroll et al. 2012) and can even consume scallops which bysally attach within the seagrass canopy (Pohle et al. 1991). Thus, the results from the mesocosms and field surveys do fall in line with earlier conclusions about seagrass habitats.

Implications for restoration

Restoration and conservation efforts often expose limitations in our knowledge of the organisms or ecosystems in question, and a major shortcoming of many restoration efforts is the failure to recognize that the environment has also changed. Management needs to take into account these “novel” ecosystems when planning restoration efforts; just because a species or habitat was found at a particular site 50 years ago is not an indication that the site is currently suitable for restoration. Land-use and water-use changes have altered the flow of freshwater into estuaries. Nutrient loading has led to algal blooms, moving SAV into shallower water or causing it to disappear all together (Valiela et al. 1992, 1997). Overharvest has removed top predators, releasing mesopredators and creating trophic cascades (Myers et al. 2007, Moksnes et al. 2008, Peterson et al. 2008). These issues need to be considered for any restoration effort.

Further, restoration plans can lead to questions about function and redundancy (McCay et al. 2003). A number of species can perform similar functions (O’Connor et al. 2008, Harwell et al. 2010, Martin and Valentine 2011), and some may be more or less suited to the new, impacted environment. Restoration efforts need to consider, at the very least, two important questions: 1) is the goal to restore ecosystem function, or 2) is the goal to restore a target species that was

there at some historic baseline? While these two questions are not necessarily mutually exclusive, the answers will ultimately help to shape restoration and management. Restoring target species may be the more common approach; however, examining which other species may serve similar ecological roles is important for restoration efforts, particularly in terms of habitat forming species.

Bay scallops are a valuable commercial species whose populations have declined throughout their geographic range. Numerous attempts have been made to restore bay scallops in areas where they were formerly abundant; these have met with mixed success (Peterson et al. 1996, Goldberg et al. 2000, Arnold et al. 2005, Tettelbach and Smith 2009). This dissertation research provided three valuable conclusions for restoration efforts that may enhance success in the future.

- 1) Any seagrass is better than no seagrass, but small patches are likely just as high quality habitat as larger, continuous meadows (Chapter 2, 3)
- 2) In the absence of seagrass, macroalgae can serve as a viable alternative, including introduced species such as *Codium fragile* (Chapter 4, 5)
- 3) Predation is important to consider, but the dominant predator, at least in New York, is the small mud crab, which can only consume scallops to ~20mm (Chapter 4, 6; Pohle et al. 1991)

This information can help future efforts for bay scallops in both New York and elsewhere. In New York, the presence of seagrass is not a metric for choosing suitable restoration sites, and restoration efforts have been successful, in part, due to the presence of alternative habitats, such as *Codium*, and in part due to planting at high densities and large sizes (Tettelbach et al. 1997, 2003, Tettelbach and Smith 2009). Other regions have limited less success, due to smaller

planting sizes and/or only utilizing ‘preferred’ seagrass habitats in Florida (Arnold et al. 2005) and Virginia (Orth, pers. comm.). Studies which have considered scallop size for restoration have had slightly more success (Goldberg et al. 2000, Tettelbach and Smith 2009, Tettelbach et al. 2011).

Therefore, specific recommendations can be made. First, presence of seagrass should not be a metric for restoration. This study suggests that any amount of seagrass is better than no seagrass, indicating that large, continuous meadows are not necessary for scallop restoration. Further, highly successful scallop plantings in New York restoration efforts occur at sites without seagrass (Tettelbach et al. 2007). The presence of more firm, sandy substrates that would prevent burial (Tettelbach et al. 1990) and planting densities exceeding 100 scallops m⁻² (Tettelbach et al. 2011) are more important for ensuring successful transplantation.

Second, a number of other habitats may be suitable for scallop restoration success. This dissertation suggests that *Codium fragile* may serve as a potential alternative habitat for scallops (Chapter 4, 5), and has been considered a valuable planting substrate in previous New York efforts (Wenzel et al. 1994). Further, other studies also suggest that scallops utilize a suite of other suitable complex structures, including *Gracilaria* and shell hash (Hernandez-Cordero et al. 2012) and cobble (Chintala 2004). Thus, any structured habitat may provide enhanced scallop survival. This adds a criteria to site selection; in addition to having a firm substrate, the presence of any structure, but not necessarily seagrass (Chapter 3, 4, 5; Tettelbach et al. 2007, Hernandez-Cordero 2012), should be considered for restoration.

The third implication involves predation. In New York, the dominant predator appears to be the small mud crab (Chapter 2, 4, 6; Pohle et al. 1991, Polyakov et al. 2007). However, in Connecticut it is the green crab, *Carcinus maenas* (Tettelbach 1986), in Virginia and North

Carolina it can be both the blue crab, *Callinectes sapidus* (Bishop and Wear 2005, Hernandez-Cordero, pers. comm.) and the cownose ray, *Rhinoptera bonasus* (Orth 1975, Peterson et al. 2001, 2008). In Florida, it is likely to be a suite of large gastropods (Bologna and Heck 1999). The identity of scallops can thus determine the size and planting season for scallops. In New York, scallops over 25mm are utilized and planted in the fall (Tettelbach et al. 2011). In Connecticut, scallops exceeding 38mm have been used (Goldberg et al. 2000). However, predators in Virginia, North Carolina and Florida are likely capable of consuming even adult scallops. In those instances, it is likely necessary to build sorts of enclosures (Fegley et al. 2008), transplant at high densities (Peterson et al. 1996) or attempt larval release at densities of thousands per square meter (Arnold et al. 2008).

Finally, bay scallops may be a model organism for other species with similar habitat requirements and associations. They are a semi-mobile, epifaunal bivalve, and so this information may apply to both sessile seagrass fauna and more mobile epifauna. This research, and the literature review, suggests that patchy seagrass habitats are viable for many associated fauna, and are not necessarily worse than continuous meadows. Further, it suggests that even habitat specialists may be able to utilize alternative habitats which offer similar function to seagrass. Last, this study suggests that identification of major predators is important for successful restoration. If the major predator is small, such as the case in New York, then raising the target species to a specific size before release becomes important, and while costly, will increase the likelihood of successful efforts.

Future research directions

This dissertation has produced many questions for future research directions. For scallops within a seascape, it would be beneficial to look at settlement vs. recruitment in natural patches.

While the artificial seagrass units controlled for confounding variables such as size and shape, shoot density and canopy height, it would be beneficial to try to relate settlement and recruitment from ASUs to those in natural patches with variable features. Additionally, the size and interiors of the ASUs, although large compared to other ASU studies, are small relative to some natural patches. Do “deeper” interiors function the same way? Another important future question is to examine hard vs. soft (gradual) edges, which would affect hydrodynamics and settlement differently. Finally, while this research suggests there may be a relatively small size patch, based on core-area index, in which survival and growth are maximized, an important step would be to determine what this minimum patch size might be. This is especially important since most seagrass restoration efforts plant small patches, so this information could inform habitat restoration as well.

There are still a suite of issues in terms of seagrass patchiness for fauna that should be investigated. While this research supports the idea of patchy seagrass as beneficial, relatively little is known about how organisms view habitat as heterogenous or homogenous. This likely varies with the size of the individual, and so different size patches will be perceived differently by organisms that vary in size, dispersal and mobility. To my knowledge, no study has attempted to quantify a suite of potential organisms across a seagrass seascape (but see Hovel et al. 2002). While some studies focus on small organisms and infauna (Eggleston et al. 1998, Attrill et al. 2000, Tanner 2005, Macreadie et al. 2010a), others focus on larger, more mobile fauna like crabs and fish (Hovel and Lipcius 2001, Gorman et al. 2009, Smith et al. 2010). An important step in determining perception is by attempting a research design across a seascape which would allow all (or as many as possible) of the potential fauna to be sampled, and then attempting to tie these densities to a series of seascape metrics – patch size, shape, within patch

location, sediment nutrients, flow, wave energy, etc. This would also be an important step toward determining secondary productivity in patchy vs. continuous seagrass meadows.

Another seascape question, and one that is beginning to be addressed, is edge effects between complex habitats. Much of the seascape literature has focused on mosaics of seagrass within a matrix of barren, unvegetated sands and muds. Thus, seagrass is likely the most desirable habitat in an otherwise featureless landscape, which may influence our perception of the importance of patches. In the tropical realm, there is research investigating seagrass-mangrove ecotones and seagrass-coral ecotones (Dorenbosch et al. 2005, Hammerschlag et al. 2010, Tuya et al. 2010), but only one study which I am aware of that attempts to look at a seagrass-complex habitat ecotone in the temperate zone (Selgrath et al. 2007). More work should be done involving seagrass-complex habitat ecotones which may influence settlement, growth and survival of a variety of species.

Positive effects of 'invasive' species should also be considered more in the literature. If an invasive species provides a resource vacated by a lost native species, including habitat, that invader can have a significant positive effect on other native species. This suggests some degree of ecological redundancy. For scallops, *Codium fragile* appears to be a suitable alternative. However, three questions arise for scallop-*Codium* associations that need to be considered. First, what is the above-bottom refuge value for *Codium* and how does that compare with eelgrass? *Codium* is much more buoyant, and thus is capable of supporting larger scallops (pers. obs.), however, it may also be easier to climb for predators, and allow larger predators access to the canopy. Preliminary lab data suggested that the *Codium* canopy offered intermediate survival between eelgrass and bare sand, but more work needs to be done to answer this question (Figure 7).

The results of this dissertation (Chapter 5) suggest that while *Codium fragile* may be beneficial, it seems that at dense algal assemblages, the positive benefit can switch to an overall negative effect. While it was unfortunately not investigated during this dissertation, a second question involves examining threshold densities of *Codium* that might switch from positive to negative impacts on scallops. It is possible that the reduced performance of scallops in year 2 at Sag Harbor may have been the result of a thicker *Codium* canopy, and thick canopies of the invasive *Caulerpa* have been implicated in the negative impacts on *Anadara trapezia* clams (Gribben et al. 2009). Further, during field surveys, it seems that in less dense stands of *Codium*, scallops are located on the bottom, but as the canopy gets thicker, scallops are found within the canopy (Tettelbach, pers. comm.). Experimental analysis of community or individual metrics should be investigated across a range of *Codium* density and/or biomass.

The third question involves community structure associated with *Codium*. Currently, the data I have presented compares potential predator densities between *Codium* and eelgrass and suggests no difference (Chapter 4). Qualitatively, there seemed to be more oyster drills, molluscivorous gastropods that can prey on scallops and other bivalves, associated with *Codium*, likely a result of the macroalgal utilization of *Crepidula fornicata* as an attachment substrate. An experimental design should be undertaken which allows for multi-dimensional analysis to assess differences in the communities between *Codium* and eelgrass, not simply different abundances. Understanding how communities differ between *Codium* and eelgrass will help restoration efforts, and also provide a better idea of production to other levels and how that may differ within the invaded habitat.

The idea of ecological redundancy also should receive more attention in the future. Many different species can perform similar functions, and thus leads to the resiliency of marine

systems. However, as certain species are lost or diminished due to both direct and indirect anthropogenic impacts, identifying which species may perform the same or similar functions will be important for restoration and management. In this case, *Codium* seems to perform similar functions as eelgrass, at least as a habitat forming species. There are likely a number of other functionally similar species which are better suited for the changing marine environments. One such species may be *Crepidula fornicata*. From my suction surveys, I recorded very high abundances of crabs, shrimp and gobies within a ‘*Crepidula* pavement (see Table 4),’ – a site in which the bottom was covered in stacks of *Crepidula fornicata* (Figure 8) – and cages placed in the area also caught larger blue crabs, toadfish and seabass. This may indicate that *Crepidula* can potentially be a subtidal oyster reef equivalent, at least in terms of habitat production and trophic transfer, although currently this is pure speculation. *Crepidula* have been shown to enhance zoobenthic diversity (de Montaudouin and Sauriau 1999) and act as a predation refuge (Thieltges 2005), despite these studies being of invasive populations of *Crepidula*. Additionally, *Crepidula* can survive and consume harmful algal species (Harke et al. 2011) and can calcify in high CO₂ environments (Ries et al. 2009), making them potentially more suitable for anthropogenically influenced estuaries. This warrants considerable further attention.

Finally, the portion of my dissertation that provided more questions than answers involves the predator impact. There are a number of avenues for potential future research. Of course first and foremost would be to extend the preliminary research involving multiple predator effects and tri-trophic interactions as a function of complexity. Both had promising, and somewhat unexpected results. MPE studies have frequently suggested that 2 predators should interact in the presence of each other and thus potentially lead to risk reduction of the prey. However, those studies tend to use sessile organisms and have no habitat component. These two components

need to be examined further, as mobile prey have a potential escape mechanism and habitat affects predation. Similarly, tri-trophic interactions are likely to be affected by habitat complexity, but studies need to incorporate multiple levels of complexity, not just presence or absence of habitat. These studies should also include behavioral components.

Additionally, the predator impact model suggests that predators are capable of controlling scallop populations and may not be satiated at their current densities. It is unknown, however, whether or not these predators are capable of driving populations of scallops to zero without investigating a functional response to changing prey densities. While other studies have shown that some of the predators investigated show a type II functional response, capable of driving prey density to zero, no studies have examined this response across a range of habitat complexity. It is possible that as habitat complexity increases and prey density decreases, it will be more difficult for predators to encounter and consume prey, but this relationship should be examined, which could then be incorporated into a better predator impact model.

Final thoughts: How important is continuous seagrass and the myth of the pristine

One of the major issues with ecological research is that studies are often conducted long after systems have been impacted to some degree by anthropogenic activities (see Jackson 2001). Because these studies took place long after impact, researchers and managers do not have a clear picture of what the estuary may have looked like. This, in turn, makes it extremely difficult to predict how changing habitats and seascapes will impact associated fauna. The equivocal results of seascape and marine macrophyte invasion studies suggest that our ideas of ‘pristine’ and/or ‘natural’ may be skewed (Figure 9). If habitat fragmentation and invasion by macroalgae were both as negative as current paradigms suggest, we would expect that results from studies would be overwhelmingly negative. This has not been the case, and many species even respond

positively to both of these ‘bad’ environmental changes. There are two plausible explanations for the highly variable results from the literature; 1) the current species being studied are habitat generalists because habitat specialists have been lost from most systems already or 2) that ‘historic’ continuous seagrass meadows were a product of human impact and species had adapted to formerly naturally fragmented seagrass.

It is possible that due to centuries of impact, that many species have been lost from our coastal and marine ecosystems. In particular, we would expect that habitat specialist species, i.e., species which have specific habitat requirements, would be disproportionately affected by anthropogenic impact. This could lead to a resulting community which has subsequently been studied as ‘natural’ to be drastically different than what actually occurred during pristine conditions. Unfortunately, little is known to the extent of impact before ecological studies, particularly marine studies, started, and as such, assumptions of what are natural and native communities could be incorrect. This could explain the majority of the neutral and positive effects of both fragmentation and invasions – it is possible the current species which are either commercially important and/or abundant enough to be studied are those which are tolerable to some degree of change. This could skew the results of studies toward the highly variable results currently observed.

Likewise, many natural processes – both biotic and abiotic disturbances – fragment seagrass meadows. In many locations, seagrass exists as a mosaic of patches which vary in size, shape and isolation, typically the result of current, water column depth, sediment composition and growth rates. However, a number of megafauna are capable of fragmenting seagrass meadows due to both direct grazing and indirectly via foraging. Many larger marine vertebrates which consume seagrass had already been impacted by humans via hunting (water fowl) or fishing (sea

turtles) before ecological studies of seagrass became common. Other grazers, such as sirenians, have experienced drastic declines and, in some cases extinctions. Further, species whose foraging activities would dig up seagrasses – such as skates and rays, and in some cases sturgeons – were also likely to be considerably less abundant by the time seagrass ecological studies commenced than what occurred naturally. Therefore, it is possible that the species which are considered to associate with seagrass habitats had evolved and adapted to a world in which most seagrass meadows were naturally fragmented, at least above-ground. Further, these adaptations might also have served to allow species to utilize other complex habitats.

It is probably impossible to determine whether or not historic human impact caused habitat specialists to be lost and/or artificially created continuous seagrass meadows. Regardless, based on the results from this dissertation and the literature, ‘fragmentation, bad’ and ‘invader, bad’ paradigms are probably not correct, at least not in marine environments. In fact, there are many examples that demonstrate both of these to be good things. Part of the problem comes from the borrowing of terrestrial ideas for marine studies. Marine environments have glaring differences in dispersal and connectivity when compared to terrestrial and freshwater systems, so making assumptions for marine environments based on terrestrial studies appears to be a poor approach. Regardless, these two major paradigms in the marine literature do not appear to be rooted in the data, which makes the fact that they are still paradigms all the more alarming. It is time to move away from application of terrestrial ideas and concepts into the marine environment.

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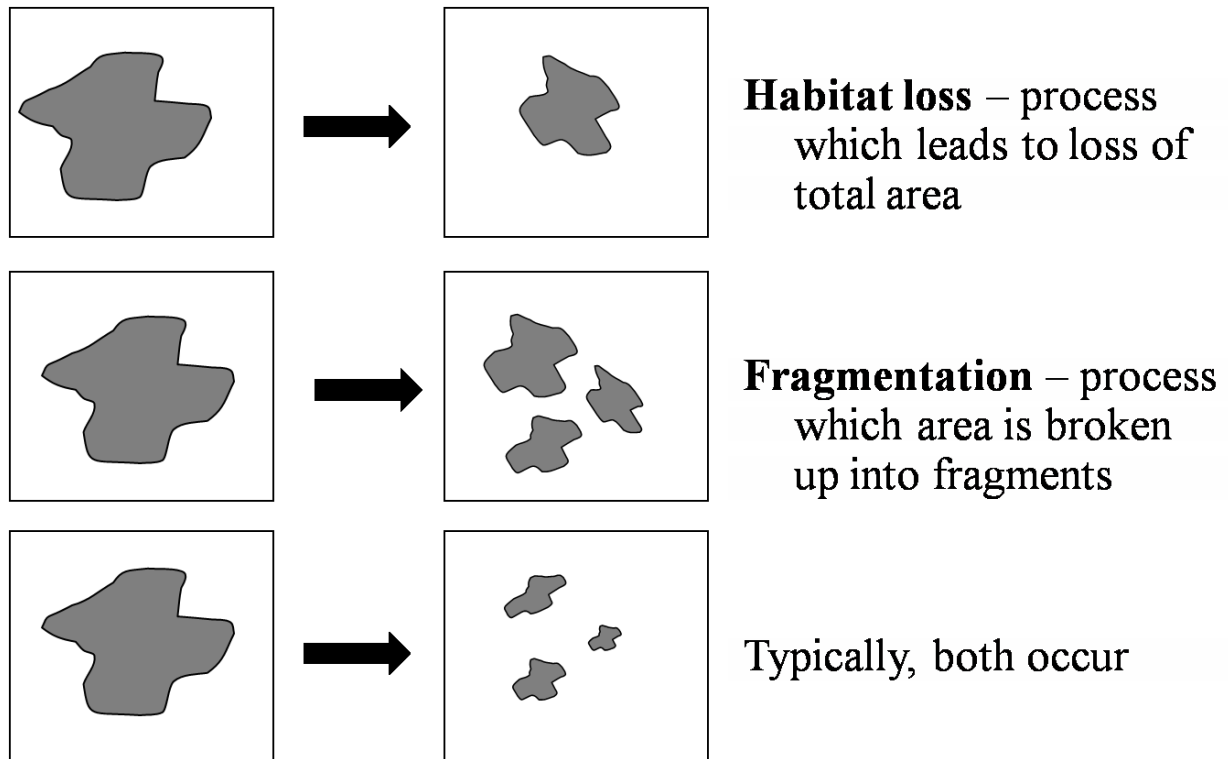
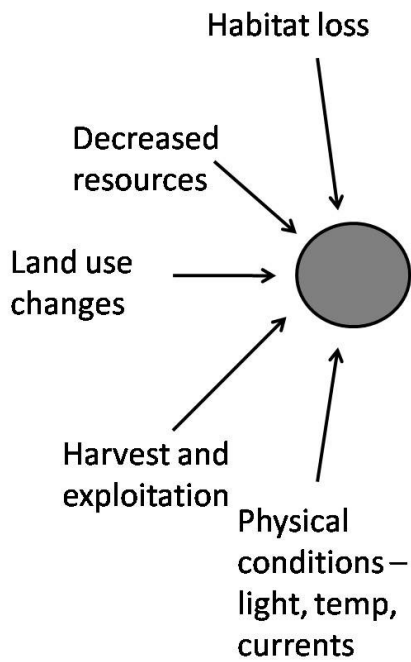


Figure 1: Diagram differentiating habitat loss and habitat fragmentation.

Environmental Stressors



Invasion

Facilitative Affects

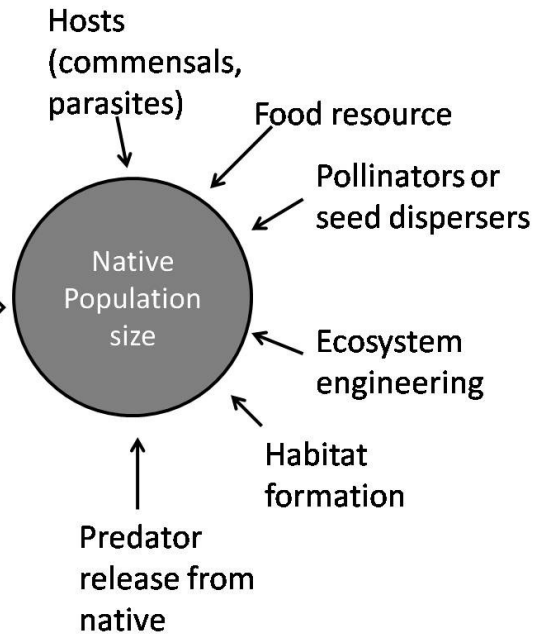


Figure 2: Conceptual diagram of illustrating stressors on native populations and invasive species' ability to alleviate these stressors, thereby facilitating growth of native populations.



Figure 3: Picture of scallop associated with *Codium fragile* in the field, illustrating its ability to remain within/above the canopy.

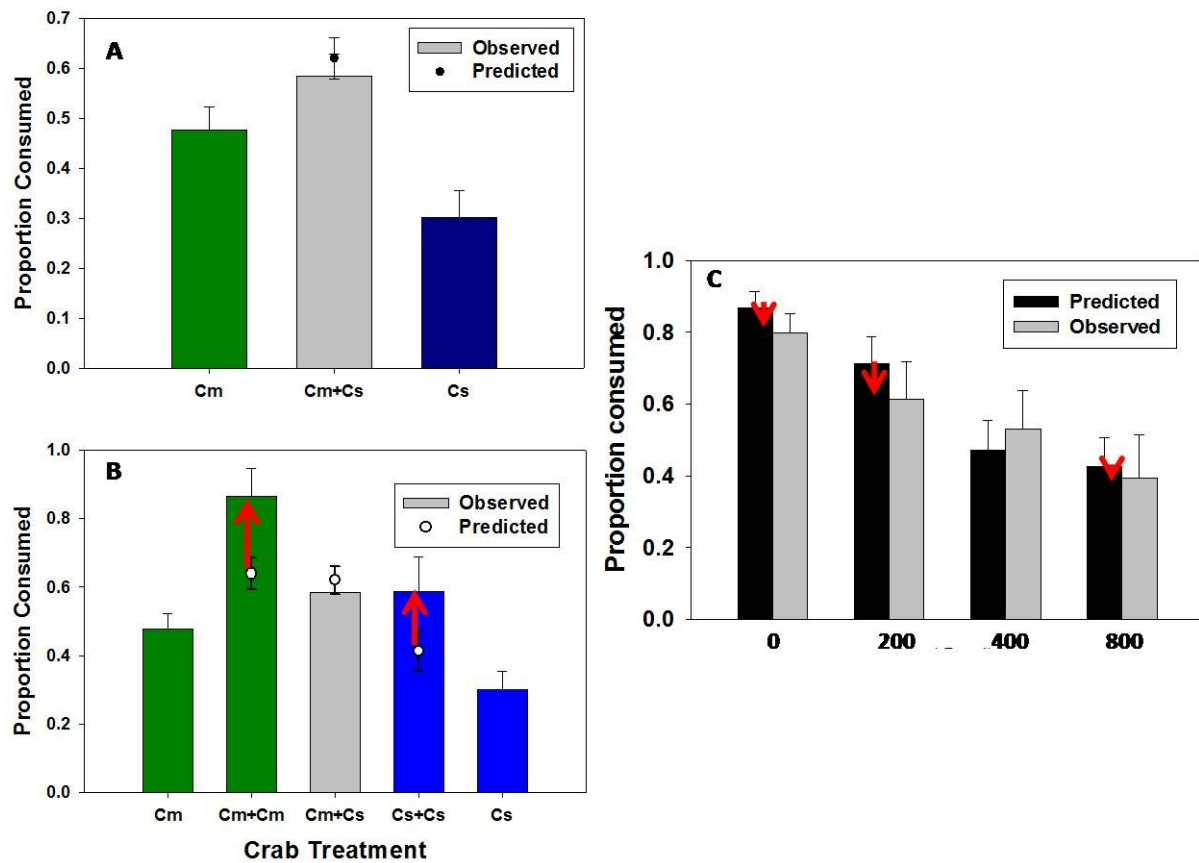


Figure 4: Preliminary data on multiple predator effects on scallop consumption by blue crabs, *Callinectes sapidus*, and green crabs, *Carcinus maenas*, as it varies with habitat complexity. A) Proportion of scallops consumed by individual predators – green bars represent green crabs, blue bars are for blue crabs – and by both predators combined (gray bars) with predicted consumption (closed circle) using formula from Sih et al 1998; B) multiple predator results expanded to show observed and predicted consumption for intraspecific treatments, red arrows illustrating risk enhancement on scallop prey in conspecific pairs; C) predicted (black bars) and observed (gray bars) consumption in multiple predator treatments across a series of habitat complexity, red arrows to highlight change in magnitude of risk reduction from low habitat to high habitat, although these results were not significant. Error bars are \pm SE.

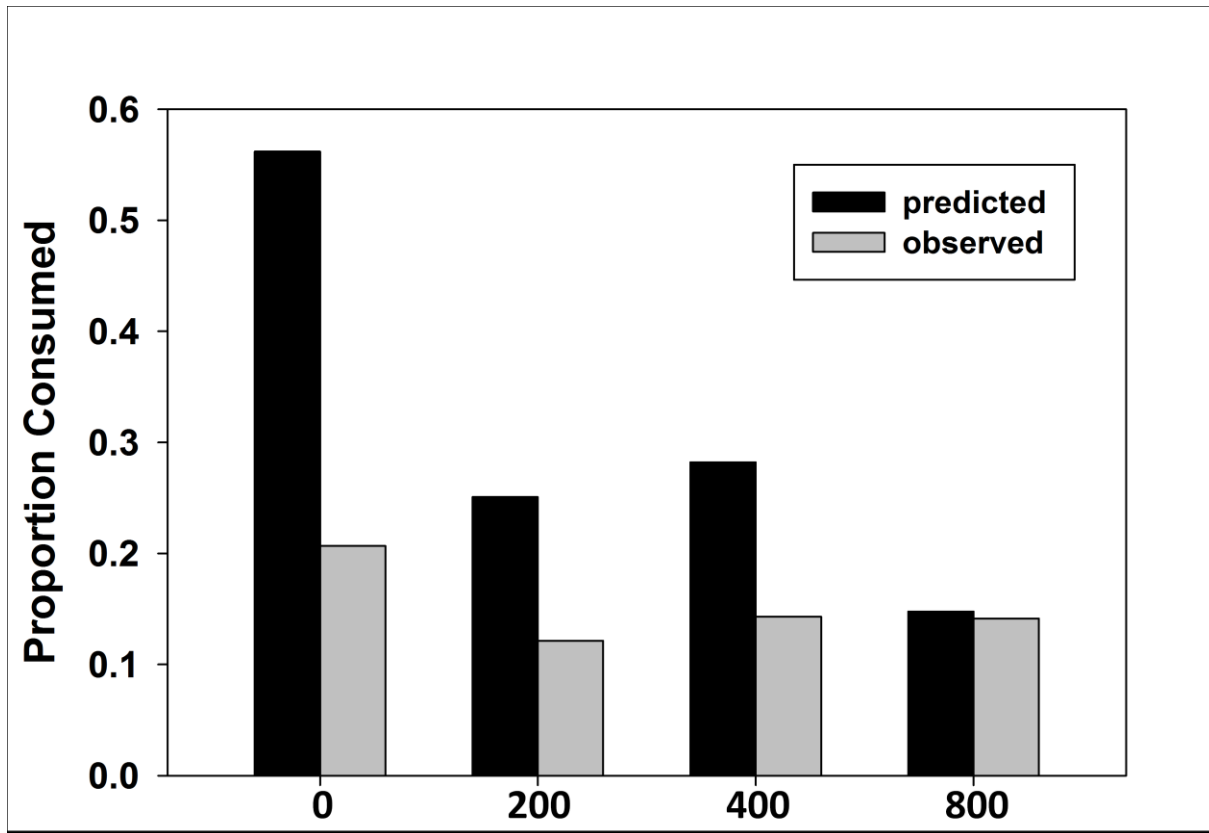


Figure 5: Preliminary data illustrating the multiple predator effects of toadfish on mud crab consumption of bay scallops as a function of habitat complexity. Black bars represent predicted values based on individual consumption rates and gray bars represent observed consumption with both predators combined.

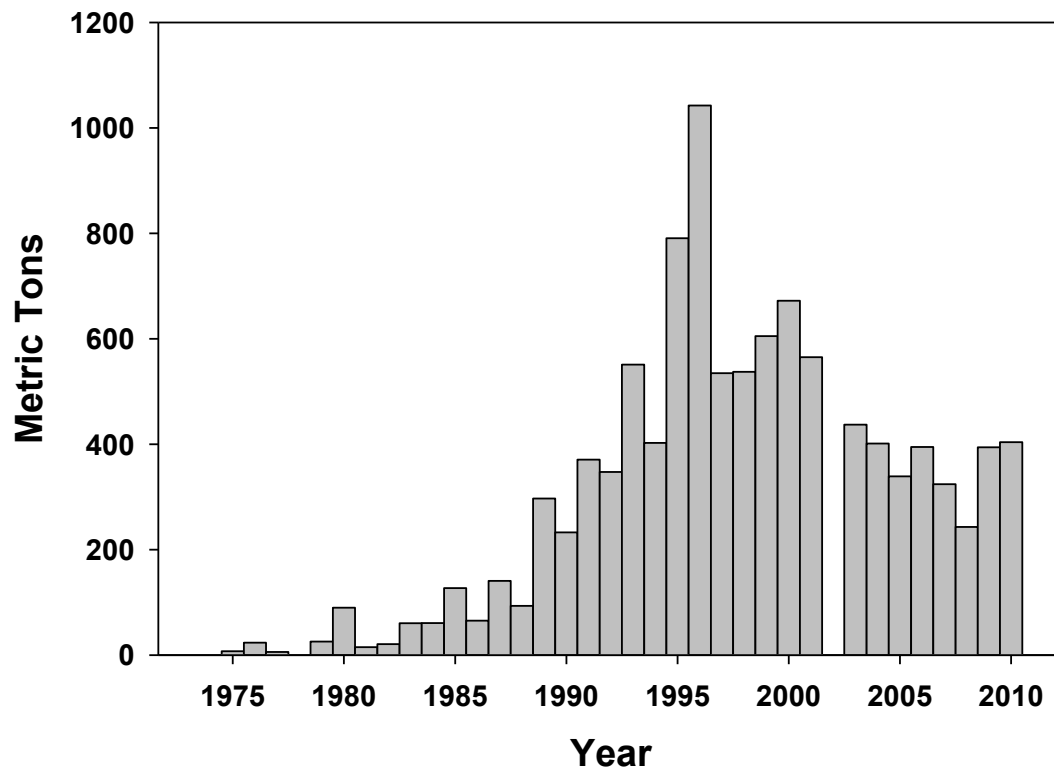


Figure 6: Blue crab landings data from the New York Department of Environmental Conservation, illustrating the annual landings in metric tons of blue crabs from 1975 to 2010.

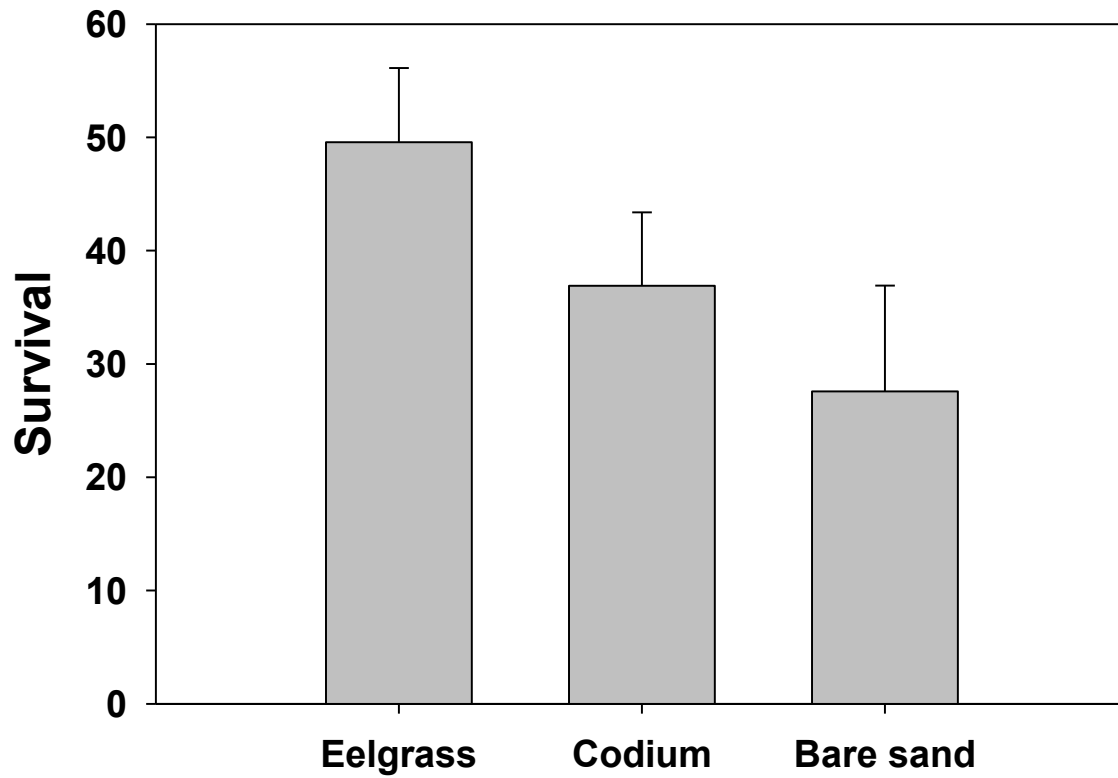


Figure 7: Comparison of survival of scallops tethered into the eelgrass and *Codium fragile* canopy or tethered on unvegetated sediments in the presence of mud crabs, *Dyspanopeus depressus*, a vegetation-climbing predator, for trials that exhibited predation. Error bars are \pm SE.



Figure 8: A photo of a ‘*Crepidula* pavement,’ where the bottom is covered in stacks of *Crepidula fornicata* and *Crepidula* shell hash. Often these areas also have *Codium fragile*, which uses *Crepidula* shells as a holdfast. This photo is from Hog Neck Bay, Southold, NY, taken in on November 3, 2010.

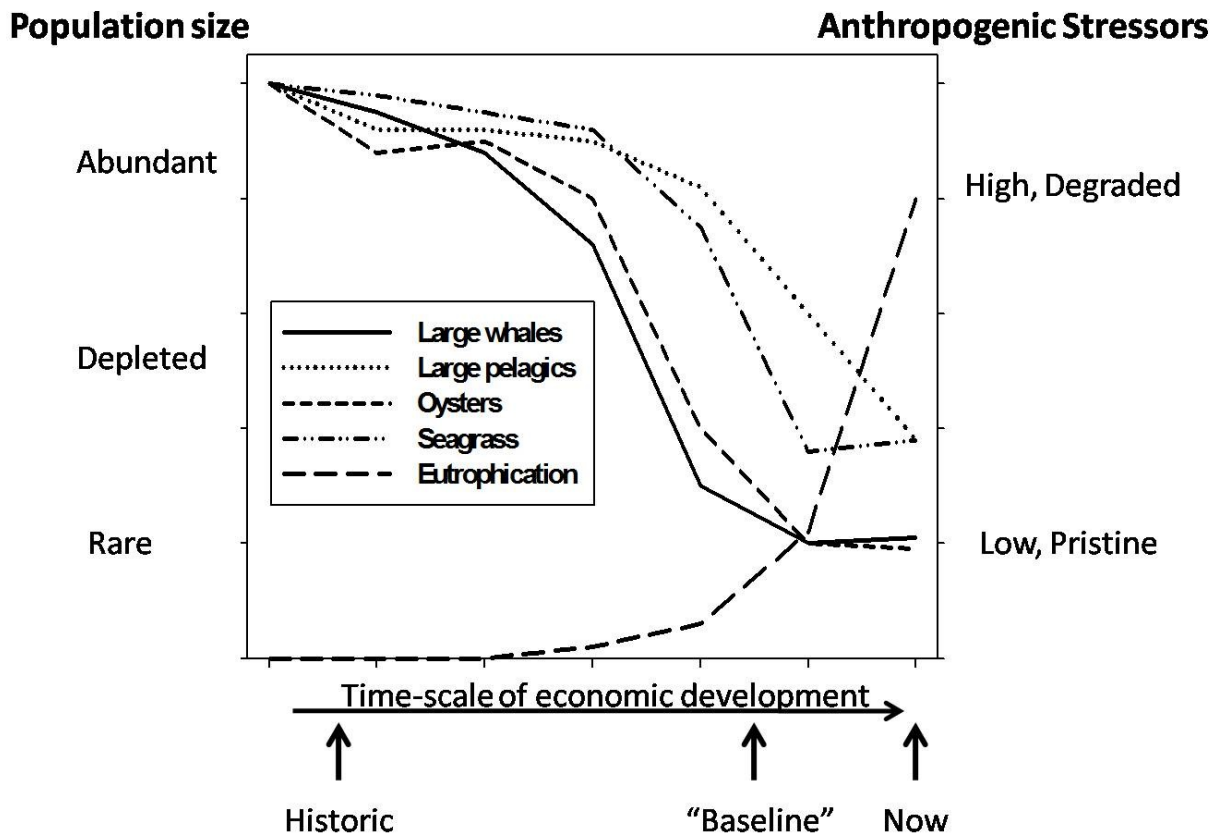


Figure 9: Conceptual diagram showing the extent of human impact on different organisms and environmental conditions, based on Lotze et al (2006), and how our 'baseline' perception of pristine ecosystems differs from actual pristine conditions, adapted from Jackson (2001).

Table 1: Summary of patterns of measured variables across a suite of species within the landscape literature. For Size + indicated the variable increases with size, - decreases with size and 0 is no difference. For Edge affect, + indicates the variable is enhanced at the edge, - indicates the variable is reduced and 0 means no effect. 1 = Multiple age classes, 2 = site variation, * = edges between two complex habitats, and n = did not differentiate between species.

Patch Attribute	Metric	Study	Fish			Invertebrates		
			+	-	0	+	-	0
Size	Density/Abundance	Bell and Westoby 1986	3	1	4	1	0	2
		Bell et al. 2001	0	0	4	1	0	7
		Bell et al. 2002	0	2	12	0	0	5
		Bowden et al 2001	-	-	-	6	4	4
		Eggleston et al. 1998	-	-	-	1	3	3
		Eggleston et al. 1999	-	-	-	0	1	4
		Hammerschlag and Serafy 2009 ^{1,*}	3	3	2	-	-	-
		Hirst and Attrill 2008	-	-	-	2	0	9
		Hovel and Lipcius 2001	5	1	4	1	0	1
		Laurel et al 2003	1	0	0	-	-	-
		Jelbrt et al. 2006	6	8	34	-	-	-
		Macreadie et al. 2009	0	0	4	-	-	-
		McNeill and Fairweather 1993	0	4	19	2	0	12
		Smith et al. 2010	1	1	0	-	-	-
		Thistle et al 2010	0	0	1	-	-	-
		This Study	-	-	-	0	0	2
		Total	19	20	84	14	8	49

	Survival	Gorman et al. 2009	0	1	0	-	-	-
		Hammerschlag et al. 2010	0	1	0	-	-	-
		Hovel and Lipcius 2001	-	-	-	0	1	0
		Hovel and Lipcius 2002	-	-	-	1	1	4
		Laurel et al 2003	0	1	0	-	-	-
		This Study	-	-	-	0	0	1
		Total	0	3	0	1	2	5
Edge	Density/Abundance	Arponen and Bostrom 2012	0	0	5	3	0	10
		Barbera-Cebrian et al 2002	-	-	-	1	2	4
		Bologna and Heck 2002	-	-	-	9	1	15
		Bowden et al. 2001	-	-	-	4	3	7
		Horunuchi 2009	9	1	2	-	-	-
		Hovel and Lipcius 2002	-	-	-	0	1	1
		Hovel et al 2002	0	1	31	0	0	32
		Jelbart et al. 2006	4	5	39	-	-	-
		Macreadie et al. 2010a	-	-	-	3	3	5
		Macreadie et al. 2010b	1	0	0	1 ⁿ	0	0
		Murphy et al. 2010	-	-	-	2	2	1
		Sanchez-Jerez et al. 1999	-	-	-	0	1	9
		Selgarth et al. 2007 ^{1,*}	-	-	-	1	1	1
		Smith et al. 2008	6	0	16	-	-	-
		Smith et al. 2010	1	1	0	-	-	-
		Smith et al. 2011	3	1	15	-	-	-
		Tanner 2005 ²	-	-	-	16	4	6
		Tuya et al. 2010 [*]	5	0	1	4	2	2

	Warry et al. 2009	-	-	-	1	0	4
	This Study	-	-	-	0	0	2
	Total	29	9	109	44	20	99
Survival	Bologna and Heck 1999	-	-	-	0	1	0
	Gorman et al. 2009	0	1	0	-	-	-
	Peterson et al. 2001 ²	-	-	-	0	1	5
	Selgarth et al. 2007 ^{1,*}	-	-	-	1	1	0
	This Study	-	-	-	0	1	0
	Total	0	1	0	1	4	5
Growth	Bologna and Heck 1999	-	-	-	1	0	0
	Reusch and Williams 1999	-	-	-	1	0	0
	This Study	-	-	-	1	0	0
	Total	-	-	-	3	0	0
Settlement	Bologna and Heck 2000	-	-	-	5	1	0
	This Study	-	-	-	1	0	0
	Total	-	-	-	6	1	0

Table 2: Comparisons of scallop shell and tissue growth rates between reported literature values and this dissertation. Some values are approximated from figures in the literature.

Shell Growth Rate (mm/d)	Tissue Growth Rate (mg/d)	Study Location	Habitat	Authors
~0.2	NA	Virginia	NA	<i>Castagna and Duggan 1971</i>
~0.4	NA	Florida	NA	<i>Barber and Blake 1983</i>
up to 0.33	NA	Connecticut	NA	<i>Tettelbach 1986</i>
NA	~4.2 – 6.5	New York	Seagrass/mix	<i>Bricelj et al. 1987</i>
~0.28	NA	New York	Seagrass	<i>Eckman 1987</i>
~0.1-0.14	NA	Florida	Seagrass	<i>Ambrose and Irlandi 1992</i>
0.27 to 0.66	~8.9 (variable)	New York	Seagrass	<i>Garcia-Esquivel and Bricelj 1993</i>
0.13-0.16	NA	Florida	Seagrass	<i>Irlandi et al 1995</i>
NA	up to 0.04	Florida	Seagrass	<i>Bologna and Heck 1999</i>
0.19 - 0.21	NA	Florida	Seagrass	<i>Irlandi et al 1999</i>
0.1 – 0.28	NA	Massachusetts	NA	<i>Shriver et al. 2002</i>
0.09 – 0.2	NA	Florida	NA	<i>Geiger et al. 2006</i>
0.28	5.2	Hallock Bay, NY	ASU center	This study
0.31	6.0		ASU edge	
0.35	8.6		Sand	
0.33 – 0.34	6.3 – 7.4	Shinnecock Bay	Eelgrass	This study
0.33 – 0.34	6.4 – 6.8		Codium	
0.31	4.6 – 5.1		Sand	
0.35 – 0.38	6.3 – 7.7	Sag Harbor	Eelgrass	
0.31 – 0.34	4.2 – 4.6		Codium	
0.34 – 0.36	5.4 – 8.0		Sand	

Table 3: The impacts of the invasive *Codium fragile* on native species, including the response variable examined and the direction of the effect.

Study	Macrophytes	Response variable	Effect
Drouin et al. 2012	Seagrass	Growth	-
Garbary et al. 2004	Seagrass	Growth	-
Jones and Thornber 2010	Epiphytes	Growth/ Density	+
Levin et al. 2002	Kelps	Recruitment	-
		Growth	0
Scheibling and Gagnon 2006	Mixed assemblage	Density/biomass	-
Schmidt and Scheibling 2006	Epiphytes		+
Sumi and Scheibling 2005	Kelps	Survival	-
Trowbridge 2001	Mixed	Density/biomass	0
	Fauna		
Bulleri et al. 2006	Mussels	Recruitment/Survival	+
Drouin et al. 2011	Total Inverts	Abundance/Richness	+
	Total Fish		+
Harris and Jones 2005	Sea slugs	Food	+
Levin et al. 2002	Urchins	Palatability	-
	Decapods	Abundance	0
	Fish (Cunner)	Abundance	-
Sauchyn and Scheibling 2009	Urchins	Food Quality	+
Scheibling and Anthony 2001	Urchins	Growth	0
Schmidt and Scheibling 2007	Decapods	Abundance	0,+
	Gastropods		0,+
	Fish		+
Trowbridge and Todd 2001	Sea slugs	Growth	+
This Study	Bay Scallops	Growth	0,+
		Survival	0,+

Table 4: The faunal assemblage found within a *Crepidula fornicata* ‘pavement’ during suction dredge surveys in the summer of 2011.

Species	Common Name	Abundance
<i>Callinectes sapidus</i>	Blue crab	2.63 ± 2.21
<i>Carcinus maenas</i>	Green crab	0.38 ± 0.26
<i>Dyspanopeus sayi</i>	Black-finger mud crab	225.50 ± 61.30
<i>Libinia</i> sp.	Spider crab	0.50 ± 0.27
<i>Pagurus longicarpus</i>	Long claw hermit crab	8.25 ± 2.70
<i>Crangon septemspinosa</i>	Sand shrimp	1.63 ± 1.03
<i>Palaemonetes</i> sp.	Grass shrimp	4.00 ± 1.77
<i>Eupleura caudate</i>	Thick-lipped oyster drill	6.50 ± 5.53
<i>Urosalpinx cinerea</i>	Atlantic oyster drill	10.38 ± 3.73
<i>Asterias forbesi</i>	Forbe’s sea star	0.38 ± 0.18
<i>Sclerodactyla briareus</i>	Sea cucumber	0.50 ± 0.43
<i>Gobiosoma bosci</i>	Naked goby	19.50 ± 7.45
Total Epifauna		281.63 ± 88.36

Table 5: Percent cover of habitat forming species found within a *Crepidula fornicata* ‘pavement’ during benthic surveys in the summer of 2011

Species	Common Name	Percent Cover
<i>Crepidula fornicate</i>	Atlantic slipper shell snail	84.5 ± 9.64
<i>Codium fragile</i>	Green fleece	31.5 ± 14.15
<i>Gracilaria</i> sp, <i>Aghardiella</i> sp	Red algae	9.17 ± 2.30
<i>Ulva lactuca</i>	Sea lettuce	1.83 ± 0.75
<i>Microcionia prolifera</i>	Red beard sponge	3.5 ± 2.5

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