

HABITAT FRAGMENTATION INFLUENCES SURVIVAL AND GROWTH OF TRANSPLANTED NORTHERN QUAHOG (*MERCENARIA MERCENARIA* LINNÉ) IN BIG LAGOON, FLORIDA

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ABSTRACT To test the effects of habitat fragmentation *per se* on the survival and growth of the northern quahog (*Mercenaria mercenaria* Linné), we stocked juvenile quahogs in 10 seagrass patches (*Halodule wrightii* Ascherson) ranging in size from 0.5–1,750 m² for two consecutive months during the summer of 2004. As a control, additional quahogs were stocked in cages located in seagrass patches that spanned the same size range. We tested for changes in shell growth, somatic growth, and mortality between caged and non-caged treatments and we estimated the strength of linear relationships between all three measures of growth and mortality with patch area, perimeter, perimeter: area ratio, seagrass aboveground biomass, and epiphyte biomass. Shell and somatic growth were each significantly greater in cages, whereas mortality was significantly less than in uncaged treatments. There were no significant relationships between clam mortality and either patch perimeter, seagrass above ground biomass, or epiphyte biomass, but during July only there was a negative relationship between clam mortality and patch area. Patch area, perimeter, perimeter: area ratio, and seagrass aboveground biomass each had some significant influence on either changes in shell height, length, or somatic growth; but this influence varied between the two trials. Our data suggest that the influence of habitat fragmentation *per se* declined from June to July, which may be the result of increasing predator densities and changes in seagrass patch characteristics.

KEY WORDS: *Mercenaria mercenaria*, quahog, habitat fragmentation, perimeter: area ratio, seagrass, *Halodule wrightii*

INTRODUCTION

Habitat fragmentation *per se* is a process that can lead to the break-up of once continuous habitats into multiple smaller habitats, thereby altering the habitat size, shape, perimeter: area ratios, interpatch distance, and the amount of habitat edge present (Saunders et al. 1991, Trzcinski et al. 1999). Habitat fragmentation *per se* is a landscape scale process; however, patch scale experiments are often successfully used to test theories associated with changes in habitat configuration (see review by [Andrén 1994, Johnson & Heck 2006a]). Typically, a reduction in patch size caused by fragmentation is accompanied by a reduction in habitat quality (i.e., decreased leaf density) (Irlandi 1994, Irlandi 1997, Hovel & Lipcius 2001, Goodsell & Connell 2002). In addition, at some threshold level where a habitat becomes extremely fragmented, functional linkages among habitats may also become disrupted, resulting in either a shift in distribution or a decline in the persistence of a population (With & Crist 1995). The decline in worldwide abundance of seagrasses caused by natural (e.g., wave energy) and anthropogenic (e.g., eutrophication, scarring) causes (Walker et al. 1989, Preen et al. 1995, Fonseca & Bell 1998, Duarte 2002), combined with the fact that seagrass meadows are often a mosaic of many different sized patches, makes seagrass meadows model systems for testing theories associated with habitat fragmentation.

Both quality and quantity of seagrass can have substantial impacts on the growth and survival of bivalves (Coen et al. 1994; Irlandi et al. 1995; Irlandi 1996; Bologna and Heck 1999). Previous studies examining habitat fragmentation and bivalves are limited; however, results suggest that fragmentation may be beneficial (or at least not detrimental). In the Gulf of Mexico,

Bologna and Heck (1999, 2000) found that bivalves had increased settlement and growth even while experiencing greater predation along patch edges, ultimately translating to a positive relationship between abundance and patch perimeter. Heck et al. (2002) found that in locations where there was consistent directionality in water movement, there were positive edge effects for northern quahog (*Mercenaria mercenaria* Linné) growth. For the mid-Atlantic coastline, bay scallops (*Argopecten irradians concentricus* Say) and northern quahogs had increased or equivalent survival in patchy rather than continuous habitats (Irlandi 1994, Irlandi et al. 1995, Irlandi 1997, Irlandi et al. 1999), and there was little if any growth advantage to residing within larger patch sizes (Irlandi 1994, Irlandi et al. 1999). In New England, within-patch location of northern quahogs did not influence growth (Heck et al. 2002). In California, *Macoma* spp. were found in greater abundances within seagrass habitats that were considered to be very patchy (Healey & Hovel 2004). Although these results agree that habitat fragmentation is not detrimental to bivalves, differences caused by species, location, time, and magnitude of responses still exist.

The northern and southern (*Mercenaria campechiensis* Gmelin) quahogs (hereafter referred to as hard clams) are two bivalves whose life cycle can depend heavily on seagrasses (Peterson 1985, Peterson 1986, Heck et al. 2002). These species are similar in size, can co-occur, and are known to hybridize (Arnold et al. 1996, Geiger et al. 2004). Unlike bivalves such as the bay scallop, hard clams are long lived and lack the ability to move extensively (Craig & Bright 1986, Devillers et al. 1998); as such, they are susceptible to consequences directly related to changes in seagrass characteristics (Irlandi 1994, Beal 2000, Bologna & Heck 2000, Bishop et al. 2005).

For hard clams, settlement within seagrass meadows can be a double edged sword. Seagrasses can provide increased food

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delivery because of disruption of water flow and increased particle deposition (Irlandi & Peterson 1991, Judge et al. 1993) and protection from lethal and sublethal predation (Peterson 1985, Coen & Heck 1991, Irlandi 1994). However, seagrasses also afford the same protection to intermediate predators such as crabs and juvenile fishes from tertiary predators like gulls and adult fishes (Beal 2000), and the mere presence of a predator can cause a reduction in clam growth rates (Irlandi & Peterson 1991, Nakaoka 1996, Nakaoka 2000). These counteracting effects are likely to explain the multitude of conflicting conclusions about the effects of seagrasses on hard clams. For example, it has been shown that hard clam lethal and sublethal predation can be either identical or less in seagrass meadows than in unvegetated substrates (Coen & Heck 1991, Irlandi & Peterson 1991, Beal 1994, Irlandi 1994, Irlandi 1997). Additionally, hard clam growth can be greater (Slattery et al. 1991, Beal 1994, Coen et al. 1994, Irlandi 1996, Beal 2000), similar (Slattery et al. 1991, Beal 2000, Heck et al. 2002), or less (Irlandi 1996, Heck et al. 2002) in seagrass meadows than in adjacent unvegetated habitats. Seagrass plant structure or patch size may or may not influence clam growth and survivorship (Kerswill 1949, Peterson et al. 1984, Beal 2000, Irlandi 1996). These variable results, as suggested earlier, have been explained by variation in horizontal food flux and the quantity of food particle settlement, temporal and spatial differences, temperature effects, seagrass morphometrics, sublethal predation, and differential current flow (Peterson & Beal 1989, Coen & Heck 1991, Irlandi & Mehlich 1996, Beal 2000, Heck et al. 2002.).

Because most of the aforementioned explanations can vary with the quality, quantity, and areal extent of seagrass meadows, it is important to understand what may happen as seagrasses are exposed to conditions that can cause their fragmentation or loss. The experiment described here was designed to evaluate if habitat fragmentation *per se* could influence hard clam growth and survival. By using caged and noncaged treatments, we measured the growth and survival of juvenile hard clams in seagrass patches of varying sizes and perimeters and with decreasing perimeter: area ratios. Because fragmentation of seagrass habitat often covaries with seagrass meadow structure (Irlandi 1997), and habitat structure can mediate predation (Orth et al. 1984, Orth & van Montfrans 2002), we incorporated aboveground seagrass and epiphyte biomass in our analyses. Previous studies suggested that certain consequences of fragmentation (e.g., increased edge and patchiness) are not detrimental to bivalves, and because greater habitat complexity often occurs in larger habitats, which potentially could also concentrate clam predators, we predicted that increased habitat fragmentation *per se* would result in enhanced growth and survival of hard clams in smaller rather than in larger seagrass patches.

METHODS

During June and July of 2004, 10 seagrass beds ranging in size between 0.5 and 1,750 m² were identified along an 800 m section of southern shoreline in Big Lagoon, Florida (30°25'N, 87°18'W) (Table 1). This shoreline was located entirely within the Gulf Islands National Seashore Federal Park. The seven smallest seagrass patches were monospecific stands of shoal grass (*Halodule wrightii* Ascherson), whereas the three largest patches contained in excess of 95% shoalgrass along with minor

TABLE 1.
Seagrass patch characteristics and quadrat replicates for June and July 2004.

Month	Patch			Replicates
	Size	Perimeter	P:A Ratio	
June	0.46	1.96	4.24	1
	4.86	7.42	1.53	3
	14.17	9.14	0.65	3
	16.00	12.75	0.80	3
	55.49	26.87	0.48	3
	166.30	73.43	0.44	3
	241.04	60.35	0.25	3
	268.92	58.93	0.22	3
	563.99	90.96	0.16	3
	1740.55	267.44	0.15	3
July	0.86	3.53	4.08	1
	1.94	5.36	2.77	2
	9.46	12.01	1.27	3
	14.17	9.14	0.65	3
	54.32	26.26	0.48	3
	176.43	73.43	0.42	3
	241.04	60.35	0.25	3
	268.92	58.93	0.22	3
	563.99	298.50	0.53	3
	1740.55	267.44	0.15	3

(<5%) amounts of turtle grass (*Thalassia testudinum* Banks ex König). Because these habitats are continually growing habitats and because different small patches were used in each trial, dimensions were estimated using a Roll-a-tape measuring wheel prior to the start of each trial. Nine of the 10 patches were approximately elliptical in shape; we measured the major and minor axes of each patch for use in area determinations. The single patch that was not elliptical was broken into several representative geometrical shapes and measurements were obtained to determine the area of each shape. The perimeter of each patch was determined by following the sand-grass interface using the measuring wheel. Both techniques have been used successfully in previous seagrass studies (Johnson & Heck 2006a). From these data, we calculated the perimeter: area (P/A) ratio for each patch. Perimeter:area ratios are a useful measure of habitat fragmentation that combines patch shape and size into a single metric (Schumaker 1996, Johnson & Heck 2006). The result is a unique measurement that can reduce the possibility of correlation between area or perimeter and other unmeasured variables and can also be independent of either area or perimeter. Because it is impossible to back-transform this value to estimate the original perimeter or area, some information pertaining to both patch area and perimeter is lost (Schumaker 1996). P/A ratios can be used at both the landscape scale and patch scale. However, at the landscape scale, mean perimeter: area ratios are used (Schumaker 1996), whereas at the patch level, individual patch measurements are used.

During May 2004, one thousand juvenile hard clams (*M. mercenaria*) were purchased from a commercial supplier in Cedar Key, FL. In the northern Gulf of Mexico, the southern quahog, *M. campechiensis*, is present, but uncommon (Coen et al. 1994, Heck et al. 2002). Thus, we used *M. mercenaria*, a

species used commonly in Gulf of Mexico aquaculture operations and one that is readily available (Arnold et al. 2003). Although the release of nonnative clams into systems is not always advisable, we believed that because *M. mercenaria* is cultured locally (Arnold et al. 2003), there is a naturally high mortality rate (Coen et al. 1994), it regularly hybridizes with *M. campechiensis* (Dillon & Hadley 1994; Arnold et al. 1996), and shares almost the same life history as *M. campechiensis* (Goodsell 1988), that adverse effects within this ecosystem would be negligible (Arnold et al. 2003).

For the duration of the experiment, all clams were held in mesh bags (~100 each) in a flow through system (temperature—24°C; salinity—26) at the Auburn Shellfish Laboratory, Dauphin Island Sea Laboratory, Dauphin Island, Alabama. By crowding clams within mesh bags, we were able to restrict growth without undue mortality in the unused clams between each trial, allowing for a similar sized clam to be used. Clams had a mean \pm SD height (measured as the longest distance between the umbo and ventral margin) of 19.5 ± 2.0 mm in June and 19.3 ± 2.6 mm in July; whereas mean length (measured as the longest distance between the anterior and posterior edges) was 22.1 ± 2.3 mm in June and 21.7 ± 2.2 mm in July. Prior to using any clams, we allowed for two weeks to pass to ensure that mortality associated with transportation had ceased. Before the deployment of each experiment, 450 clams were measured for height and length, and labeled in groups of 15 using waterproof vinyl tags and cyanoacrylic glue.

For each month, clams were transported from the laboratory to the study site in aerated seawater within ice chests. Upon arrival, ambient seawater was exchanged with that in ice chests over a period of 1 h to acclimate the clams to local conditions. Depending on the size of each seagrass patch, we deployed between one and three 0.5 m^2 frames made from 2.5 cm PVC for a total of 24 frames to delineate placement areas (Table 1), a technique used successfully in previous experiments (Marelli & Arnold 1996). The frames were held to the bottom using stakes made from reinforcing bar. Within each of the frames, 15 clams were released, resulting in a stocking density of 30 m^{-2} . Locally reported clam densities are typically much lower than this (Coen et al. 1994); however, this density is well within the reported range of hard clam densities in the Gulf of Mexico (Craig & Bright 1986). After stocking each trial, any unused, tagged clams were frozen for initial biomass calculations. For each of the two trials, we deployed three, $0.5 \times 0.5 \times 0.5\text{-m}$ cages in a range of seagrass patch sizes similar to those stocked for the noncaged treatments. During June, cages were placed in patches that were 55.5, 268.9, and 1740.6 m^2 . During July, cages were placed in patches that were 0.52, 0.76, and 1.02 m^2 . Plastic mesh on the cages was 1 cm^2 and they were staked to the bottom using guywires and reinforcing bar. Clams were stocked in the cages at the same density as the noncaged treatments. Any clams not used during either trial were frozen to derive a baseline regression equation between clam biomass and either height or weight. The purpose of this equation was to allow us to estimate the initial biomass of the clams used during the experiments.

After approximately four weeks, the clams were collected from the frames and cages by hand, and the area surrounding the frames was also searched. The number of clams remaining in each frame was recorded and the clams were stored on ice for transportation. As an estimate of seagrass above ground bio-

mass and epiphyte biomass, two replicate 10 cm^2 quadrats were haphazardly place in the area near each frame and all the above ground seagrass biomass was removed and stored for further processing. After collection, the clams and seagrass were transported to the Dauphin Island Sea Laboratory and frozen for analysis.

Processing of the clams consisted of remeasuring clam height and length and determining soft tissue biomass. Biomass was determined by removing all the soft tissue and calculating the ash free dry weight (AFDW) to the nearest 0.0001 g. To calculate AFDW, the clam tissue was removed and dried at 80°C to a constant weight (DW). It was then placed in a muffle furnace at 500°C for five hours (AW) and then allowed to cool in a desiccator. AFDW was calculated by subtracting AW from DW. Above ground seagrass and epiphyte biomasses were determined by removing all epiphytes from at least 10 shoal-grass leaves with a razor blade. The clean seagrass leaves and the removed epiphytes were placed into two separate pans, whereas the remaining unscrapped seagrass leaves were carefully rinsed and placed into a third weighing pan. These pans were placed into a drying oven (80°C) for at least 24 h and then weighed to the nearest 0.0001 g. The samples were subsequently placed into a muffle furnace (500°C) for five hours and reweighed to calculate the ash free dry weight. Total above ground seagrass biomass and epiphyte loads were calculated by determining the percentage of epiphytes present in the subsample, (e.g., % of epiphytes = [epiphyte AFDW/seagrass AFDW] * 100), then applying this value to the remaining unscrapped leaves.

Mortality was calculated as the proportion of clams surviving after each trial. For height and length, we measured the change in size between the initial measurement and the measurements after the clams were sampled. Somatic growth was determined as the difference between the initial estimated clam biomass and the final biomass. For the initial biomass determination, a power regression model was fitted using any extra clams and the tagged unused clams from June and July ($n = 83$), resulting in the equation: Initial AFDW = $0.0079(\text{Final AFDW})^{7.458}$; $r^2 = 0.96$.

We analyzed mortality and clam growth (somatic, shell height, and shell length) for each month using a full-factorial multiple regression model (SPSS 2002) where seagrass above-ground biomass, epiphyte biomass, and either patch size, perimeter, or perimeter: area ratios (P/A) were the independent variables. To test if relationships between clam growth and patch characteristics that were significant during June and July remained constant between the two trials, we conducted an ANCOVA where month was the covariate. Differences for mean mortality and growth between treatments that were caged and uncaged were compared using ANOVA.

RESULTS

Mortality

During June, 106 of 450 (24%) clams were recovered alive. Sixty-two of the clams were from uncaged treatments and 43 were from the caged treatments. Although more clams were collected from noncaged treatments, the 62 clams represented only 15% of clams deployed, whereas 43 clams recovered from cages represented 96% of clams deployed. This large difference in recovery rates between the caged and uncaged treatments was

significant ($F_{1,29} = 89.12$; $P \leq 0.001$) (Fig. 1). Clam recovery after four weeks in July was less than in June. A total of 36 clams were recovered (9%) from uncaged treatments. For caged treatments, all three cages were destroyed or disturbed by unknown causes and data were not available.

In June, the mean mortality ranged between 80% and 93% for 9 of 10 patches. The remaining patch (268.9 m², 8th largest patch) had a mean mortality of $64 \pm 6\%$. There was a general decline in mortality with patch size (Fig. 2), although there were no significant relationships between mortality and patch size, seagrass above ground biomass, or epiphyte biomass. The smallest patch (0.5 m²) had the highest mortality ($93 \pm 0.07\%$) and the 8th largest patch (269 m²) had the lowest mortality ($64 \pm 0.06\%$). During July, clam mortality for all patches was between 80% and 100%, with the four smallest and the second largest patches having mortalities in excess of 96%. The remaining patches had mortalities that ranged between 93% and 80%. There was a significant negative relationship between mortality and patch area ($F_{1,24} = 4.33$, $P = 0.048$) (Fig. 2) and a significant interaction between perimeter:area ratios and seagrass biomass ($F_{1,24} = 7.95$, $P = 0.009$). During July, there were no significant relationships between clam mortality and either patch perimeter, seagrass above ground biomass, or epiphyte biomass.

Growth

Growth for uncaged clams was minimal during June and significantly less than compared with clams that were caged (Fig. 1). In the uncaged treatments, mean somatic growth for

both months combined was negative, indicating an overall loss in body mass during the trials. Mean clam height increased approximately 0.6 mm and length increased approximately 0.4 mm during the trials. Compared with the uncaged treatments, growth in the caged treatments was approximately three times greater for somatic and shell growth (Fig. 1). As a result, during June there was a significant difference between the caged and noncaged treatments for changes in somatic growth ($F_{1,105} = 6.47$; $P = 0.012$), shell height ($F_{1,105} = 90.43$; $P \leq 0.001$), and shell length ($F_{1,105} = 86.07$; $P \leq 0.001$).

Analysis of changes in clam height, length, and somatic growth as it relates to seagrass patches resulted in several significant relationships during June and July. During June, the change in clam height was significantly and positively related to patch area ($F_{1,61} = 5.88$; $P = 0.018$) (Fig. 3), perimeter ($F_{1,61} = 4.89$; $P = 0.031$) (Fig. 3), and P/A ratios ($F_{1,61} = 4.27$; $P = 0.043$) (Fig. 4), with area and perimeter being positive and P/A ratios being negative relationship. Changes in clam length was not significantly related to patch area or perimeter, but there was a significant negative relationship with P/A ratios ($F_{1,61} = 4.43$; $P = 0.040$) (Fig. 4). For somatic growth, there were no significant relationships with patch size, perimeter, P/A ratio, seagrass above ground biomass, or epiphyte biomass. During July, seagrass above ground biomass, patch area, and perimeter each influenced clam growth. Clam height was significantly and negatively related to patch size ($F_{1,35} = 7.33$; $P = 0.010$) and perimeter ($F_{1,35} = 8.99$; $P = 0.005$) (Fig. 3). Additionally, for clam height there was a significant interaction ($F_{1,35} = 4.81$; $P = 0.035$) between perimeter: area ratios and

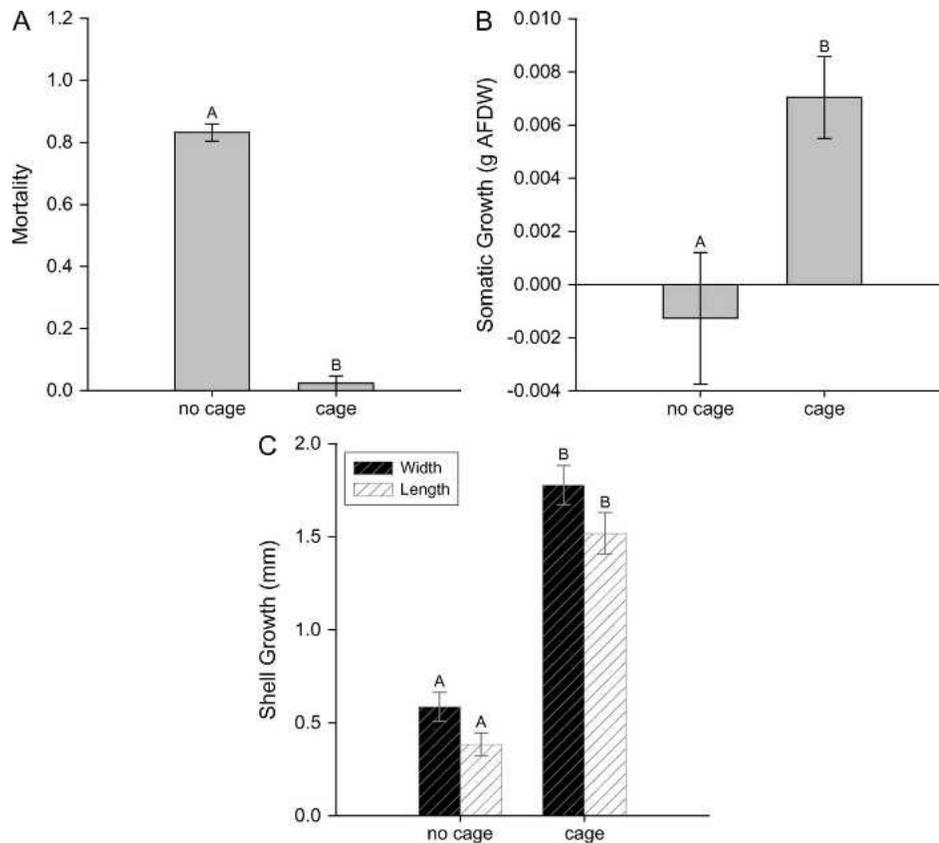


Figure 1. Mean \pm SE differences between June caged and noncaged treatments for clam (A) mortality, (B) biomass, and (C) shell measurements.

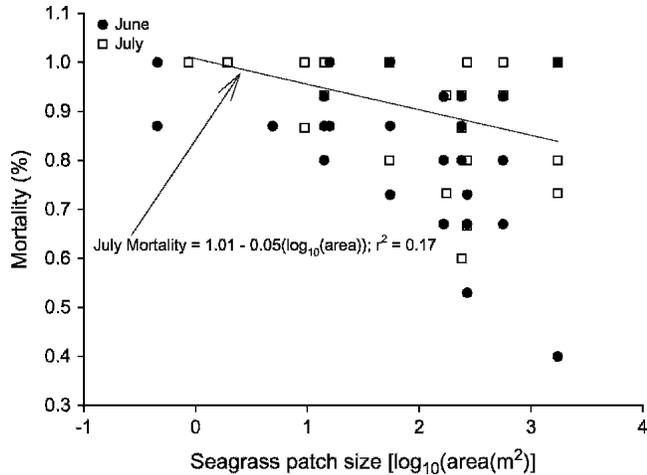


Figure 2. Clam mortality versus seagrass patch size during June and July of 2004. The significant regression model is for July only.

seagrass biomass. Regression analysis of changes in clam length and both patch area and patch P/A ratio resulted in significant multivariate models that included significant interactions for both patch area and P/A ratio with seagrass biomass and epiphyte biomass (Table 2). When patch perimeter was the independent variable, the result was a significant model that included seagrass biomass and \log_{10} (perimeter) (Table 2). For somatic growth, the regression including patch area resulted in a significant model that also included seagrass biomass and \log_{10} (area). The regression analysis that included patch perimeter, resulted in a significant relationship between somatic growth and \log_{10} (perimeter) (Fig. 4), whereas the analysis with P/A ratios resulted in a significant interaction term between P/A ratios and seagrass biomass (Table 2).

When we examined the relationship between growth and patch descriptors across trials, there was a significant change in the relationship between clam height and both patch size and perimeter between June and July (Fig. 3). Results from our ANCOVAs indicated that there were significant interactions between months for patch size (interaction term: $F_{4,82} = 8.45$; $P \leq 0.001$) and perimeter (interaction term: $F_{1,82} = 20.67$; $P \leq 0.001$), indicating that the relationship between changes in clam height and patch size and perimeter varied between trials.

DISCUSSION

For hard clams that reside in seagrass habitats, there must be a balance between the risks of predation and the need to obtain resources for growth and reproduction. Our results showed that in larger patches clams had increased shell growth during June, but during July there was better survival in larger patches and patches with larger perimeters had better somatic growth. Predation rates on hard clams in Big Lagoon increased from June to July, especially in small patches, and when faced with increased predation risk, growth was reduced and energy was partitioned away from somatic growth and toward shell growth.

Previous studies examining habitat fragmentation *per se* often cite differential effects of predators as the reason for inconsistencies within results (Bologna & Heck 1999, Hovel & Lipcius 2002, Johnson & Heck 2006b). During June and July,

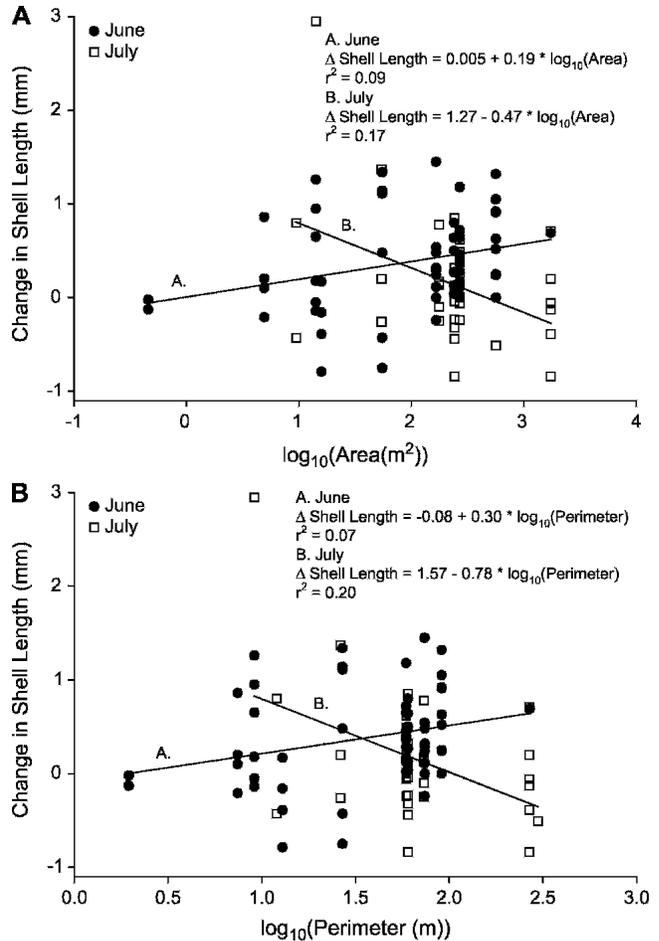


Figure 3. Significant regressions for changes in clam shell height during June and July 2004. Panel A contains significant relationships between changes in shell height and patch area. Panel B contains significant relationships between changes in shell height and patch perimeter.

our data suggested that there were changes in the processes governing hard clam populations within Big Lagoon. This may have been caused by increasing numbers of adult blue crabs (*Callinectes sapidus* Rathbun), a known predator of hard clams (Bisker & Castagna 1989, Beal 2000), coupled with increased growth of shoal grass in small patches. Regardless of treatment location or month, crushed hard clam shells, indicative of blue crab predation, were present during clam retrieval. As is typical of many areas, during the summer the adult blue crab population increases because of seasonal migrations (Perry & McIlwain 1986, Kenney 2001, Murphy et al. 2001). This migration reaches an apex during the late summer or early fall (Perry & McIlwain 1986, Kenney 2001, Posey et al. 2005), and presumably so does the predation risk to hard clams.

During June, the lack of significant relationships between mortality and either patch descriptors or seagrass and epiphyte biomass suggested that habitat fragmentation *per se* had little effect on hard clams. In addition, the positive relationship between clam shell growth and patch area and perimeter, without the subsequent increase in somatic growth, may indicate increased disturbance by crab predators in the larger patches. Nonlethal handling of bivalves by potential predators

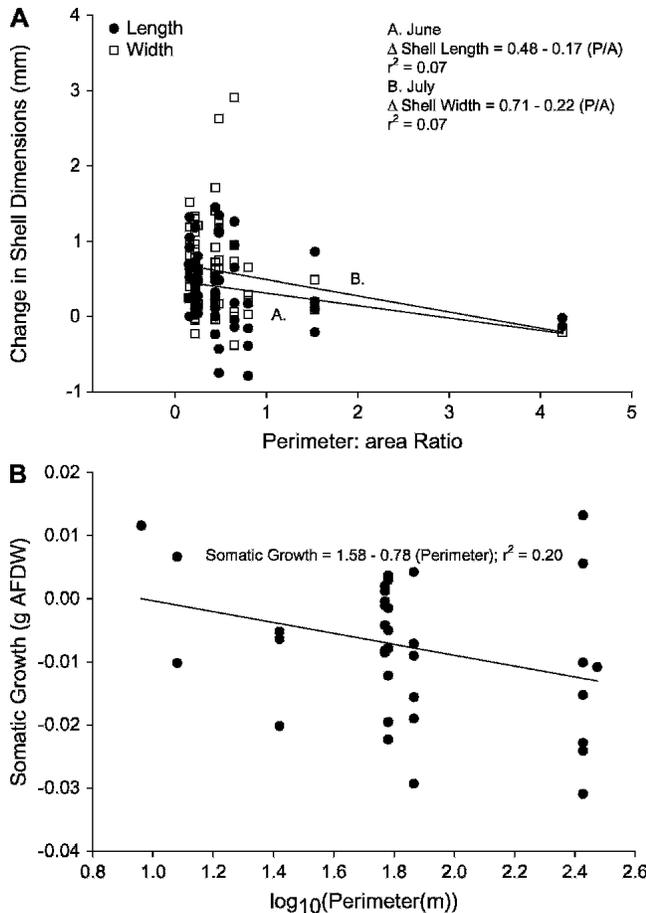


Figure 4. Significant regressions for changes in clam growth (height (●), length (□), and biomass) during 2004. Panel A contains significant relationships between changes in shell height and length with perimeter: area ratios during June. Panel B contains significant relationships between somatic growth and patch perimeter during July.

can trigger increased shell growth (Boulding 1984, Leonard et al. 1999, Smith & Jennings 2000, Dietl 2003). Chemical cues from the close proximity of predators can cause a hard clam to remain buried, resulting in a decrease in shell and somatic

growth (Nakaoka 2000). Because shell growth was positive, our results suggested increased handling.

During June there was a significant positive correlation between patch area and above ground seagrass biomass (Pearson's $r = 0.465$; $P = 0.010$). Because juvenile blue crabs are subject to extensive conspecific predation (Moksnes et al. 1997) and blue crab survival and abundance can be positively related to the complexity of seagrass habitats (i.e., shoot density and/or biomass) (Schulman et al. 1996, Pardieck et al. 1999, Hovel & Lipcius 2002, Orth & van Montfrans 2002), there may have been an increased abundance of juvenile blue crabs in the larger patches. During July, there was no longer a significant correlation between patch size and above ground seagrass biomass, indicating that the small patches had seagrass densities similar to the larger patches. Additionally, there was a significant negative relationship between patch size and mortality, between both patch size and perimeter with shell height, and between perimeter with somatic growth. These results may indicate that the smaller blue crabs that were utilizing the larger and denser seagrass beds as protection during June were able to exit the larger patches and inhabit smaller patches. If this is correct, our variable results may be because of a complex interaction between habitat complexity, patch size, and predator behavior.

Hard clams are not as abundant in the northern Gulf of Mexico as in the eastern and western Gulf (Craig & Bright 1986, Coen et al. 1994, Bologna 1998, Heck et al. 2002, Arnold et al. 2003). Like many other marine invertebrates, the fecundity of hard clams is very high (Arnold et al. 2002, Peterson 2002), suggesting that postsettlement processes in locations like Big Lagoon most likely explain the low numbers of adult clams. As such, consequences of habitat fragmentation *per se* may only indirectly affect hard clams by influencing the predators that routinely consume them. As predicted by terrestrial researchers, larger patches provided increased refuge, thereby reducing clam mortality (Saunders et al. 1991). Previous workers had found that hard clam survival was not related to patch size (Irlandi 1994, Irlandi 1997) and our results show that the responses by hard clams can vary depending on location, as have other habitat fragmentation *per se* studies (Healey & Hovel 2004, Johnson & Heck 2006a). Our results seemingly contradict the emerging opinion that fragmentation within marine habitats does not influence community structure and function in a consistent

TABLE 2.

Significant regression models for changes in northern quahog growth during July 2004. Abbreviations are as follows: Per = perimeter; P/A = perimeter: area ratio; SG = aboveground seagrass biomass; Epi = epiphyte biomass.

Height (mm)	df	F	p	Model
Length (mm)	1,35	7.33	0.01	Δ Shell Height = 1.27 - 0.477 [$\log_{10}(\text{Area})$]; $r^2 = 0.17$
	1,35	8.99	0.00	Δ Shell Height = 1.58 - 0.78 [$\log_{10}(\text{Per})$]; $r^2 = 0.20$
	1,35	4.81	0.04	Δ Shell Height = -0.16 + 1.13 (P/A*SG); $r^2 = 0.12$
Somatic (g AFDW)	3,33	5.64	0.00	Δ Shell Length = -0.02 + 2.44 (SG) - 0.45 [$\log_{10}(\text{Area})$ *SG] - 0.35 [$\log_{10}(\text{Area})$ *Epi]; $r^2 = 0.34$
	2,34	5.66	0.01	Δ Shell Length = 0.972 + 0.496 (SG) - 0.547 [$\log_{10}(\text{Per})$]; $r^2 = 0.25$
	2,34	7.69	0.00	Δ Shell Length = -0.19 + 3.97 (P/A*SG) - 19.96 (P/A*Epi); $r^2 = 0.31$
Somatic (g AFDW)	2,34	13.17	0.00	Somatic Growth = -0.002 + 0.012 (SG) - 0.006 [$\log_{10}(\text{Area})$]; $r^2 = 0.44$
	1,35	8.99	0.00	Somatic Growth = 1.58 - 0.78 (Per); $r^2 = 0.20$
	1,35	4.81	0.04	Somatic Growth = -0.16 + 1.58 (P/A*SG); $r^2 = 0.12$

manner (McNeill & Fairweather 1993, Hovel & Lipcius 2001, Hovel et al. 2002, Johnson & Heck 2006b). However, it is important to note that all but three significant relationships explained less than 30% of the variation within the models, suggesting that other unmeasured factors may ultimately be better predictors of clam mortality and growth. In addition, we must point out that the power of our tests was between approximately 0.40 and 0.50. This can be considered to be less than optimal (<0.80) for statistical testing; however, it does not suggest that the patterns evident are not valid, just that the possibility of making a Type II error is inflated (Sokal & Rohlf 1981).

Because Big Lagoon's seagrass meadows contain many patches in excess of 2,000 m² (M. Johnson pers. obsv.), conditions should be favorable for clam survival. Reductions in hard clam abundances must occur between the time of settlement and the point at which clams obtain a size refuge in larger patches. Typically, bivalve predation can be extensive during this period (Hiddink et al. 2002, Hunt & Mullineux 2002, Walton et al. 2002, Mistri 2004). For three species of bivalves, Beukema & Dekker (2005) found that post larval predation by the shrimp (*Crangon crangon* Linnaeus) lead to successive recruitment failures of bivalves in the Wadden Sea. High, near-shore flats had low shrimp biomass and appeared to provide the only refuge for bivalves during years of high predation pressure. Potential predators of bivalve spat (i.e., shrimp, pinfish (*Lagodon rhomboides* Linnaeus), and blue crabs) (Hill & Wassenberg 1992, van der Veer et al. 1998, Bullard et al. 1999, Costantini & Rossi 2001) can reach densities in excess of 400 m⁻² in Big Lagoon (Johnson & Heck 2006a) and may be responsible for much of the post settlement mortality. If no high quality refuge habitat exists within the Big Lagoon complex, this may explain the relatively low hard clam abundances.

Predators (Hovel & Lipcius 2001, Hovel et al. 2002) and seagrass characteristics (Holmquist 1997, Hovel 2003) can each

be influenced by changing patch sizes, and differential effects by predators as well as variable seagrass characteristics have been used to explain the results of previous experiments (Bologna & Heck 1999, Bologna & Heck 2000, Hovel & Lipcius 2002). If habitat fragmentation *per se* was responsible for the significant relationships, we found the response was more similar to terrestrial studies (Debinski & Holt 2000, Ribas et al. 2005) than other marine studies (Bell et al. 2001, Johnson & Heck 2006a). The reason for this different response may be the inability of hard clams to move extensively after settlement, and typically, organisms that lack the ability to migrate or move are more susceptible to changes in habitat configuration (Andr n 1994, Debinski & Holt 2000).

In conclusion, the complexity of our results highlights the need to discriminate between the effects of habitat fragmentation *per se*, predators, and habitat structure. This is difficult, because often each covaries with seagrass patch size and shape (Hovel 2003); nevertheless, there is still a pressing need to know if patch configuration is an important cause of ecological patterns or if it is simply correlated with other more important ecological variables.

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