1992

Survival of juvenile queen conch, Strombus gigas, in natural habitats: Impact of prey, predator and habitat features

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Recommended Citation

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https://dx.doi.org/doi:10.25773/v5-2vbq-jc63

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The College of William and Mary, 1992

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Survival of juvenile queen conch, *Strombus gigas*, in natural habitats: Impact of prey, predator and habitat features

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A Dissertation

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the degree of

Doctor of Philosophy

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by

Livingston S. Marshall, Jr.

December 1992

APPROVAL SHEET

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

Doctor of Philosophy

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DEDICATION

To my wonderful family:
my mom and dad, Shirley & Livingston, Sr.;
my sisters Juanita, Patricia, Delglicia, Sandra & Pamela;
my brother John; and
my nieces and nephews:
Octavia, Terrell, Nadia, Tristan, Omar, Oran & Ayanna.

And with much love,
To Michelle Paulette Penn

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ACKNOWLEDGMENTS

Each of my advisory committee members deserves recognition for their contributions throughout the course of my studies. My major professor, Dr. Romuald N. Lipcius, deserves special and appreciated thanks for his enthusiastic support and guidance. I am especially thankful to Drs. Herbert M. Austin and Evon P. Ruzecki whose unwavering support and encouragement were always welcomed. I thank Robert I. Wicklund, Carl H. Hobbs, and Professor Bori L. Olla for their time and patience in providing valuable comments in shaping the outcome of my research.

Additional thanks are extended to Robert Wicklund and Gerri Wenz of the Caribbean Marine Research Center (CMRC) for their unselfish logistical, administrative and financial support. Their confidence and belief in my academic abilities from the inception of this work will always be cherished. Members of the VIMS Crustacean Ecology Group spent many long hours assisting me with field work; I am extremely grateful. Karen Metcalf, Geno Olmi, Luis Coba-Cetina, Paul Gerdes, Bruce Layman and Lyn Cox-McCarthy deserves special thanks. I am especially indebted to Dr. David B. Eggleston, a true friend and colleague who spent countless hours assisting me in all aspects of this research.

Although I could never fully thank everyone who contributed toward the successful completion of this work, there are individuals who deserve special mention and thanks: Rodney M. Williams, Gwen Vennings, Liston Cyrus, Danny Gouge, Neville Wisdom, Gerry Wisdom, Dwayne Cooper, Foster and Annette Dorsette, Kathy French, and Dr. William Head. I could not have completed this work without their special support.

I am most grateful for the support and encouragement provided by my entire family throughout my many years of academic studies.

This work was funded by several sources including the Caribbean Marine Research Center (NOAA-NURP), Commonwealth of Virginia, Central Intercollegiate Athletic Association, Lyford Cay Foundation (Nassau, Bahamas), my dad, Livingston S. Marshall, Sr., and Rodney M. Williams (Pickett Foods Ltd., Nassau, Bahamas).

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ABSTRACT

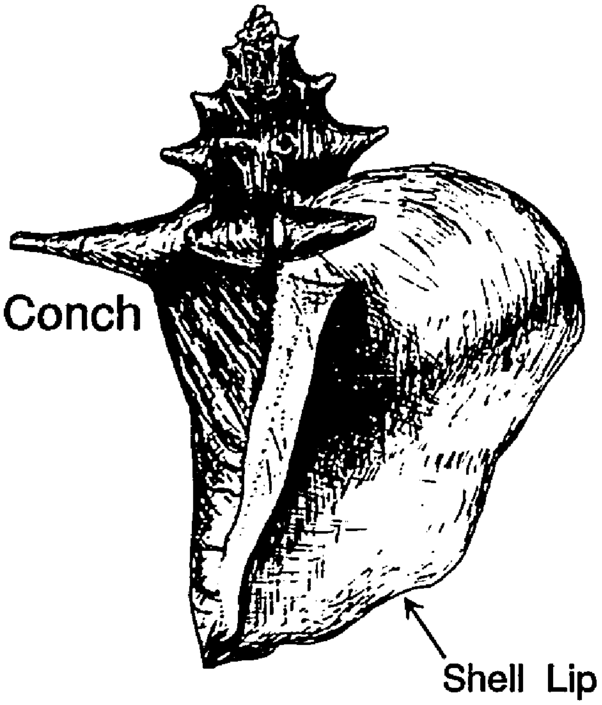
In this dissertation, I experimentally examine predation-induced mortality upon juvenile queen conch, *Strombus gigas*, and assess the importance of select habitat predator and conch characteristics affecting predation intensity. Experiments were conducted during the summer and early fall of 1987, 1988, 1990 and 1991 in seagrass beds and adjacent sand flats near Lee Stocking Island, Exuma Cays, Bahamas. These experiments indicate that various factors act interactively to produce habitat-specific mortality rates in queen conch due to predation. These include (1) habitat type, whereby seagrass beds offer some protection; (2) local population dynamics, such that populated seagrass beds appear to enhance conch survival; (3) population density in some seagrass beds, such that mortality is inversely density-dependent; (4) conch size, such that larger conch have higher survival rates, depending on the specific type of habitat; and (5) predation intensity and predator guilds, which likely differ across habitats, producing habitat-specific mortality rates. When integrated with complementary studies of queen conch trophodynamics, these results provide critical information regarding key ecological factors affecting conch survival. In particular, results from the hatchery-reared experiments demonstrate the potential use of hatchery-reared stocks in natural habitats, and hence a valuable option for enhancement of fishery stocks throughout the Caribbean. In general, the integration of results obtained in this dissertation, with complementary studies of queen conch trophodynamics, should provide valuable suggestions of queen conch habitats, densities and scales of patchiness producing highest survivorship and growth rates in nature.

SURVIVAL OF JUVENILE QUEEN CONCH, *STROMBUS GIGAS*, IN NATURAL HABITATS: IMPACT OF PREY, PREDATOR AND HABITAT FEATURES

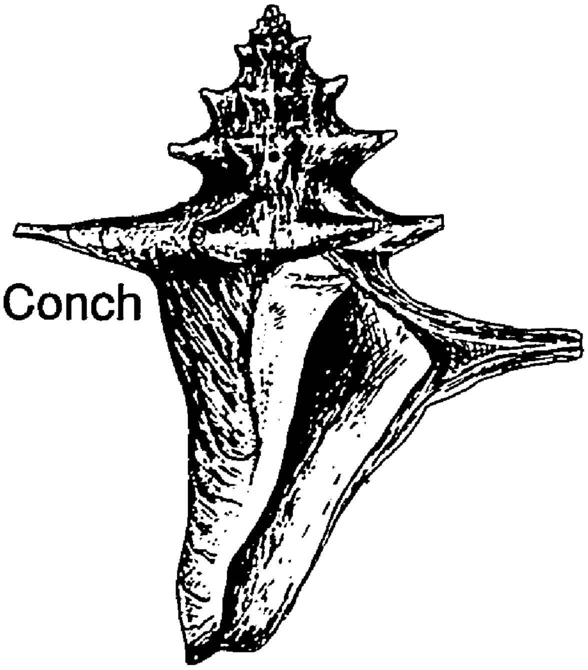
GENERAL INTRODUCTION

The queen conch, *Strombus gigas*, is a prosobranch gastropod widely distributed throughout shallow waters of Bermuda, the Bahamas, southern Florida, and the Caribbean (Randall 1964). Its population biology has been studied in various locations including the Berry Islands, Bahamas (Iversen et al. 1986), Cuba (Alcolado 1976), Puerto Rico (Appeldoorn 1987), the Virgin Islands (Randall 1964), Venezuela (Weil and Laughlin 1984) and Caicos Islands (Hesse 1979). Queen conch are most common in shallow-water beds of turtle grass, *Thalassia testudinum*, and manatee grass, *Syringodium filiforme*, and in sandy bottoms with algal patches (Weil and Laughlin 1984). Juveniles probably remain buried in sandy habitats during their first year, emerging only at night to feed (Iversen et al. 1986). At 50-70 mm total shell length (TSL = tip of spire to distal end of siphonal canal), juvenile conch (0^+ year-class) emerge to reside in shallow seagrass meadows. There they remain for the next two to three years before migrating to deeper waters near the onset of maturity. Adults are distinguished by their well-formed shell lip (Fig. 1). During warmer months, adults migrate to shallow inshore waters for mating and egg laying (Robertson 1959, Randall 1964, Weil and Laughlin 1984). Population densities usually vary between 0.04 and 2.0 individuals/m^2 (Alcolado 1976, Weil and Laughlin 1984, Wicklund et al. 1988), but juvenile conch in densities up to 250 conch/m^2

Figure 1. Adult and juvenile queen conch, *Strombus gigas*, depicting a key morphological shell difference - the lack of a well formed lip area in juveniles.



Adult Queen Conch



Juvenile Queen Conch

undergo mass migrations in shallow seagrass meadows near Lee Stocking Island, Exuma Cays, Bahamas (Stoner et al. 1988, Lipcius et al. 1991).

Throughout its geographic range, the queen conch is an important commercial species, but has recently experienced dramatic declines in many areas largely due to over-exploitation (Adams 1970, Brownell et al. 1977, Brownell and Stevely 1981). Recent attempts to manage and enhance existing populations have been hindered by a lack of knowledge regarding key ecological factors affecting queen conch survival in natural habitats.

Predation is a potentially major cause of *S. gigas* mortality (Jory 1982, Jory and Iversen 1983); mass mortalities and macroparasites of conch are rare (Iversen et al. 1986). Conch are preyed on by crustaceans, fishes and molluscs (Robertson 1961, Randall 1964, Jory 1982, Jory and Iverson 1983, Iversen et al. 1986), including the tulip snail (*Fasciolaria tulipa*), apple murex (*Murex pomum*), giant hermit crab (*Petrochirus diogenes*), Caribbean spiny lobster (*Panulirus argus*), Florida horse conch (*Plueroploca gigantea*), spotted eagle ray (*Aetobatis navinari*), permit (*Trachinotus falcatus*), hogfish (*Lachnolaimus macunus*), queen triggerfish (*Balistes vetula*) and porcupine fish (*Diodon hystrix*). Predation on large, mature conch appears to be limited to large gastropods, hermit crabs, certain sharks, rays, loggerhead turtles (*Caretta*) and octopus.

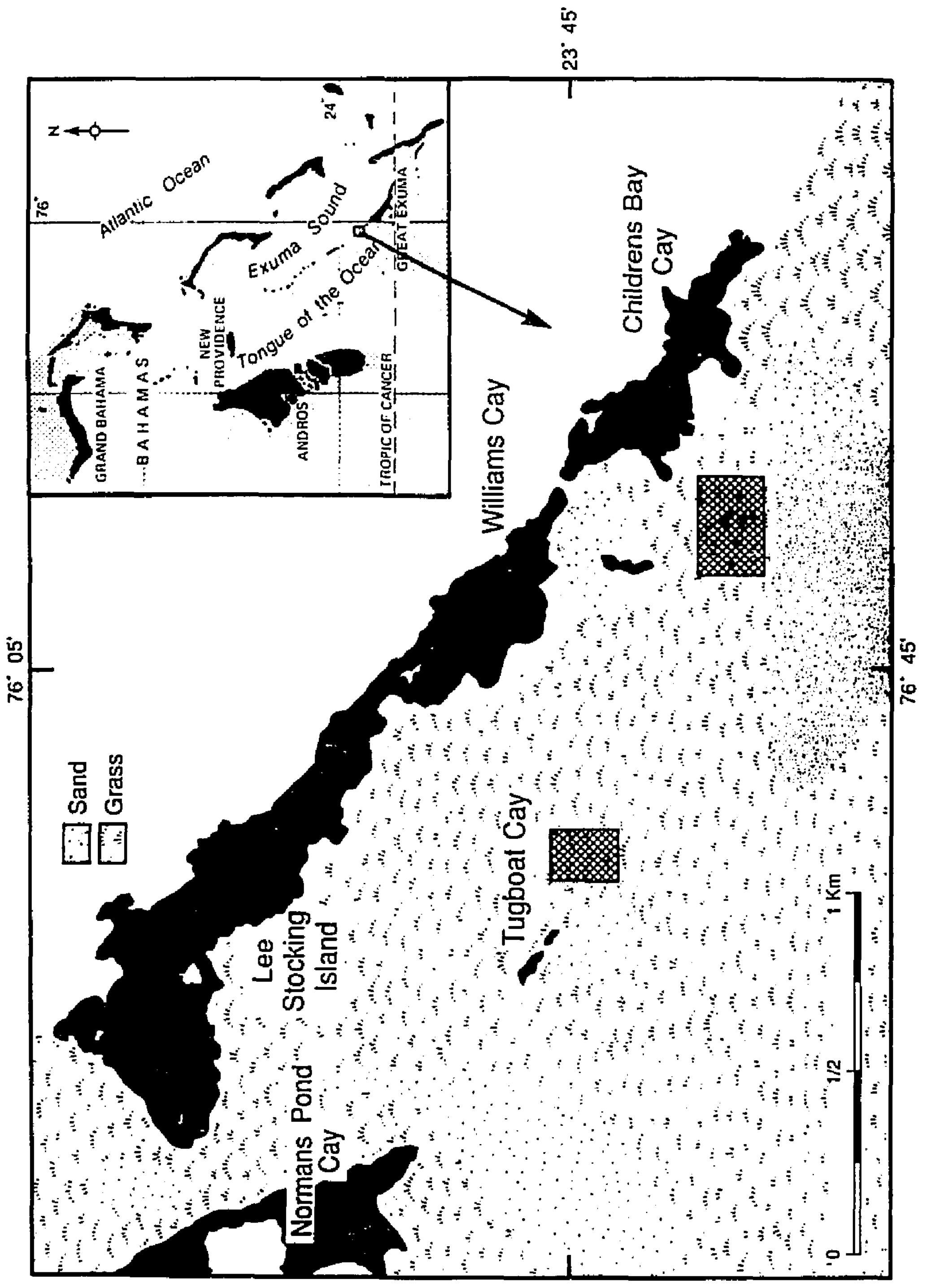
Previous studies on survival of juvenile queen conch in natural habitats have failed to incorporate the interactive features of predators, prey and habitat. In addition, the majority of past studies have utilized four basic approaches, each with its accompanying benefits and disadvantages. Laboratory studies have generally focused on identification of predator types and their modes of attack (Randall 1964, Jory and Iversen 1983, Iversen et al. 1986), comparisons of predation rates upon hatchery-reared and wild conch (e.g., Jory 1982), and categorization of shell-damage features useful in identifying natural predators (Jory and Iversen 1983). Field observations have documented the incidence of damaged shells, which at best provide estimates of relative rates of predation by various predator types (Iversen et al. 1986). Growth and mortality rates due to varying levels of predation intensity have been quantified in field enclosures, with experimental results highly dependent upon the quality of the enclosures (Jory and Iversen 1983). In these cases, however, a lack of controls for cage artifacts in predator-prey interactions precludes meaningful comparisons of these rates with those in natural habitats. Finally, mark-recapture studies incorporating techniques useful in quantifying natural emigration and mortality rates (Appeldoorn 1984, 1985; Iversen et al. 1986) have failed to distinguish between emigration and mortality in the experimental designs, precluding unbiased estimates of natural mortality rates.

In concordance with the hypothesis that juvenile queen conch suffer high mortality rates, length-frequency analyses and survivorship curves (Randall 1964, Alcolado 1976, Iversen 1983) have generally yielded extremely high field mortality estimates. Mortality rates decrease exponentially with increasing size (Appeldoorn 1984), and stabilize after conch attain sexual maturity at approximately 3-3.5 years of age (Appeldoorn and Ballantine 1986). If most of this mortality is due to predation, then predators can potentially exert significant control over queen conch population dynamics at the juvenile stage (Appeldoorn and Ballantine 1986).

In this investigation, I examine several features of juvenile queen conch predator-prey dynamics in a shallow seagrass system near Lee Stocking Island (LSI), Exuma Cays, Bahamas (Fig. 2). Lee Stocking Island is located at the southeastern edge of the Great Bahama Bank (23^0 45' N, 76^0 05' W), adjacent to Exuma Sound. Depths in the nearshore areas average 2-10 m, increasing to 10-20 m within 1 km offshore. Closer inshore and toward the banks, the channels widen into shallows (1-5 m depths) that are characterized by patches of coral heads, turtle grass beds, scattered patches of calcareous algae, and calcareous sand. Stoner et al. (1988), Wicklund et al. (1988), and Herrnkind and Lipcius (1989) provide additional descriptions of the area.

To the west and southwest of LSI, large portions (0.5-3 hectares) of uniform seagrass beds serve as nursery grounds for 0^+-3^+ year-class juvenile queen conch. These juveniles have consistently been observed at moderate to high densities in at least two locations in seagrass beds near LSI (Wicklund et al. 1988; pers. obs.; Fig. 2), offering ideal habitats for manipulative experiments. The nursery grounds are generally characterized by shallow water depths of 3-4 m; year-round surface water temperatures between 22^0-32^0 C; underwater visibility between 15-25 m; poorly

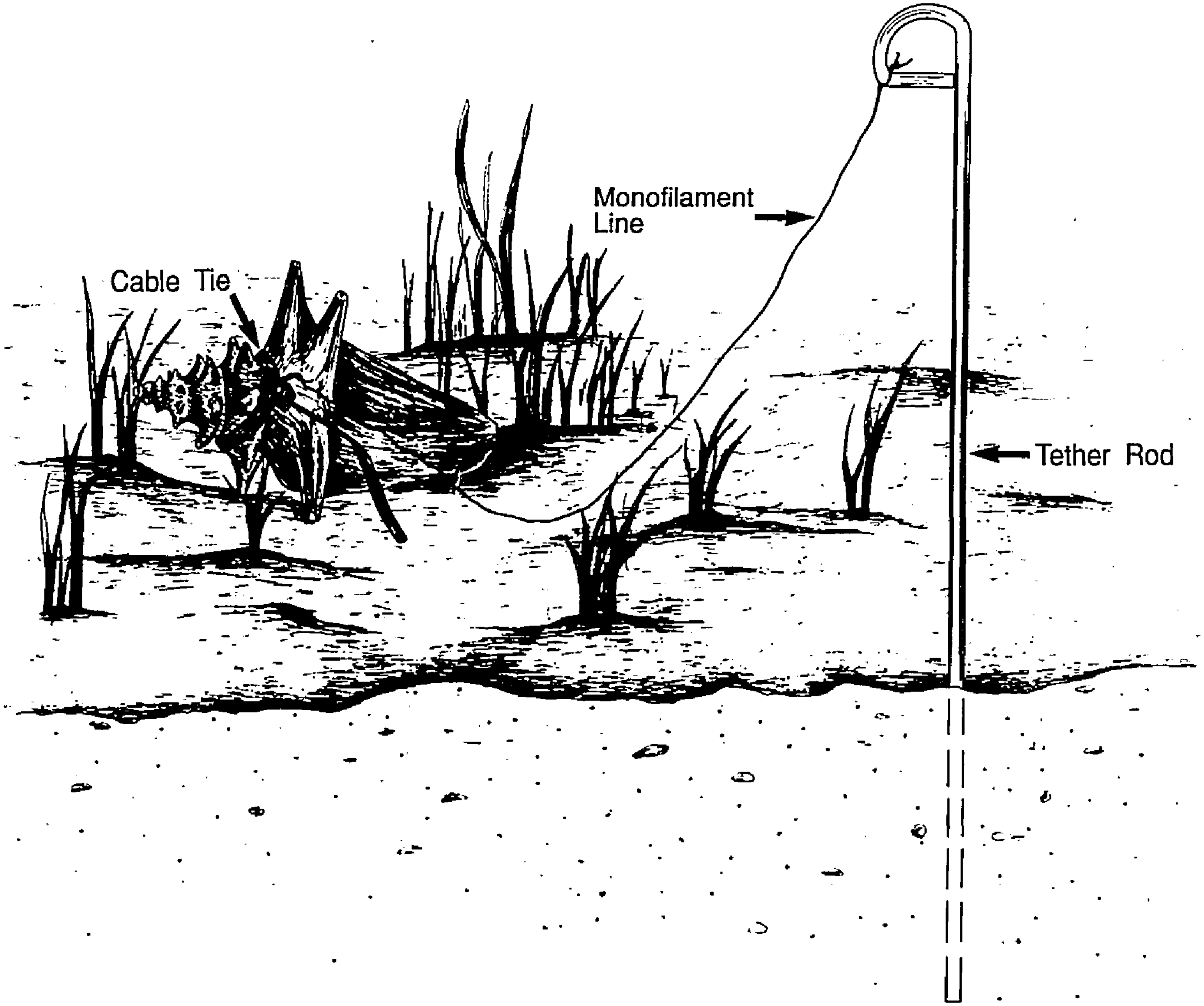
Figure 2. Juvenile conch resident aggregations near Lee Stocking Island, Exuma Cays, Bahamas.


Sand
Grass
76° 05'
23° 45'
76° 45'
Lee Stocking Island
Normans Pond Cay
Tugboat Cay
Williams Cay
Childrens Bay Cay
0
1/2
1 Km
Atlantic Ocean
Exuma Sound
Tongue of the Ocean
GRAND BAHAMA
BAHAMAS
NEW PROVIDENCE
ANDROS
TROPIC OF CANCER
GREAT EXUMA
76°
24°
N

sorted, medium to coarse grained calcareous sediments; and dense to sparse cover of *Thalassia testudinum*, *Syringodium filiforme*, *Penicillus capitatus* and other calcareous algae.

In Chapter 1 of this dissertation, I examine the survival of juvenile conch as a function of conch size, conch density, and habitat type. Chapter 2 compares the survival, growth and burial activity of wild and hatchery-reared juvenile conch in natural seagrass habitats. Chapter 3 examines the hypothesis that juvenile conch survival in seagrass beds is due to variations in predation-induced mortality. This chapter also examines conch survival as a function of the proximity to habitats containing resident conch. Lastly, Chapter 4 examines the use of tethering (Fig. 3) as a tool for estimating juvenile conch survival in natural habitats. In addition, Chapters 2 and 3 provide quantitative data on conch size frequencies, conch densities and epibenthic predator densities within experimental sites.

Figure 3. Schematic of tethering apparatus used to measure relative predation-induced mortality rates of juvenile conch. Prior to the initiation of an experiment, the rod is inserted flush with the sediment surface, and excess length of the cable tie is removed.


Cable Tie
Monofilament Line
Tether Rod

Chapter 1

PREDATION-INDUCED MORTALITY IN NATURAL HABITATS

INTRODUCTION

One of the major ecological issues regarding the distribution and abundance of marine species concerns habitat selection and its regulatory factors. In general, higher densities of organisms are found in vegetated (i.e., structurally complex in terms of biomass and plant density) than unvegetated (e.g., sand) habitats, and the sizes of both predator and prey organisms often vary with habitat type (see review by Cooper and Crowder 1979). The three biotic factors most likely responsible for such patterns are food availability, intraspecific competition, and predation. Of these, predation is often believed to be a major determinant of species abundance and distribution patterns (Connell 1975).

Numerous studies have investigated the role of habitat complexity in marine predator-prey interactions (e.g., Orth et al. 1984, Gotceitas and Colgan 1989). Habitat structural complexity (i.e., plant density or biomass) provides cover for prey by reducing predator capture rates and search capabilities. With few exceptions (Marinelli and Coull 1987), predator foraging success declines with increasing habitat complexity (see reviews in Orth et al. 1984, Ryer 1988), although there may be some threshold level of complexity below which predator foraging success is not reduced significantly (Gotceitas and Colgan 1989).

The relative sizes of predator and prey also determine the effect of structural complexity upon predator-prey interactions (Ryer 1988). Prey size selection has been demonstrated for marine predators feeding on various species of gastropods, bivalves and fish (e.g., Hughes and Elner 1979, Peterson 1982, Werner et al. 1983, Lawton and Hughes 1985). Moreover, sizes below and above those preferred by predators are provided some refuge from predation pressure (Paine 1976).

Prey density is often positively correlated with habitat structure, both in macroinvertebrates (e.g., Stoner 1980, Summerson and Peterson 1984) and fish (Cooper and Crowder 1979, Bell and Westoby 1986, Gotceitas and Colgan 1989). However, many species show compromises with respect to habitat choice when faced simultaneously with the needs to forage and avoid predation (Werner and Hall 1988). In situations where a compromise is necessary, prey may choose a habitat with some intermediate level of complexity in an attempt to maximize their feeding rate while minimizing the risk of predation.

Predators generally respond to varying prey densities in several ways. Predator consumption or searching efficiency may decline with decreasing prey densities or increasing predator densities (Katz 1985, Mansour and Lipcius 1991). Theoretically, decreases in consumption rates will result in the migration of predators to other patches (Hassell 1978), thereby preventing the overexploitation of prey items within a patch. As a result, high- density prey patches or patchily distributed systems will experience higher proportional mortality rates than low-density prey patches (Katz 1985).

In this chapter, I examine the impact of three features -- habitat type, conch size and conch density -- on predation-induced mortality of juvenile *Strombus gigas* in natural habitats. Specifically, I tested the following hypotheses:

(1) that predation-induced mortality in vegetated seagrass sites is lower than

that in an unvegetated, sand site;

(2) that predation-induced mortality is higher for small than large conch; and,

(3) that juvenile conch at low densities experience higher mortality rates than those in high densities.

Specific hypotheses were combined within a single experimental design in manipulative field experiments at LSI. Foraging behavior of potential epibenthic predators is also described.

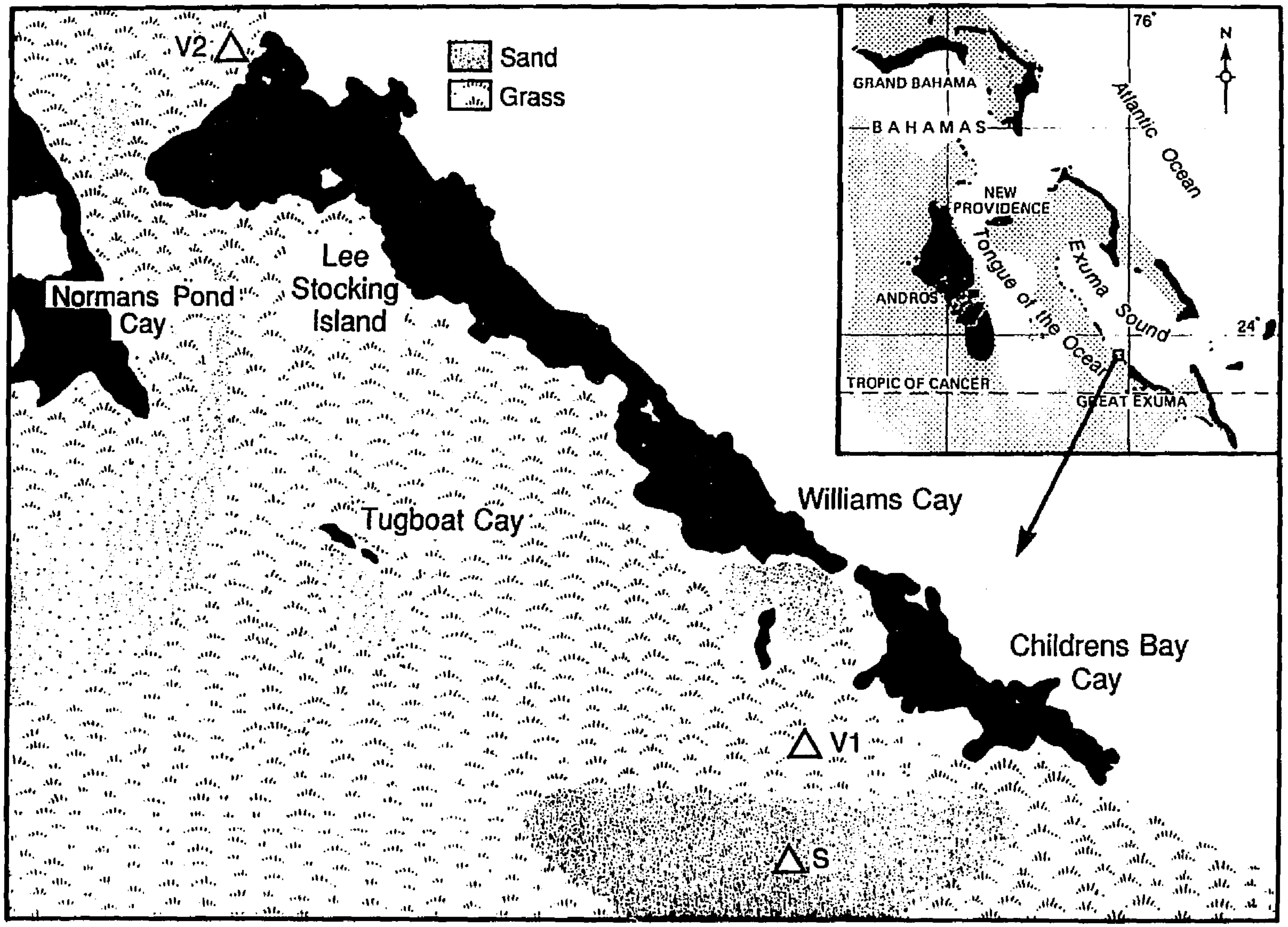
MATERIALS AND METHODS

Study Site

All investigations were conducted in subtidal habitats near LSI (Fig. 4). Experimental plots were set up in two seagrass beds and one sand flat (Fig. 4). The seagrass sites (vegetated 1 (V1) and vegetated 2 (V2)) were established on 17-20 June 1987, whereas the unvegetated, sand (S) site was established on 11 July 1987. The seagrass beds contained poorly-sorted, medium to coarse-grained calcareous sediments, and moderate to low densities of turtle grass (Stoner et al. 1988). Calcareous green algae, including *Halodule wrightii* and *Rhipocephalus phoenix*, were also sparsely distributed throughout the area, along with abundant seagrass detritus.

Site V1 was characterized by average water depths of 3-4 m, current velocities of 60-100 cm/s during maximum flow (Dill et al. 1986), and average juvenile queen

Figure 4. Lee Stocking Island, Exuma Cays, Bahamas. Approximate location of study sites (V1, V2, S) are denoted by triangles. V1 = vegetated seagrass site with resident juvenile conch; V2 = vegetated seagrass bed without resident conch, S = sand site.


V2
Sand
Grass
Normans Pond Cay
Lee Stocking Island
Tugboat Cay
Williams Cay
Childrens Bay Cay
V1
S
GRAND BAHAMA
BAHAMAS
NEW PROVIDENCE
ANDROS
Tongue of the Ocean
Exuma Sound
Atlantic Ocean
TROPIC OF CANCER
GREAT EXUMA
76°
24°
N

conch densities typically near 1.0 conch/m^2 (Wicklund et al. 1988, Stoner 1989, Stoner and Waite 1990).

Site V2 was uninhabited by queen conch. Water depths and bottom features were similar to those at site V1, but currents were weak since the site lies within a protected cove.

Site S was a large sand flat located approximately 50 m southwest of site V1, with sparse stands of turtle grass and manatee grass. A thin, surface algal mat, consisting mainly of blue-green algae typified the area. Water depth averaged 1.5-2.0 m with generally strong tidal currents. Juvenile queen conch were patchily distributed throughout the sand flat at lower densities (0.68 conch/m^2) than those in neighboring seagrass beds (pers. obs.).

Water temperatures during the study period (June-August, 1987) ranged from 26.5^0-31.5^0 C; salinities from 35 to 37 ppt.

Experimental Procedure

In the field experiments I employed tethering, which measures relative predator-induced mortality rates between experimental treatments (Heck and Thoman 1981, Herrnkind and Butler 1986, Wilson et al. 1987, Eggleston et al. 1990). The technique is not intended to measure absolute rates of predation.

Juvenile queen conch were collected by SCUBA divers from areas outside the study sites, and subdivided into two size classes approximating 1 and 2 years of age, respectively (Table 1). Conch were then tethered by fastening one end of a 20-lb-test monofilament line to the locking portion of a cable tie (Fig. 3). The cable tie was then secured around the spire of each conch and excess tie removed. The other end of the monofilament line was tied to the top bent portion of a 33-cm stainless-steel rod (3.2 mm dia.). A numbered tag identifying each animal was attached to the top of each rod, which was sunk in the sediment such that only the top few centimeters of the rod and tag were visible. The tether-rod system did not provide discernible visual or mechanical cues to predators, and did not appear to impede movement of conch in the tether area. The total tether length was approximately 40 cm between the stake and attached cable tie, providing each conch with a circular foraging area of approximately 0.5 m. Recent studies have shown that tethered juvenile queen conch grow at habitat-specific rates approximating those of untethered individuals (L. S. Marshall, Jr. and R. N. Lipcius unpubl.).

Two separate but related sets of field experiments were established to examine predator-induced mortality rates of juvenile *S. gigas*. Experiment I compared mortality rates between two seagrass beds: one with resident conch (site V1), and one without resident conch (site V2). Experiment II examined mortality rates in a sand habitat (site S). In each seagrass bed, eight circular plots (3-m radius) were set up in two parallel rows of four. Four of these plots received six tethered conch for a nominal plot density of 0.21 conch/m^2, equivalent to low to moderate natural densities in the area.

Table 1. Experimental Design

Analysis	Factor	Levels	Descriptions
Exp. I	Site	2	Two seagrass beds - V1 and V2 [a]
	Size	2	Large: 120-150 mm TSL [b]
			Small: 80-100 mm TSL
	Density	2	High: 0.85/m^2
			Low: 0.21/m^2
Exp. II [c]	Size	2	Large: 120-150 mm TSL
			Small: 80-100 mm TSL

[a] V1 contained resident juvenile conch; V2 was uninhabited by conch.

[b] TSL = total shell length: from tip of spire to distal end of siphonal canal.

[c] Experiment II was conducted in the unvegetated sand habitat.

The remaining four plots received 24 tethered conch for a nominal plot density of 0.85 conch/m^2, equivalent to moderate to high natural densities. Two replicates of each factor combination (density and size) were thereby established in each of the seagrass sites (e.g., two replicates of low density/large conch per seagrass site, two replicates of high density/small conch per seagrass site). In total, 60 small and 60 large juvenile conch were tethered within plots in sites V1 and V2, with all experimental treatments systematically interspersed.

In the sand flat site, six plots (4 m radius) were aligned in a single row. Each plot received 11 tethered conch, thereby establishing the same nominal density (0.21 conch/m^2) as the low-density treatment in the seagrass plots. Plots containing large conch were alternated with plots containing small conch. Larger plots in the sand flat were chosen to accommodate more conch, and thus reduce the variance in the proportional mortality estimates for each plot, while concurrently maintaining plot densities comparable to those in the vegetated sites.

Initial set up of experimental plots in sites V1 and S required the removal of conch from those plots to control conch densities. Potential epibenthic predators encountered during conch removal were quantified and left undisturbed in the sites. Sites V1 and S also contained resident juvenile conch in areas surrounding the experimental plots. The resident conch in site V1 persisted throughout the experimental period, with individuals immigrating into the study areas, thus necessitating their removal prior to each sampling. Shortly after the establishment of experimental plots in the sand flat, the resident conch began to migrate from the shallow sand areas towards the slightly deeper seagrass meadows. Hence, immigrants were only removed from the experimental plots during the first two weeks of the study. In contrast, site V2 was devoid of queen conch, precluding the need to remove conch from experimental plots. Plots at sites V1 and V2 were monitored weekly for 10 weeks, whereas site S was monitored for 7 weeks. All conch lost weekly were noted, then replaced with individuals of the same size.

The following criteria were used to determine conch losses due to predation-induced mortality or conch escape:

Predation-induced mortality:

- Empty conch shells found intact on the tethering apparatus, with shells often showing chipped areas around the lip. This category, as well as the following category, were considered to reflect predation-induced mortality and not mortality due to physical stress or ill health because 100 % of 40 conch tethered in cages survived over the full experimental period.
- Hermit crabs (*Petrochirus diogenes*) occupying undamaged or partially damaged shells (chip marks) that remained attached to the tethering apparatus.
- The occurrence of crushed shells and absence of tethered conch in the immediate vicinity of the stake, monofilament line and cable tie (often chewed).
- Actual sighting of conch being eaten by epibenthic predators, including the tulip snail (*Fasciolaria tulipa*), apple murex (*Murex pomum*), and hermit crab (*Petrochirus diogenes*).

- Absence (disappearance) of entire conch plus tethering apparatus. These were attributed to the actions of large pelagic or benthic predators rather than escape because in pilot trials (1) conch were unable to remove the tether rod from the substrate, and (2) conch locations were noted and their shells were detected with 100% accuracy in all sites.

Escape:

- Conch missing from tethering apparatus, with cable tie open or locked.

Experimental Design and Data Analysis

Weekly conch proportional mortality rates were standardized using the following formula:

$$X_i = E/(T \times D);$$

where E = number of conch eaten over the duration of the experiment,

T = duration of experiments in each site (10.0, 10.6 and 6.7 weeks for sites V1, V2 and S, respectively),

D = initial number of conch per experimental plot (24 conch at high densities and 6 at low densities in sites V1 and V2; 11 per plot in site S), and

X_i = average weekly proportional mortality for plot i during the full experimental period.

Thus, mortality data from each plot generated a single, independent value for statistical analyses. Two a priori, full-factorial and balanced ANOVA designs were employed to test the effects of conch size, density, and habitat type on conch proportional mortality rates in the seagrass sites. Levels of these factors included: large and small conch sizes, high and low conch densities, and vegetated and unvegetated habitat types (Table 1). A three-way ANOVA was employed to analyze data from sites V1 and V2, with Site, Conch Size and Density as factors. A one-way ANOVA was also used to analyze data from the sand site (S), with Conch Size as the only factor. Proportional mortalities were arc-sine square-root transformed to meet statistical assumptions (Underwood 1981). Hartley's F-max test was used to test for homogeneity of variance (Sokal and Rohlf 1981); in all cases either variances were homogeneous or the ANOVA results were significant at a probability level lower than that for Hartley's F-max test (Underwood 1981). In cases where the overall F-ratio was significant, Ryan's Q test (Day and Quinn 1989) was used to compare treatment means. When significant interaction effects precluded singular conclusions concerning main effects, the data were analyzed with Ryan's Q test within levels of main factors (Underwood 1981).

During each sampling period in site V1, the number of non-experimental (immigrant) conch within experimental plots were recorded, permitting analysis of proportional mortalities as a function of ambient conch densities (ambient conch density = (number of experimental + immigrant conch per plot) / total area of plot). Ambient densities were sorted and ranked from lowest to highest, then grouped into three levels of 1.0 conch/m^2 intervals ranging up to 3.0 conch/m^2.

RESULTS

Predator Observations

The most frequently occurring epibenthic predator was the hermit crab *Petrochirus diogenes*, followed by the apple murex, *Murex pomum*, and tulip snail, *Fasciolaria tulipa* (Table 2). Remains of previously tethered conch shells, broken monofilament lines, and large (1-2 m^2) cropped seagrass areas within and nearby experimental plots indicated the periodic presence of large vertebrate predators, such as sea turtles, sharks or rays. *P. diogenes*, *M. pomum*, and *F. tulipa* often attacked tethered conch in the experimental plots. Small to medium-sized *Petrochirus* (60-140 mm TSL) were frequently observed manipulating conch shells with their chelae, then reaching into the opening of the conch shell in an attempt to extract the animal from its shell by the operculum. Conch typically responded by withdrawing fully into the shell, thereby continuing a long battle (often 1 h or more) until the predator was either successful in extracting the conch from the shell, or the conch managed to escape the predator's grasp. Unsuccessful attempts by some small ($<$ 70 mm TSL) *Petrochirus* to extract a conch usually resulted in further attempts with nearby smaller conch. In contrast, *Petrochirus* larger than 140 mm TSL typically chipped away at the lip area of the conch shell, soon exposing the prey for consumption.

Murex were usually found attacking conch in groups of two or more. They were also observed with *Petrochirus*, apparently feeding on tethered animals that succumbed to multiple attacks. When attacking solitarily, *Murex* attached to the

Table 2. Summary characteristics of potential epibenthic predators within experimental plots.

SITE	CHARACTERISTICS	PREDATORS		
		Petrochirus	Murex	Fasciolaria
V1	No. Observed	145	73	6
	% Of Total	64.7 %	32.6 %	2.7 %
	Mean Size[a]	88.4 mm	86.8 mm	89.3 mm
	Size Range	10-164 mm	58-108 mm	66-118 mm
	Frequency (%)[b]	63.6 %	42.0 %	6.8 %
V2	No. Observed	51	6	1
	% Of Total	87.9 %	10.4 %	1.7 %
	Mean Size	101.0 mm	65.4 mm	93.0 mm
	Size Range	10-200 mm	40-75 mm	--
	Frequency (%)	33.0 %	6.8 %	2.3 %
S	No. Observed	26	2	1
	% Of Total	89.7 %	6.9 %	3.4 %
	Mean Size	93.8 mm	59.5 mm	113 mm
	Size Range	10-132 mm	32-87 mm	--
	Frequency (%)	26.2 %	4.8 %	2.4 %

[a] Mean sizes in TSL. Juveniles (< 50 mm TSL) were counted in Total No. Observed, but not in Mean Size and Size Range calculations.

[b] Frequency of occurrence (%) equals mean number of plots with one or more predators per week.

outside lip area of the conch, inserted the proboscis into the shell opening, then rasped at the flesh. On two separate occasions, *Murex* was observed drilling through the spire of conch shells tethered within experimental plots. The presence of partially consumed conch appeared to attract *Petrochirus* and *Murex* as possible scavengers.

Although only observed in low numbers, *Fasciolaria* elicited the most distinct predator evasion response from conch. Queen conch almost instantaneously began to flee with short, quick, hopping motions when approached by *Fasciolaria.* This behavior is a characteristic response to large epibenthic predators (Schmitt 1982). Once successful in capturing a conch, *Fasciolaria* was very effective in killing and consuming its prey through insertion of its proboscis into the conch shell opening, followed by rasping of the flesh.

Tethering Experiments

In experiment I at sites V1 and V2 (Factors = *Site*, *Size*, *Density*) there was a significant *Density* effect and a significant *Site* x *Density* interaction effect; *Size* was not significant (Table 3). When analyzed by *Site*, *Density* was significant for site V1 (Ryan's Q test, Critical F = 7.71, df = 4, $P < 0.05$; Fig. 5a), but not for site V2 (Ryan's Q test, Critical F = 7.71, df = 4, $P > 0.05$; Fig. 5a). When analyzed by *Density*, *Site* was not significant in either case (Ryan's Q test; low density: Critical F = 7.71, df = 4, $P > 0.05$; high density: Critical F = 7.71, df = 4, $P > 0.05$). At site V1 proportional mortality was inversely density-dependent for the two experimental densities, with highest proportional mortalities in low-density plots (Fig. 5a).

The non-tethered resident conch in site V1 migrated into the experimental plots, thereby inflating plot densities into the range of naturally occurring intermediate to high conch densities. These ambient conch densities differed significantly from nominal experimental densities (ANOVA, $F = 20.61$, df = 1, $P < 0.001$). Thus, I also analyzed proportional mortality of experimental conch as a function of ambient conch density (Fig. 5b). Proportional mortality was inversely-density dependent: highest at low ambient conch densities, moderate at intermediate ambient conch densities, and lowest at highest ambient conch densities; however, this trend was not statistically significant (ANOVA, $F = 2.71$, df = 2, $P = 0.07$).

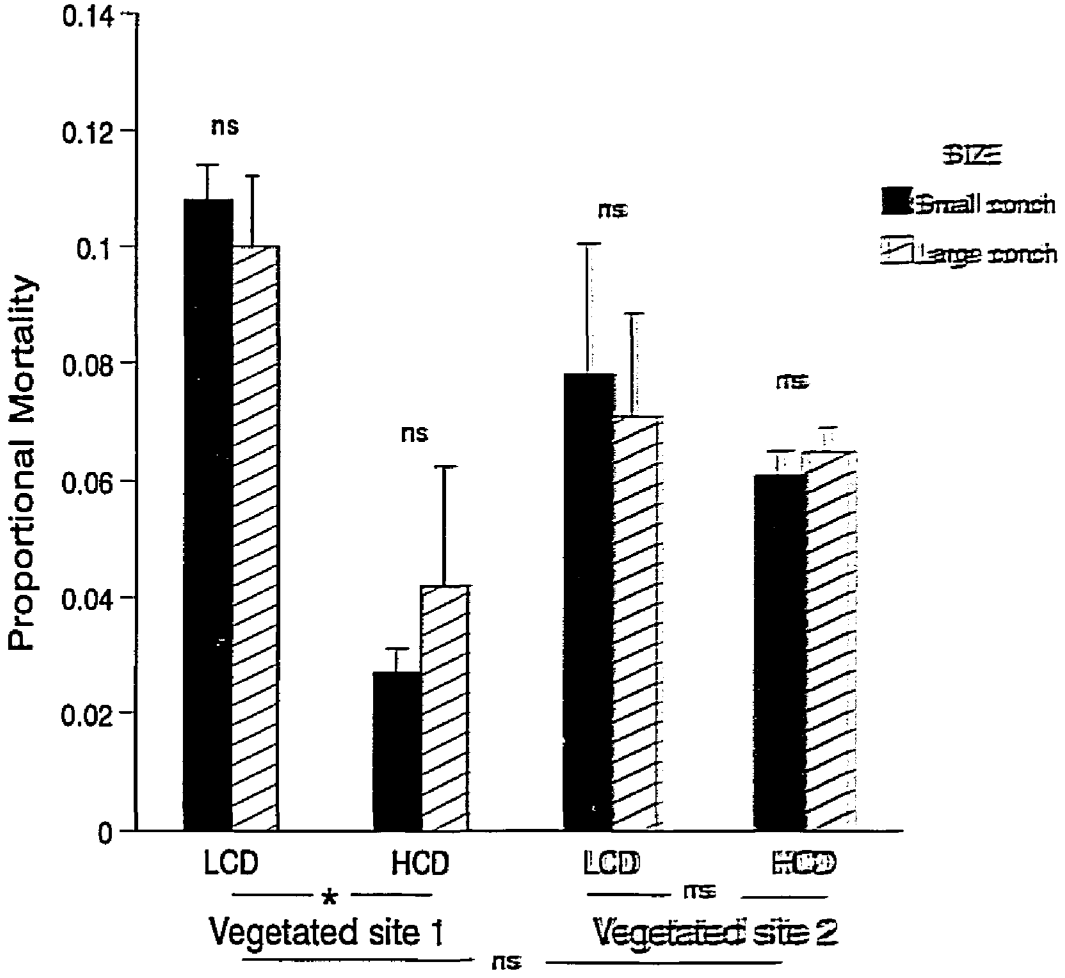
In experiment II, mean proportional mortality rates did not differ significantly by *Size* (ANOVA, $F = 1.45$, df = 1, $P = 0.295$) for conch tethered in the sand site (S). Though not significant, there was a trend toward higher mortality rates for small conch over large conch. This non-significance may have been due to low sample sizes, as indicated by a power test showing a required sample size of at least 10 plots per treatment combination (at power = 0.80) to detect a proportional mortality difference of 0.03.

Table 3. Three-way ANOVA on data from sites V1 and V2 (dependent variable = arc-sine square-root transformed proportional mortalities).

Source of variation	DF	MS	F
Site	1	0.985	0.10 ^{ns}
Density	1	91.059	9.43 *
Size	1	0.146	0.02 ^{ns}
Site X Density	1	54.723	5.67 *
Site X Size	1	0.381	0.04 ^{ns}
Density X Size	1	3.754	0.39 ^{ns}
Size X Density X Size	1	0.566	0.06 ^{ns}
Error	8	9.655	

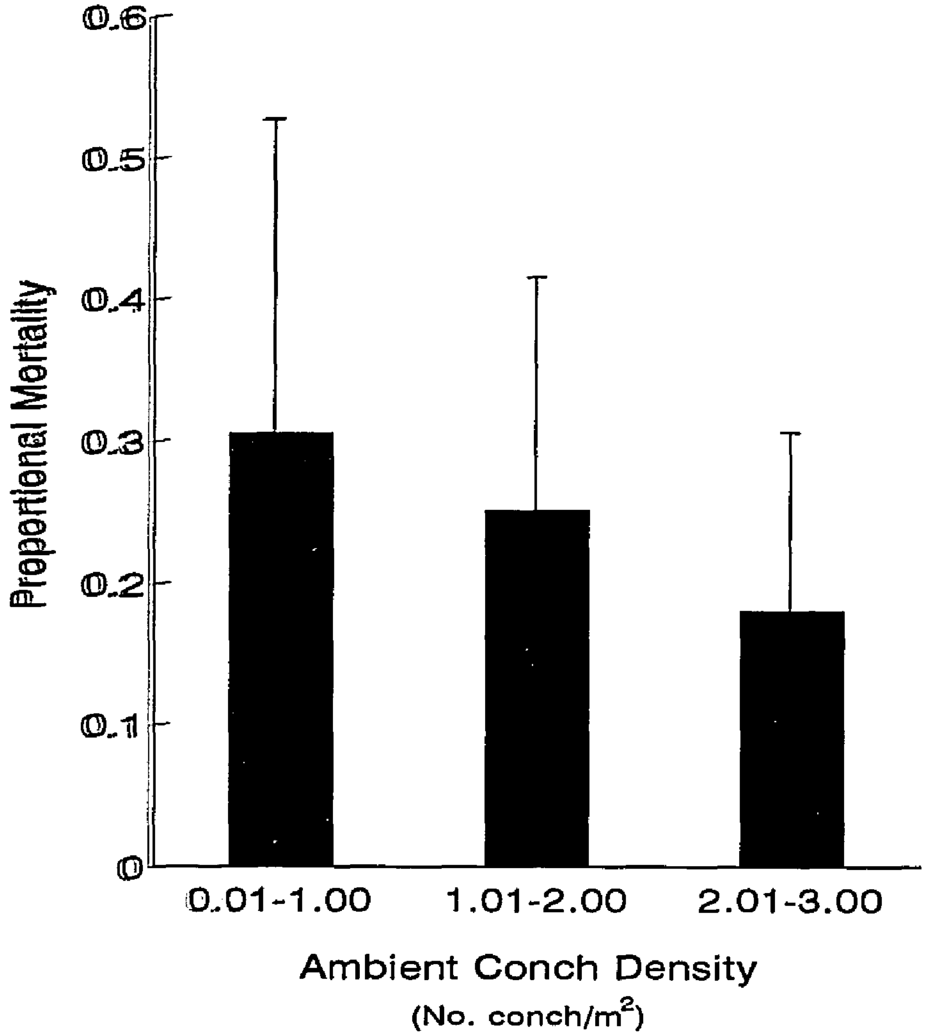
^{ns} $P > 0.05$, * $P < 0.05$

Figure 5a. Proportional mortalities for small (S) and large (L) conch in sites V1, V2. Sites V1 and V2 received low (0.21 conch/m^2) and high (0.85 conch/m^2) density treatments. Vertical lines on top of bars denote one standard error.



LCD = Low Conch Density, HCD = High Conch Density

Figure 5b. Inversely-density dependent proportional mortality of experimental conch as a function of ambient conch density in site V1. Vertical lines on top of bars represent one standard deviation.


Proportional Mortality
0.6
0.5
0.4
0.3
0.2
0.1
0
0.01-1.00
1.01-2.00
2.01-3.00
Ambient Conch Density
(No. conch/m^2)

DISCUSSION

These field experiments demonstrated inversely density-dependent mortality rates of juvenile queen conch in a seagrass bed with naturally occurring resident conch. Inverse density-dependent predation has been previously documented in both field (Katz 1985) and laboratory (Hildrew and Townsend 1977, Thompson 1978, Spitze 1985, Lipcius and Hines 1986, Eggleston 1990a, b,) experiments. The present study is the first to identify such a mortality pattern in a tropical field system.

The occurrence of such a pattern in juvenile queen conch has a number of critical implications. First, mortality is inversely density-dependent if there is a reduced risk of mortality as prey density increases. Inverse density-dependence may produce a partial refuge from predation for some segments of the conch population, mainly those conch in microhabitats with high ambient conch densities. Such a phenomenon could contribute to the continued persistence of juvenile conch in seagrass beds, similarly to that postulated in other systems (Murdoch and Oaten 1975, Hassell 1978, Lipcius and Hines 1986, Eggleston et al. 1990). Second, the survival of newly recruited juvenile conch (0^+ year-class) in seagrass beds may be significantly affected by the inversely density-dependent patterns of predation-induced mortality. Ambient conch densities at the scale of meters to tens and hundreds of meters naturally range through the low, intermediate, and high conch densities tested herein (Wicklund et al. 1988, Marshall, Jr. and Lipcius unpubl.). Recently emerged recruits from the 0^+ year-class that are in high density patches similar to the conch densities tested in this investigation conceivably experience the lowest mortality rates in the local population, relative to those newly emerged juveniles residing in low conch density patches. Hence there may be selection for recently recruited juveniles to move into high density patches within seagrass beds with resident conch.

Third, the occurrence of mass migrations of juvenile queen conch within seagrass beds (Stoner et al. 1988, Lipcius et al. 1991) may also be explained in part by the inversely density-dependent mortality. For instance, mortality rates that are relatively low at high conch densities may result in a relative prey refuge from predation for conch migrating en masse, similar to that postulated for the mass migration of spiny lobster (Herrnkind 1980). Furthermore, there was a relative paucity of epibenthic predators within the band of mass-migrating juvenile conch, and an apparent absence of visible signs of predation-induced mortality (pers. obser., June-August, 1988). Therefore, I suggest that one reason juvenile conch migrate en masse is to avoid high predation-induced mortality rates; migration per se is probably due to other causes such as food limitation.

These field experiments further demonstrate that predation-induced mortality of juvenile queen conch and the inversely density-dependent effect observed in one seagrass bed varies across habitats. In particular, predation rates were affected significantly by conch density in the seagrass bed with resident conch but not in a second seagrass bed without resident conch. I postulate that variations in proportional mortality rates in our experiments may be due to (1) habitat-related variation, (2) variation in the composition, efficiency and abundance of epibenthic predators at each site (see Table 2), or a combination of both. Juvenile queen conch burial as a means of avoiding predation has been hypothesized by Appeldoorn (1984), and experimental animals in the sand site were observed on several occasions in partially buried states. In the vegetated sites, burial activity would be reduced or hindered due to the presence of plant, detrital, and below-ground root material. A combination of these two latter phenomena may partially explain the occurrence of lower mortality rates in the unvegetated site relative to the vegetated sites.

The structure of the suite of predators in the three experimental sites was dominated by *Petrochirus diogenes*, followed by *Murex pomum*, then *Fasciolaria tulipa*. Perhaps only some portion of this guild is responsible for the recorded mortality in the experimental sites. This situation would be analogous to that reported by Menge (1982) where *Thais lapillus* is evidently the only functionally important predator (though others are present) feeding on benthic prey in a New England rocky intertidal area. Closer to the subtidal, *T. lapillus* is joined by starfish, crabs, and possibly fish as functionally important predators. Differences in predation intensity could also simply reflect differences in prey abundances (Menge 1978a, b); however, additional information is needed on predator behavior to determine the precise cause of varying predation intensity in the respective habitats.

Although prey size selection is evident in various epibenthic predators feeding on gastropod molluscs (Hughes and Elner 1979, Lawton and Hughes 1985), there was little evidence for such a phenomenon in these experiments. Indiscriminate consumption of both large and small (conch) prey occurred in all three experimental sites, though small conch in the sand site showed a trend for higher proportional mortality rates than large conch. This lack of prey size selectivity by epibenthic predators was surprising considering that the suite of epibenthic predators observed in experimental sites were capable of handling the available range of conch sizes. Nonetheless, our use of a limited size range of large conch may have precluded discrimination of size selectivity by predators.

These experimental field results indicate that juvenile queen conch survival in natural habitats is site-specific, with patterns of predation-induced mortalities being a combined function of habitat type and prey availability. Additional manipulative investigations into predator and prey characteristics such as size, morphology, behavior, and local patch dynamics are needed to explain the role of predator-prey interactions in structuring queen conch populations in a wide range of habitats.

SUMMARY

In this chapter, I examined predation-induced mortality of juvenile queen conch with field experiments in shallow subtidal habitats near LSI. The survival of tethered juveniles was measured as a function of (1) conch size (80-100 mm and 120-140 mm TSL), (2) conch density (0.21-3.0 conch/m^2), and (3) habitat type (seagrass with resident conch, seagrass without resident conch, and sand). In addition, epibenthic predator distribution and abundance were quantified within experimental sites. There was no effect of conch size on predation-induced mortality in any of the experimental sites. Mortality rates did not differ significantly between the two vegetated sites; however, the impact of nominal conch densities on mortality rates differed within the two vegetated sites. In the seagrass bed with resident conch, conch mortality was inversely density-dependent, with highest proportional mortalities at the nominal low density. A similar pattern was observed when proportional mortality was analyzed as a function of ambient conch density. There were no significant density effects in the seagrass site without resident conch. The mortality pattern observed in the seagrass containing resident conch in part explains the continued persistence of juvenile conch within the experimental area. Differences in the patterns of observed proportional mortalities may be partially related to meso-scale conch densities in the site containing resident conch or by differences in predator composition and abundance between the sites.

Chapter 2

SURVIVAL OF WILD AND HATCHERY-REARED JUVENILE QUEEN CONCH IN NATURAL HABITATS

INTRODUCTION

The release of hatchery-reared juveniles into natural habitats for stock enhancement has been documented for various benthic marine invertebrates, though few attempts have experienced long-term success (Tegner 1989, Polovina 1990). In theory, the advantages of such releases are twofold (Polovina 1990): first, hatchery-reared juveniles released into natural habitats might rapidly supplement natural stocks such that the release of hatchery-reared animals can be discontinued once natural stocks recover; and second, hatchery-reared juveniles added to natural stocks on a long-term basis might increase harvest levels of a fishery over levels achieved from natural stocks alone.

Despite success in larval and juvenile culture of the queen conch, *Strombus gigas*, (Siddall 1983, Davis et al. 1987), recent attempts to enhance natural populations of *S. gigas* by transplanting hatchery-reared juveniles into natural habitats have failed due to several factors. Foremost are the difficulties associated with placement of hatchery-reared conch in suitable micro-habitats (Appeldoorn and Ballantine 1983), high predation-related mortalities (Jory and Iverson 1983), and the possibility that behavioral responses of hatchery-reared conch differ significantly from those of wild conch. In addition, physical stress resulting from the transport of conch to the field may augment mortalities in the field.

Past investigations utilizing hatchery-reared queen conch have been limited to: (1) large field releases with subsequent studies on growth, survival, and movements (Appeldoorn and Ballantine 1983, Appeldoorn 1985); (2) field investigations to determine the effects of size on mortality (Appeldoorn 1984); and (3) laboratory experiments to quantify density-growth relationships (Appeldoorn and Sanders 1984). Field experiments are typically characterized by low or variable survival rates, precluding meaningful site comparisons (Appeldoorn and Ballantine 1983).

Field experiments using juvenile conch in subtidal habitats have been logistically difficult and problematic to date. Natural habitats harbor many predators and permit long-range movement and concealment (i.e., burial) of juvenile conch, thus making small animals or their shells difficult to recover. If hatchery-reared conch are to be used to enhance natural populations, it is essential to evaluate whether differences in predation-related mortality rates exist between cultured and wild animals. Baseline rates of mortality due to factors other than predation (i.e., stress and mortality associated with handling and transport) also need to be established. Furthermore, determination of differential predation and growth rates between habitats is necessary if outplanted conch are to be placed in habitats suitable for maximum survival (Stoner 1989, Stoner and Sandt 1991).

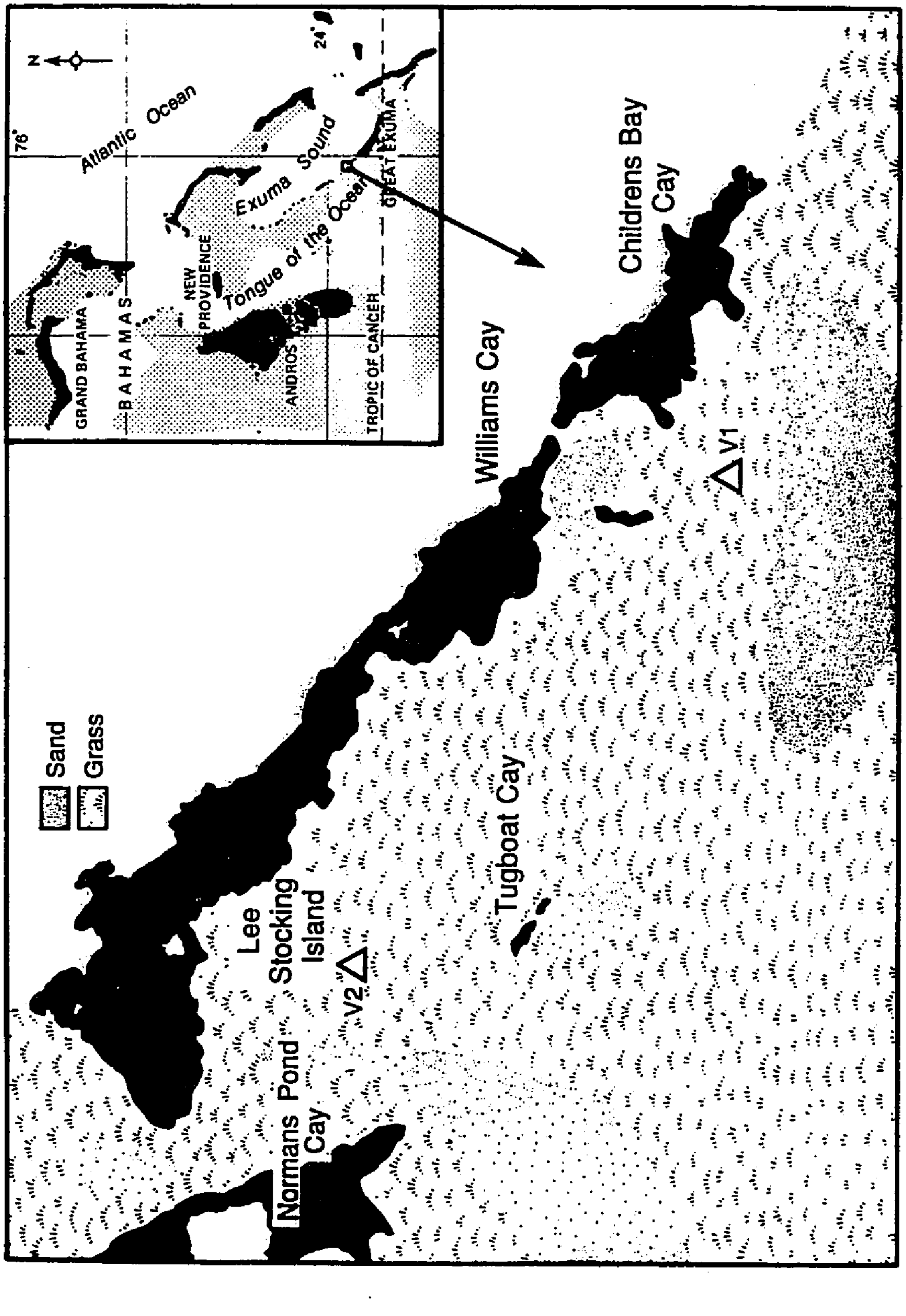
This study quantifies mortality and growth rates of hatchery-reared and wild juvenile queen conch in an experimental framework using cages and tethering in two natural habitats near Lee Stocking Island, Exuma Cays, Bahamas. Behavioral (burial) activity was also measured in both stock types. Specifically, I tested the hypothesis that hatchery-reared *Strombus gigas*, growth rates are significantly lower than those of wild conch; predation-induced mortalities of hatchery-reared conch are higher than those of wild animals; and, that hatchery-reared conch behavioral activity differs significantly from those experienced by wild, naturally occurring juvenile conch.

METHODS AND MATERIALS

Study Sites

Tethering experiments were conducted in seagrass habitats near LSI (Fig. 6). Two experimental sites (V1, V2) were chosen on the basis of their similarities in environmental features (Fig. 6). Both seagrass beds were characterized by poorly-sorted, medium to coarse-grained sediments, and low to moderate densities of turtle grass (*Thalassia testudinum*: 27.0 - 72.0 g dry wt/m^2; Stoner and Waite 1990). Calcareous green algae, including *Halimeda incrassata* and *Rhipocephalus phoenix*, were also sparsely distributed throughout the area, along with abundant detritus. Average water depth in both experimental sites was approximately 3-4 m, with current velocities of 60-100 cm/s during maximum flood (Dill et al. 1986). A key difference between site V1 and V2 was in the abundance of resident benthic organisms: initial survey of site V1 indicated varying densities of juvenile conch and associated epibenthic predators, while site V2 was devoid of resident conch but contained a small number of epibenthic predators (less than 2 predators per 20 m^2). Water temperature throughout the study period ranged from 25.0-29.0^0 C; salinity ranged from 35-37 psu.

Figure 6. Lee Stocking Island, Exuma Cays, Bahamas. Approximate location of study sites (V1, V2) used to compare survival of hatchery-reared and wild conch.


Sand
Grass
Normans Pond Cay
Lee Stocking Island
V2
Tugboat Cay
Williams Cay
V1
Childrens Bay Cay
N
76°
24°
Atlantic Ocean
Exuma Sound
Tongue of the Ocean
GRAND BAHAMA
BAHAMAS
NEW PROVIDENCE
ANDROS
TROPIC OF CANCER
GREAT EXUMA

Size-Frequency and Density Estimates

Size-frequency and density estimates were simultaneously obtained from site V1, before, during and at the conclusion of the first 11 wks of the field tethering experiment. A final size-frequency and density estimate from site V1 was taken during January 1989. Density estimates were obtained by sampling six haphazard 2.5-m-radius circular plots. All conch within each of the six plots were collected and their total shell lengths (TSL: from tip of spire to distal end of siphonal canal in mm) measured with calipers underwater; conch were then haphazardly redistributed within the plots. Samples from the circular plots were used to construct size-frequency histograms. Additional conch were collected until sample sizes of approximately 200 were obtained per sampling period. The latter task was accomplished by collecting conch from an area outside the circular plots: all conch encountered were selected irrespective of size until the required sample size was attained.

Experimental Animals

The hatchery-reared juveniles used in our experiments were first generation (pers. comm., M. Davis, Project Coordinator, Turks and Caicos Conch Farm). After 9-10 months of laboratory rearing, the animals (50-60 mm TSL) were placed in fully enclosed 1 m^2 wire-mesh oyster bags (mesh size: 1 cm x 1 cm) at densities approximating 25 conch/m^2. These bags were then placed in shallow, nearshore subtidal areas (1.5 m depth) characterized by a mixture of hardbottom, sandy areas, *Thalassia* seagrass, and macroalgae (*Laurencia* and *Batophora* spp.). Conch were fed an abundance of *Laurencia* once per week but were also exposed to additional food sources growing on mesh bags and the natural bottom. Laboratory growth rates prior to field transfer averaged 0.25 mm/d, but decreased to approximately 0.15 mm/d following field transfer, probably as a result of changes in diet (M. Davis, pers. comm.). Hatchery-reared animals were in the field approximately three mths. prior to their shipment to LSI.

This study focused on wild and hatchery-reared juvenile queen conch ranging between 60-82 mm TSL. A total of 200 hatchery-reared conch arrived at LSI approximately 24 h after being packed and shipped from the Turks and Caicos Conch Farm. Upon arrival, the conch were left in their shipping bags (100 animals per bag, equally divided onto four large, egg-carton trays), and immediately placed in a large circular pool with open circulating seawater for acclimation. Four hours later the conch were removed from their shipping bags and transferred into three fully enclosed wire-mesh cages (mesh size: 1 cm x 1 cm; cage size: 1.4 m x 1.4 m x 1.2 m) for further acclimation. Shipping-related mortalities were assessed at this point.

Wild juvenile queen conch were collected from the vicinity of Childrens Bay Cay, approximately 250 m outside the experimental area. These conch were also held in wire-mesh cages to standardize treatment of experimental animals, to observe behavior (e.g., feeding and locomotion activity), and to facilitate their retrieval. Acclimation cages were located in a protected embayment. Both hatchery-reared and wild animals were cage-acclimated for 48 h.

EXPERIMENTAL DESIGN

Cage-Control Experiment

A cage-control experiment using hatchery-reared and wild conch was conducted concurrently with the field tethering experiment to (1) determine mean growth rates of caged conch, and (2) estimate mortalities due to factors other than predation. The cage-control experiment was performed from 1 September 1988 to 16 November 1988 (11 wks). Four fully enclosed wire-mesh cages initially used for acclimation were used in the cage experiment. Cages were oriented such that the enclosed conch had a 1.96 m^2 bottom area over which they could move and feed. Each of two cages received either 20 hatchery-reared conch or 20 wild conch, for a density of $10/m^2$. Prior to caging, the TSL of each conch was recorded to calculate the mean initial TSL (mm) for each cage treatment. Based on earlier findings by Stoner and Sandt (1991), conch were fed weekly with detrital material (seagrass detritus and algae) during the entire 11 wk period. In addition, caged animals were observed feeding on algal material growing on the inside of enclosed cages. Upon termination of the cage experiment, all surviving conch were again measured to determine mean final TSL (mm) so that growth of cage-held, hatchery-reared and wild conch over 11 wks could be calculated.

To establish non-predation-induced mortality rates, conch in all four cages were examined daily during the first week of the experiment, and then weekly for the next 10 weeks. Dead conch or their empty shells were removed without replacement.

Field Experiment

The field tethering experiment was established in the two experimental sites (V1, V2) on 1 September 1988. Initial set up of experimental plots in site V1 required the removal of conch from those plots to establish nominal experimental conch densities. Potential epibenthic predators encountered during conch removal were quantified and left undisturbed. The resident conch in site V1 persisted throughout the experimental period, with individuals immigrating into the experimental plots, thus necessitating their removal prior to each sampling. In contrast, site V2 remained devoid of resident queen conch. Conch were tethered in a manner similar to those described in Chapter 1. Prior to the introduction of tethered animals into experimental plots, the TSL (mm) of each experimental conch was recorded.

A total of 12 experimental plots, each 4.4 m x 4.4 m, was set up in each of the two experimental sites (V1 and V2). Six plots per site were designated for tethering wild animals, while the remaining six received tethered hatchery-reared animals. With a plot size of 19.4 m^2 and the inclusion of eight animals per plot, densities were established at 0.41 conch/m^2, well within the range of natural queen conch densities (Stoner 1989). In total, 96 hatchery-reared and 96 wild juvenile conch were tethered within plots in sites V1 and V2. All experimental treatments were systematically interspersed.

Approximately 48 h after introducing the tethered animals to the field, we collected data on the burial activity of all experimental conch. Conch were considered to be buried if at least two-thirds of their shells were submerged beneath seagrass detritus or bottom sediments. The burial data were converted to proportions of conch buried (i.e., total number of conch buried per plot divided by the total number of conch (8) per plot), then analyzed for Stock (hatchery-reared, wild) and Site (V1, V2) effects using a fixed-factor, 2-way ANOVA model.

Tethered conch in experimental plots were sampled daily during the first week for mortalities, and weekly for the next 10 wks. Potential epibenthic predators encountered in experimental plots during sampling were identified, measured, and left in the plots. I used criteria similar to those described in Chapter 1 to ascribe conch losses to predation-induced mortality or conch escape.

Weekly sampling of tethered conch in sites V1 and V2 to record mortality rates was suspended at the end of 11 wks, but the experiments was continued unmonitored until 7 January 1989 at which time mortality and growth rates were again recorded. A final sampling was conducted on 10 July 1989 to record mortality and growth rates. All conch surviving at the end of 11, 18 and 33 wks were measured to determine final TSL (mm) and overall growth rates. Thus, we were able to estimate and analyze mortality and growth rates over three distinct periods during the course of our tethering experiments: 1 September - 16 November 1988 is designated as 'Period I', 1 September 1988 - 7 January 1989 is designated as 'Period II', while 1 September 1988 - 10 July 1989 is designated as 'Period III'.

I used the *t*-test and a series of 1-, 2-, and 3-way analysis of variance (ANOVA) models (after procedures in Underwood 1981) to test the effects of Site, Stock, and Time on conch proportional mortality, and growth during the two experimental periods.

Use of the mortality data generated a single, independent value from each plot for statistical analyses. Proportional mortality and proportional burial data were arc-sine, square-root transformed to meet statistical assumptions (Underwood 1981). Hartley's F-max test was used to test for homogeneity of variance (Sokal and Rohlf 1981); in all cases either variances were homogeneous or the ANOVA results were significant at a probability level lower than that for Hartley's F-max test (Underwood 1981).

RESULTS

Size-Frequency and Density Estimates

Ambient conch densities averaged 1.3-2.3 per m^2 in site V1 throughout Period I, while January 1989 estimates averaged 2.7 per m^2 (Table 4). Site V1 was generally inhabited and numerically dominated by two size classes of juvenile conch with approximate year-class boundaries at 95 mm TSL and 160 mm TSL (Fig. 7). Conch less than 95 mm TSL were 1^+, while those between 95-160 mm TSL were 2^+. It is also likely that those greater than 150 mm TSL were older 2^+ or 3^+. In the four samples, all conch larger than 165 mm TSL exhibited a well-formed shell lip characteristic of adult conch (Randall 1964). These adults represented less than 2% of all animals sampled.

Size and Growth

Caged conch

At the initial set up of control cages, mean TSL differed significantly between hatchery-reared (68.0 mm) and wild conch (73.7 mm) (Table 5). However the difference between these two means (5.7 mm) is not considered biologically meaningful since both groups represent a narrow size range within a single year-class (Fig. 7). Despite the availability of a large and continuous food supply, neither hatchery-reared nor wild conch grew significantly over Period I (11 wks) (Table 5).

Tethered Conch

Mean initial TSL of the 96 wild conch (74.3 mm) was significantly larger than that of the 96 hatchery-reared conch (71.7 mm) (3-way ANOVA; $F = 23.46$, df = 1, $P < 0.001$); again this difference was not considered biologically meaningful. There were no significant *Site* effects or *Site* x *Stock* interactions at the beginning of the study (3-way ANOVA; *Site*: $F = 2.32$, df = 1, $P = 0.130$; *Site* x *Stock*; $F = 0.01$, df = 1, $P = 0.984$).

At the end of Period I, 17 hatchery-reared and 6 wild conch had been killed in site V1, compared with 44 hatchery-reared and 37 wild conch killed in site V2. Mean initial TSL of those conch killed did not differ significantly from that of surviving conch (Table 6). A comparison of TSL between stock types for all surviving conch in the two experimental sites indicated significant *Site*, *Stock*, and *Time* (initial versus final) effects

Table 4. Juvenile queen conch densities in site V1 on four sampling dates. Each plot sampled (N=6) consisted of a 2.5 m radius circle. Mean densities over time are not significantly different (1-way ANOVA, F = 1.11, df = 3, P > 0.05).

Sampling date	N	Mean density (conch/m^2 ± sd)	Range of densities (conch/m^2)
08/29/88	159	1.3 ± 1.7	0.1 - 4.1
10/24/88	192	1.6 ± 1.1	0.3 - 3.3
11/14/88	267	2.3 ± 1.7	0.5 - 4.4
01/06/89	312	2.7 ± 1.1	1.4 - 4.5

Figure 7. Size frequency of resident juvenile conch in site V1. Samples were taken on three separate dates during 1988 (fig. a, b, c) and once during 1989 (fig. d). Values shown are the total number of conch per size interval (Total Shell Length, TSL in mm).

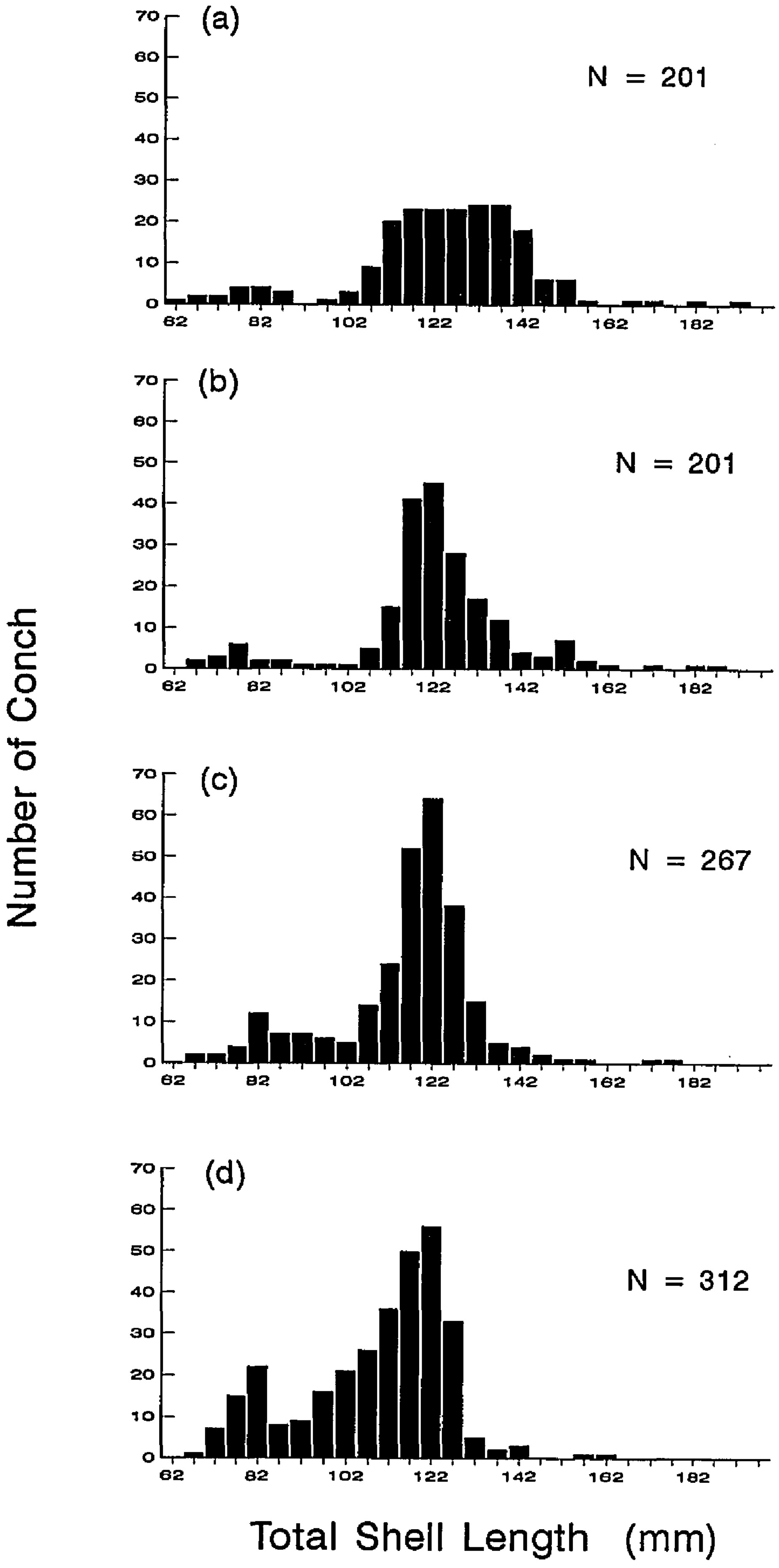

Number of Conch
(a)
N = 201
(b)
N = 201
(c)
N = 267
(d)
N = 312
0
10
20
30
40
50
60
70
62
82
102
122
142
162
182
Total Shell Length (mm)

Table 5. Two-way ANOVA (cage nested within stock) comparing mean TSL (mm) of hatchery-reared and wild conch over time (time 1 = initial set-up, time 2 = final: end of 11 weeks) for Period I.

Source of Variation	df	MS	F
Stock	1	982.5	68.8 ****
Time	1	2.2	0.2 ^{ns}
Cage (Stock)	2	21.0	1.5 ^{ns}
Stock x Time	1	8.0	0.6 ^{ns}
Time x Cage (Stock)	2	5.4	0.4 ^{ns}
Error	142	14.3	

^{ns} $P > 0.05$, **** $P < 0.001$

with no significant interaction effects (Tables 6 and 7). In all cases, mean final TSL for surviving conch were significantly higher than mean initial TSL; both TSL values were slightly higher in site V2 than V1. By the end of Period I, tethered conch in both sites had grown significantly. There were no significant differences between average daily growth rates for hatchery-reared and wild conch in site V1 (*t*-test, t = -0.45, df = 51, P = 0.65) or site V2 (*t*-test, t = -0.26, df = 4, P = 0.81) during Period I (Table 8).

Growth patterns observed during Period II were similar to those observed in Period I (Table 8). In site V1, 24 hatchery-reared and 35 wild conch remained, compared to only 4 wild conch in site V2. Comparisons between stock types for surviving conch in site V1 indicated significant *Site*, *Stock*, and *Time* effects with no significant interactions (2-way ANOVA; *Stock*: F = 11.82, df = 1, P = 0.001; *Time*: F = 14.72, df = 1, P < 0.001; *Stock* x *Time*: F = 0.01, df = 1, P = 0.96). There were no significant differences between average daily growth rates for hatchery-reared (0.027) and wild (0.026) animals (*t*-test, t = 0.08, df = 37, P = 0.94). Although 3 of the 4 surviving conch in site V2 indicated positive growth rates, there were no significant differences between mean initial and mean final TSL (*t*-test, t = -1.23, df = 5, P = 0.27).

By the end of Period III of the field tethering experiments, no conch survived in site V2. In contrast, 9 hatchery-reared and 12 wild conch survived in site V1. For these surviving conch there was a significant difference between mean initial TSL (77.5 mm) and mean final TSL (83.5 mm); there were no significant Stock or interaction effects

Table 6. Summary data of tethered hatchery-reared and wild conch at the end of Period I. Outcome represents those conch surviving (alive) and dead (killed) at the end of Period I. Time: I = initial, F = final. X ± sd (mm) = mean TSL (mm) of conch used ± one sd. N = number of conch.

Outcome	Site	Stock	Time	X ± sd (mm)	N	Size Range
Alive	V1	Hatchery	I	71.3 ± 3.1	31	67 - 79
			F	74.9 ± 3.7	31	68 - 83
		Wild	I	73.7 ± 4.6	42	60 - 81
			F	77.6 ± 5.2	42	61 - 88
	V2	Hatchery	I	73.5 ± 1.3	4	72 - 75
			F	77.8 ± 3.8	4	74 - 83
		Wild	I	75.6 ± 3.7	11	69 - 80
			F	80.6 ± 4.0	11	73 - 86
Dead	V1	Hatchery	I	71.3 ± 2.7	17	68 - 76
		Wild	I	74.8 ± 4.0	6	69 - 81
	V2	Hatchery	I	72.0 ± 2.7	44	69 - 81
		Wild	I	74.4 ± 4.3	37	67 - 81

Table 7. Three-way ANOVA on growth data from the field tethering experiment examining the effects of site (V1, V2), stock (hatchery-reared, wild) and time (initial, final) at the end of period I.

Source of variation	df	MS	F
Site	1	123.0	6.9 **
Stock	1	128.4	7.2 **
Time	1	346.6	19.5 ***
Site X Stock	1	0.1	0.0 ^{ns}
Site X Time	1	3.8	0.2 ^{ns}
Stock X Time	1	1.2	0.1 ^{ns}
Site X Stock X Time	1	0.1	0.0 ^{ns}
Error	168	17.8	

^{ns} $P > 0.05$, ** $P < 0.01$, *** $P < 0.005$

Table 8. Summary growth data for Period I, II and III of the field tethering experiment. Note: There were no conch surviving in site V2 at the end of Period III, therefore no growth data available. * Values in bracket represents mean cumulative growth (mm) for the conch in the respective sites and Periods.

Period	Site	Stock	No. Conch surviving*	Changes in TSL (mm)	Mean daily growth ($mm.d^{-1}$ ± sd)
I	V1	Hatchery	31 (3.6)	-2 - 13	0.046 ± 0.04
		Wild	42 (3.9)	0 - 9	0.050 ± 0.03
	V2	Hatchery	4 (4.3)	1 - 11	0.055 ± 0.06
		Wild	11 (4.9)	-2 - 10	0.064 ± 0.04
II	V1	Hatchery	24 (3.4)	-2 - 14	0.027 ± 0.04
		Wild	35 (3.3)	-2 - 9	0.026 ± 0.03
	V2	Hatchery	0 (---)	---	---
		Wild	4 (2.8)	-2 - 8	0.022 ± 0.03
III	V1	Hatchery	9 (8.0)	2 - 18	0.034 ± 0.02
		Wild	12 (4.0)	0 - 8	0.017 ± 0.01

(2-way ANOVA; *Time*: $F = 12.60$, df = 1, $P = 0.001$; *Stock*: $F = 0.01$, df = 1, $P = 0.974$; *Time* X *Stock*: $F = 1.40$, df = 1, $P = 0.244$). Average daily growth rates of tethered conch surviving at the end of Period III in site V1 were not significantly different for hatchery-reared and wild conch (*t*-test, $t = 1.74$, df = 10, $P = 0.11$) (Table 8).

Mortality

Caged Conch

There was 100% survivorship of wild conch in control cages. By week eight, one of 40 hatchery-reared conch in control cages had died, followed by a mean of 1.5 deaths per cage per wk during the final three wks of the cage experiment (i.e., 10 of 40). This 25% loss of hatchery-reared conch is attributable to factors other than predation-induced mortality since no predators were found in the cages.

Cumulative Mortality Patterns in Tethered Conch

During the first week of the field-tethering experiment, cumulative mortality rates were recorded daily for each of the experimental treatments (Fig. 8). By day seven, wild tethered conch in sites V1 and V2 were experiencing the lowest and highest cumulative mortality rates respectively; those for hatchery-reared conch were intermediate. During the second week of the tethering experiments, cumulative mortality rates were lower for wild and hatchery-reared conch in site V1 than rates for both stock types in site V2. The difference in cumulative mortality rates between the two sites continued to widen into the third week, with hatchery-reared conch in site V2 suffering the highest losses, followed closely by wild conch in the same site. This general pattern persisted until the experiment was terminated at the end of 33 wks (Fig. 9).

By the end of Period I, 23 of 96 tethered conch had been killed in site V1 compared to 81 of 96 in site V2. Of the 23 conch killed in site V1, three had chip marks around the shell lip areas, six were categorized as missing, while the remaining 14 were found as either empty shells or shells containing hermit crabs. In the case of the last 14, all shells were found intact on the tethers. The remains of broken shells, broken tether lines and mangled cable ties indicated that approximately 18% (8 of 44) of the hatchery-reared and 27% (10 of 37) of the wild conch had been killed by crushing predators in site V2. There was no evidence of any tethered conch having been killed by crushing predators in site V1. In site V2, three shells from the 81 killed conch showed chip marks in the shell lip area, one was categorized as missing, while 59 were found as either empty shells or shells containing hermit crabs.

Two approaches were used to examine proportional mortality rates of tethered conch in Period I of the experiments. The first compared cumulative proportional mortality rates for both stock types within and between the two experimental sites; at week 4 and at week 11 (Fig. 10, a, b). At the end of week 4, there was a significant *Site* effect (2-way ANOVA; $F = 32.15$, df = 1, $P < 0.001$), but non-significant *Stock* (2-way ANOVA; $F = 1.54$, df = 1, $P = 0.229$) and interaction (2-way *ANOVA*, $F = 0.08$, df = 1, $P = 0.781$) effects. At week 11, cumulative

Figure 8. Cumulative mortality of hatchery-reared and wild juvenile conch in sites V1 and V2 during the first three weeks of the field tethering experiments. Values plotted are total number of conch killed per day (week 1) and per week (week 2 and 3).

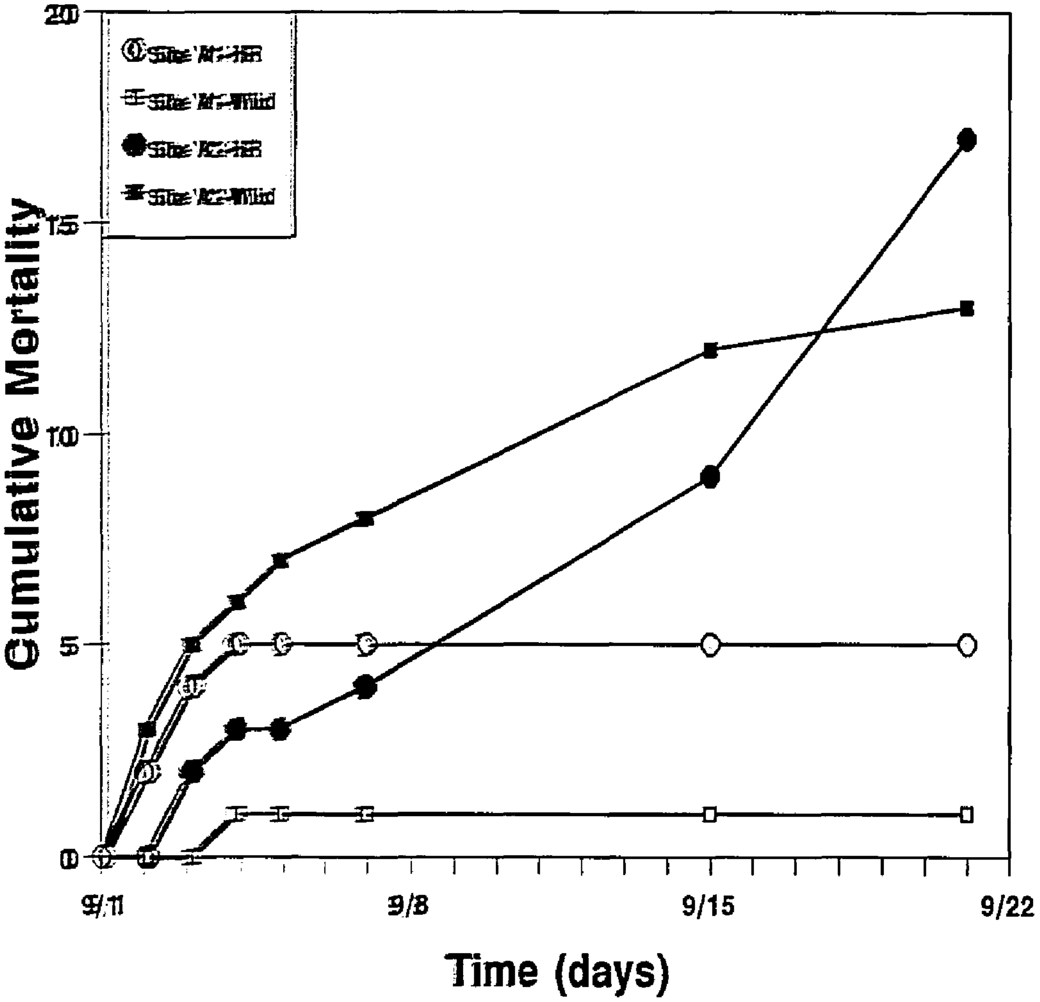
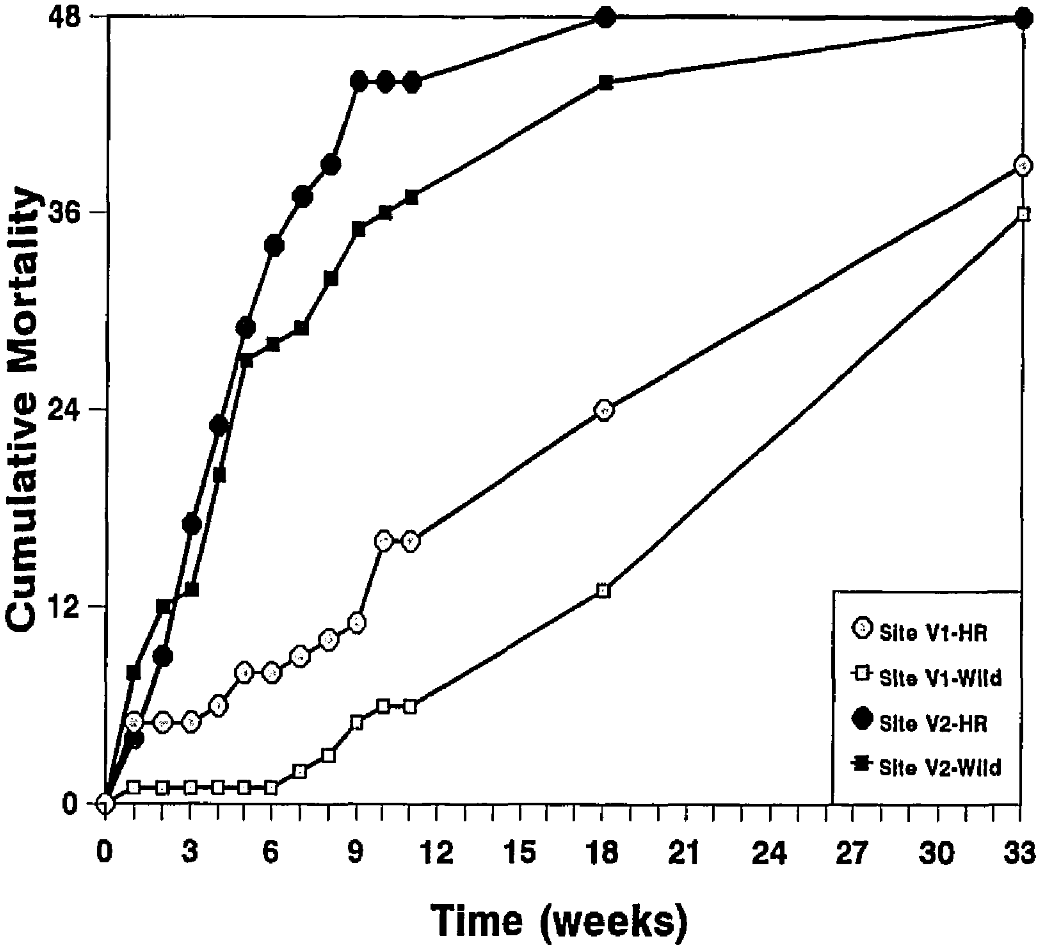
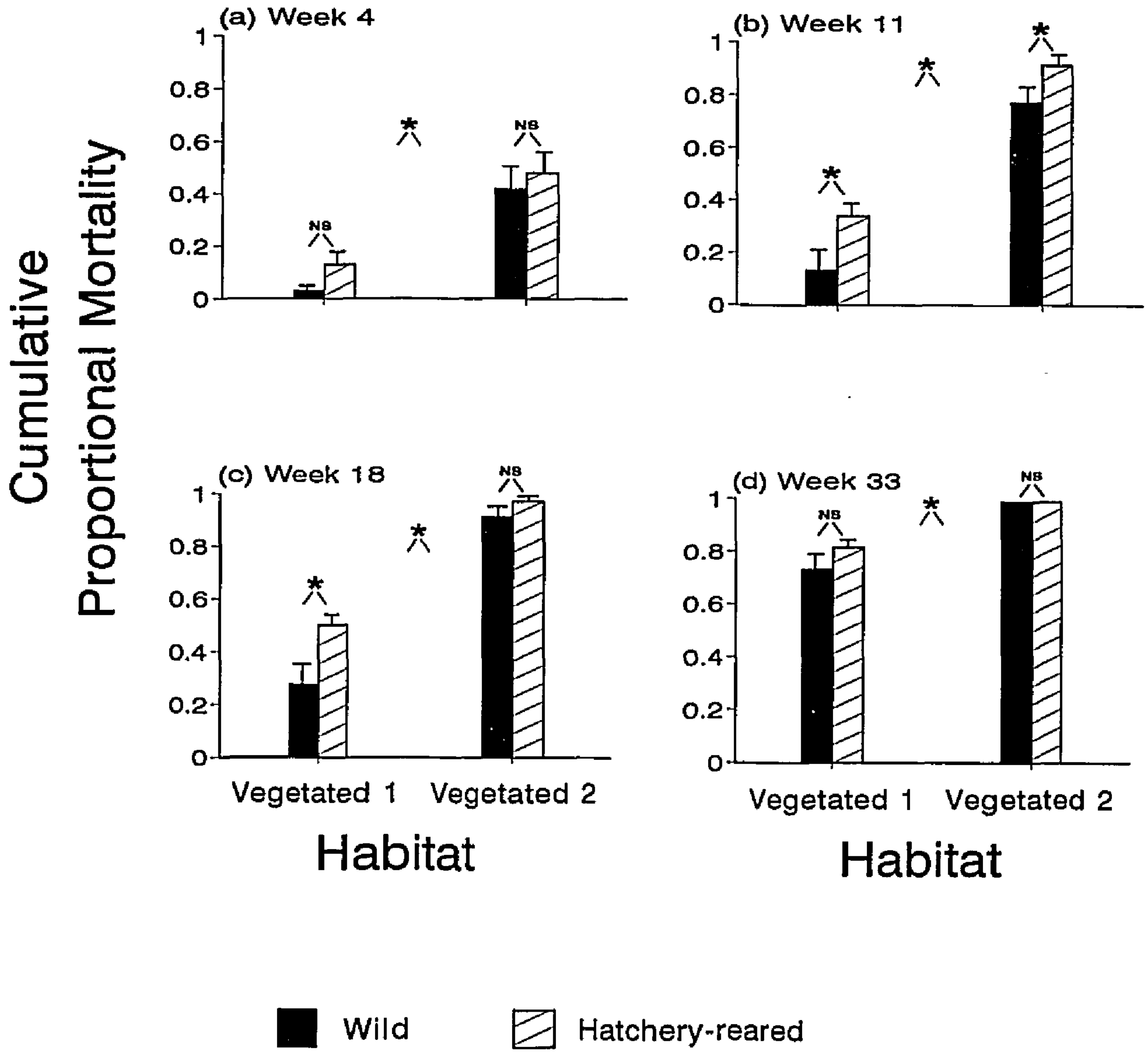

Site 'A1-HR'
Site 'A1-Wild'
Site 'A2-HR'
Site 'A2-Wild'
Cumulative Mortality
0
5
10
15
20
9/1
9/8
9/15
9/22
Time (days)

Figure 9. Cumulative mortality of hatchery-reared and wild juvenile conch in sites V1 and V2 during the full course (33 weeks) of the field tethering experiments. Values plotted are the total number of conch killed per week.



48
36
24
12
0
Cumulative Mortality
0
3
6
9
12
15
18
21
24
27
30
33
Time (weeks)
Site V1-HR
Site V1-Wild
Site V2-HR
Site V2-Wild

Figure 10. Cumulative proportional mortalities of hatchery-reared and wild conch in sites V1 and V2 during (a) week 4, (b) 11 (Period I), (c) week 18 (Period II) and (d) week 33 (Period III). Vertical line on top of each bar denotes one standard error.


Cumulative
Proportional Mortality
(a) Week 4
(b) Week 11
(c) Week 18
(d) Week 33
0
0.2
0.4
0.6
0.8
1
NS
*
Vegetated 1
Vegetated 2
Habitat
Wild
Hatchery-reared

proportional mortality rates were significantly higher for hatchery-reared conch in both sites (2-way ANOVA; $F = 10.72$, df = 1, $P < 0.005$), and significantly higher in site V2 than V1 (2-way ANOVA; $F = 79.44$, df = 1, $P < 0.001$). The *Site* x Stock interaction effect was not significant (2-way ANOVA; $F = 0.30$, df = 1, $P > 0.05$).

Secondly, I subtracted the non-predation-induced proportional mortality rate (i.e., 0.25) observed in the hatchery-reared cages from field tethered hatchery-reared animals, thereby yielding a conservative estimate of predation-induced proportional mortality rates. In this case, the significant *Site* effect observed in the cumulative proportional mortality analysis (Fig. 10, a) remained significant (i.e., predation-induced mortality was significantly higher in site V2 than site V1; 2-way ANOVA; $F = 80.77$, df = 1, $P < 0.001$). In contrast, the predation-induced proportional mortality rates did not differ by *Stock* (2-way ANOVA; $F = 0.498$, df = 1, $P > 0.05$). The *Site* x *Stock* interaction effect was not significant (2-way ANOVA; $F = 0.91$, df = 1, $P > 0.05$).

By the end of Period II (Fig. 10, c), the significant *Site* effect continued, with tethered animals in site V2 experiencing significantly higher mortality rates than those in site V1 (2-way ANOVA; $F = 116.99$, df = 1, $P < 0.001$). Mortality rates of the two stock types were significantly different in site V1 (ANOVA; $F = 6.03$, df = 1, $P = 0.034$), but not in site V2 (ANOVA; $F = 1.80$, df = 1, $P = 0.209$). There were no significant *Site* x *Stock* interaction effects (2 way ANOVA; $F = 2.69$, df = 1, $P = 0.117$).

During Period III, mortality rates in site V2 were significantly higher than those in site V1, but the *Stock* effect was not significant (Fig. 10, d; 2-way ANOVA, *Site*: $F = 95.79$, df = 1, $P < 0.005$; *Stock*: $F = 1.415$, df = 1, $P > 0.05$). With the termination of the cage experiment at the end of the eleventh week, I have no estimates of non-predation-induced proportional mortality rates during the remainder of the field tethering experiment (i.e., for Periods II and III). Hence I provide no analysis and estimates of predation-induced mortality for the latter portion of our field-tethering experiment.

Burial Activity

Behavioral observations over the first 48 h after initiation of the tethering experiments showed a total of 17 conch (4 hatchery-reared, 13 wild) buried in site V1, compared to 19 (8 hatchery-reared, 11 wild) in site V2. The proportion of hatchery-reared and wild conch buried did not differ significantly by *Stock*, *Site*, or *Stock* x *Site* (2-way ANOVA, *Stock*: $F = 2.67$, df = 1, $P = 0.118$; *Site*: $F = 0.04$, df = 1, $P = 0.837$; *Stock* x *Site*: $F = 2.77$, df = 1, $P = 0.112$). However, wild conch showed a trend toward higher mean burial rates (0.223) over hatchery-reared (0.131) conch. A power test dictated a required sample size of at least 76 plots (power = 0.80) to detect a difference of 0.090 (i.e., the observed difference) between the proportions of buried hatchery-reared and wild conch. Given that such a large sample size is required to statistically detect the observed difference in mean proportion buried between hatchery-reared and wild conch, I conclude that such a difference in burial rates is not biologically significant. Throughout the remainder of the experiment, both hatchery-reared and wild conch were observed in various stages of "protective cover:" either fully or partially buried, or positioned low in the grassbeds.

Predator Observations

The most frequently observed epibenthic predators in the plots with tethered conch in the two experimental sites during Period I included the tulip snail (*Fasciolaria tulipa*), apple murex (*Murex pomum*), and giant hermit crab (*Petrochirus diogenes*) (Table 9). Portunid crabs were frequently observed within experimental plots but no data was collected on their occurrence since their observation and capture were difficult. Two Caribbean spiny lobster, *Panulirus argus*, (approximately 80-100 mm carapace length) were also observed in the vicinity of the experimental plots in site V1. Other potential predators occasionally observed, but not quantified, included octopus, nurse sharks, loggerhead turtles, and rays.

DISCUSSION

Caging and tethering experiments were used to examine the survival and growth of juvenile hatchery-reared and wild queen conch, *Strombus gigas*, in shallow seagrass habitats near Lee Stocking Island, Exuma Cays, Bahamas. These provide the first comprehensive examination of survival of hatchery-reared and wild juvenile queen conch in natural habitats. My most important finding was that survival of

Table 9. Summary of results from field observations of potential epibenthic predators from within experimental plots at sites V1 and V2 during Period I of the field tethering experiments. Results below are pooled from 12 plots in each of the two experimental sites. All plots were sampled weekly during Period I.

Site	Predator type	Total abundance (%)	Mean density per plot	Size (TSL, mm)		
				Mean	Min.	Max.
V1	Hermit crab	48 (38.7%)	0.33	72.0	48	104
	Apple murex	73 (58.9%)	0.51	85.1	60	105
	Tulip snail	3 (2.4%)	0.02	80.0	51	99
V2	Hermit crab	20 (54.0%)	0.14	57.4	25	111
	Apple murex	17 (46.0%)	0.12	74.2	54	91
	Tulip snail	---	---	---	---	---

hatchery-reared and wild juvenile conch was primarily influenced by habitat type, and secondarily by stock type. Furthermore, both hatchery-reared and wild conch exhibited positive growth rates, with little difference in growth between stock types. Conch burial rates were independent of stock type, though the trend was for higher burial rates in wild conch. Finally, a portion of the mortality rates observed for hatchery-reared conch was likely due to factors other than predation. These findings indicate that although there are some survival and behavioral differences between hatchery-reared and wild juvenile conch, the utilization of hatchery-reared conch can be a viable strategy in the replenishment, augmentation, and management of wild queen conch stocks. Caution should however be exercised in generalizing conclusions since the performance of outplanted hatchery-reared individuals will likely vary depending on habitat type, local predator guilds, and attributes of the hatchery-reared animals (e.g., genetic stock, size at outplant, prior growth history, handling and transport).

Mortality

Numerous studies have examined how vegetation density affects predator-prey interactions (e.g., Heck and Thoman 1981, Crowder and Cooper 1982, Heck and Wilson 1987, Gotceitas and Colgan 1989), but have not necessarily provided an understanding of how prey mortality rates may vary in similar habitats. Results from my experiments indicate that mortality rates of tethered conch differed significantly between two apparently similar seagrass beds differing primarily in the abundance of resident conch.

Field observations, combined with the recovery of damaged shells, empty shells, or shells occupied by hermit crabs, suggest that three abundant epibenthic predators are primarily responsible for the observed conch mortalities. Empty shells or shells containing hermit crabs indicate predation by tulip snails or apple mureces (pers. obs.), since these animals characteristically feed on the soft tissue parts, leaving the shell undamaged. Although the total number of tulip snails observed in the two sites was low, tulip snails are common in seagrass beds and efficient predators on juvenile conch (Randall 1964, Jory 1982, pers. obs.). Most often, tulip snails remained buried within and outside experimental plots, suggesting that they fed on tethered conch at night. Chipped shells or shells showing evidence of having the lip area "peeled" away usually indicated the activity of large hermit crabs. Randall (1964) also observed similar evidence for hermit crabs feeding on juvenile conch.

The recovery of shell fragments and broken tether lines from experimental plots in site V2 suggest predation by large pelagic predators (e.g., rays, sharks, turtles). The similarity in the number of hatchery-reared and wild conch killed by epibenthic and crushing predators is inconsistent with the hypothesis that juvenile hatchery-reared conch may be more susceptible to crushing predators because of thinner shells or the lack of well-developed spines (Jory and Iversen 1988). Occurrence of crushed shells in site V2 and absence of such evidence in site V1 also suggest that the suite of predators in the two sites differed: the suite at site V1 apparently was mostly epibenthic, while site V2 was dominated by epibenthic predators with occasional large crushing predators.

Growth

One possible explanation for the observed lack of growth in cage-held conch is cage overcrowding, since the initial cage density was approximately 10 conch/m^2. Juvenile conch growth rates are generally density-dependent with growth being greatly reduced at higher densities (Appeldoorn and Sanders 1984, Weil and Laughlin 1984, Stoner 1989). In contrast to this general finding however, Iversen (1983) found no difference in growth rates for caged 10-15 cm TSL wild conch at low densities (1 and 2 per m^2) and caged individuals were generally characterized by low growth rates (0.0-0.06 mm/d). In field studies at Lee Stocking Island, Stoner (1989) showed reduced growth rates for caged and free-ranging juvenile conch at high conch densities, with growth rates for conch caged at high densities (4 and 8 per m^2) almost zero after 8 wks and negative after 19 wks. This finding was attributed to reduced food availability or behavioral interference interactions. Given that the densities in my cage experiment exceeded the high densities used by Stoner (1989), it is likely that caged conch were highly affected by these two attributes. Given this lack of growth in cages for both hatchery-reared and wild animals, the 25% mortality rate recorded for hatchery-reared animals was most likely due to starvation, stress induced by overcrowding, or stress associated with handling and transport. A combination of these possibilities, particularly the latter, seems most likely, especially considering that hatchery-reared and wild conch were caged and fed in the same manner, yet wild conch experienced no mortality. The absence of predators within the fully enclosed cages indicate that predation-induced mortality was not a contributing factor.

Mean daily growth rates for tethered hatchery-reared and wild conch in both sites during Period I of my experiments (0.046-0.064 mm/d) were lower than those recorded for free ranging hatchery-reared (0.17 mm/d; Appeldoorn and Ballantine 1983) and wild conch (e.g. 0.19-0.30 mm/d; Laughlin and Weil 1983); but within the lower range of those recorded for laboratory-held hatchery-reared individuals (0.02-0.15 mm/d; Appeldoorn and Sanders 1984, Laughlin and Weil 1983, Appeldoorn and Ballantine 1983). However, rates recorded in Period I of this study were comparable to those found for free-ranging, wild juvenile conch at Lee Stocking Island (0.075 mm/d over 13 wks) by Stoner (1989). Iversen (1983), and Appeldoorn (1985), have shown that growth rates in juvenile conch are related to water temperature. Temperatures during the study by Stoner (1989) ranged from 28-31° C. Water temperatures during Period I of my experiments were slightly lower (26-29° C), and possibly account for the reduced growth rates. The low average daily growth rates recorded during the remainder of these experiments (Periods II and III) probably reflect the reduction in growth activity during the cooler months of the study, or possible food limitations due to overgrazing.

Survival and Growth of Hatchery-Reared and Wild Conch

My study is the first to use tethering techniques to quantify growth and survival of hatchery-reared and wild juvenile conch in natural habitats. Barshaw and

Able (1990) suggest that tethering to assess predation in different habitats should be evaluated for each new species under consideration because species-specific behavior patterns could create habitat-specific tethering artifacts. I emphasize that growth and mortality rates reported here are only relative measures recorded in representative seagrass habitats and may not reflect natural growth and mortality rates. Field observations indicated that hatchery-reared conch behavior was similar to that of wild conch: both stock types were observed displaying feeding activities and the characteristic stromboid predator escape response (quick "hopping" motion). In the latter case, both stock types were sometimes observed to escape an advancing predator (tulip nails). These observations suggest that there were no biases of tethering on the behavior of hatchery-reared compared to wild conch, neither was behavior markedly different for the two stock types. Similar field-tethering experiments by Heck and Thoman (1981), Heck and Wilson (1987) and Barshaw and Able (in press), utilizing tethered crabs as prey, did not observe any differences in behavior of crabs tethered in different substrates. The non-significant differences in average daily growth rates of hatchery-reared and wild conch in the two experimental sites indicate that hatchery-reared conch grow in natural habitats, and that their growth rates approximate those of wild animals. The survival of nine hatchery-reared and twelve wild conch after 33 wks further indicate that hatchery-reared conch survive at similar rates as wild conch, and that tethering is an effective technique for measuring relative growth and mortality rates of juvenile queen conch.

Juvenile queen conch burial in natural habitats has been hypothesized as a means of avoiding predation (Appeldoorn 1984, Iversen et al. 1986). Given the artificial nature of the environment in which hatchery animals are raised (e.g., lack of natural substrate, absence of predators), hatchery-reared animals are believed to lack the necessary behavioral responses necessary for avoiding predators; the result is extremely high mortality rates immediately following outplant. My test of this hypothesis revealed a number of conch in partially or completely buried states with a trend toward higher burial rates in wild conch. However, there were no significant differences in burial rates between stocks or sites. Hatchery-reared abalone seed have been reported to behave different from wild abalone of the same size, perhaps resulting in their increased susceptibility to predation (Schiel and Welden 1987, Tegner and Butler 1989). Appeldoorn and Ballantine (1983) confirmed immediate burial activity for hatchery-reared conch between 20-50 mm TSL on an offshore sand and algal plain. In contrast, no conch were observed burying in shallow seagrass beds, probably due to the anoxic conditions just below the surface. Conch were however found low in the beds or often beneath clumps of macroalgae, a finding similar to those reported in this study. These results suggest that hatchery-reared conch display similar anti-predator behavioral responses as wild conch.

One obvious weakness of this study is that I did not adequately determine the source of non-predation-induced mortality for hatchery-reared conch in the control cages. Hence, estimates of field predation-induced mortality rates for hatchery-reared animals may be too conservative (i.e., very little and possibly none of the 25% mortality subtracted from hatchery-reared field rates may be due to non-predation-induced mortality). If this latter possibility exist then it is likely that the mortalities recorded in the field were due solely to predation; hence mortality rates between stock types remain significantly different.

Field tethering experiments indicated significant growth rates for both hatchery-reared and wild conch in both seagrass sites, with growth rates slightly higher in the seagrass meadow without resident conch than the one with resident conch. However, the consistently low mortality rates in the seagrass bed with conch and consistently high mortality rates in the seagrass bed without conch indicate that the seagrass bed with resident conch is best for release of hatchery-reared juvenile conch. Good growth rates but high mortality rates in the seagrass bed without conch support the hypothesis that this site is not necessarily a poor habitat type, but that the activities of epibenthic and pelagic predators may be sufficient to prevent the establishment of resident conch in the habitat.

The success of juvenile conch in natural habitats may be regulated by several biotic and abiotic mechanisms. In an effort to determine habitat quality, Stoner and Sandt (1991) quantified epiphyte, seagrass, detrital, sediment and other habitat variables in a seagrass bed known to contain high densities of juvenile conch consistently. By comparison, there exist large seagrass areas with similar habitat variables which are not only devoid of resident conch, but usually produce poor growth and survivorship for transplanted juvenile conch (R. N. Lipcius and L. S. Marshall Jr., unpubl. data). In some cases the absence of resident conch in these areas may be due to recruitment limitations, with such limitations being a function of larval supply or ontogenetic movement of the species (Stoner and Waite 1990). In other cases where recruitment is not limited, newly-settled recruits may simply suffer high rates of post-settlement mortality. Further, there may be other variables present in these unpopulated seagrass beds that have yet to be measured or identified which may be influencing habitat quality for conch.

The relationships between mortality, growth, and burial activity for hatchery-reared and wild juvenile conch suggest that the use of hatchery-reared juvenile conch to replenish depleted natural stocks is a viable strategy; however, caution should be exercised in the selection of suitable habitats. Finally, the component approach undertaken here, considering growth, behavior, predation and non-predation induced mortality in similar habitat types, rather than overall mortality rates, may provide a clearer understanding of the mechanisms regulating the survival of wild and hatchery-reared juvenile conch in natural habitats.

SUMMARY

The survival of wild and hatchery-reared juvenile queen conch in nature depends critically on the selection of habitats that minimize mortality and maximize growth. With field caging and tethering experiments I examined survival and growth of hatchery-reared and wild juvenile queen conch, in shallow seagrass habitats near LSI. The factors tested were stock type (wild or hatchery-reared) and habitat (seagrass beds with and without resident conch). The dependent variables included (1) growth, (2) an anti-predator behavioral response (burial activity), and (3) mortality (predation-induced and non-predation-induced). Mortality was dependent upon the habitat into which conch were outplanted, with the habitat effect overwhelming the effect of stock type upon mortality. Both hatchery-reared and wild conch exhibited significantly lower mortality in a seagrass bed with resident conch than in a seagrass bed without resident conch; a portion of the mortality observed in hatchery-reared conch may have been due to factors other than predation (e.g. handling stress). The habitat effect was apparently due either to the presence of resident conch, or to some factor associated with the seagrass bed harboring resident conch. Growth and burial rates did not differ between the two stock types. Although there were some differences in survival between hatchery-reared and wild conch, these findings indicate that habitat features are more important in the control of conch survival, and therefore that the use of hatchery-reared juvenile conch can be a viable strategy in the replenishment, augmentation, and management of wild queen conch stocks, if habitats are selected wisely.

Chapter 3

SURVIVAL IN COMPARABLE SEAGRASS HABITATS

INTRODUCTION

The role of predation in regulating community structure has been documented for a wide range of rocky and soft-bottom marine systems (Paine 1966, 1980, Mann 1977, Virnstein 1977, 1979, Menge 1978a, 1983, Woodin 1981, Posey 1986, Hines et al. 1989). Further, Connell (1975) suggested that predation is the most important biotic factor regulating community structure. The impact of predation and its intensity on community organization is often a function of environmental rigor (Connell 1975, Menge 1976, 1983, Menge et al. 1986), with numerous studies contrasting the character and intensity of predation in vegetated and unvegetated habitats (Young et al. 1976, Vince et al. 1976, Orth 1977, Nelson 1979, 1981, Stoner 1980, 1982, Peterson 1982, Summerson and Peterson 1984).

Throughout its geographical range, the queen conch, *Strombus gigas*, is found in diverse habitats including sand flats, seagrass and algal beds, and rubble areas (Brownell and Stevely 1981). Juvenile conch utilize shallow (<5 m depth) seagrass beds as nursery habitat (Randall 1964, Weil and Laughlin 1984, Stoner and Waite 1990); however, their occurrence within seagrass beds reflects a patchy nature: often conch are dense in one bed, but absent from a nearby comparable bed. In particular, large seagrass beds (≥ 0.5 km^2) occur near LSI, which appear suitable in sediment, depth, and macrophyte cover for juvenile conch. Juvenile conch are found in only a few distinct geographic locations within these seagrass beds, with two such areas consistently having resident juvenile conch over the past several years (Wicklund et al. 1988, Stoner 1989, Stoner and Sandt 1991, pers. obs.). Given this patchy distribution, I hypothesize that such a pattern results in part from variations in predation-induced mortality due to the distribution of prey and predators. Further, there may be a positive feedback mechanism in the population such that young juveniles survive at higher rates when conch abundance is relatively high. These hypotheses were examined by tethering juvenile queen conch in three replicated treatments: two seagrass beds with resident conch, and two seagrass sites each at 50 m and 350 m outside the area containing resident conch. Abundance and foraging behavior of three potential epibenthic predators were also described and quantified.

METHODS AND MATERIALS

Study Site

Field tethering experiments were conducted in subtidal habitats near LSI. In this study, two replicate experimental locations (Site 1: Childrens Bay Cay (CBC); Site 2: Tugboat Cay (TB); Fig.11) were chosen on the basis of their similarity in environmental features. Three subsites were then selected at CBC and designated as CBC-0, -50, and -350 m subsites; similar subsites were established at TB to serve as replicates (Fig. 12). CBC-0 and TB-0 were located within the central region of a juvenile conch concentration; CBC-50 and TB-50 were located approximately 50 m beyond the outermost edge of the area containing resident conch; and CBC-350 and TB-350 were approximately 350 m away from the area containing resident conch. Neither of the subsites at 50 m and 350 m contained resident conch. A thorough

Figure 11. Location of juvenile conch resident aggregations (cross-hatched, boxed areas) in *Thalassia* seagrass beds near Less Stocking Island, Exuma cays, Bahamas.

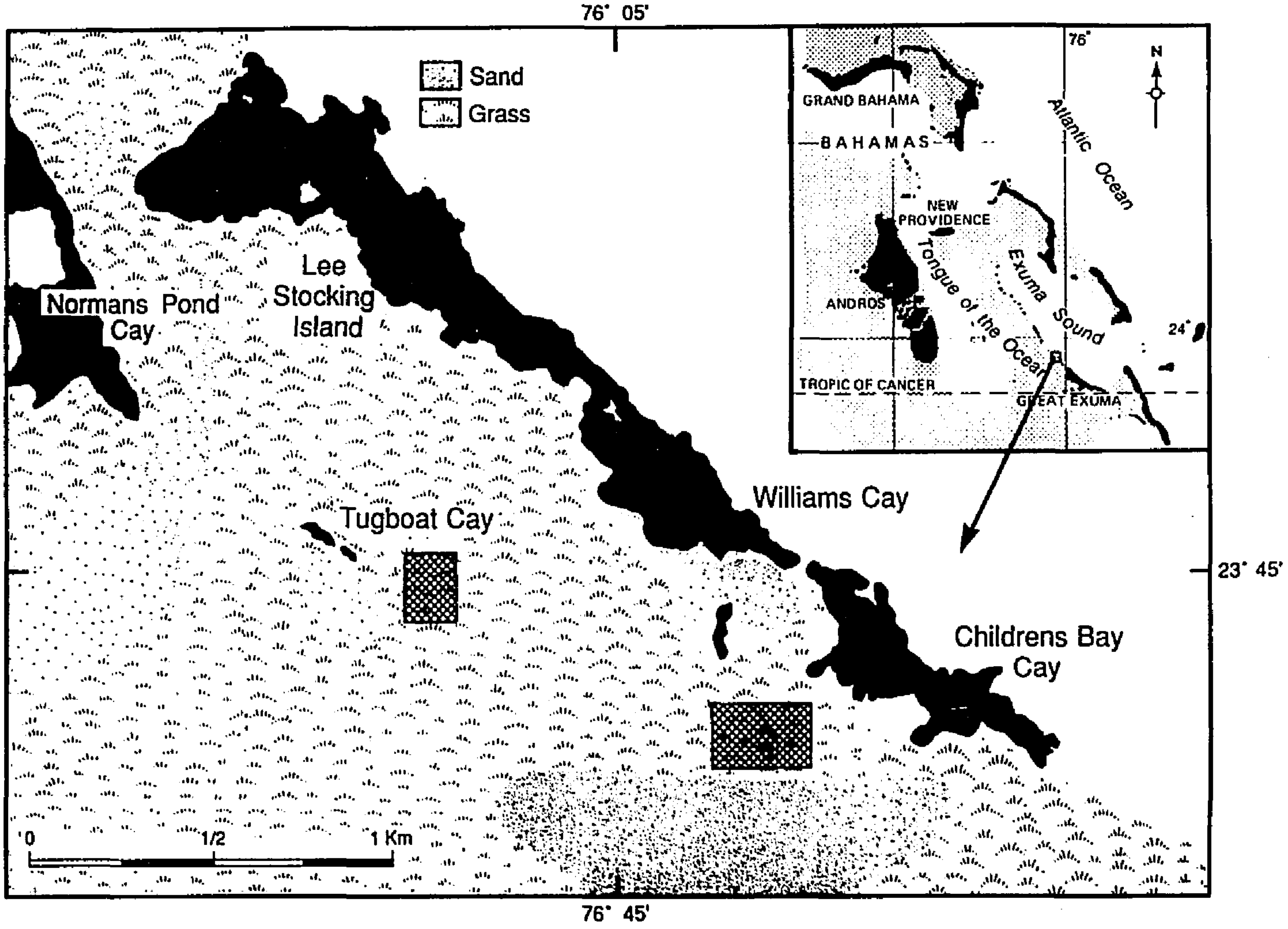
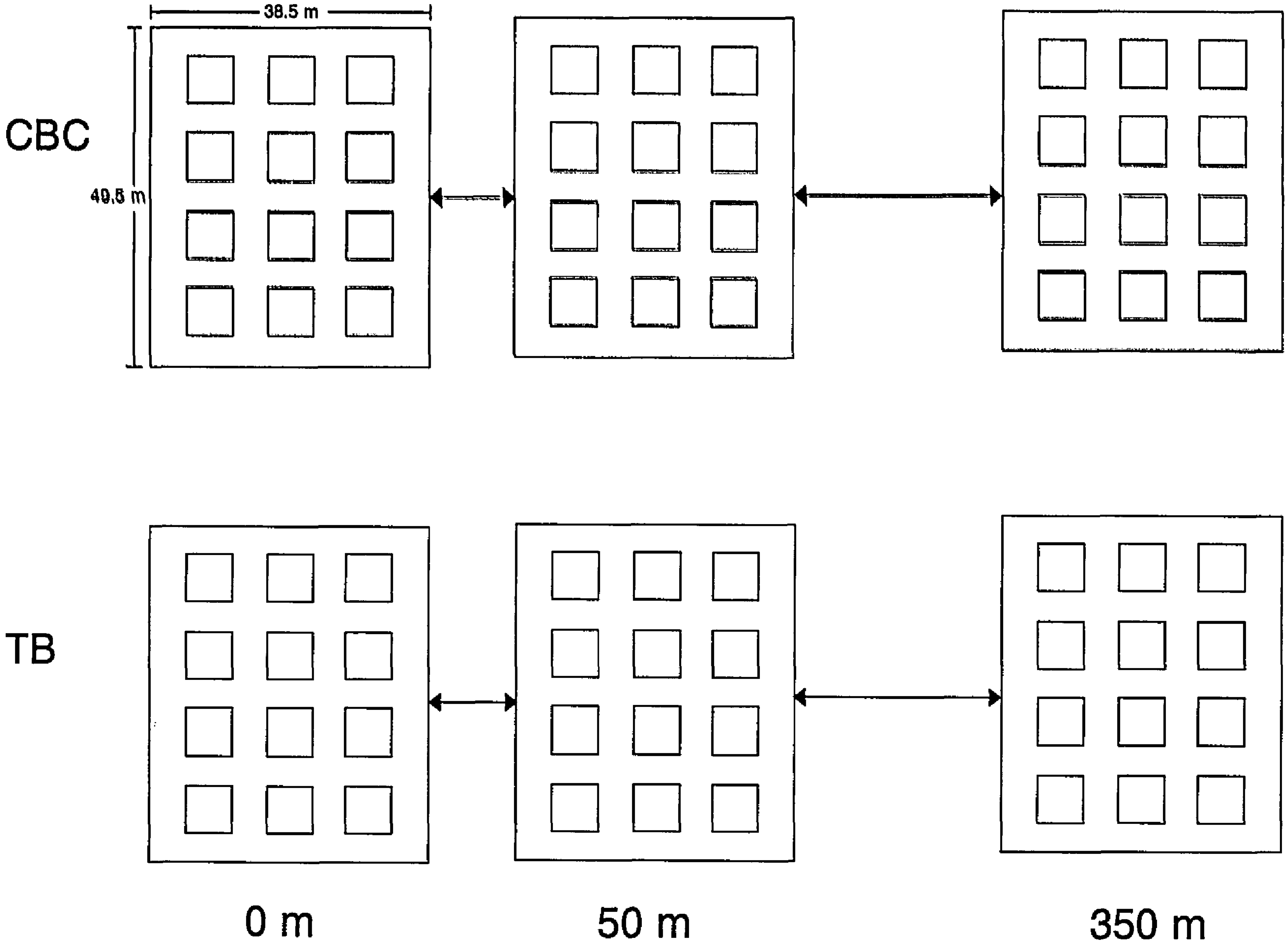

76° 05'
Sand
Grass
Normans Pond Cay
Lee Stocking Island
Tugboat Cay
Williams Cay
Childrens Bay Cay
23° 45'
76° 45'
0
1/2
1 Km
GRAND BAHAMA
BAHAMAS
NEW PROVIDENCE
ANDROS
Tongue of the Ocean
Exuma Sound
Atlantic Ocean
76°
24°
N
TROPIC OF CANCER
GREAT EXUMA

Figure 12. Schematic of 1990 site layout at Childrens Bay Cay (CBC) and Tugboat Cay (TB).


CBC
38.5 m
49.5 m
TB
0 m
50 m
350 m

survey in each of the four subsites without resident conch indicated an occasional (1-2) milk conch, *Strombus costatus*; these were removed from the experimental area prior to experiments.

In general, sites at CBC and TB were characterized by poorly-sorted, medium to coarse-grained calcareous sediments, and low to moderate densities of turtle grass, *Thalassia testudinum*. Calcareous green algae, including *Halodule wrightii* and *Rhipocephalus phoenix*, were also sparsely distributed throughout the area, along with abundant seagrass detritus. Average water depth in both locations ranged between 2.5-4 m, with current velocities of 60-100 cm/s during maximum flood tide (Dill et al. 1986). Water temperatures during the study period (June-October 1990) ranged between 26.5^0 C and 31.5^0 C; salinities from 35 to 37 psu.

Biomass Determination

Differences in live and dead seagrass biomass, between and within the two seagrass sites, were determined at the conclusion of the field experiments by measuring above-ground dry-weight biomass (g) in 0.25 m^2 quadrats. Two replicate samples of macrophyte and detrital material (mainly live and dead turtle grass blades, respectively) were collected at each subsite by haphazardly placing a quadrat within six randomly selected experimental plots in each of the six subsites. All above-ground material within each quadrat was gathered into 3.0-mm-mesh nylon bags, and later separated in the laboratory. Since the live biomass consisted of almost 99% *Thalassia*, the remaining 1% (*Syringodium filiforme* and *Penicillus capitatus*) was not quantified. Sorted live and dead samples were oven dried at 80-100^0 C for 24 h to constant weight, then weighed to determine mean dry weight (g) within each of the six subsites.

Size-Frequency and Density Estimates

Conch size-frequency and density estimates were simultaneously obtained in the two subsites containing resident conch (CBC-0, TB-0) during June, July and August. The June and July samples were collected prior to the introduction of tethered juvenile conch; the August samples were collected approximately 3 weeks following the introduction of tethered conch. Density estimates were obtained by sampling six haphazard 30.25 m^2 (3.1 m radius) circular plots. All conch within each of the six plots were collected by SCUBA divers, and their total shell length (TSL in mm) measured underwater with calipers; conch were then haphazardly redistributed within the plots. Additional conch were collected until sample sizes of approximately 200 were obtained each sampling period. The latter task was accomplished by collecting from a randomly selected area outside the circular plots: all conch encountered were measured until the required sample size was attained.

Experimental Procedure

Juvenile queen conch were collected by SCUBA divers from the two experimental subsites containing resident conch (CBC-0 m, TB-0 m). Collections were from areas outside and at least 100 m away from the area established for tethering experiments. Conch collected at CBC-0 m subsite were tethered in the CBC-0, -50 and -350 m subsites, while conch collected at TB-0 m site were tethered in the TB-0, -50 and -350 m subsites. Juvenile conch 100-120 mm TSL (estimated 1-2 year olds) were selected for tethering since this size range represented the numerically dominant group at the CBC and TB subsites. Conch were tethered in a manner similar to that described in Chapter 1, except that the tether line was lengthened to approximately 60 cm between the stake and attached cable tie, providing each conch with a circular foraging area of approximately 1.5 m^2.

Within-Site Layout

Within each of the six experimental subsites a rectangular area measuring 49.5 m x 38.5 m (1905.8 m^2) was marked off using PVC stakes. This large area was further divided into 63 equal-sized cells, each measuring 5.5 m x 5.5 m (30.3 m^2). Twelve of the 63 cells were randomly selected to receive experimental (tethered) animals, with the requirement that each of these twelve cells was bordered on all sides by a non-experimental cell. Six of these plots received six tethered conch each for a plot density of 0.21 conch/m^2, equivalent to low natural densities in the area. The remaining six plots received 20 tethered conch for a plot density of 0.66 conch/m^2, equivalent to moderate natural densities. Experimental treatments within each site were systematically interspersed (Fig. 12). Hence, six replicates of high and low conch densities were established in each of the replicated seagrass sites at the three experimental distances. In total, 720 and 216 juvenile conch were tethered within high and low density treatments, respectively.

Initial set up of experimental plots at CBC-0 and TB-0 required quantification of resident conch within those plots (i.e., counts of non-tethered resident conch within experimental plots). In contrast, the replicated 50 m and 350 m subsites were devoid of resident conch, precluding the need to remove conch from experimental plots. Tethered animals were placed into experimental plots between 26 July and 6 August 1990. Experimental plots were sampled approximately 1 wk after introduction of tethered animals, once during the next 3 wks and weekly during the last 6 wks, providing a total of eight samples during the 11 wk experimental period. Potential epibenthic predators (> 50 mm TSL) encountered during sampling were observed, recorded and left undisturbed. In several instances underwater video cameras were used to document natural predation sequences of epibenthic predators, particularly the tulip snail, *Fasciolaria tulipa.* Criteria identical to those outlined earlier in Chapter 1 were used to determine conch losses due to predation-induced mortality. In addition, killed conch were replaced with live animals of a similar size (100-120 mm TSL). Thus, individual plot densities were returned to nominal experimental densities (0.66 conch/m^2 or 0.21 conch/m^2) at the end of each sampling period.

Data Manipulation and Statistical Analysis

A two-way analysis of variance (ANOVA) model was used to compare mean conch sizes and densities in the two subsites containing resident conch (CBC-0 m and

TB-0 m subsites). Factors tested were *Site* (CBC, TB) and *Time* (time 1 = June, 2 = July, 3 = August).

Separate two-way ANOVA models were used to examine live and dead biomass as a function of *Site* and *Distance*. Data were log transformed to satisfy statistical criteria of normality and homogeneity of variance. Following transformations, sample variances were homogeneous or the ANOVA results were tested for significance at a probability level lower than that for Cochran's test for homogeneity of variance (Underwood 1981).

The number of conch killed in each plot at the end of the 11 wk experimental period were summed, generating a single independent cumulative mortality value (i.e., each of 72 plots produced a single cumulative mortality value). A full-factorial and balanced two-way ANOVA design tested for the main and interactive effects of *Site* (CBC, TB) and *Distance* (0, 50, 350 m). Cumulative mortality data were also log transformed to meet statistical assumptions (Underwood 1981).

In cases where the overall F-ratio was significant, Ryan's Q test (Day and Quinn 1989) was used to compare treatment means. When interaction effects were significant, the data were analyzed with Ryan's Q test within levels of main factors (Underwood 1981). All statistical tests were performed at an alpha level of 0.05.

RESULTS

Size-Frequency and Density Estimates

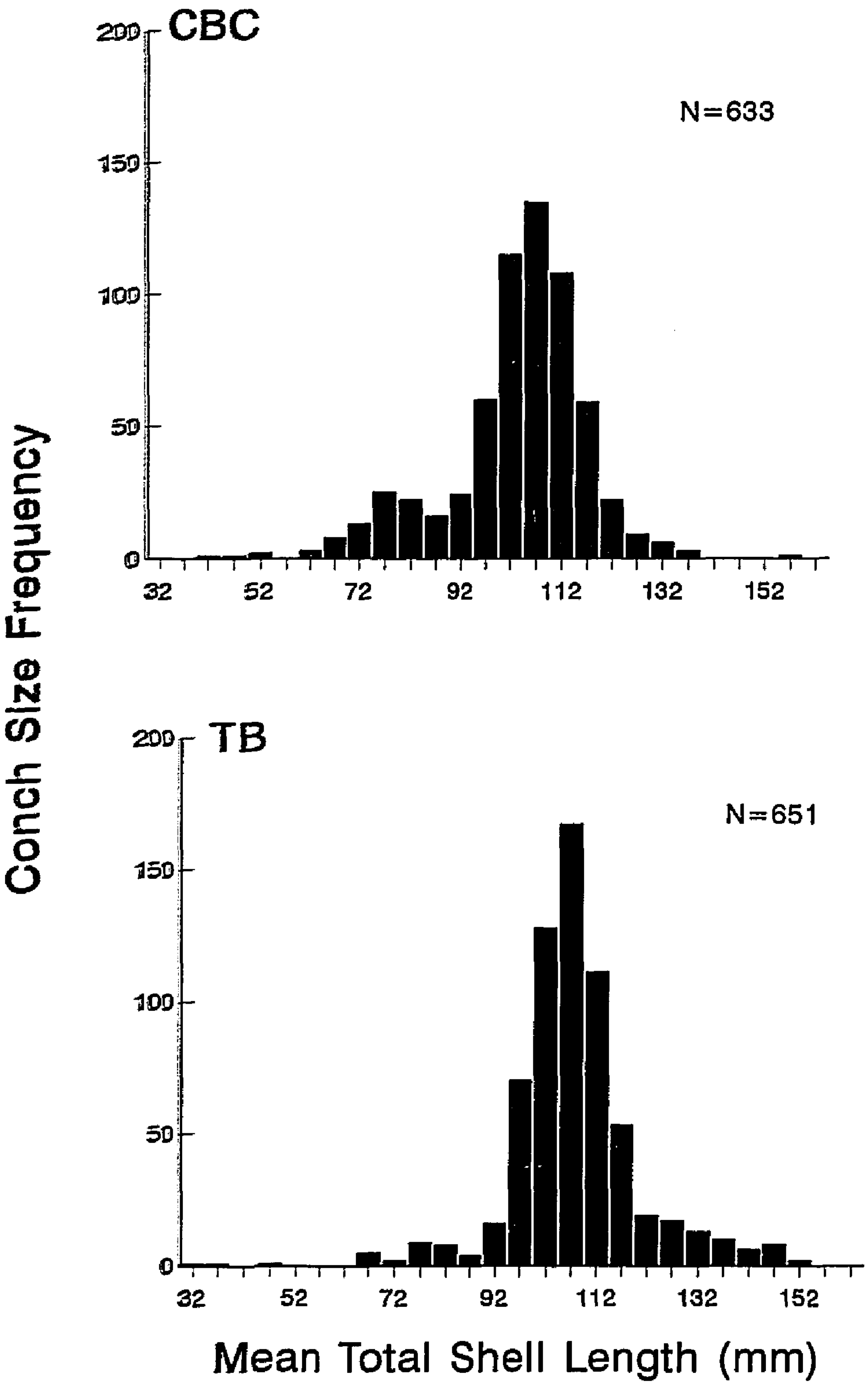
During June, July and August, the CBC-0 m subsite was generally inhabited by two size classes of juvenile conch separated at about 90-95 mm TSL; the former represented 1^+ years of age, while the numerically dominant class (i.e., greater than 95 mm TSL) was composed of 2^+ age conch (Fig. 13). At the TB-0 subsite there were fewer juveniles in the 1^+ year class and more larger conch (i.e., 125-155 mm TSL) than at CBC-0 (Fig. 13). An increase in juveniles <95 mm TSL was observed in the July and August samples, especially in the CBC subsites (Fig. 14).

Mean size (TSL) of ambient conch differed significantly by *Site* and *Time*; the *Site* x *Time* interaction was not significant (Table 10a, 10b, Fig. 15). Conch density did not differ significantly between CBC and TB, but did differ significantly over time (Table 11a, 11b, Fig. 16). Samples taken during June (0.93 conch/m^2) and July (1.07 conch/m^2) did not differ significantly, although these two samples were significantly higher than the August sample (0.61 conch/m^2) (Ryan's Q test, Critical F = 4.17, no. of means = 2, df = 30; and, F = 3.32, no. of means = 3, df = 30; $P < 0.05$).

Biomass

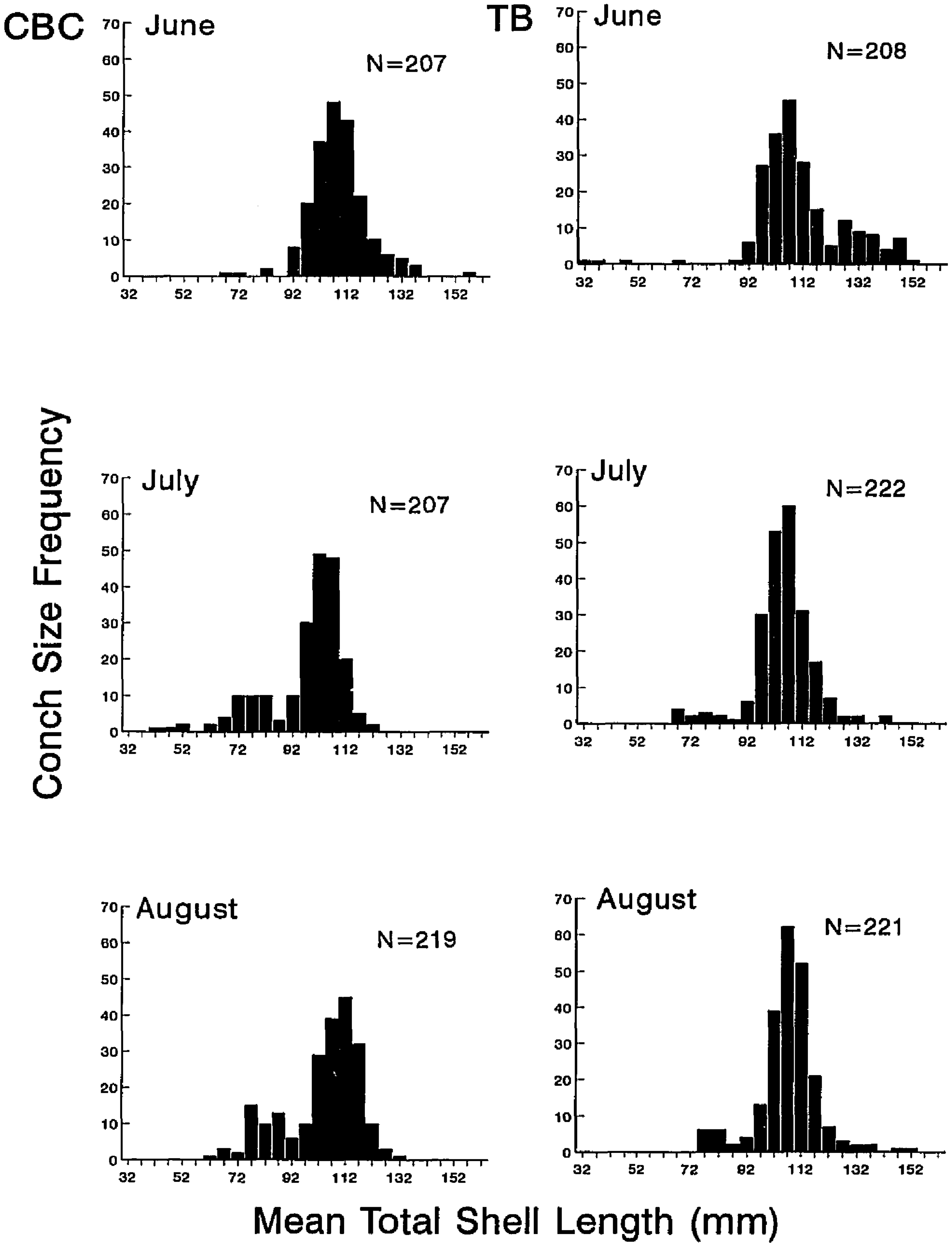
The analysis of dead biomass indicated a significant *Site* x *Distance* interaction, precluding singular conclusions regarding the significant main effect of *Distance* (Table 12). Subsequent analysis of the *Site* x *Distance* interaction effect revealed no significant differences due to *Distance* at CBC (Ryan's Q test, MSE = 0.054, df = 33, $P > 0.05$) (Fig. 17). At TB, mean dead biomass was not

Figure 13. Juvenile conch size structure at Childrens Bay Cay and Tugboat Cay during summer 1990. Values shown are the total number of conch per size interval (Total Shell Length in mm).



* 32=30-34, 37=35-39, etc.

Figure 14. Monthly size-frequency comparisons between the 0-m subsites at CBC and TB during June, July and August 1990. Values shown are the total number of conch per size interval (Total Shell Length, TSL in mm).



* 32=30-34, 37=35-39, etc.

Table 10a. Two-way analysis of variance comparing mean conch size (TSL, in mm) at CBC-0 and TB-0 m subsites during June, July and August 1990.

Source of Variation	df	MS	F
Site	1	223.00	9.64 ***
Time	2	165.65	7.16 ***
Site x Time	2	3.05	0.13 ^{ns}
Error	30	23.12	

^{ns} $P > 0.05$, *** $P < 0.005$

Table 10b. Mean size and size ranges (TSL ± sd, in mm) of juvenile conch in the 0-m subsites at CBC and TB on three sampling dates. N = total number of conch collected in six, 3.1 m radius circles.

Site	Date	N	Mean size	Size Range
CBC	June	130	111.5 ± 3.7	74 - 161
	July	167	103.2 ± 1.8	49 - 126
	August	113	107.9 ± 6.9	68 - 131
TB	June	208	115.8 ± 7.4	35 - 159
	July	222	109.3 ± 3.6	70 - 148
	August	108	112.4 ± 2.6	82 - 157

Figure 15. Mean conch size at CBC-0 and TB-0 m subsites during June, July and August 1990. Vertical lines on top of bars denote one standard deviation.

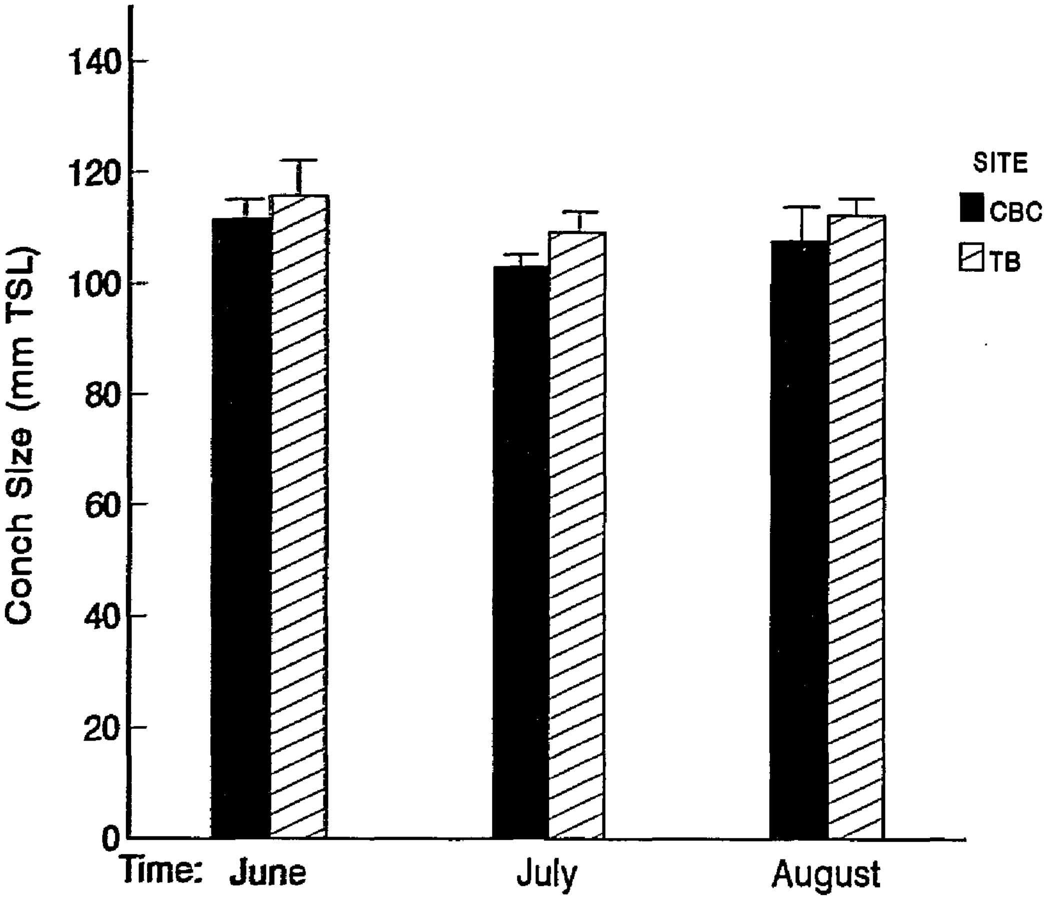

Conch Size (mm TSL)
140
120
100
80
60
40
20
0
Time: June
July
August
SITE
CBC
TB

Table 11a. Two-way analysis of variance for conch density (no./m^2) at CBC-0 and TB-0 m subsites during June, July and August 1990.

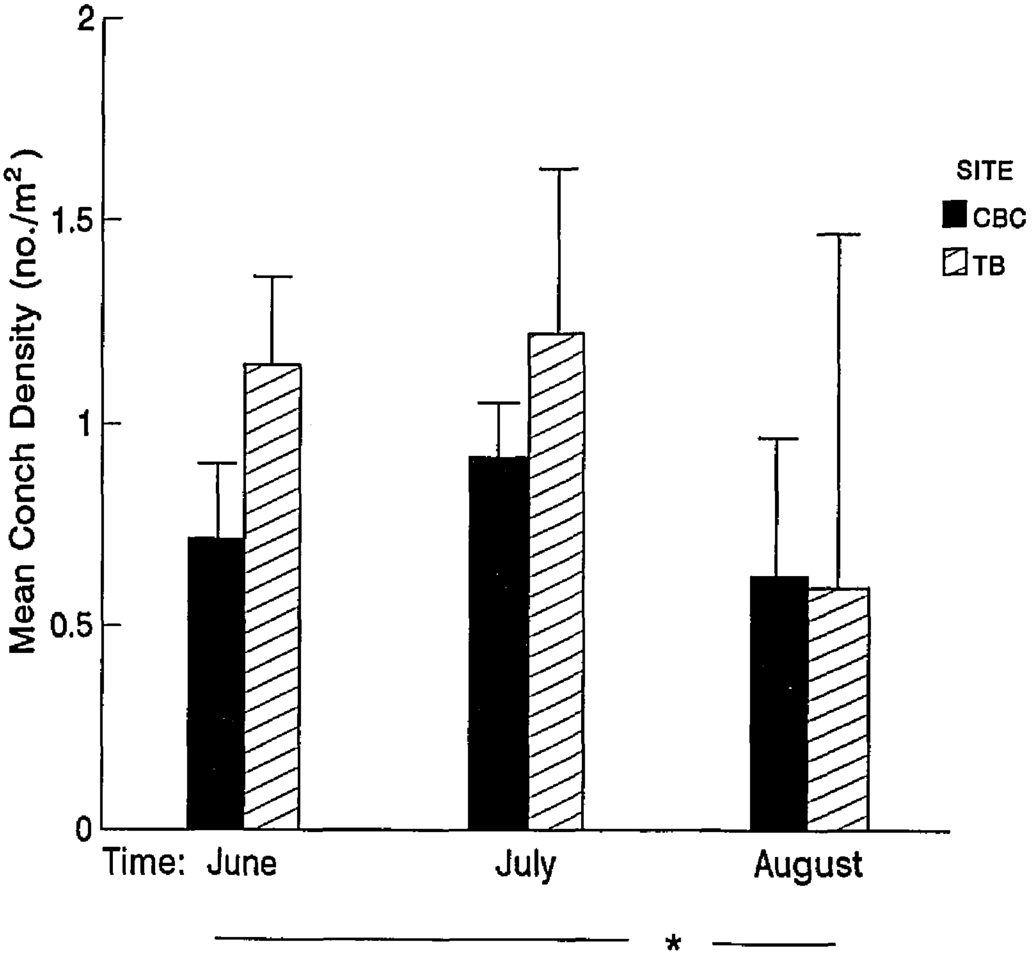
Source of Variation	df	MS	F
Site	1	0.50	3.41 ^{ns}
Time	2	0.68	4.64 *
Site x Time	2	0.17	1.15 ^{ns}
Error	30	0.15	

^{ns} $P > 0.05$, * $P < 0.05$

Table 11b. Means and ranges for conch density (nos./m^2 ± sd) in the CBC-0 and TB-0 m subsites. N = total number of conch collected in six, 3.1 m radius circles.

Site	Date	N	Mean density	Range of densities
CBC	June	130	0.7 ± 0.3	0.3 - 1.1
	July	167	0.9 ± 0.2	0.6 - 1.3
	August	113	0.6 ± 0.4	0.03 - 1.1
TB	June	208	1.1 ± 0.3	0.9 - 1.8
	July	222	1.2 ± 0.6	0.6 - 2.2
	August	108	0.6 ± 0.3	0.3 - 1.1

Figure 16. Mean conch density at CBC-0 and TB-0 m subsites during June, July and August 1990. Treatment levels that are not significantly different at the 0.05 level share an underline. Vertical lines on top of bars denote one standard deviation.


2
1.5
1
0.5
0
Mean Conch Density (no./m²)
SITE
CBC
TB
Time: June
July
August
*

significantly different between the 0 and 50 m subsites; however, these subsites differed from the 350 m subsite (Ryan's Q test, MSE = 0.020, df = 33, $P < 0.05$). In the analysis of *Site* within *Distance*, mean dead biomass differed significantly between subsites at all distances (Ryan's Q test; 0 m: MSE = 0.039, df = 22, $P < 0.05$; 50 m: MSE = 0.031, df = 22, $P < 0.05$; 350 m: MSE = 0.041, df = 22, $P < 0.05$) (Fig. 17).

Although live *Thalassia* biomass did not differ significantly by *Site* and *Distance*, there was a significant *Site* x *Distance* interaction (Table 13; Figure 18). Analysis of the three distances within each *Site* indicated a significant difference in mean *Thalassia* biomass between the 0, 50 and 350 m subsites at CBC (Ryan's Q test, MSE = 0.007, df = 33, $P < 0.05$), with mean *Thalassia* biomass inversely related to distance from the site containing resident conch. At TB there were no significant differences in *Thalassia* biomass between the 0 and 50 m subsites; however, the 350 m subsite was significantly higher in biomass than these two subsites (Ryan's Q test, MSE = 0.006, df = 33, $P < 0.05$). Analysis of *Sites* within *Distance* indicated significant differences between the two 0 m subsites (Ryan's Q test, MSE = 0.009, df = 22, $P < 0.05$), and the two 350 m subsites (Ryan's Q test, MSE = 0.004, df = 22, $P < 0.05$), but none between the two 50 m subsites (Ryan's Q test, MSE = 0.006, df = 22, $P > 0.05$) (Fig. 18).

Table 12. Two-way analysis of variance comparing mean (log(x+1)) dead biomass (g dry wt/0.25 m^2) within experimental sites (CBC, TB) and across distance (0, 50, 350 m).

Source of Variation	df	MS	F
Site	1	0.02	0.51 ^{ns}
Distance	2	0.17	4.49 *
Site x Distance	2	0.35	9.47 ****
Error	66	0.04	

^{ns} $P > 0.05$, * $P < 0.05$, **** $P < 0.001$

Figure 17. Estimates of dead biomass (g dry wt/0.25 m^2) collected in the six subsites at the conclusion of field experiments. Treatment levels that are not significantly different at the 0.05 level share an underline. Vertical lines on top of bars denote one standard deviation.

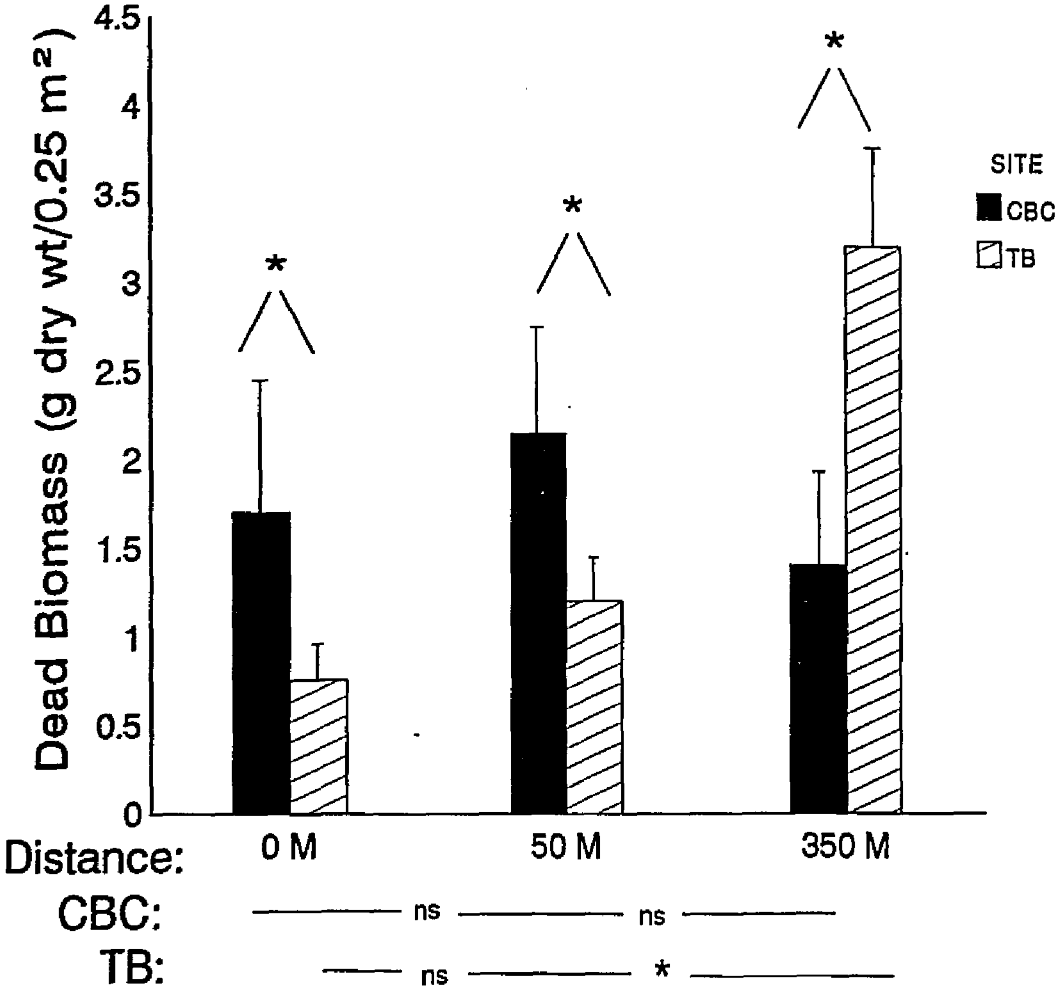
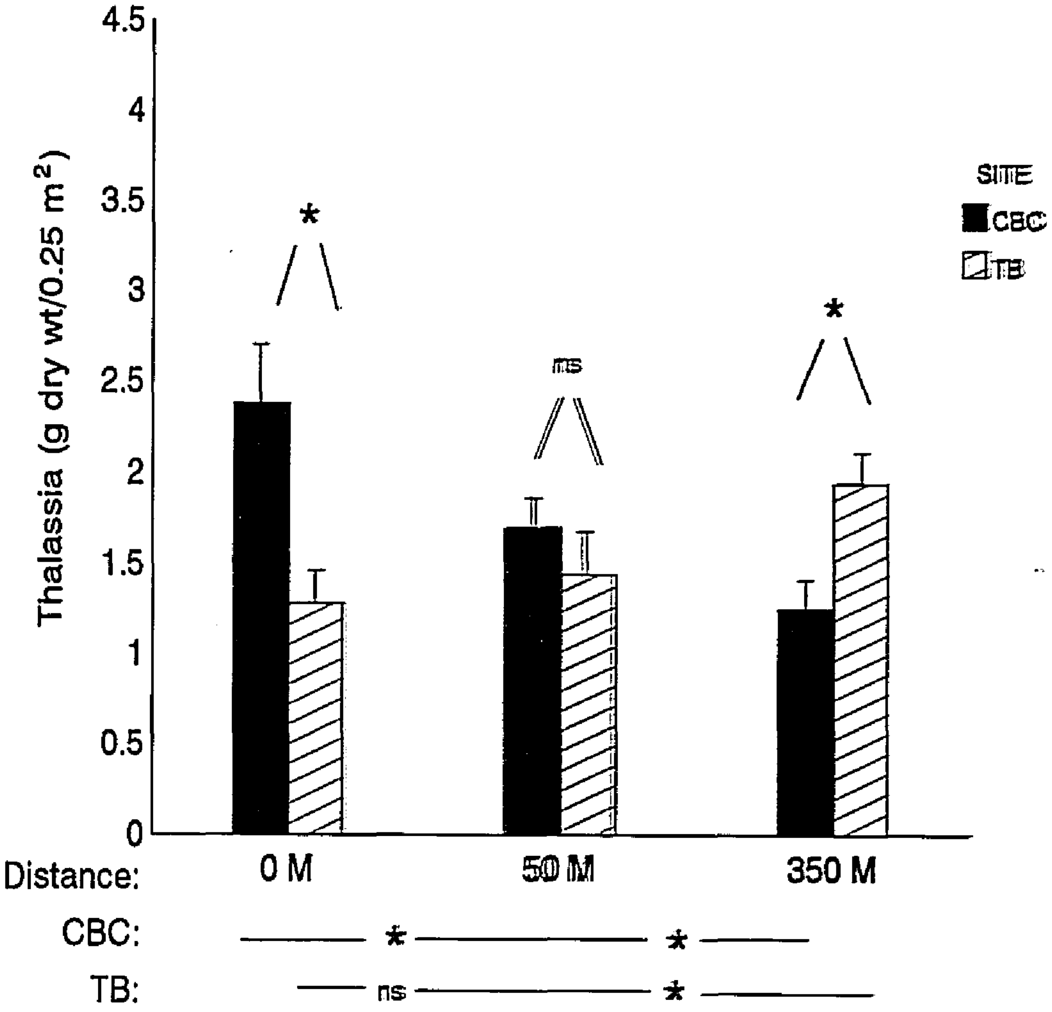

Dead Biomass (g dry wt/0.25 m^2)
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
SITE
CBC
TB
*
*
*
Distance:
0 M
50 M
350 M
CBC:
ns
ns
TB:
ns
*

Table 13. Two-way analysis of variance examining effects of site (CBC, TB) and distance (0, 50, 350 m) on mean (log (x+1)) *Thalassia* biomass (g dry wt/0.25 m^2).

Source of Variation	df	MS	F
Site	1	0.02	2.98 ^{ns}
Distance	2	0.01	1.35 ^{ns}
Site x Distance	2	0.12	18.24 ****
Error	66	0.01	

^{ns} $P > 0.05$, **** $P < 0.001$

Figure 18. Estimates of live (*Thalassia*) biomass (g dry wt/0.25 m^2) collected in the six subsites at the conclusion of field experiments. Vertical lines on top of bars denote one standard deviation.


Thalassia (g dry wt/0.25 m²)
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
SITE
■ CBC
▨ TB
*
ns
*
Distance:
0 M
50 M
350 M
CBC: * *
TB: ns *

Tethering Experiments

Analysis of cumulative mortality at nominal densities (Factors = *Site*, *Distance*) indicated significant *Site* and *Distance* effects, but also a significant *Site* x *Distance* interaction effect (Table 14, Fig. 19). At CBC, cumulative mortality did not differ significantly between the 50 and 350 m experimental subsites; however mortality in the 0 m subsite was significantly lower than that at 50 and 350 m (Ryan's Q test, MSE = 0.055, df = 33, $P < 0.05$). At TB, mortality was lowest in the 0 m subsite, intermediate in the 50 m subsite and highest in the 350 m subsite (Ryan's Q test, MSE = 0.069, df = 33, $P < 0.05$). When analyzed by *Site* at each distance, the 0 and 350 m subsites did not differ between CBC and TB (Ryan's Q test; 0 m: MSE = 0.053, df = 22, $P > 0.05$; 350 m: MSE = 0.074, df = 22, $P > 0.05$); mortality did however differ significantly between subsites at 50 m (Ryan's Q test, MSE = 0.058, df = 22, $P < 0.05$). In summary, conch mortality at CBC and TB sites was consistently low at 0 m, consistently high at 350 m, but variable at 50 m (Fig. 19).

Predator Observations

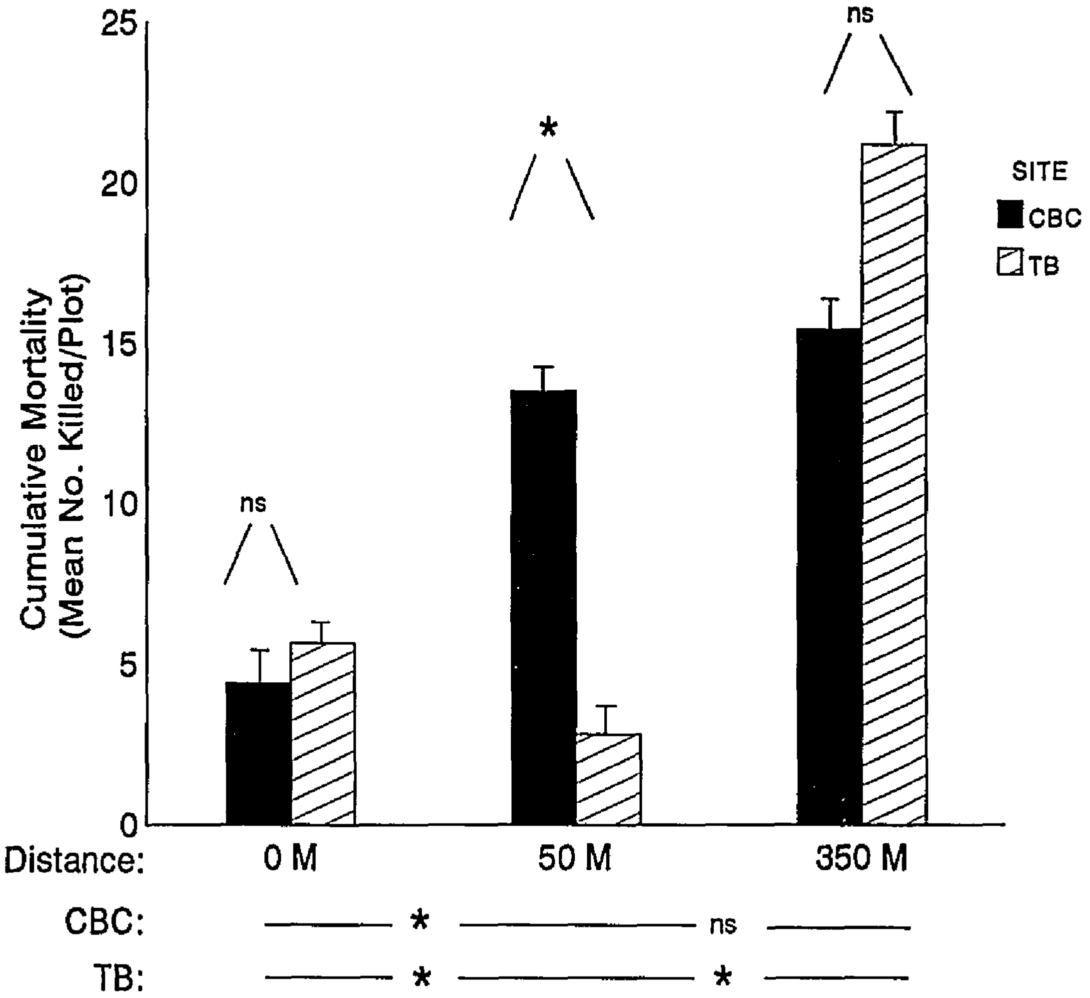
The most frequently occurring potential epibenthic predator in the six subsites was the hermit crab *Petrochirus diogenes*, followed by the apple murex, *Murex pomum*, and tulip snail, *Fasciolaria tulipa* (Table 15a, 15b). Epibenthic predators were not concentrated in subsites containing resident conch; at the TB subsites,

Table 14. Two-way analysis of variance examining the effects of site (CBC, TB) and distance (0, 50, 350 m) on cumulative mortality (log (x+1)) of tethered conch.

Source of Variation	df	MS	F
Site	1	0.25	4.07 *
Distance	2	1.72	27.60 ****
Site x Distance	2	0.95	15.32 ****
Error	66	0.06	

^{ns} $P > 0.05$, * $P < 0.05$, **** $P < 0.001$

Figure 19. Cumulative mortality of tethered conch (mean no. killed/plot) in the six experimental subsites. Vertical lines on top of bars denote one standard deviation.


Cumulative Mortality
(Mean No. Killed/Plot)
25
20
15
10
5
0
ns
*
ns
SITE
CBC
TB
Distance:
0 M
50 M
350 M
CBC:
*
ns
TB:
*
*

abundance of hermit crabs was lowest in the 0 m subsite, increased in the 50 m subsite, and highest in the 350 m subsite. This pattern was not observed at CBC subsites; neither was the pattern repeated for apple murex or tulip snails at either CBC or TB.

Within each site (i.e., CBC, TB), the percent total composition of epibenthic predators varied for hermit crabs and apple murex. At the CBC-0 and -350 m subsites, hermit crabs constituted almost 50% of the total percentage of epibenthic predators, compared to almost 31% at the 50 m subsite. In contrast, hermit crabs made up almost 82% of all epibenthic predators in each of the three subsites at TB. In particular, hermit crabs constituted almost 95% of the epibenthic predator composition at the TB-50 m subsite. Tulip snail proportions remained characteristically low (< 3%) in all experimental sites.

Mean size of hermit crabs ranged between 80-93 mm TSL. Apple murex were slightly smaller, with mean sizes ranging between 74-82 mm TSL. Tulip snails were consistently the largest of the three epibenthic predators with mean sizes ranging between 104-128 mm TSL. The low abundance of tulip snails (19 at CBC, 24 at TB) probably reflects reduced activity of tulip snails during daytime; several snails were observed in partially buried states within experimental plots. Tulip snails were also observed to depart from experimental plots immediately upon completion of feeding activity. Video recordings indicated conch could and often did escape attacks by *Fasciolaria*. A juvenile conch typically eluded *Fasciolaria* by thrusting its foot and

Table 15a. Summary characteristics of potential epibenthic predators observed within experimental plots in the three subsites at Childrens Bay Cay (CBC).

SITE	CHARACTERISTICS	PREDATORS		
		Petrochirus	Murex	Fasciolaria
0 m	No. Observed	287	290	8
	% Of Total	49.1 %	49.6 %	1.4 %
	Mean Size	81.3 mm	82.4 mm	117.4 mm
	Size Range	50-134 mm	59-105 mm	102-132 mm
50 m	No. Observed	315	142	3
	% Of Total	68.5 %	30.9 %	0.7 %
	Mean Size	88.4 mm	79.7 mm	113.3 mm
	Size Range	50-144 mm	63-99 mm	100-127 mm
350 m	No. Observed	196	174	8
	% Of Total	51.9 %	46.0 %	2.1 %
	Mean Size	84.3 mm	75.7 mm	128.7 mm
	Size Range	54-198 mm	61-91 mm	108-154 mm

Table 15b. Summary characteristics of potential epibenthic predators observed within experimental plots in the three subsites at Tugboat Cay (TB).

SITE	CHARACTERISTICS	PREDATORS		
		Petrochirus	Murex	Fasciolaria
0 m	No. Observed	211	41	4
	% Of Total	82.4 %	16.0 %	1.6 %
	Mean Size	81.7 mm	78.4 mm	104.0 mm
	Size Range	51-155 mm	62-94 mm	67-122 mm
50 m	No. Observed	263	11	4
	% Of Total	94.6 %	4.0 %	1.4 %
	Mean Size	87.0 mm	73.7 mm	104.7 mm
	Size Range	50-140 mm	53-89 mm	85-133 mm
350 m	No. Observed	579	48	16
	% Of Total	90.0 %	7.5 %	2.5 %
	Mean Size	93.8 mm	82.5 mm	125.5 mm
	Size Range	50-180 mm	51-105 mm	104-164 mm

operculum against the substrate in an arc-like stabbing motion, causing the shell to be lifted and propelled forward by hopping over the substrate.

DISCUSSION

The value of seagrass habitats in providing refuge from predation has been experimentally demonstrated for various marine species (e.g., Nelson 1979, Heck and Thoman 1981, Peterson 1982, Minello and Zimmerman 1983, Herrnkind and Butler 1986, Wilson et al. 1987, Eggleston et al. 1990). However, relatively few studies have addressed the survival of conspecifics within similar seagrass habitats as a function of distance from conspecific aggregations. This study demonstrates that predation-induced mortality of juvenile queen conch varies across similar seagrass habitat types in association with the presence and absence of resident conch. In particular, mortality was consistently lowest in seagrass sites containing resident conch and highest in sites farthest from the resident conch aggregations. Mortality was variable in the sites bordering the resident conch aggregation, being significantly higher at one site than the other. Quantification of potential epibenthic predators in experimental sites indicate a variable pattern of occurrence; epibenthic predators were not always concentrated in areas containing resident conch. Variations in predation-induced mortalities in experimental sites appear to be related to (1) the presence and absence of resident conch, (2) epibenthic predator-induced mortalities, and (3) variations in habitat biomass characteristics (this study, Stoner 1989, Stoner and Waite 1990, Stoner and Sandt 1991).

The presence of resident conch appears to exert a positive influence on juvenile conch survival. This finding is consistent with findings reported earlier in this dissertation (Chapter 1 and 2). Although the direct mechanism for such an occurrence has yet to be identified, it is likely that the increased survival of experimental conch in the presence of resident conch is related to interactions between conch and their predators within a local population. For instance, large numbers of conch at densities similar to those measured in the two 0-m subsites could potentially swamp predators, thereby reducing proportional mortality rates of juvenile conch.

The dynamics of the two subsites containing resident conch may also partially explain the increased survival of experimental conch. The increased influx of animals < 95 mm TSL during July and August, particularly at CBC, reflects the periodic influx of new recruits. Such an increase in total numbers could serve to induce or maintain the predator swamping mechanism mentioned above. The low numbers of such recruits (< 95 mm TSL) at the TB site probably reflect differences in recruitment intensity or timing between the two (TB, CBC) local areas. In the Exuma Cays, adult conch spawn between April and October, with subsequent emergence of recruits between August and October (Stoner and Waite 1990). Size frequency and density estimates during this study clearly point to the arrival of new recruits during July, especially at the CBC site.

The influence of habitat features in mediating predation has long been recognized (Huffaker 1958). Several researchers (see review by Kikuchi 1980) have suggested that areas of greater seagrass and algal biomass should have lower levels of predation than areas of lesser biomass. In the case of juvenile conch, seagrass shoot density and biomass can be used to predict juvenile conch densities within nursery habitats, with 1^+ - 2^+ age conch generally preferring intermediate seagrass biomass areas and avoiding areas with high and low biomass (Stoner and Waite 1991). Initial comparisons of cumulative proportional mortality and *Thalassia* abundance patterns within and between replicate treatments suggest no clear relationship between these two variables. However, when viewed on a broader scale, the estimated *Thalassia* abundance in the respective sites does provide insight into the survival of juvenile conch in seagrass habitats. Mean *Thalassia* abundance in the six subsites ranged between 4.8-9.2 g dry wt./m^2, values well within ranges previously reported for juvenile conch habitats at LSI (Stoner and Waite 1991). More importantly, values comprising this range represent measurements taken in the two subsites containing resident conch (TB: 4.8 g dry wt/m^2; CBC: 9.2 g dry wt/m^2). Hence the values recorded in the four sites without resident conch are within the range of values recorded for sites containing resident conch. This finding plus the occurrence of resident conch in two geographically separate locations (TB and CBC 0-m subsites) with *Thalassia* biomass spanning a range of abundances, suggest that in terms of *Thalassia* biomass abundance, the four subsites without resident conch are suitable as habitats for resident conch. Given the consistent occurrence of juvenile conch in the two 0-m subsites (Wicklund et al. 1988; pers. obs.), it is likely that seagrass biomass (dead and green) recorded in these sites are representative of suitable seagrass biomass abundances for juvenile conch. This view is supported by previous experiments: in sites known to serve as natural habitats for juvenile conch, Stoner and Sandt (1991) noted a direct relationship between seagrass biomass and habitat quality, as measured by conch growth.

The varying levels of predation intensity recorded in the experimental sites, despite the overall similarity in *Thalassia* abundance, suggest that *Thalassia* biomass is not the major factor regulating predation intensity. For example, similar levels of *Thalassia* biomass were measured in the two 50-m subsites, yet the two subsites differed significantly in their levels of predation-induced mortality. Of the six experimental subsites, lowest predation-induced mortalities were measured in the TB 50-m subsite. This finding indicates that certain habitats without resident conch provide low levels of predation-induced mortality comparable to those in sites containing resident conch. Epibenthic predator characteristics and biomass abundances measured in this particular subsite were, in general, similar to those measured in the other subsites. It is likely that other predator or seagrass characteristics play an important role in determining site-specific predation intensity.

Dead biomass (dead seagrass blades and detrital material) occurrence primarily reflects live *Thalassia* abundance, and secondarily conch feeding activity. Biomass occurrence in experimental sites provides a food source for juvenile conch (Stoner and Waite 1991), and adds structural complexity to the habitat. On numerous occasions, tethered and non-tethered conch were observed partially or fully buried beneath dead grass blades and detritus, demonstrating the sheltering potential of dead biomass in combination with live *Thalassia* blades. Conversely, dead seagrass biomass in combination with high abundances of *Thalassia* blades may have the opposite effect of increasing conch vulnerability to predation through a reduction in conch mobility and escape. Juvenile conch mobility probably determines the upper limit of seagrass densities with which they associate (Stoner and Waite 1990). High shoot densities, trapping heavy accumulations of dead biomass, and combined with thick stands of seagrass and soft sediments could inhibit conch movements. Conch typically move by thrusting the foot (operculum) against the substrate, propelling the shell forward in a hopping motion (Parker 1922); locomotion is therefore more efficient on sparse to moderately vegetated substrate.

Differences in predation intensity may also reflect differences in prey abundance. Initial occurrence of potential epibenthic predators prior to the introduction of tethered conch suggests that predators had an established source of prey. With the introduction of tethered conch, especially within sites without resident conch, it is likely that tethered conch became additional prey. Hence, in some sites, predation intensity may reflect (1) the degree to which epibenthic predators switched from their initial prey items to feed on juvenile conch, and (2) the availability of alternative prey items. In either case, predation intensity on tethered conch would be impacted. Differences in predation intensity in the experimental sites may also be related to the efficiency and abundance of epibenthic predators at each site. The structure of the characteristic suite of predators in the three experimental sites revealed a domination of *Petrochirus diogenes*, followed by *Murex pomum*, then *Fasciolaria tulipa*. Perhaps only some portion of this observed predator guild is responsible for the recorded predation intensity in the respective sites. For instance, only predators larger than 100 mm TSL may be effective in killing and consuming the available tethered conch ranging between 100-120 mm TSL.

The patchy occurrence of juvenile conch in similar seagrass beds is only partially explained by the results of these experiments. Juvenile conch absence from seagrass beds may reflect variations in recruitment dynamics: pelagic larvae may not be dispersed to certain areas, dispersed larvae may not settle, or settled larvae may suffer high post- settlement mortalities. Juvenile conch absence in certain seagrass beds may also reflect habitat suitability in terms of food limitations (Stoner 1989). Lastly, juvenile conch absence from apparently suitable areas may be due to yet unmeasured variables (e.g., physical parameters such as salinity, tidal flow) which are important components of habitat suitability, though the experimental sites did not appear particularly stressful in physical conditions.

Given the observed patterns of predation-induced mortalities in experimental sites, the hypothesis that predation is partially responsible for the patchy distribution of juvenile conch in natural habitats is supported. Finally, survival of juvenile conch in natural habitats appears to be site-specific and mediated to a degree by interactions including the presence and absence of juvenile conch, habitat biomass abundance, and epibenthic predator composition.

SUMMARY

Juvenile queen conch, *Strombus gigas*, are patchily distributed in shallow seagrass meadows near Lee Stocking Island, Exuma Cays, Bahamas, probably due to habitat-specific predation. I examined this hypothesis with field experiments by tethering juvenile conch (100-120 mm TSL) within three replicated habitat types: a seagrass bed with resident conch, and two seagrass beds at 50 m and 350 m outside the area containing resident conch. In addition, potential epibenthic predator distribution and abundance were quantified within each experimental site. Cumulative mortalities varied significantly as a function of site and distance: mortalities were characteristically low in experimental sites containing resident conch (0 m sites), and highest in experimental sites furthest away (350 m) from sites with resident conch. Mortalities in experimental sites bordering areas containing resident conch were intermediate in magnitude and variable, being significantly higher at one 50 m site than the other. Furthermore, epibenthic predators were not concentrated in areas containing resident conch. Hence, seagrass beds with resident conch appear to enhance conch survival. The observed pattern of predation-induced mortalities in juvenile conch is only partially explained by seagrass biomass densities and epibenthic predator occurrences, both of which varied significantly between and across experimental sites. From these findings I conclude that juvenile conch survival in the experimental seagrass sites is site-specific: the presence of resident conch appears to have a positive impact on the survival of juvenile queen conch.

Chapter 4

EVALUATION OF TETHERING AS A TOOL FOR ASSESSING PREDATION-INDUCED MORTALITY OF JUVENILE QUEEN CONCH

INTRODUCTION

The importance of predation in structuring marine communities is an often-debated topic in ecology, but it is difficult to assess due to the problems associated with conducting experiments (Sih et al. 1985). Even when experimental studies can be conducted to examine the importance of predation, they are often limited in their conclusions by the quality of the experimental techniques used to assess predation estimates.

Predation is a major cause of natural mortality in juvenile queen conch, *Strombus gigas*, but despite numerous attempts, the accurate estimation and control of juvenile conch natural mortality have not been accomplished. Previous investigations of predation upon conch have used four basic techniques, each with its accompanying benefits and disadvantages (ref. General Introduction Section). In particular, the use of field enclosure experiments that estimate growth and mortality rates under varying levels of predation intensity depends upon qualities of the enclosure (Jory and Iversen 1983). Unfortunately, extrapolation of these mortality estimates to field situations has been difficult owing to lack of information regarding cage artifacts upon predator-prey interactions.

When used as a technique during predation studies, tethering is intended to measure relative predator-induced mortality rates between experimental treatments (Heck and Thoman 1981); the technique is not intended to measure absolute rates of predation. Within the last decade, the use of tethering has increased in popularity, being utilized in experiments of predator-prey interactions with brachyuran and hermit crabs (Heck and Thoman 1981), the blue crab, *Callinectes sapidus* (Wilson 1985, Wilson et al. 1987, Heck and Wilson 1987, Wilson et al. 1990), Caribbean spiny lobster, *Panulirus argus* (Herrnkind and Butler 1986, Eggleston et al. 1990), the American lobster, *Homarus americanus* (Barshaw and Able 1990) and several fish species (Shulman 1985, McIvor and Odum 1988). With the exception of two studies (Herrnkind and Butler 1986, Barshaw and Able 1990), none of these sought to address artifacts of tethering as a tool for assessing predation-induced mortality. Below I describe results from field experiments designed to assess the use of tethering in quantifying predation-induced mortality rates of juvenile conch in natural habitats. Experimental objectives included (1) comparison of predation-induced mortalities on tethered, tagged, and untethered juvenile conch within enclosures, and (2) effects of the presence and absence of resident conch on survival of experimental animals. These experiments examined the hypotheses (1) that tethering causes minimal artifacts on experimental predation-induced mortality of juvenile queen conch; and, (2) that juvenile conch tethered within treatments containing resident conch experience lower mortality rates compared to conch in treatments without resident conch.

METHODS AND MATERIALS

Study Site

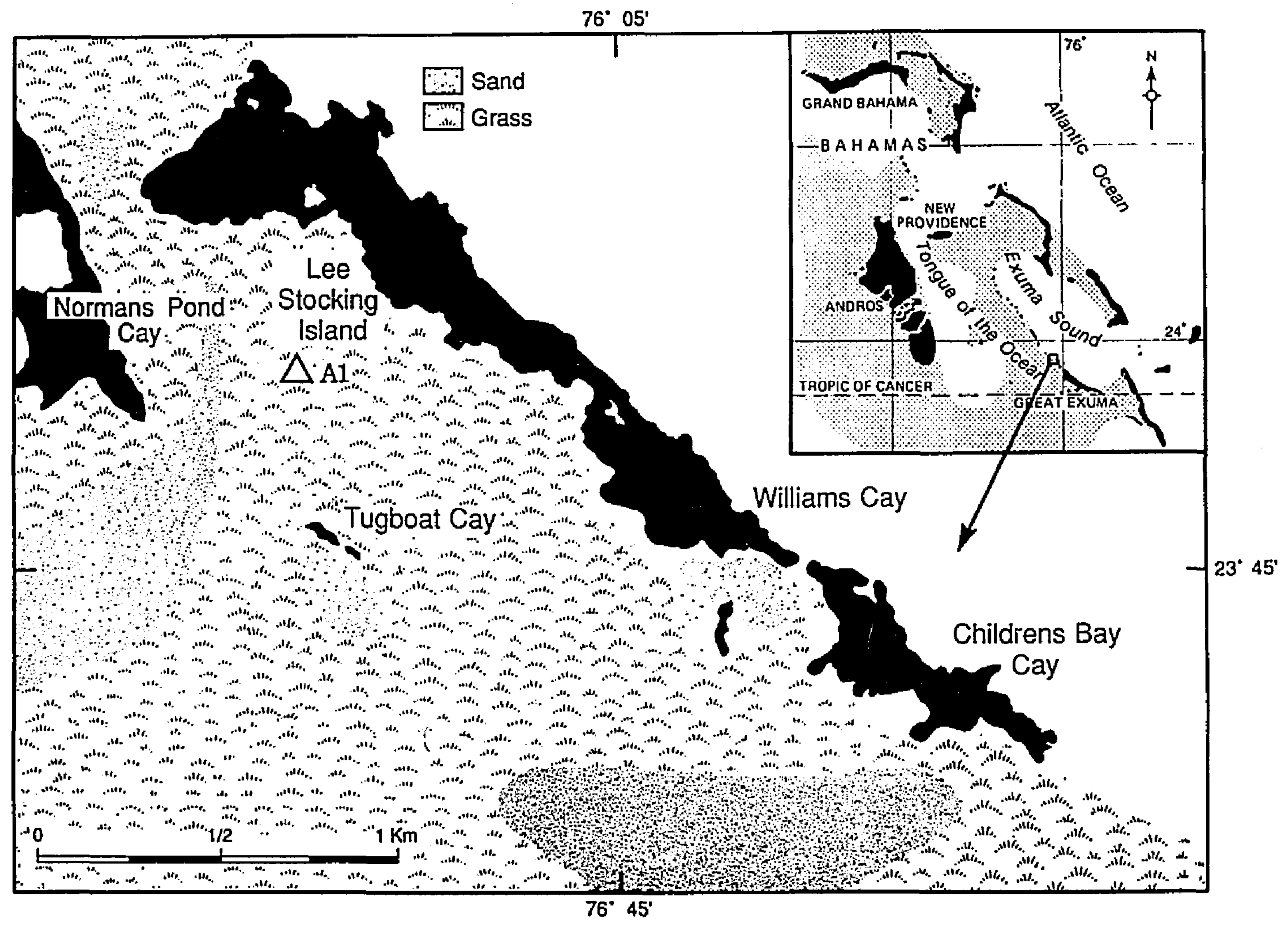
The experiment was conducted during late summer and fall, 1991 in a shallow turtle grass bed (*Thalassia testudinum)* west of LSI. This particular seagrass site was used in earlier tethering experiments, and is illustrated as site A1 (Fig. 20). The area characteristically contains moderate densities of *Thalassia* (see Chapter 3, Methods section; also Stoner and Sandt 1991). Other general characteristics of the site include a mean water depth of 3 m, strong tidal currents (to 100 cm/s, Dill et al. 1986) and the absence of resident conch.

Field enclosures (cages) were constructed using 2.5 cm x 2.5 cm wire mesh forming circular walls 30.5 cm high and 4 m in diameter. The cages were held erect with 1.25-cm-diameter reinforcement bars (rebar) hammered into the sediment and wired to the plastic mesh. The 8-12 bars per cage held the cages intact despite strong currents during maximum flood and ebb tides. Additionally, the wire-mesh cage walls were pushed almost 4 cm into the sediment to prevent conch escape. Cages were topless, to permit immigration and emigration of potential pelagic and epibenthic predators.

Within-site Layout

The plot layout in this experiment was similar to that utilized during 1990 tethering experiments (Chapter 2). Briefly, a rectangular area measuring 49.5 m x 38.5 m was marked off using PVC stakes driven into the sediment. This large area was further divided into 63 equal-sized squares (cells), each measuring 5.5 m x 5.5 m (30.25 m^2). Cells were systematically numbered 1-63, after which a random numbers table was used to select 24 of the 63 cells randomly for cage assignments (Fig. 21).

Figure 20. Approximate location of study site (A1, denoted by triangle), used during 1991 tethering artifact experiment.


76° 05'
Sand
Grass
Normans Pond Cay
Lee Stocking Island
A1
Tugboat Cay
Williams Cay
Childrens Bay Cay
23° 45'
0
1/2
1 Km
76° 45'
GRAND BAHAMA
BAHAMAS
NEW PROVIDENCE
ANDROS
Tongue of the Ocean
Exuma Sound
Atlantic Ocean
76°
24°
N
TROPIC OF CANCER
GREAT EXUMA

Experimental Animals

Juveniles in this experiment were 0^+ - 3^+ year-class conch ranging in size from 80-180 mm TSL. In this study, resident conch are defined as those untethered, non-tagged, free-ranging juveniles placed in cage treatments to simulate free ranging juveniles in the wild. Residents were typically juveniles and subadults between 60-180 mm TSL. Tethered conch are those animals attached to a tether-rod apparatus in a manner similar to that described in Chapter 1. Tagged conch were those animals with cable ties locked around the shell spire (latter 1/3 portion of the shell), with excess portions of each tie removed. Transparent (off-white) color ties were used; the cable ties were used to distinguish free-ranging, untethered conch from free-ranging residents and mimic the tethering apparatus without the tether line. Sizes of both tethered and tagged conch ranged between 80-100 mm TSL. Hereafter, the tethered and the tagged conch collectively are distinguished as experimental conch.

Both experimental and resident conch were collected from an area approximately 0.5 km northwest of Norman's Pond Cay, and about 2 km from the experimental site. The collection technique and the size range collected depended on the experimental treatment to which conch were assigned. For experimental treatments in which resident conch were to be utilized, two divers placed 3, 50-m-long transects, each spaced 5 m apart, in the central region of the resident conch. Beginning at the 0-m transect mark, each diver swam the distance of the transect stopping every 10 m to gather into a large mesh bag the 10 conch nearest to the 10-m

Figure 21. Schematic of 1991 site layout for tethering artifact experiment.

				○	○	
		▨		▨		
	○	▨	▨		⊞	
	⊞					
●			⊞	▨	⊞	
	⊞	●	○		○	
○		●		⊞		
		▨	●		●	●

Treatment Replicates:

● Tethers, Without Resident conch
▨ Tethers, With Resident conch
○ Untethered, without Resident Conch
⊞ Untethered, with Resident conch

interval markings. The 10 conch were collected irrespective of size or shell fouling condition. Transect interval markings that failed to produce 10 animals were bypassed for the next markings, and the process continued until the required 12 bags containing 10 conch each were collected (N=120).

Experimental conch were collected outside the immediate areas in which resident conch were collected. The sizes required for this portion of the study involved collection of 0^+ juveniles, 80-100 mm TSL. Given these relatively smaller sizes, collections required continuous haphazard searching until the required sample size (N=120) was obtained. Experimental animals were collected following the collection of resident conch, thus avoiding potential bias in the size ranges available for use as resident conch. Conch exposure out of the water was minimized by measurement underwater. Following collections, animals were transported (in large, seawater-filled containers) to the experimental site and placed in their respective cage treatments. The bottom area within each cage was thoroughly examined for epibenthic predators, with such predators being removed from cages prior to the introduction of juvenile conch.

Experimental Procedure

The four replicated treatment combinations randomly assigned to the 24 cages were:

- Tethered, with resident conch;
- Tethered, without resident conch;

- Untethered, with resident conch; and
- Untethered, without resident conch.

Six replicate cages of each treatment combination were established (N=24 cages; Fig. 21). A total of 10 experimental conch per cage (0.8 conch/m^2) were enclosed in each of the treatments requiring no resident conch; experimental conch included either tethered conch or tagged conch. The addition of 10 resident conch to the remaining two treatments doubled the individual cage densities to 1.6/m^2. Both cage densities are well within the range of natural densities consistently observed in natural populations in the vicinity of LSI (i.e., 1-2 conch/m^2; Stoner et al. 1988, Wicklund et al. 1988, Marshall et al., in press).

During cage sampling periods, the following protocol was utilized:

- The number of conch killed/cage was recorded;
- The number of resident conch in the respective treatments was maintained at initial nominal densities (10/cage); those killed by predators were replaced during each sampling visit. Conch used to replace these animals were collected in the same manner as that described above;
- Remains of broken, crushed or empty conch shells were removed from the cages, along with the tethering apparatus. Killed experimental conch were not replaced.
- Determination of predation-induced mortality followed the criteria outlined in Chapter 1.

All experimental treatments were initiated on 24 July 1991, sampled bimonthly during August and September, and sampled monthly during October and November (N=6 sampling visits). During sampling visits, each cage was examined for openings in the walls or at the cage wall/sediment interface. Cages were maintained to minimize escape of enclosed conch. During the final sampling visit in November, openings at the cage-wall/sediment interface large enough to permit the passage of conch or epibenthic predators were observed in two cages; three resident conch escaped from one cage, while all enclosed animals were accounted for in the second cage. The escaped animals were not included in statistical analyses.

Data Analysis

The cumulative number of conch killed per cage in each of the four experimental treatments provided independent data values for statistical analyses. In treatments containing resident conch, the cumulative number of residents killed were determined separately from the number of experimental conch killed. Cumulative number of conch killed per cage was converted to a proportion by dividing the total number killed by initial nominal densities (N=10). Hence, each of the six individual cages in the four experimental treatments generated a single cumulative proportional mortality value. Cochran's homogeneity of variance test on un-transformed data was not statistically significant, permitting direct analysis of un-transformed data. A two-way analysis of variance (ANOVA) model was used to examine the effects of Tether ((1) conch with tether; and (2) conch tagged without tether), Conch ((1) cages with resident conch; and (2) cages without residents) and the Tether x Conch interaction with cumulative proportional mortality as the dependent variable. The two-way interaction effect provided information on potential experimental artifacts. Underwood (1981) stated that "In the general sense, interactions occur when the effects of the levels of one factor differ when in the presence of different levels of another factor (and necessarily vice versa). Thus, the effects of the two factors are not additive, and are not independent of each other." In the present experiments significant interaction effects between Tether and Conch would suggest the presence of tethering artifacts.

In the two treatments containing tethered and tagged conch with residents, I generated 95% confidence intervals and tested the hypothesis that the mean cumulative proportional mortality of both tethered and tagged conch were significantly different from zero.

RESULTS

Predators and Related Observations

Observations on epibenthic predator occurrences within enclosures suggested a composition similar to that previously recorded in this site: a numerical dominance of the hermit crab *Petrochirus diogenes*, followed by apple murex, *Murex pomum*, and the tulip snail, *Fasciolaria tulipa*. Hermit crabs were observed in 15 of the 24 cages (1-2 per cage) during each sampling visit, while apple murex were observed less frequently (about 1 per cage in 6 of 24 cages during each visit). Hermit crabs were frequently observed crawling on cage walls, into and out of the cages. The small cage mesh size (2.5 cm x 2.5 cm) excluded some larger (80-160 mm TSL) epibenthic predators. Crushed shells were found inside cages on three separate occasions, indicating feeding by large predators (e.g., sharks and rays). Most of the conch were killed by predators which left the shells undamaged or slightly damaged (i.e., with chipped shell openings).

Mortality

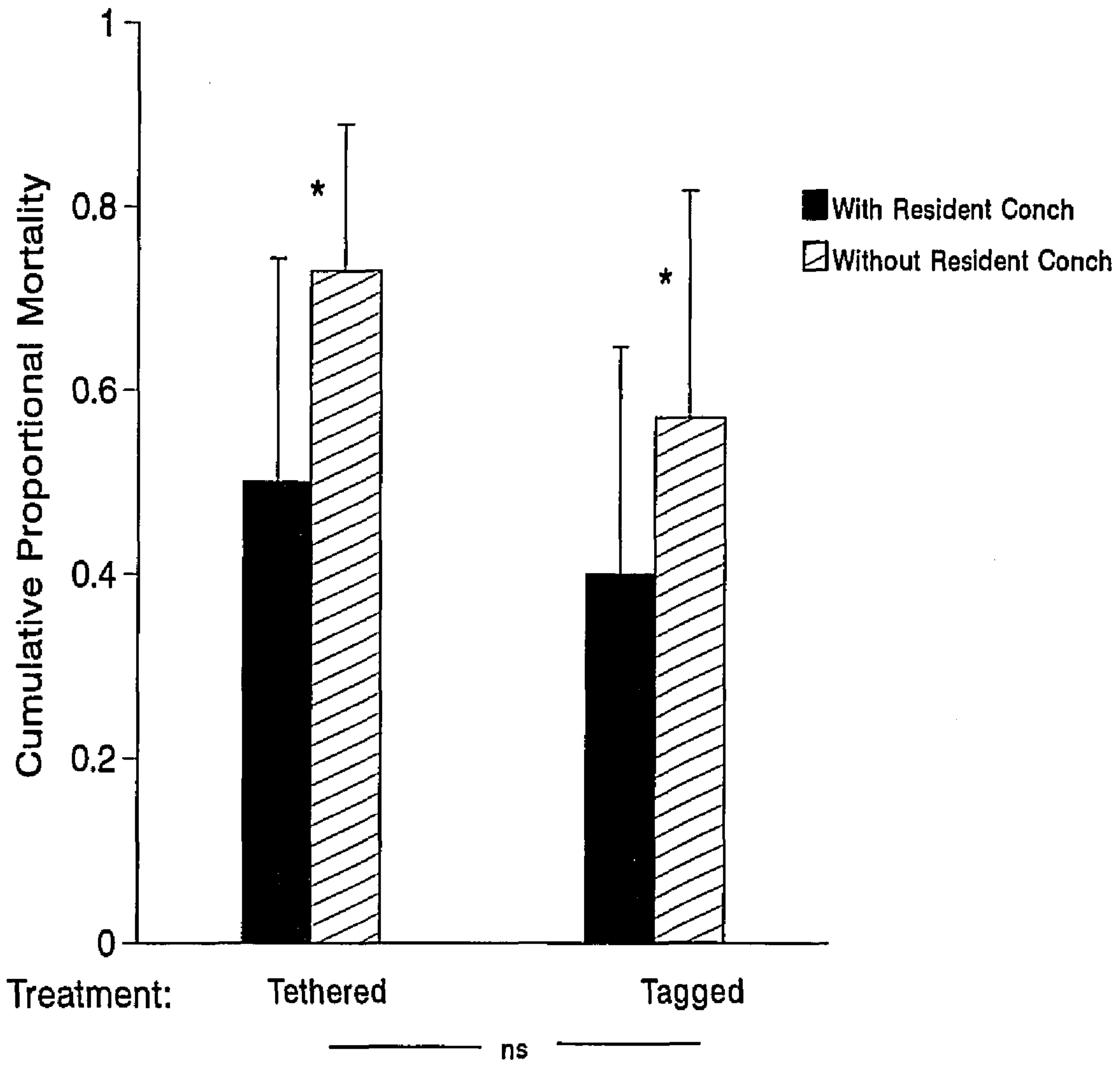
There were no significant differences in mortality between tethered (0.62) and tagged (0.48) conch; mortality was significantly higher in treatments without resident conch (0.65) than in treatments with residents (0.45); the Tether x Conch interaction effect was not significant (Table 16; Fig. 22). Highest mortalities were recorded in the cages containing tethered conch only (0.73) followed respectively by cages containing untethered, tagged conch and no residents (0.56), tethered conch with residents (0.50) and untethered, tagged conch with residents (0.40). The power of the ANOVA for the non-significant Tether factor was estimated to be 0.25. A subsequent analysis of required sample size indicated that a minimum of 47 cages per treatment would be needed to obtain a power of 0.80. Such a large sample size (N = 47 x 4 treatment combinations) suggest that the small difference observed between tethered and tagged conch is not biologically significant. In the two treatments containing resident conch, cumulative proportional mortalities of residents were not significantly different from those of tethered and tagged conch (Table 17).

Table 16. Two-way ANOVA examining the effects of Tether (conch with tether, conch tagged without tether) and Conch (presence of resident conch, absence of resident conch) on conch mortality. Dependent variable = untransformed cumulative proportional mortality.

Source of Variation	df	MS	F
Tether	1	0.107	2.07 ^{ns}
Conch	1	0.236	4.57 *
Tether x Conch	1	0.007	0.13 ^{ns}
Error	20	0.052	

^{ns} $P > 0.05$, * $P < 0.05$

Figure 22. Two-way ANOVA examining the effect of Tether and Conch (dependent variable = untransformed cumulative proportional mortality).



Cumulative Proportional Mortality
1
0.8
0.6
0.4
0.2
0
*
*
With Resident Conch
Without Resident Conch
Treatment:
Tethered
Tagged
ns

Table 17. Confidence interval analysis for tethered and tagged conch. Factor means within the 95 percent confidence interval (C.I.) are not significantly different from zero.

Factor	N	Mean	Stdev	SE Mean	95% Percent C.I.
Tether	6	0.150	0.152	0.062	(-0.009, 0.309)
Tags	6	0.217	0.286	0.117	(-0.083, 0.517)

DISCUSSION

Tethering techniques have been used in experiments of predator-prey interactions in fish (Shulman 1985, McIvor and Odum 1988), and various marine invertebrates (Heck and Thoman 1981, Wilson 1985, Wilson et al. 1987, Heck and Wilson 1987, Wilson et al. 1990, Herrnkind and Butler 1986, Barshaw and Able 1990, Eggleston et al. 1990). With the exception of Herrnkind and Butler (1986) and Barshaw and Able (1990), none of these studies sought to experimentally examine potential artifacts of the technique. In field experiments designed to address this issue, my results indicate that predation-induced mortalities on tethered juvenile *Strombus gigas* are similar to those of untethered animals. Specifically, an absence of significant statistical interaction effects suggests that the use of tethering presented minimal experimental artifacts. Hence, predation-induced mortality estimates are representative of relative rates of predation within the study site. Additionally, mortality of tethered animals varied significantly in the presence or absence of resident conch, with treatments containing residents experiencing lowest mortality rates. Combining these findings with mortality estimates derived from experiments conducted under similar field conditions in nearby seagrass sites during previous years, I conclude that tethering techniques provide consistent and reliable estimates of relative predation-induced mortality rates on juvenile conch in natural habitats.

Mortality estimates derived for the respective treatments are considered to be strictly predation-induced mortality and not cage-induced, starvation-related mortalities. Conch densities used in the respective treatments (0.80 and 1.60/m^2)

were well within the natural range of juveniles in the wild; it is therefore unlikely that cages produced overcrowding or food limitations. The study site consistently has a moderate to high standing crop of seagrass detritus and algae, two primary foods for juveniles in the size range (0^+ - 3^+ year classes) utilized in this experiment (Stoner 1989, Stoner and Waite 1991).

The simultaneous use of caging and tethering deserves further comparison given their efficacy in measuring predation-induced mortality. Cages were constructed to prevent and minimize potential conch escape, and also permit immigration and emigration of pelagic and epibenthic predators. In both cases, cages proved highly effective: a total of three (of 240 +) conch escaped during the four-month experimental period, whereas potential epibenthic predators were observed within enclosures during each sampling visit. The occurrence of crushed shells within cages confirm some feeding activity by crushing pelagic predators. Hence, cage use appears to have been effective in containing enclosed animals while permitting access to some epibenthic and pelagic predators. The combination of caging and tethering permitted the accurate retrieval of almost 100% of all enclosed conch, thus enhancing the overall predictive power of the experiment.

Tethered conch were expected to experience higher predation-induced mortality than untethered conch due to restrictions on conch escape by tethers. The nonsignificant differences between the tethered and untethered conch suggest that despite the potential restrictive nature of tether lines, tethered conch experience mortality rates similar to those experienced by untethered animals. Hence, the use of tethering to measure relative predation rates on juvenile conch appears to yield comparable mortality rates for both tethered and untethered conch under these experimental conditions. Additionally, free- ranging resident conch and tagged, untethered conch were also expected to experience similar mortalities, both of which should be significantly lower than tethered animals. Such a pattern was observed, with measured differences in mortalities between resident and experimentally treated animals likely due to differences associated with the size of resident conch. On average, resident conch were larger (60-180 mm TSL) than experimental (i.e., tethered and tagged) conch, which ranged between 80-100 mm TSL. Juvenile conch mortality is inversely related to size (Appeldoorn 1984). It is therefore likely that resident conch experienced higher survival than experimental conch due to their larger size, and concurrently enhanced the survival of experimental conch.

The mortality rates measured during this study are comparable to those measured within the study site during previous investigations. In a 1988 study comparing relative predation-induced mortalities of hatchery-reared and wild animals (60-82 mm TSL), cumulative mortality rates for wild conch averaged 0.8 at the end of 11 weeks (Chapter 2). In a similar 11-week 1989 study, cumulative proportional mortalities averaged 0.50 for juveniles between 60-80 mm TSL within this same study site, while mean cumulative mortalities of 0.71 were measured in a nearby unpopulated site (Windsock Cay) with similar seagrass biomass (Lipcius and Marshall, Jr., unpub. data). All of these investigations were conducted during late summer through early fall.

Results indicating increased survival for animals in cages containing resident conch also support findings from previous experiments, where mortalities recorded for conch tethered in areas containing resident juvenile conch were consistently lower than those in areas without residents (Chapter 2 and 3). Although this study was not designed to measure differences in predation-induced mortalities as a function of conch density, the finding of lowest mortalities in treatments containing resident conch and highest mortality in treatments without residents further supports the hypothesis of inversely density-dependent predation in seagrass beds containing resident conch (Chapter 1).

Barshaw and Able (1990) suggest that tethering to assess predation in different habitats should be evaluated for each new species under consideration because species-specific behavior patterns could create habitat-specific tethering artifacts. However, observations derived from a study comparing survival of hatchery-reared and wild stocks in natural habitats indicate that behavior of tethered conch (e.g., escape response, feeding activity and burial) was similar to that of untethered conch (Chapter 2). This finding, combined with findings from the present study, suggests that artifacts of tethering in juvenile queen conch predation studies are minimal, and that my estimates of predation-induced mortalities are reliable and unbiased. Ideally, future experiments to estimate mortality rates of juvenile conch in natural habitats should incorporate experimental designs which measure mortality rates without the aid of artificially introduced techniques. Meanwhile, the use of tethering appears to be a viable technique in providing estimates of predation-induced mortalities on juvenile queen conch in natural habitats.

SUMMARY

I examined the potential artifacts of tethering in deriving estimates of relative rates of predation-induced mortality of juvenile queen conch, in natural habitats. Field experiments were conducted during summer and fall 1991 in a moderately dense portion of a turtle grass bed near LSI, Bahamas. Conch survival was compared between tethered and tagged, 80-100 mm TSL conch in the presence and absence of resident conch (60-180 mm TSL). Mortality rates of tethered conch did not differ significantly from tagged conch, whereas conch (tethered or tagged) enclosed with free-ranging resident conch experienced significantly lower mortalities than those without residents. The latter finding provides further evidence consistent with the hypothesis that resident conch enhance survival of recruits through a positive feedback mechanism. In treatments containing both experimental and resident conch, mortality rates did not differ significantly between residents and experimental conch though residents suffered lower mortalities. Since resident conch were generally larger than experimental conch, their slightly increased survival was likely due to their larger size. The absence of significant statistical interaction effects indicates that minimal artifacts were introduced by the tethering technique. These results, combined with behavioral observations from previous similar tethering experiments, indicate that tethering provides consistent and reliable estimates of relative rates of predation on juvenile queen conch in different seagrass habitats.

CONCLUSIONS

Results from these experiments indicate that various factors act interactively to produce habitat-specific mortality rates in queen conch due to predation. These include (1) habitat type, whereby seagrass beds offer some protection; (2) local population dynamics, such that populated seagrass beds appear to enhance conch survival; (3) population density in some seagrass beds, such that mortality is inversely density-dependent; (4) conch size, such that larger conch have higher survival rates, depending on the specific type of habitat; and (5) predation intensity and predator guilds, which likely differ across habitats, producing habitat-specific mortality rates. When integrated with complementary studies of queen conch trophodynamics, these results provide critical information regarding key ecological factors affecting conch survival. In particular, results from the hatchery-reared experiments demonstrate the potential use of hatchery-reared stocks in natural habitats, and hence a valuable option for enhancement of fishery stocks throughout the Caribbean. In general, the integration of results obtained in this dissertation, with complementary studies of queen conch trophodynamics, should provide valuable suggestions of queen conch habitats, densities and scales of patchiness producing highest survivorship and growth rates in nature.

LITERATURE CITED

Adams, J. E. (1970). Conch fishing industry of Union Island, Grenadines, West Indies. J. Trop. Sci. 12: 279-288.

Alcolado, P. J. (1976). Growth, morphological variations of the shell and some biological data of the conch *Strombus gigas* L. (Mollusca: Mesogastropoda). Acad. Cien. Cuba Ser. Oceanol. 34: 1-26 (English Translation).

Appeldoorn, R. S. (1984). The effect of size on mortality of small juvenile conchs (*Strombus gigas* Linne and *S. costatus* Gmelin). J. Shell. Res. 4 (1): 37-43.

Appeldoorn, R. S. (1985). Growth, mortality, and dispersion of juvenile laboratory-reared conchs, *Strombus gigas* and *S. costatus*, released at an offshore site. Bull. Mar. Sci. 37: 785-793.

Appeldoorn, R. S. (1987). Assessment of mortality in an offshore population of queen conch, *Strombus gigas* L., in southwest Puerto Rico. Fish. Bull., U. S. 85: 797-804.

Appeldoorn, R. S., Ballantine, D. L. (1983). Field release of cultured queen conchs in Puerto Rico: implications for stock restoration. Proc. Gulf Caribb. Fish. Inst. 35: 89-98.

Appeldoorn, R. S., Ballantine, D. L. (1986). Assessment of fisheries of queen conch, *Strombus gigas*, in Puerto Rico. Final Report to Nat. Mar. Fish. 62 p.

Appeldoorn, R. S., Sanders, I. M. (1984). Quantification of the density-dependent growth relationship in hatchery-reared juvenile conchs (*Strombus gigas* Linne and *S. costatus* Gmelin). J. Shellfish Res. 4: 63-66.

Barshaw, D. E., Able, K. W. (1990). Tethering as a technique for assessing predation rates in different habitats: an evaluation using juvenile lobsters *Homarus americanus*. Fish. Bull., U. S. 88: 415-417.

Barshaw, D. E., Able, K. W. (In press). Deep burial as a refuge for lady crabs *Ovalipes ocellatus*: comparisons with blue crabs *Callinectes sapidus*. Mar. Ecol. Prog. Ser.

Bell, J. D., Westoby, M. (1986). Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia 68: 205-209.

Brownell, W. N., Stevely, J. M. (1981). The biology, fisheries and management of the queen conch, *Strombus gigas*. Mar. Fish. Rev. 43(7): 1-12.

Brownell, W. N., Berg, C. G., Haines, K. C. (1977). Fisheries and aquaculture of the conch, *Strombus gigas* in the Caribbean. FAO Fish. Rept. 200: 59-69.

Connell, J. H. (1975). Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460-490 in M. L. Cody and J. Diamond, (eds.), Ecology and Evolution of Communities. Belknap Press, Cambridge, Mass., USA.

Cooper, W. E., Crowder, L. E. (1979). Patterns of predation in simple and complex environments. In: R. H. Shoud and H. Clopper, (eds.), Predator prey systems in fisheries management. Sport Fish. Inst., Washington, DC.

Crowder L. B., Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802-1813.

Davis, M., Hesse, C., Hodgkins, G. (1987). Commercial hatchery produced queen conch, *Strombus gigas*, seed for research and grow-out market. Proc. Gulf. Caribb. Fish. Inst. 38: 326-335.

Day, R. W., Quinn, G. P. (1989). Comparisons of treatments after an analysis of variance in Ecology. Ecol. Monog. 59: 433-463.

Dill R. F., Shinn, E. A., Jones, A. T., Kelly, K., Steinen, R. P. (1986). Giant subtidal stromatolites forming in normal salinity waters. Nature 324: 55-58.

Eggleston, D. B. (1990a). Foraging behavior of the blue crab, *Callinectes sapidus*, on juvenile oysters, *Crassostrea virginica*: effects of prey density and size. Bull. Mar. Sci. 46: 62-82.

Eggleston, D. B. (1990b). Behavioral mechanisms underlying variable functional response of blue crabs, *Callinectes sapidus* feeding on juvenile oysters, *Crassostrea virginica*. J. Anim. Ecol. 59(2): 615-630.

Eggleston, D. B., Lipcius, R. N., Miller, D. L., Coba-Cetina, L. (1990). Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. Mar. Ecol. Prog. Ser. 62: 79-88.

Eggleston, D. B., Lipcius, R. N., Hines, A. H. (1992). Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Mar. Ecol. Prog. Ser. 85: 55-68.

Gotceitas, V., Colgan, P. (1989). Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80: 158-166.

Hassell, M. P. (1978). The dynamics of arthropod predator-prey systems. Monographs in Population Biology 13. Princeton University Press, Princeton, NJ, 237 p.

Heck, K. L., Jr., Thoman, T. A. (1981). Experiments on predator-prey interactions in vegetated aquatic environments. J. Exp. Mar. Biol. Ecol. 53: 125-134.

Heck, K. L., Wilson, K. A. (1987). Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. J. Exp. Mar. Biol. Ecol. 107: 87-100.

Herrnkind, W. F. (1980). Spiny lobsters: patterns of movement. In: J. S. Cobb and B. F. Phillips (eds.), The biology and management of lobsters, Vol. I, Physiology and behavior. Academic press, NY, p. 349-407.

Herrnkind, W. F., Butler, M. J. (1986). Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. Mar. Ecol. Prog. Ser. 34: 23-30.

Herrnkind, W. F., Lipcius, R. N. (1989). Habitat use and population biology of Bahamian spiny lobster. Proc. Gulf Caribb. Fish. Inst. 39: 265-278.

Hesse, K. O. (1979). Movement and migration of the queen conch (*Strombus gigas*), in the Turks and Caicos Islands. Bull. Mar. Sci. 29: 303-311.

Hildrew, A. G., Townsend, C. R. (1977). The influence of substrate on the functional response of *Plectrocnemia conspersa* (Curtis) larvae (Trichoptera: Polycentropodidae). Oecologia 32: 21-26.

Hines, A. H., Posey, M. H., Haddon, P. J. (1989). Effects of adult suspension- and deposit-feeding bivalves on recruitment of estuarine infauna. The Veliger 32: 109-119.

Huffaker, C. B. (1958). Experimental studies on predator-prey oscillations. Hilgardia 27: 343-383.

Hughes, R. N., Elner, R. W. (1979). Tactics of a predator, *Carcinus maenas* and morphological responses of the prey, *Nucella lapillus*. J. Anim. Ecol. 48: 65-78.

Iversen, E. S. (1983). Feasibility of increasing Bahamian conch production by mariculture. Proc. Gulf Caribb. Fish. Inst. 35: 83-88.

Iversen, E. S., Jory, D. E., Bannerot, S. P. (1986). Predation on queen conchs, *Strombus gigas* in the Bahamas. Bull. Mar. Sci. 39: 61-75.

Jory, D. E. (1982). Predation by tulip snails, *Fasciolaria tulipa*, on queen conch, *Strombus gigas*. Unpublished M.S. thesis, University of Miami, Coral Gables, Florida.

Jory, D. E., Iversen, E. S. (1983). Queen conch predators: not a roadblock to mariculture. Proc. Gulf Caribb. Fish. Inst. 35: 108-111.

Jory, D. E., Iversen, E. S. (1988). Shell strength of queen conch, *Strombus gigas* L.: aquaculture implications. Aqua. Fish. Manag. 19: 45-51.

Katz, C. H. (1985). A nonequilibrium predator-prey interaction. Ecology 66: 1426-1438.

Kikuchi, T. (1980). Faunal relationships in temperate seagrass beds. In R. C. Phillips and C. P. McRoy (eds.), Handbook of seagrass biology: An ecosystem perspective, p. 153-172. Garland Press, NY.

Laughlin, R. A., Weil, E. (1983). Queen conch mariculture and restoration in the Archipelago de Los Roques: Preliminary results. Proc. Gulf Caribb. Fish. Inst. 35: 64-72.

Lawton, P., Hughes R. N. (1985). Foraging behavior of the crab *Cancer pagurus* feeding on the gastropods *Nucella lapillus* and *Littorina littorea*: comparisons with optimal foraging theory. Mar. Ecol. Prog. Ser. 27: 143-154.

Lipcius, R. N., Hines, A. H. (1986). Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. Ecology 67: 1361-1371.

Lipcius, R. N., Stoner, A. W., Marshall Jr., L. S., Bardales, A. T. (1991). Mass migration of juvenile queen conch, *Strombus gigas*, in the Bahamas. Proc. Gulf Caribb. Fish. Inst. 40: 299-302.

Mann, K. (1977). Destruction of kelp beds by sea urchins. A cyclical phenomenon of irreversible degradation? Helgol. Wiss. Meersunters. 30: 455-467.

Mansour, R. A., Lipcius, R. N. (1991). Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. Mar. Ecol. Prog. Ser. 72: 239-246.

Marinelli, R. L., Coull, B. C. (1987). Structural complexity and juvenile fish predation on meiobenthos: an experimental approach. J. Exp. Mar. Biol. Ecol. 108: 67-81.

McIvor, C. C., Odum, W. E. (1988). Food, predation risk and micro-habitat selection in a marine fish assemblage. Ecology 69: 1341-1351.

Menge, B. A. (1976). Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs 46: 355-393.

Menge, B. A. (1978a). Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. Oecologia 34: 1-16.

Menge, B. A. (1978b). Predation intensity in a rocky intertidal community. Effects of an algal canopy, wave action and desiccation on predatory feeding rates. Oecologia 34: 17-35.

Menge, B. A. (1982). Reply to a comment by Edwards, Conover and Sutter. Ecology 63: 1180-1184.

Menge, B. A. (1983). Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia 58: 141-155.

Menge, B. A., Lubchenco, J., Ashkenas, L. R. (1986). Experimental separation of effects of consumer on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. J. Exp. Mar. Biol. Ecol. 100: 225-269.

Minello, T. J., Zimmerman, R. J. (1983). Fish predation of juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. J. Exp. Mar. Biol. Ecol. 72: 211-231.

Murdoch, W. W., Oaten, A. (1975). Predation and population stability. In: A. MacFadyen (ed.), Advances in ecological research, Volume VIX. Academic Press, NY, p. 2-131.

Nelson, W. G. (1979). Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. J. Exp. Mar. Biol. Ecol. 38: 225-245.

Nelson, W. G. (1981). The role of predation by decapod crustaceans in seagrass ecosystems. Kieler Meeresforsch, Sonderh. 5: 529-536.

Orth, R. J. (1977). The importance of sediment stability in seagrass communities. Pages 281-300, in B. C. Coull, (ed.), Ecology of marine benthos. Univ. South Carolina Press, Columbia.

Orth, R. J., Heck, Jr., K. L., van Montfrans, J. (1984). Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7: 339-350.

Paine, R. T. (1966). Food web complexity and species diversity. Amer. Nat. 100: 65-75.

Paine, R. T. (1976). Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology 57: 858-873.

Paine, R. T. (1980). Food webs, linkage interaction strength, and community infrastructure. J. Anim. Ecol. 49: 667-685.

Parker, G. H. (1922). The leaping of the *Stromb* (*Strombus gigas* Linn.). J. Exp. Zool. 36: 205-209.

Peterson, C. H. (1982). Clam predation by whelks (*Busycon* spp.): experimental tests on the importance of prey size, prey density and seagrass cover. Mar. Biol. 66: 159-170.

Polovina, J. J. (1990). Evaluation of hatchery release of juveniles to enhance rockfish stocks, with application to pacific ocean perch, *Sebastes alutus*. Fish. Bull., U. S. 89: 129-136.

Posey, M. (1986). Predation of a borrowing shrimp: Distribution and community consequences. J. Exp. Mar. Biol. Ecol. 103: 143-161.

Randall, J. E. (1964). Contributions to the biology of the queen conch, *Strombus gigas*. Bull. Mar. Sci. 14: 246-295.

Robertson, R. (1959). Observations on the spawn and veligers of conch (*Strombus*) in the Bahamas. Proc. Malacol. Soc. Lond. 33: 164-172.

Robertson, R. (1961). The feeding of *Strombus* and related herbivorous marine gastropods. Notulae Naturae 343: 1-9.

Ryer, C. H. (1988). Pipefish foraging and the effect of altered habitat complexity. Mar. Ecol. Prog. Ser. 48: 37-45.

Schiel, D. R., and B. C. Welden. (1987). Responses to predators of cultured and wild red abalone, *Haliotis rufescens*, in laboratory experiments. Aquaculture 60: 173-188.

Shulman, M. J. (1985). Recruitment and coral reef fishes: effects of distribution of predators and shelter. Ecology 66: 1056-1066.

Siddall, S. E. (1983). Biological and economic outlook for hatchery production of juvenile queen conch. Proc. Gulf Caribb. Fish. Inst. 35: 46-52.

Sih, A., Crowley, P., Mcpeek, M., Petranka, J., Strohmeir, K. (1985). Predation, competition and prey communities: A review of field experiments. Annu. Rev. Ecol. Syst. 16: 269-311.

Sokal, R. R., Rohlf, F. J. (1981). Biometry. W. H. Freeman and Co., San Francisco. 859 p.

Spitze, K. (1985). Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. Ecology 66: 938-949.

Stoner, A. W. (1980). The role of seagrass biomass in the organization of benthic macrofauna assemblages. Bull. Mar. Sci. 30: 537-551.

Stoner, A. W. (1982). The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linn.). J. Exp. Mar. Biol. Ecol. 58: 271-284.

Stoner, A. W. (1989). Density-dependent growth and grazing of juvenile queen conch *Strombus gigas* L. in a tropical seagrass meadow. J. Exp. Mar. Biol. Ecol. 130: 119-133.

Stoner, A. W., Sandt, V. J. (1991) Experimental analysis of habitat quality for juvenile queen conch in seagrass meadows. Fish. Bull., U. S. 89: 693-700.

Stoner, A. W., Waite, J. M. (1990). Distribution and behavior of queen conch *Strombus gigas* relative to seagrass standing crop. Fish. Bull., U. S. 88: 573-585.

Stoner, A. W., Waite, J. M. (1991). Trophic biology of queen conch in nursery habitats: diets and primary food sources in seagrass meadows. J. Mollusc. Stud. 57: 451-460.

Stoner, A. W., Lipcius, R. N., Marshall, Jr., L. S., Bardales, A. T. (1988). Synchronous emergence and mass migration in juvenile queen conch. Mar. Ecol. Prog. Ser. 49: 51-55.

Summerson, H. C., Peterson, C. H. (1984). Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Mar. Ecol. Prog. Ser. 15: 67-77.

Tegner, M. J. (1989). The feasibility of enhancing red sea urchin, *Stronglocentrotus franciscanus*, stocks in California: An analysis of the options. Mar. Fish. Rev. 51(2): 1-22.

Tegner, M. J., Butler, R. A. (1989). Abalone seeding. In K. O. Hahn (editor), Handbook of culture of abalone and other marine gastropods, p. 157-182. CRC press, Boca Raton, Fla.

Thompson, D. J. (1978). Towards a realistic predator-prey model: the effect of temperature on the functional responses and life history of larvae of the damselfly *Ischnura elegans*. J. Anim. Ecol. 47: 757-767.

Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Ann. Rev. 19: 513-605.

Vince, S., Valiela, I., Backus, N., Teal, J. M. (1976). Predation by the saltmarsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. J. Exp. Mar. Biol. Ecol. 23: 255-266.

Virnstein, R. W. (1977). The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58: 1199-1217.

Virnstein, R. W. (1979). Predation on estuarine infauna: response patterns of component species. Estuaries 2: 69-86.

Weil, M. E., Laughlin, R. A. (1984). Biology, population dynamics and reproduction of the queen conch, *Strombus gigas* (Linne.) in the Archipelago de Los Roques National Park. J. Shell. Res. 4: 45-62.

Werner, E. E., Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69: 1352-1366.

Werner, E. E., Gilliam, J. F., Hall, D. J., Mittlebach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548.

Wicklund, R. I., Hepp, L. J., Wenz, G. A. (1988). Preliminary studies on the early life history of the queen conch, *Strombus gigas* in the Exuma Cays, Bahamas. NURP Res. Rep. 88(4): 347-363. Natl. Undersea Res. Prog., NOAA, Rockville, MD 20852.

Wilson, K. A. (1985). Physical and biological interactions that influence habitat use of mangrove crabs. Ph.D. diss., Univ. Pennsylvania, Philadelphia, 187 p.

Wilson, K. A., Heck, Jr., K. L., Able, K. W. (1987). Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. Fish. Bull. 85: 53-58.

Wilson, K. A., Able, K. W., Heck, Jr., K. L. (1990). Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). Mar. Ecol. Prog. Ser. 58: 243-251.

Woodin, S. A. (1981). Distribution and community structure in a shallow water sand flat. Ecology 62: 1052-1066.

Young, D. K., Buzas, M. A., Young, M. W. (1976). Species densities of macrobenthos associated with seagrass: a field experimental study of predation. J. Mar. Res. 34: 577-592.

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