

Abstract. — A study was conducted on shallow banks near Lee Stocking Island, Bahamas, to determine habitat associations of queen conch *Strombus gigas* L. within seagrass meadows of *Thalassia testudinum*. Transect data showed that conch density and biomass increased directly with increasing macrophyte cover up to an optimal level of moderate-density seagrass (608–864 shoots/m²), after which conch density decreased sharply. Up to the optimal level, conch density and biomass were closely correlated with seagrass and detritus biomass, shoot density, and depth. Seagrass shoot density was the best predictor of conch abundance. Results of habitat choice experiments showed that two different juvenile size classes (75–100 mm and 125–150 mm shell length) are proficient in detecting and choosing habitats with moderate seagrass density over bare sand, low or high seagrass density. Larger conch appear to prefer habitat with higher shoot density than conch of smaller size classes; adult conch were less specialized in their habitat association. These results provide data on one of the key environmental variables, seagrass structure, which will be useful in predicting conch distributions in the field and for planning conch outplanting.

Distribution and Behavior of Queen Conch *Strombus gigas* Relative to Seagrass Standing Crop

Allan W. Stoner
Janice M. Walte

Caribbean Marine Research Center, 100 E. 17th Street
Riviera Beach, Florida 33404
and
Lee Stocking Island, Exuma Cays, Bahamas

Seagrass meadows, common in protected shallow waters, are known to be important sources of food and shelter for numerous fishes and invertebrates from high to low latitudes (Kikuchi 1980, Ogden 1980, Virnstein et al. 1984). Living seagrasses are consumed by a few animals such as surgeonfishes, halfbeaks, parrotfishes (Randall 1964, Ogden 1980), urchins (Lawrence 1975), green sea turtles (Ogden 1980), and sirenia (Bertram and Bertram 1968); however, most nonpredaceous fauna of seagrass meadows consume seagrass epiphytes or detritus (Zimmerman et al. 1979, Leber 1983, Fry 1984, Howard 1984, Kitting et al. 1984, Van Montfrans et al. 1984). Sheltering from predation has been shown experimentally for many seagrass inhabitants, particularly crustaceans (Nelson 1979, 1981; Heck and Thoman 1981; Coen et al. 1981; Stoner 1982; Leber 1985; Wilson et al. 1987).

The queen conch *Strombus gigas* L. is a large gastropod mollusc which derives both food and shelter from seagrass beds of the Caribbean region (Bermuda and southeastern Florida to Brazil). After the first year of life, of which little is known, queen conch juveniles emerge from the sediment and feed epibenthically in seagrass meadows where there are large quantities of algal and detrital foods (Randall 1964). Juvenile queen conch are important grazers of seagrass

detritus, and conch densities may be limited by food abundance (Stoner 1989). Recent experiments conducted in the Bahamas have shown that seagrasses reduce predation rates on juvenile conch in nursery areas (Marshall and Lipcius, In review).

Throughout its geographic range, the queen conch is an important commercial species which has been severely depleted in many areas (Adams 1970, Brownell et al. 1977). For this reason, there is increasing interest in improving the management of conch, and seeding of depleted areas with hatchery-reared juveniles has been proposed (Berg 1976, Brownell and Stevely 1981, Laughlin and Weil 1983, Coulston et al. 1987). Successful management of the fishery and/or outplanted populations will require detailed information on the relationships between queen conch and environmental variables. This study was conducted to examine the role of macrophyte cover in the distribution of juvenile conch in two nursery areas of the Exuma Cays, Bahamas. In addition to seagrass shoot density and biomass, abundance of detritus, sediment characteristics, and depth were considered for their potential influence on the density, distribution, and biomass of conch. Field experiments were conducted to determine the role of habitat selection in natural conch distributions.

Table 1

Habitat characteristics of the two seagrass meadow study sites. Units for each are: depth (meters at low water), sediment grain size (Φ), organics (% dry wt), *Thalassia* shoots (n/m^2), *Thalassia* and detritus biomass (g dry wt/ m^2). Values are means \pm SD. n = number of measurements from three transects.

	Stations						
	1	2	3	4	5	6	7
Children's Bay Cay							
Depth ($n = 3$)	1.0 \pm 0.1	1.2 \pm 0.1	1.8 \pm 0.2	2.7 \pm 0.3	3.4 \pm 0.3	—	—
Sediment grain size ($n = 3$)	1.50 \pm 0.11	1.38 \pm 0.31	1.50 \pm 0.07	1.83 \pm 0.59	2.44 \pm 0.51	—	—
Organics ($n = 3$)	2.44 \pm 0.20	2.35 \pm 0.25	2.61 \pm 0.06	2.98 \pm 0.44	3.88 \pm 0.45	—	—
July							
<i>Thalassia</i> shoots ($n = 6$)	0.0 \pm 0.0	64.0 \pm 16.0	304 \pm 48.0	576 \pm 48.0	704 \pm 80.0	—	—
<i>Thalassia</i> biomass ($n = 6$)	0.0 \pm 0.0	3.5 \pm 1.1	16.0 \pm 4.7	48.0 \pm 4.8	65.6 \pm 14.4	—	—
Detritus ($n = 6$)	0.0 \pm 0.0	0.80 \pm 0.80	3.68 \pm 1.9	30.9 \pm 18.6	104 \pm 44.8	—	—
February							
<i>Thalassia</i> shoots ($n = 6$)	0.0 \pm 0.0	67.2 \pm 19.2	304 \pm 72.0	736 \pm 208	864 \pm 160	—	—
<i>Thalassia</i> biomass ($n = 6$)	0.0 \pm 0.0	8.6 \pm 9.9	13.9 \pm 4.6	56.0 \pm 20.8	80.0 \pm 19.2	—	—
Detritus ($n = 6$)	0.0 \pm 0.0	0.64 \pm 0.80	0.64 \pm 1.28	48.0 \pm 36.8	125 \pm 96.0	—	—
Shark Rock							
Depth ($n = 3$)	1.6 \pm 0.1	1.7 \pm 0	2.0 \pm 0	2.5 \pm 0.1	2.8 \pm 0.1	3.3 \pm 0.3	3.2 \pm 0.1
Sediment grain size ($n = 3$)	1.58 \pm 0.06	1.68 \pm 0.21	1.96 \pm 0.18	2.00 \pm 0.13	2.20 \pm 0.35	2.57 \pm 0.01	2.53 \pm 0.10
Organics ($n = 3$)	2.44 \pm 0.03	2.33 \pm 0.22	2.34 \pm 0.12	2.70 \pm 0.11	3.21 \pm 0.22	3.57 \pm 0.46	2.85 \pm 0.47
July							
<i>Thalassia</i> shoots ($n = 6$)	0.0 \pm 0.0	72.0 \pm 12.8	256 \pm 44.8	528 \pm 46.4	669 \pm 56.0	741 \pm 88.0	728 \pm 123
<i>Thalassia</i> biomass ($n = 6$)	0.0 \pm 0.0	5.28 \pm 1.4	20.3 \pm 4.6	54.4 \pm 8.0	62.4 \pm 14.4	83.2 \pm 1.6	97.6 \pm 20.8
Detritus ($n = 6$)	0.0 \pm 0.0	0.48 \pm 0.64	3.2 \pm 2.7	13.8 \pm 13.1	64.0 \pm 22.4	96.0 \pm 40.0	176 \pm 41.6
February							
<i>Thalassia</i> shoots ($n = 6$)	0.0 \pm 0.0	68.8 \pm 19.2	292 \pm 81.6	452 \pm 54.4	608 \pm 101	816 \pm 217	764 \pm 128
<i>Thalassia</i> biomass ($n = 6$)	0.0 \pm 0.0	6.9 \pm 4.8	36.8 \pm 17.6	68.8 \pm 33.6	78.4 \pm 14.4	80.0 \pm 9.6	115 \pm 36.8
Detritus ($n = 6$)	0.0 \pm 0.0	8.0 \pm 1.1	1.3 \pm 1.9	14.7 \pm 15.4	157 \pm 35.2	84.8 \pm 4.8	309 \pm 174

Site description

This study was conducted in the Exuma Cays, Bahamas, at two sites characterized by turtlegrass *Thalassia testudinum* König and known juvenile queen conch populations (Wicklund et al. 1988). The first site (CBC) was located 1.5 km west of Children's Bay Cay (23° 44.3'N, 76° 04.5'W). The second site (SR) was located just southwest of Shark Rock (23° 45.0'N, 76° 07.5'W), a rock outcrop off the southern end of Norman's Pond Cay. There is a gradient in depth at both sites from a shallow sand bar (<1.0 m) to a depth of approximately 3.5 m, accompanied by a gradient in seagrass and detritus biomass (Table 1). Tidal range in the area is approximately 1 m and both sites are subject to strong reversing tidal currents, sometimes exceeding 50 cm/second.

Conch density was highest ($\sim 2.0/m^2$), near the population centers, decreasing in density towards their peripheries. At each site three transects were made, each separated by approximately 50 m. Divers were towed by a small boat around each site to place buoys on the edges of each population. Transects were then

positioned through the population centers, parallel to the depth gradient. Transect lengths were an average of 61 m at CBC and 142 m at SR. Stations marked by stakes were placed along each transect (5 for CBC and 7 for SR) from bare sand to the highest density seagrass. *Thalassia* shoot density was used to set all stations of equivalent number in similar habitats for both sites. Station 1 of each transect was placed on bare sand, with no seagrass or detritus. Stations 2, 3, 4, and 5 were placed in the following approximate shoot densities, respectively: 70, 300, 550, and 700 shoots/ m^2 . Stations 6 and 7 at SR were characterized primarily by increasing accumulated detritus and higher seagrass biomass and not increasing shoot density.

Methods and materials

Field measurements

Counts were made in July 1988 and February 1989 to test for seasonal differences in conch distribution. In February at CBC we found that the center of the population had moved north of its July location, and

so transect 1 (the southernmost transect) was moved between transects 2 and 3 for the February sampling. Measurements, including station depth, conch density and shell lengths, macrophyte shoot density and biomass, and amount of macroscopic detritus, were taken at each station along the transects within a circle of 2.5 m radius around each stake. Sediment grain-size and organic content were measured in July 1988.

Depths were measured at low water using an electronic depth sounder on a 17-foot Boston Whaler, adjusting for the depth of the transducer below the surface. Using scuba, conch were gathered within each 2.5-m circle at each station, counted, and measured for shell length using large calipers.

A separate collection of 80 conch ranging from 17 to 196 mm in siphonal length was made to generate a length-weight curve. After freezing, the conch were extracted from their shells, washed to remove feces, blotted to remove excess water, and weighed. The following equation describes the significant correlation ($r^2 = 0.987$, $F = 5233.4$, $p < 0.001$) between shell length and wet weight:

$$\log_{10}(\text{wet weight}) = 3.403 \times \log_{10}(\text{length}) - 5.569$$

The equation was used to convert length-frequency data to biomass values.

Two replicate samples of macrophytes and macroscopic detritus (mostly senescent seagrass blades and debris) were collected at each station by haphazardly placing a quadrat with 25-cm sides within each circle. The number of shoots within the quadrat were counted and then collected along with the macrophyte detritus into nylon bags (3.0-mm mesh). *Thalassia* blades (using only aboveground parts), and macrodetritus were separated in the laboratory and dried at 80°C for approximately 24 hours to constant weight. Dry-weight biomass was determined for the individual components.

A core of 40 mm diameter, with a penetration depth of 5 cm, was taken for determination of sediment grain-size distribution and organic content. A subsample of approximately 100 g wet weight was dried at 80°C to constant mass and incinerated at 550°C for 4 hours to determine sediment organic content. Organic content was quantified as the percent difference between dry weight and ash-free dry weight. Another sediment subsample of approximately 50 g was used to determine sediment grain-size. After washing to remove salts and to extract the silt-clay fraction, sand-sized particles were analyzed using standard Ro-Tap procedures. Silt-

clay fractions were analyzed using standard pipet procedures (Folk 1966). Product moment statistics were generated for mean grain size and sortedness (McBride 1971).

Habitat preference experiments

Experimental manipulations of plots of seagrasses were made at the Shark Rock site to test for habitat preference in conch of various size classes. Cages 3.6 m diameter (10.2 m²) were constructed of black plastic mesh with 20-mm openings. The cages were 25 cm high and supported by 1-m long pieces of reinforcement bar driven into the sediment. The bottom edge of the screen was pushed into the sediment approximately 3 cm to prevent escape of conch. No losses occurred during the experiments.

Four cages were built in locations similar to station 5 (see above), characterized by *Thalassia* shoot densities of 700 shoots/m² (Moderate Density). Two cages were built near stations 3 with approximately 300 shoots/m² (Low Density), and two cages were built in high biomass habitats similar to station 7 with approximately 750 shoots/m² plus a heavy layer of detritus (High Density). Macrophytes in two of the moderate-density cages were manipulated so that one-half of each was reduced to 300 shoots/m² (Low Density) (Table 2). This was accomplished by placing a rope across the cage through the center and parallel to the direction of flood tide current. (Manipulations were oriented with the current because juvenile conch at the study site are known to move either up or down current during migration.) Then shoots were systematically pulled from one-half of the cage to achieve the desired shoot density. The two cages for this Moderate/Low treatment were manipulated to provide mirror images of one another. The other two moderate-density plots were manipulated in a similar fashion to provide Moderate/Sand treatments, where all seagrass shoots were removed from one side of each cage. Replicate Low/Sand treatments were constructed by manipulating the two low-density plots. High/Moderate treatments were set up by manipulating the high-density plots. About 80% of the loose detritus (comprised mostly of senescent seagrass blades) was removed from half of the high-density plots. Final shoot densities in the high- and moderate-density areas were similar (656 and 672 shoots/m², respectively), and removal of detritus yielded a macrophyte environment similar to the moderate-density areas (Table 2). The manipulations required maintenance such as removing new growth and accumulated detritus. Except for the removal of detritus which accumulated along the edges of the cages, maintenance of the plots was performed between the short habitat preference runs.

Table 2

Summary of biological conditions presented in experiments of habitat preference in queen conch. There were no significant differences between plots in any of the four treatment levels (ANOVA, $p > 0.05$).

Treatment	<i>n</i>	Seagrass shoots (<i>n</i> /m ²)	Seagrass biomass (g dry wt/m ²)	Detritus (g dry wt/m ²)
Sand	8	0 ± 0	0 ± 0	0 ± 0
Low Density	8	272 ± 32	27 ± 13	3.0 ± 3.5
Moderate Density	12	672 ± 80	72 ± 20	58 ± 37
High Density	4	656 ± 64	98 ± 11	269 ± 66

Between 27 September and 28 October 1988 three conch size-classes were tested for their preferences for habitat type. The classes included animals between 75 and 100 mm shell length (~1 year old), conch between 125 and 150 mm (2 and 3 years old), and adults with the fully developed flare of the shell lip (~4 years or more). All were collected from the seagrass beds around the experimental enclosures. To provide a conch density similar to that in nature, 10 juveniles of a size-class were added to each enclosure (1.0 conch/m²) after removal of all large invertebrates such as urchins, hermit crabs, and conch. For runs with the adults, 8 animals were placed in an enclosure.

Preliminary experiments showed that the distribution of conch in both Moderate/Low and Moderate/Sand treatments did not change significantly between 1 and 5 days; therefore, all runs were terminated at 3 days. At the end of a run, the numbers of conch found on each side of the cage were recorded, and the animals were removed. Because the animals touching the screen may have been moving around the periphery of the enclosure, they were not included in the counts. Three or four runs were made for each size-class and treatment, except those in the High/Moderate enclosures where two runs were made in each cage. No significant differences were found in the distribution of animals in a size-class in any of the pairs of cages providing similar combinations of macrophytes (Fisher's Exact Test, $p > 0.05$); therefore, the paired cages were considered to be replicates.

Results

Station characteristics

Average depths for the five stations at CBC increased from station 1 (1.0 m) to station 5 (3.4 m). Average station depths for SR increased from station 1 (1.6 m) to station 6 (3.3 m) and then decreased slightly at station 7 (3.2 m). *Thalassia* shoot density, biomass, and detritus biomass all increased with increasing station

number and depth, with a few exceptions (see Table 1). At CBC shoot density ranged from 0.0 to 864 shoots/m², *Thalassia* biomass from 0.0 to 80 g dry wt/m², and detritus biomass from 0.0 to 125 g dry wt/m². At SR shoot density ranged from 0.0 to 765 shoots/m², *Thalassia* biomass from 0.0 to 115 g dry wt/m², and detritus biomass from 0.0 to 309 g dry wt/m².

Sediment grain-size at the CBC transects was relatively constant (1.38–1.83 Φ) between stations 1 and 4, but finer at station 5 (2.44 Φ). Sediment organic content increased slightly over the transects from low-biomass to high-biomass stations. At the SR transects mean grain diameter decreased (increasing Φ) from stations 1–6, while stations 6 and 7 had nearly equal grain size (2.57 and 2.53 Φ). Organic content was highest at SR station 6, but values ranged only from 2.33 to 3.50% of dry sediment weight.

Children's Bay Cay and the Shark Rock site showed highly significant correlations among all of the variables: water depth, seagrass shoot density, above-ground seagrass biomass, and standing crop of macrodetritus (Table 3). Weakest correlations ($r = 0.586$ to 0.631) occurred between detritus and the other variables at Shark Rock in February, when abundance of detritus was low. Correlations between macrophyte and depth characteristics remained highly significant when all sites, stations, and dates were included in regression models (Table 3) suggesting that the relationships are relatively universal in the study area. The highest correlation occurred between seagrass shoot density and water depth ($r = 0.930$), and weakest correlations were found between detritus biomass and the other variables.

Conch density patterns

At CBC there was an increase in conch density in both July and February along the transects from station 1–5, except for a small decrease in February from station 4 to station 5 (Fig. 1). Densities in July were similar

Table 3

Pearson correlation matrices showing the relationships among depth and macrophyte variables at the seagrass meadow study sites. The upper and lower sections of the first two matrices are for July and February collections, respectively. The bottom matrix is for all stations and dates combined. Shoots = density of *T. testudinum* shoots; *Thalassia* = biomass of *T. testudinum*; Detritus = biomass of macrodetritus.

	Depth	Shoots	<i>Thalassia</i>	Detritus
Children's Bay Cay				
Depth	—	0.966**	0.938**	0.911**
Shoots	0.968**	—	0.961**	0.817**
<i>Thalassia</i>	0.873**	0.880**	—	0.839**
Detritus	0.728**	0.752**	0.826**	—
Shark Rock				
Depth	—	0.969**	0.964**	0.839**
Shoots	0.950**	—	0.954**	0.769**
<i>Thalassia</i>	0.877**	0.891**	—	0.889**
Detritus	0.631*	0.586*	0.623*	—
Combined sites and dates				
Depth	—	—	—	—
Shoots	0.930**	—	—	—
<i>Thalassia</i>	0.871**	0.887**	—	—
Detritus	0.648**	0.628**	0.726**	—

* $p < 0.05$; ** $p < 0.01$.

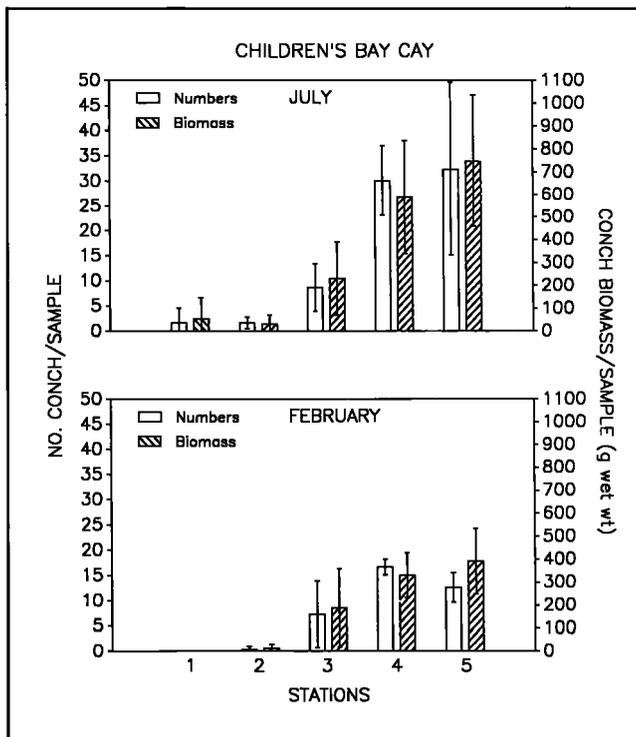


Figure 1

Number of conch and conch biomass sampled within a 2.5-m radius circle at Children's Bay Cay, July 1988 and February 1989, at each station. Values are means \pm SD.

to those in February at stations 1, 2, and 3. Stations 4 and 5 had densities almost twice as high in July as those in February. At SR, the general pattern was an increase in conch density from station 1-5 (except a small decrease in July at station 4) (Fig. 2). In July, the density then decreased sharply at stations 6 and 7. In February, the density increased further at station 6 and then decreased at station 7. More pronounced than at CBC, the densities at SR in February at stations 3, 4, and 5 were lower than the July densities.

After log transformation of the data to improve heterogeneity in the variance, a multi-way ANOVA was used to test for differences and interactions in conch density between sites, dates, transects, and stations (Table 4). Transects were examined as blocks, and hence there were no interaction terms with transect. Since SR had 7 stations as opposed to 5 at CBC, stations 6 and 7 at SR were not used in this analysis where CBC and SR were compared.

There were no significant interaction terms or block (transect) effects in the ANOVA ($p > 0.05$); therefore, the effects of date, site, and station may be interpreted directly. It is clear from Figures 1 and 2 that conch densities were higher in July than in February at both CBC and SR at most stations. Significant site effects appear to be related to the low numbers of conch at SR, particularly in February and at station 1-3. Station effects occurred because of the increase in conch

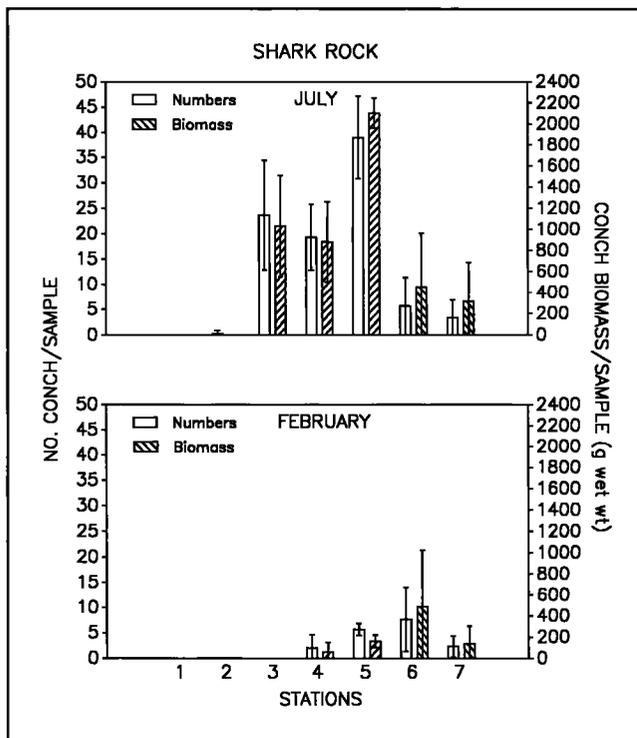


Figure 2

Number of conch and conch biomass sampled within a 2.5-m radius circle at Shark Rock, July 1988 and February 1989, at each station. Values are means \pm SD.

density between stations 1 and 5 at all sites and dates, except SR station 4.

A one-way ANOVA and a Newman-Keuls multiple range test were used to test for differences in log transformations of conch density among stations 1-5 combining all sites and dates (CBC-July, SR-July, CBC-February, SR-February). There was a significant difference between stations ($F = 22.02$, $p < 0.0001$). Conch densities increased with increasing station number, ranging from $0.42 (\pm 1.38)$ to $22.4 (\pm 15.8)$. Newman-Keuls tests showed that the logs of conch density at stations 1 and 2 were significantly different from all other stations, though not from one another, as were stations 4 and 5. Station 3 was significantly different from all other stations (Newman-Keuls, $p < 0.05$).

Conch biomass patterns

As with conch density, there was an increase in conch biomass at CBC, from stations 1 to 5. The pattern was strong for both July and February, although the actual biomass values were higher in July at stations 4 and 5 than in February. At SR the biomass also increased from stations 1 to 5 (with a slight decrease at station

Table 4

Results of multi-way analysis of variance for conch density in seagrass meadows. Data were log-transformed and transects were examined as blocks.

Source	df	MS	F	p
Date	1	2.503	22.755	<0.0001
Site	1	0.753	6.846	0.011
Transect	2	0.032	0.289	0.750
Station	6	2.400	21.820	<0.0001
Date * Site	1	1.047	3.058	0.086
Date * Station	6	0.539	1.574	0.171
Site * Station	6	0.160	0.468	0.829
Date * Site * Station	6	0.228	0.642	0.696
Error	56	0.355		

Table 5

Results of multi-way analysis of variance for conch biomass in seagrass meadows. Data were log-transformed and transects were examined as blocks.

Source	df	MS	F	p
Date	1	9.349	15.564	<0.0001
Site	1	3.025	5.036	0.028
Transect	2	0.155	0.258	0.773
Station	6	11.511	19.162	<0.0001
Date * Site	1	3.838	2.372	0.129
Date * Station	6	1.868	1.154	0.343
Site * Station	6	1.614	0.997	0.436
Date * Site * Station	6	1.032	0.610	0.722
Error	56	1.692		

4 in July). In July, biomass decreased sharply at station 6 and 7, while in February the biomass continued to increase at station 6 and decreased at station 7. In July stations 3, 4, and 5 had much higher biomass values than in February.

After log transformations of the biomass data, a multi-way ANOVA was used again to test for differences or interactions between dates, sites, transects, and stations in conch biomass with transects examined as blocks (Table 5). Where CBC and SR were compared, stations 6 and 7 at SR were not used.

There were no significant interaction terms and no block effects on the ANOVA ($p > 0.05$), therefore the effects of date, site, and station are interpreted directly. As mentioned above, conch biomass at both CBC and SR was higher in July than in February at most stations. Site differences appear to be due to low biomass values in February at SR, especially at stations 1-3. Station differences clearly resulted from the increase of conch biomass with the increase in station number, at all sites and dates, except SR station 4.

Table 6

Pearson correlation coefficients for relationships between measures of conch abundance and characteristics of seagrass habitat for different months and sites. CBC = Children's Bay Cay site; SR = Shark Rock site. At the Shark Rock site, analyses were made with 5 and 7 stations because of decreasing numbers of conch at stations 6 and 7 (see text).

	CBC		SR		SR	
	July	Feb.	(5 stations) July	Feb.	(7 stations) July	Feb.
Conch density						
Depth	0.868**	0.868**	0.813**	0.837**	0.168	0.650**
Shoots	0.860**	0.851**	0.831**	0.787**	0.314	0.726**
<i>Thalassia</i>	0.910**	0.753**	0.779**	0.803**	0.141	0.495*
Detritus	0.608*	0.753**	0.701**	0.853**	0.141	0.495*
Conch biomass						
Depth	0.774**	0.892**	0.850**	0.801**	0.216	0.530*
Shoots	0.874**	0.831**	0.863**	0.741**	0.423	0.634**
<i>Thalassia</i>	0.886**	0.781**	0.836**	0.799**	0.270	0.353
Detritus	0.680**	0.597*	0.827**	0.780**	0.004	0.244
Combined sites and dates (5 stations)						
	Conch density		Conch biomass			
Depth	0.603**		0.492**			
Shoots	0.636**		0.513**			
<i>Thalassia</i>	0.513**		0.433**			
Detritus	0.330*		0.266*			

* $p < 0.05$; ** $p < 0.01$.

A one-way ANOVA and a Newman-Keuls multiple range test were used to test for differences in log transformations of conch biomass among stations for all date-site samples. There was a significant difference in the log of conch biomass across stations. Conch biomass increased from 13.4 g wet weight (± 44.5) at station 1 to 851 g wet weight (± 766) at station 5. The log of conch biomass at stations 1 and 2 were not different from one another but were each significantly different from stations 3, 4, and 5. Stations 3 and 5 were each significantly different from all stations but station 4 (Newman-Keuls, $p < 0.05$).

Relationships between conch and the independent variables

There were highly significant correlations between both density and biomass of conch in the field and the depth and macrophyte characteristics of the habitat (Table 6). Tested by individual date at Children's Bay Cay, correlations between conch density and depth, shoot density, and seagrass biomass were high and relatively similar (r values between 0.753 and 0.910), while correlations with detritus were significant but lower. Similar patterns held for conch biomass. At

Shark Rock in July, conch numbers and biomass were highest at station 5 (Fig. 2) and did not increase over the entire range of seagrass shoot density or biomass. Therefore, linear regressions of conch density and biomass with depth and macrophyte characteristics did not yield high or significant correlations in most cases when data from all seven stations were included (Table 6). Highly significant correlations were found using the first five stations; all of the habitat characteristics yielded correlation coefficients between 0.701 and 0.863 (Table 6).

In regression models including data from all dates, sites, and stations 1–5, all of the environmental variables yielded significant correlations with conch density and biomass (Table 6). Highest correlations occurred between seagrass shoot density and both conch density and conch biomass. Lowest correlation coefficients occurred with detritus.

Two stepwise multiple regressions were run to determine the best multiple regression models for conch density and conch biomass using all of the data for stations 1–5 (all dates and sites combined). Alpha to enter and remove from the models was set at 0.150. The regression model for conch density included first shoot density followed by detritus standing crop, and yielded a

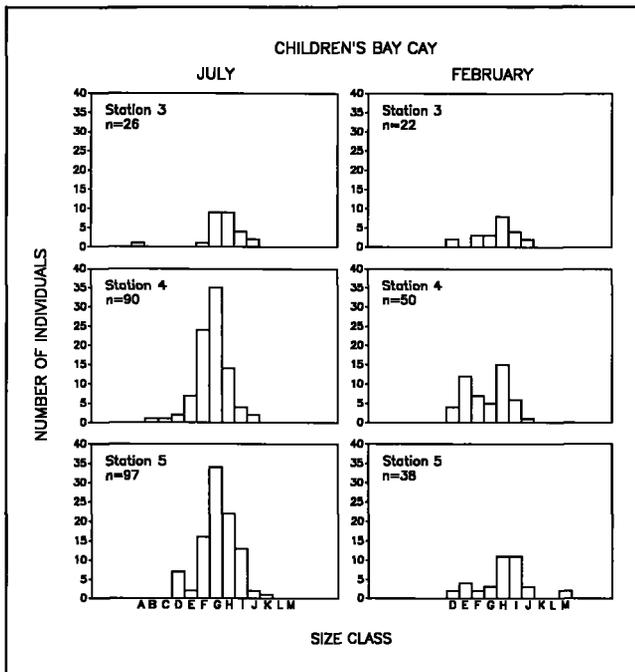


Figure 3

Number of individuals per sample (2.5-m radius circle) within each conch size-class for each station at Children's Bay Cay, July 1988 and February 1989. Size-classes are as follows: A = 40–49 mm, B = 50–59 mm, C = 60–69 mm, D = 70–79 mm, E = 80–89 mm, F = 90–99 mm, G = 100–109 mm, H = 110–119 mm, I = 120–129 mm, J = 130–139 mm, K = 140–149 mm, L = 150–159 mm, M = 160–169 mm, N = 170–179 mm, O = 180–189 mm, P = 190–199 mm, and Q = 200–209 mm.

multiple correlation coefficient of 0.664 ($p < 0.001$). The stepwise multiple regression model for conch biomass included only shoot density and provided a multiple regression coefficient of 0.513 ($p < 0.001$). No other variables contributed significantly to the correlation.

Results of the regressions and the Newman-Keuls tests for conch density across stations indicate that stations 3–5 provide a suitable habitat for conch larger than 70 mm SL with habitat characteristics ranging as follows: 256–864 mean shoots/m², 13.9–80.6 mean g dry wt of *Thalassia*/m², and 0.64–157.12 mean g dry wt of detritus/m². In addition, the correlation between conch and macrophyte characteristics are linear only up to station 5 (608–864 mean shoots/m², 62.4–80.6 mean g dry wt of *Thalassia*/m², 64.0–157.1 mean g dry wt of detritus/m²) which appears to be the near-optimal habitat for juvenile conch larger than 70 mm.

Conch length-frequency patterns

The Kolmogorov-Smirnov two-sample test was used to test for significant differences in the length-frequency distribution of conch at different stations. Only stations

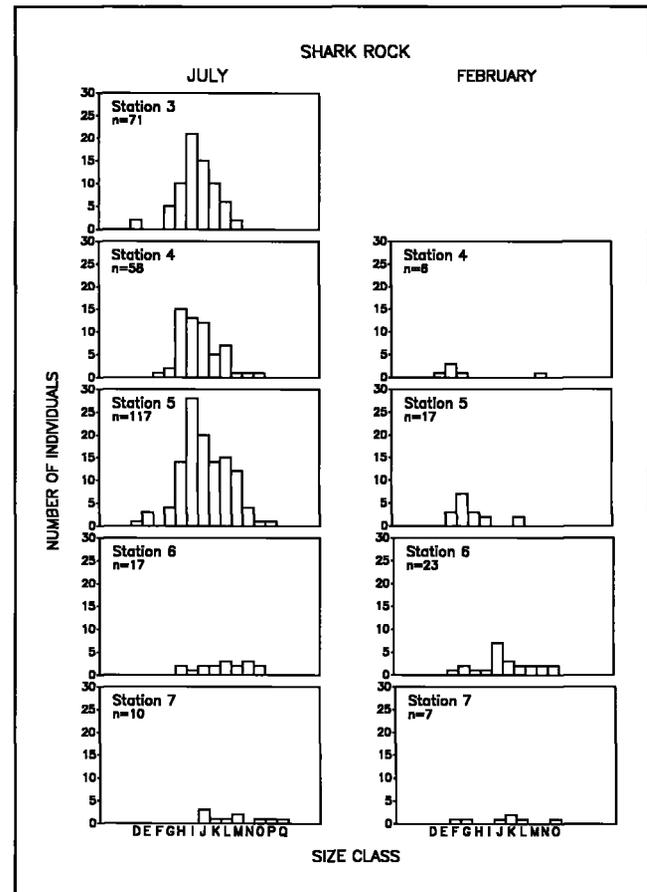


Figure 4

Number of individuals per sample (2.5-m radius circle) within each conch size-class for each station at Shark Rock, July 1988 and February 1989. For size-classes see Figure 3.

with at least 10 conch were used in the analysis (CBC stations 3–5 in both July and February; SR stations 3–7 in July and stations 5–6 in February).

In July, CBC stations 3, 4, and 5 all had significantly different conch length-frequencies (stations 3 and 4, $p < 0.0001$, stations 3 and 5, $p = 0.015$, stations 4 and 5, $p < 0.0001$). Mean lengths varied only from 102 to 111 mm, and the statistical differences were a result of subtle differences in the shape of the distributions (Fig. 3). In February at CBC, the length-frequency distribution of conch at station 3 was different significantly from that at station 4 ($p = 0.004$), and the distribution at station 4 was different significantly from that at station 5 ($p < 0.0001$). The length-frequencies at stations 3 and 5 were not different ($p = 0.062$); the mean values and shapes of the distribution were similar (Fig. 3).

In July, conch length-frequency patterns at SR stations 3, 4, and 5 were not different (stations 3 and 4, $p = 0.220$; stations 4 and 5, $p = 0.260$), and had means

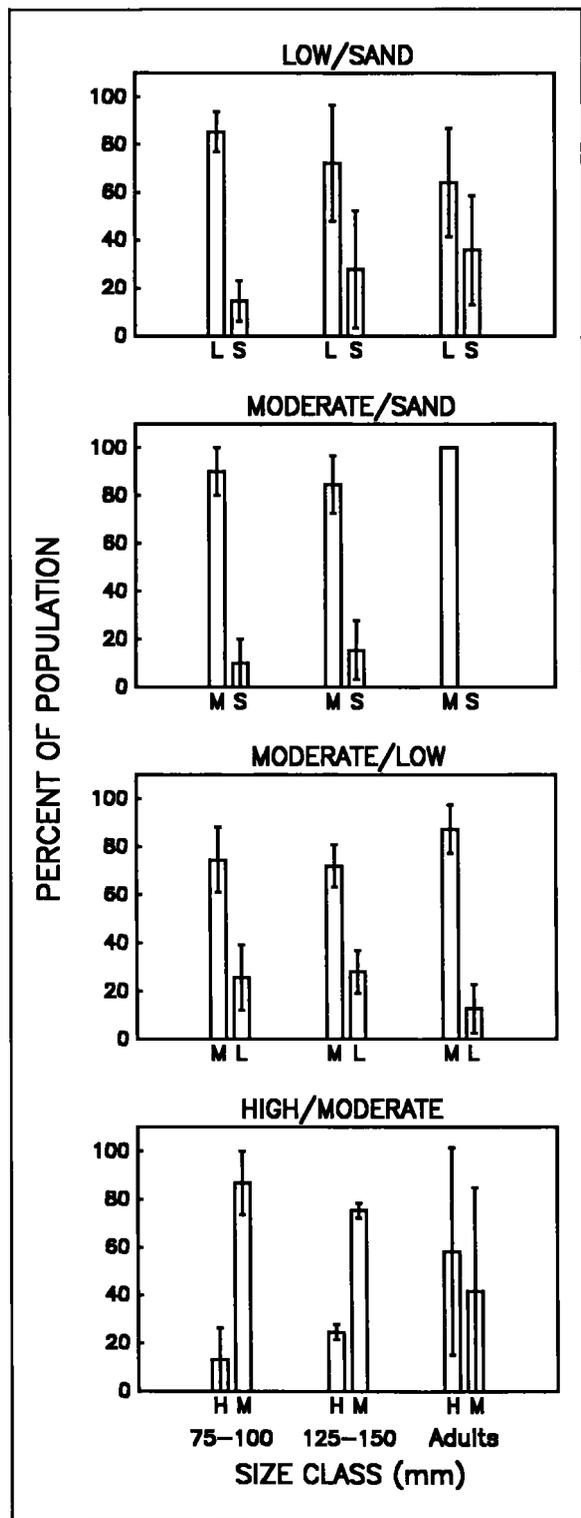


Figure 5

Percentage of conch in three size-classes found within a habitat type from a choice of two types. Choices included combinations of bare sand, low and high seagrass biomass.

Table 7

Results of G-tests on habitat choice by three size-classes of conch presented with paired habitats.

Size-class (mm)	No. of runs	Total no. of conch in the habitats	G_{adj}	p
Low/Sand treatments				
75-100	6	37/6	24.86	<0.01
125-150	6	28/9	10.24	<0.01
Adults	6	6/5	0.09	>0.05
Moderate/Sand treatments				
75-100	6	53/7	42.99	<0.01
125-150	8	61/10	36.41	<0.01
Adults	6	33/0		<0.01
Moderate/Low treatments				
75-100	6	44/17	12.27	<0.01
125-150	6	38/22	9.72	<0.01
Adults	6	31/5	20.89	<0.01
High/Moderate treatments				
75-100	4	2/23	20.72	<0.01
125-150	4	8/25	9.19	<0.01
Adults	4	4/3	0.14	>0.05

between 129 and 136 mm. Distributions at stations 6 and 7 were not different ($p = 0.749$) (Fig. 4). This pattern of size-frequency distribution showed that, in July, conch were significantly larger at the stations with higher macrophyte biomass (stations 6 and 7), while smaller conch were found at sites with moderate-to-low seagrass biomass (stations 3, 4, and 5). In February, the two SR stations with more than 10 conch—stations 5 and 6—had significantly different length-frequencies ($p < 0.0001$) (Fig. 4). Again, the large conch were associated with high seagrass biomass.

Habitat preference experiments

Results of the habitat preference experiments showed that conch were proficient in detecting and choosing habitats with different macrophyte characteristics (Fig. 5). Of the conch in all size classes, 90% were associated with the moderate density plots as opposed to sand habitat (10%). Habitat selectivity was less strong in the other habitat pairs, but it is clear that plots with seagrass present were selected over bare-sand habitats, and moderate-density seagrass was selected over either high- or low-density seagrass.

Heterogeneity G tests showed that the results of runs within all of the individual habitat preference tests were homogeneous ($p < 0.05$) except one (Low vs. Sand; 125-150 mm; $G_H = 14.37$, $p > 0.05$). Standard G tests were used with the pooled data to test the null hypothesis that animals were distributed equally over

the two sides of the enclosures. All treatments and size-classes resulted in highly significant differences ($p < 0.01$), except for two cases (Table 7). Adults in the Low/Sand treatment and adults in the High/Moderate treatment showed no significant habitat preference ($p > 0.05$). In these two experiments adult conch were highly motile, and more than 50% of the individuals were found traveling around the walls of the enclosures. Because only animals not touching the walls were included in the analysis, the numbers for analysis were small and highly variable (Table 7, Fig. 5). Where a high-preference habitat (Moderate Density) was paired with a low-preference habitat (Low Density or Sand), adult conch were not found against the walls of the enclosures in such high numbers (28%) and habitat selection was highly significant (Table 7).

Discussion

Many marine organisms are known to prefer seagrass beds over bare sand. For example, amphipods, tanaidaceans, decapods, and fishes have all been found to be more abundant in seagrass beds than on bare sand (Heck and Thoman 1981, Holt et al. 1983, Stoner 1983, Heck et al. 1989). Also, abundance of animals within seagrass beds appears to be influenced strongly by the local amount of macrophyte structure. Numbers of both decapod and peracarid crustaceans have been correlated with seagrass biomass (Heck and Orth 1980, Stoner 1980a, Lewis 1984). A direct linear relationship between seagrass biomass and harpacticoid abundance and diversity was attributed to an increase in habitable space, nutritional resources, and reduced levels of predation (Hicks 1980). Communities of epibenthic fish on the banks of Florida Bay were associated with areas of high seagrass biomass and with accumulations of seagrass detritus (Sogard et al. 1987). Detritus was thought to provide a rich food source as well as a refuge from predators.

The general association of queen conch with turtlegrass *Thalassia testudinum* is well known (Randall 1964, Hesse 1979, Weil and Laughlin 1984), but quantitative relationships between the mollusc and seagrass beds are reported for the first time in this study. The distributional patterns of queen conch near Lee Stocking Island were similar to patterns found for other taxa, with few individuals associated with bare sand and low-density seagrass. As was true for other species, juvenile conch densities increased with macrophyte biomass and shoot density over a wide range; however, optimal levels of macrophyte cover were found, beyond which only larger individuals were associated. The observed association of juvenile queen conch with moderate amounts of macrophyte cover

(shoot density, biomass, etc.) probably results from a combination of mechanisms: (1) a simple inability of the animals to maneuver into or through heavy stands of seagrass and detritus, (2) active habitat choice for specific seagrass cover, and (3) differential survivorship associated with different macrophyte densities, especially in the smaller size-classes.

The upper limit of seagrass density with which juvenile queen conch are associated is probably set by their locomotory abilities. Randall (1964) speculated that thick stands of seagrass obstruct the movements of small conch. High shoot density is also responsible for heavy accumulations of detritus and soft sediments which may impede locomotion. Given that queen conch propel their heavy shells with thrusts of a pointed operculum on the end of a muscular foot, locomotion is most efficient on a firm substratum.

The direct relationship between conch density and seagrass density below the optimal level is most likely linked to more complex interactions. It is known that abundance of food can be limiting for juvenile conch in the field at natural density (Stoner 1989). The primary sources of food for juvenile conch in nursery habitats are macrodetritus and algal epiphytes (Stoner and Waite, In review); both of these food items increase with seagrass density. Blade and detritus productivity increase with shoot density, and seagrasses have the effect of increasing the entrapment of fine sediments and detritus (den Hartog 1967, Orth 1977, this study), useful only up to the point of impeded locomotion. Algae consumed by conch in the seagrass nursery areas are primarily those growing as epiphytes on *Thalassia* blades. Production of these epiphytes can be as high as 50% of the seagrass production (den Hartog 1979), and increases with seagrass shoot density. The increase in density of conch with seagrass shoot density, therefore, may be a function of habitat choice by individuals for areas with greater abundance of foods and/or a function of food limitation in the population.

The relationship between conch density and seagrass shoot density can also be a response to predation. This response could be direct, whereby the survivorship of conch increases with increasing seagrass structure, or indirect, where habitat preference for high-structure habitats has evolved as a response to predators. In either case, the role of seagrass biomass in protecting prey species is known for a wide variety of predator-prey combinations (Coen et al. 1981, Stoner 1982, Leber 1985, Heck and Wilson 1987), and experiments with crustaceans have shown that prey species are proficient in choosing high-density seagrass (Stoner 1980b, Coen et al. 1981, Bell and Westoby 1986). The fact that small conch were more proficient in selecting habitats of particular seagrass biomass or shoot density than

large individuals suggests that there is strong selective pressure for habitat choice in small conch, probably via size-specific mortality. Susceptibility of juveniles to predation is known to decrease with increasing conch size (Appeldoorn 1984).

Whether the observed distributional patterns are ultimately a response to foods and/or predators cannot be determined from data presented here; however, new experiments using artificial structures and predator manipulations would be useful. In any case, strong habitat preferences suggest that evolved behavioral mechanisms are influential, and the evolution of habitat choice in conch is probably related to both procuring sufficient foods and avoiding predators.

Significant effects of date in the density and biomass of conch in the seagrass beds was related to the normal seasonality of reproduction and recruitment in conch of the Exuma Cays. The 1+ year-class (~40–100 mm), spawned during the previous summer (1987), was most abundant in July. In the Exuma Cays, spawning occurs between April and October (Stoner et al. In review), with greatest recruitment to the benthos probably occurring between August and October. Juvenile conch spend most of their first year buried in the sediment; therefore, only the 1987 and older cohorts were surveyed in July 1988 and February 1989. In February, the 1988 cohort had not yet emerged from the sediment and, therefore, the 1+ year-class was not found in that survey.

Information on the settlement and distribution of juvenile conch in their first year of life will be particularly useful in elucidating mechanisms of distribution and abundance. Conch less than 40 mm have been found in very shallow, unvegetated subtidal sediments, moving to deeper waters or seagrass beds with age (Weil and Laughlin 1984; Stoner and Sandt, unpubl. data). Highest abundance of 1-year-old conch in sparse seagrass close to sand shoals, therefore, could be a result of ontogenetic migration.

The relationship between juvenile conch and easily measured characteristics of the macrophyte community should prove useful in predicting conch distributions and in planning stock-enhancement programs involving the seeding of hatchery-reared conch. The lack of statistical interaction among the factors site, station, and date suggests that the strong relationships between conch and seagrass shoot density (and other macrophyte characteristics) are relatively universal. It must be pointed out, however, that the surveys were conducted within areas known to be long-term conch nursery sites, and there are extensive areas of seagrasses on the Exuma Bank near Lee Stocking Island which appear to have similar habitat characteristics but no resident conch populations. Recent transplant experiments have shown that many of the habitats with

appropriate seagrass, sediment, and detritus characteristics do not provide good growth or survivorship in juvenile conch (Stoner and Sandt, In press). Clearly, there are unmeasured variables in the seagrass meadows which are important aspects of habitat quality for conch. Habitats without natural conch populations, which produced good growth and survival rates, may be recruitment limited. Such limitation may be a function of larval supply or ontogenetic movements in the species. This study demonstrates that there is a strong relationship between conch density and biomass and the amount of seagrass structure in the habitat; however, general seagrass characteristics cannot be used as predictors of conch distribution independent of other variables such as food quality, presence of predators, hydrographic considerations, and recruitment processes.

Acknowledgments

This research was supported by a grant from the National Undersea Research Program, NOAA, U.S. Department of Commerce. We thank P. Bergman, L. Cox, B. Olla, K. McCarthy, V. Sandt, C. Tanner, R. Wicklund, and E. Wishinski for assistance in the field and for discussion of the field data. R. Appeldoorn, L. Marshall, L. Riggs, C. Ryer, V. Sandt, and R. Wicklund provided thoughtful criticism of the manuscript.

Citations

- Adams, J.E.**
1970 Conch fishing industry of Union Island, Grenadines, West Indies. *J. Trop. Sci.* 12:279–288.
- Appeldoorn, R.S.**
1984 The effect of size on mortality of small, juvenile conchs (*Strombus gigas* Linne and *S. costatus* Gmelin). *J. Shellfish Res.* 4:37–43.
- Bell, J.D., and M. Westoby**
1986 Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. *Oecologia (Berl.)* 68: 205–209.
- Berg, C.J. Jr.**
1976 Growth of the queen conch, *Strombus gigas*, with a discussion of the practicality of its mariculture. *Mar. Biol. (Berl.)* 34:191–199.
- Bertram, G.C.L., and C.K.R. Bertram**
1968 Bionomics of dugongs and manatees. *Nature (Lond.)* 218:423–426.
- Brownell, W.N., and J.M. Stevely**
1981 The biology, fisheries, and management of the queen conch, *Strombus gigas*. *Mar. Fish. Rev.* 43(7):1–12.
- Brownell, W.N., C.J. Berg Jr., and K.C. Haines**
1977 Fisheries and aquaculture of the conch *Strombus gigas* in the Caribbean. *FAO Fish. Rep.* 206:59–69.

- Coen, L.D., K.L. Heck Jr., and L.G. Abele**
1981 Experiments on competition and predation among shrimps of seagrass meadows. *Ecology* 62:1484-1493.
- Coulston, M.L., R.W. Brey, A.C. Dempsey, and P. Odum**
1987 Assessment of the queen conch (*Strombus gigas*) population and predation studies of hatchery reared juveniles in Salt River Canyon, St. Croix, U.S. Virgin Islands. *Proc. Gulf Caribb. Fish. Inst.* 38:294-306.
- den Hartog, C.**
1967 The structural aspect in the ecology of seagrass communities. *Helgol. Wiss. Meeresunters.* 15:648-659.
1979 Seagrasses and seagrass ecosystems, an appraisal of the research approach. *Aquat. Bot.* 7:105-117.
- Folk, R.L.**
1966 A review of grain-size parameters. *Sedimentology* 6: 73-93.
- Fry, B.**
1984 $^{13}\text{C}/^{12}\text{C}$ ratios and the trophic importance of algae in Florida *Syringodium filiforme* seagrass meadows. *Mar. Biol. (Berl.)* 79:11-20.
- Heck, K.L. Jr., and R.J. Orth**
1980 Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. *In* Kennedy, V.S. (ed.), *Estuarine perspectives*, p. 449-464. Acad. Press, NY.
- Heck, K.L. Jr., and T.A. Thoman**
1981 Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* 53:125-134.
- Heck, K.L. Jr., and K.A. Wilson**
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.
- Heck, K.L. Jr., K.W. Able, M.P. Fahay, and C.T. Roman**
1989 Fishes and decapod crustaceans of Cape Cod eelgrass meadows: Species composition, seasonal abundance patterns and comparison with unvegetated substrates. *Estuaries* 12: 59-65.
- Hesse, K.O.**
1979 Movement and migration of the queen conch, *Strombus gigas*, in the Turks and Caicos Islands. *Bull. Mar. Sci.* 19: 303-311.
- Hicks, G.R.F.**
1980 Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. *J. Exp. Mar. Biol. Ecol.* 44:157-192.
- Holt, S.A., C.L. Kitting, and C.R. Arnold**
1983 Distribution of young red drums among different seagrass meadows. *Trans. Am. Fish. Soc.* 112:267-271.
- Howard, R.K.**
1984 The trophic ecology of caridean shrimps in an eelgrass community. *Aquat. Bot.* 18:155-174.
- Kikuchi, T.**
1980 Faunal relationships in temperate seagrass beds. *In* Phillips, R.C., and C.P. McRoy (eds.), *Handbook of seagrass biology: An ecosystem perspective*, p. 153-172. Garland Press, NY.
- Kitting, C.L., B. Fry, and M.D. Morgan**
1984 Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecologia (Berl.)* 62:145-149.
- Laughlin, R.A., and E. Weil M.**
1983. Queen conch mariculture and restoration in the Archipelago de Los Rogues: Preliminary results. *Proc. Gulf Caribb. Fish. Inst.* 35:64-72.
- Lawrence, J.M.**
1975 On the relationships between marine plants and sea urchins. *Oceanogr. Mar. Biol. Annu. Rev.* 13:213-286.
- Leber, K.M. III**
1983 Feeding ecology of decapod crustaceans and the influence of vegetation on foraging success in a subtropical seagrass meadow. Ph.D. thesis, Florida State Univ., Tallahassee, 166 p.
1985 The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology* 66: 1951-1964.
- Lewis, F.G. III**
1984 Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule*, and bare sand substrata. *Mar. Ecol. Prog. Ser.* 19:101-113.
- Marshall, L.S. Jr., and R.N. Lipcius**
In review Density-dependent mortality of juvenile queen conch and predator aggregation. *Mar. Ecol. Prog. Ser.*
- McBride, E.F.**
1971 Mathematical treatment of size distribution data. *In* Carver, R.E. (ed.), *Procedures in sedimentary petrology*, p. 109-127. Wiley, NY.
- 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.
1981 Experimental studies of decapod and fish predation on seagrass macrobenthos of the Indian River, Florida. *Mar. Ecol. Prog. Ser.* 5:141-149.
- Ogden, J.C.**
1980 Faunal relationships in Caribbean seagrass beds. *In* Phillips, R.C., and C.P. McRoy (eds.), *Handbook of seagrass biology: An ecosystem perspective*, p. 173-198. Garland Press, NY.
- Orth, R.J.**
1977 The importance of sediment stability in seagrass communities. *In* Coull, B.C. (ed.), *Ecology of marine botany*, p. 281-300. Univ. South Carolina Press, Columbia.
- Randall, J.E.**
1964 Contributions to the biology of the queen conch, *Strombus gigas*. *Bull. Mar. Sci. Gulf Caribb.* 14:246-295.
- Sogard, S.M., G.V.N. Powell, and J.G. Holmquist**
1987 Epibenthic fish communities on Florida Bay banks: Relations with physical parameters and seagrass cover. *Mar. Ecol. Prog. Ser.* 40:25-39.
- Stoner, A.W.**
1980a The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull. Mar. Sci.* 30:537-551.
1980b Perception and choice of substratum by epifaunal amphipods associated with seagrasses. *Mar. Ecol. Prog. Ser.* 3:105-111.
1982 The influence of benthic macrophytes on the foraging behavior of pinfish *Lagodon rhomboides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 58:271-284.
1983 Distributional ecology of amphipods and tanaidaceans associated with three seagrass species. *J. Crust. Biol.* 3: 505-518.
1989 Density dependent growth and the grazing effects of juvenile queen conch (*Strombus gigas* L.) in a tropical seagrass meadow. *J. Exp. Mar. Biol. Ecol.* 130:119-133.
- Stoner, A.W., and V.J. Sandt**
In press Transplanting as a test procedure before large-scale outplanting of juvenile queen conch. *Proc. Gulf Caribb. Fish. Inst.*

Stoner, A.W., and J.M. Waite

In review Trophic biology of queen conch in nursery habitats: diets and primary food sources in seagrass meadows. Mar. Ecol. Prog. Ser.

Stoner, A.W., I.F. Boidron-Metairon, and V.J. Sandt

In review Reproductive activity of queen conch, *Strombus gigas*, and the abundance of veligers. Bull. Mar. Sci.

Van Montfrans, J., R.L. Wetzel, and R.J. Orth

1984 Epiphyte-grazer relationships in seagrass meadows: Consequences for seagrass growth and predation. Estuaries 7:289-309.

Virnstein, R.W., W.G. Nelson, F.G. Lewis III, and R.K. Howard

1984 Latitudinal patterns in seagrass epifauna: Do patterns exist and can they be explained. Estuaries 7:310-330.

Weil M., E., and R. Laughlin G.

1984 Biology, population dynamics, and reproduction of the queen conch, *Strombus gigas* Linne, in the Archipelago de Los Rogues National Park. J. Shellfish Res. 4:45-62.

Wicklund, R.I., L.J. Hepp, and G.A. Wenz

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., K.L. Heck Jr., and K.W. Able

1987 Juvenile blue crabs, *Callinectes sapidus*, survival: An evaluation of eelgrass, *Zostera marina*, as refuge. Fish. Bull., U.S. 85:53-58.

Zimmerman, R., R. Gibson, and J. Harrington

1979 Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Mar. Biol. (Berl.) 54:41-47.