

Abstract.—Transplants of juvenile queen conch *Strombus gigas* L. were conducted in the southern Exuma Cays, Bahamas, to test the relationship between large-scale patterns of distribution and differential habitat quality (as indicated by conch mortality and growth). One-year-old conch (mean shell length 93 mm) were transplanted to two locations within known conch nursery habitats, one with low and one with moderate seagrass biomass. Transplants were also made to six sites without resident conch: two sites similar to the moderate biomass site, two sites similar to the low biomass site, one site with heavy seagrass, and one on bare sand.

Mortality was low at stations with natural conch populations and/or moderate seagrass biomass. Mortality was high at all other sites, and increased with time at the sand site and at one of the low biomass sites. Growth rate was high and relatively constant through the experiment at the stations with natural conch populations and at one site with moderate seagrass biomass and no resident conch (C2). Rapidly declining growth rates were found at all other sites despite depth, sediment, and macrophyte characteristics similar to sites with resident conch. Data on standing crops of macrodetritus at the beginning and end of the experiment indicated food limitation at one site where growth was low. Until the distribution of queen conch is understood, small-scale transplanting will provide a useful tool for evaluating distributional mechanisms and a test for habitats proposed for stock enhancement.

Experimental Analysis of Habitat Quality for Juvenile Queen Conch in Seagrass Meadows

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Seagrass meadows are important nursery habitats for many fishes and invertebrates from high to low latitudes (Thayer et al. 1975, Kikuchi and Peres 1977, Weinstein and Heck 1979, Stoner 1983, Pollard 1984, Robblee and Zieman 1984, Sogard et al. 1987). The queen conch *Strombus gigas* L. is a large gastropod mollusc (to >250 mm shell length) which uses the seagrass habitat as a nursery (Randall 1964, Weil and Laughlin 1984, Stoner and Waite 1990). Food value makes the queen conch an important commercial species throughout the Caribbean region (Brownell and Stevely 1981, Berg and Olsen 1989).

Hatchery data suggest that pelagic larvae of the queen conch spend 18 to 40 days in the water column (Brownell 1977, Davis et al. 1987, Mianmanus 1988). The larvae settle and metamorphose in the benthos and live for the first several months in places and in ways mostly unknown at this time. Juveniles are usually 35–40 mm shell length when first observed on sandy shoals and in shallow seagrass meadows (Stoner and Sandt, unpubl. data). Primary foods for juvenile stages are seagrass detritus and algae (Stoner 1989a, Stoner and Waite 1991). In seagrass beds of the Bahama, Turks, and Caicos Is., Virgin Is., Cuba, and Venezuela, juvenile queen conch densities of 1 to 2 animals/m² are common (Alcolado 1976, Hesse 1979, Weil and Laughlin 1984, Iversen et

al. 1987, Stoner 1989a). Recent investigations in the Bahamas show that highest densities of juvenile queen conch are associated with seagrass beds of intermediate shoot density (Stoner and Waite 1990). Older juveniles move to deeper water (Weil and Laughlin 1984), and sexual maturity is attained at approximately 3.5 to 4.0 years (Randall 1964, Appeldoorn 1988).

Large seagrass habitats (hundreds of hectares) are found near Lee Stocking I., in the Exuma Cays, Bahamas. Much of this habitat appears to be appropriate for juvenile queen conch (depth, sediments, macrophyte cover); however, conch are associated with certain geographic areas within the seagrass meadows. Five discrete juvenile populations have been observed in particular localities near Lee Stocking I. from 1984 to the present (Wicklund et al. 1988, Stoner, unpubl. data).

Reported here are the results of experimental transplants designed to examine qualities of seagrass meadows which provide optimal habitat for juvenile queen conch. The following two hypotheses were tested using conch survivorship and growth as indicators of habitat quality: (1) habitat quality is directly related to seagrass biomass; and (2) Habitats with similar depth, sediments, and macrophyte biomass have equivalent qualities as nurseries for juvenile conch.

Site description

Experiments with juvenile queen conch were conducted during the summer of 1988, at eight sites in the southern Exuma Cays, Bahamas, near Lee Stocking I. (Fig. 1). These sites included two which have natural populations of queen conch juveniles, Children's Bay Cay site 1 (C1) and Neighbor Cay site 1 (N1). Site C1 had moderate turtlegrass *Thalassia testudinum* biomass, and N1 had low biomass (Fig. 2). Site N1 had lower seagrass biomass than the optimal for juvenile conch reported by Stoner and Waite (1990) but has had a persistent population of conch since at least 1986. Two sites were chosen with macrophyte, sediment, and depth characteristics similar to C1, but with no resident conch populations. Children's Bay Cay site 2 (C2) was in the same seagrass bed as C1 but 0.5 km to the southeast; the other site was west of Lee Stocking I. (L1). An additional two sites were chosen for similarity to N1: one site was north of Lee Stocking I. (L3) and the second near Windsock Cay (W1).

To examine the effects of seagrass biomass in extreme cases, two additional sites were chosen. A sand bank site, Children's Bay Cay site 3 (C3), was selected where there was no macrophyte cover but which has a regular transience of juvenile conch. One additional site, Lee Stocking I. site 2 (L2), was chosen for high seagrass and detrital biomass, 300 m northwest of L1.

Methods and materials

Two topless cages were constructed at the eight experimental sites with 2.0 cm black plastic mesh wired to reinforcement bar driven into the sediment. The

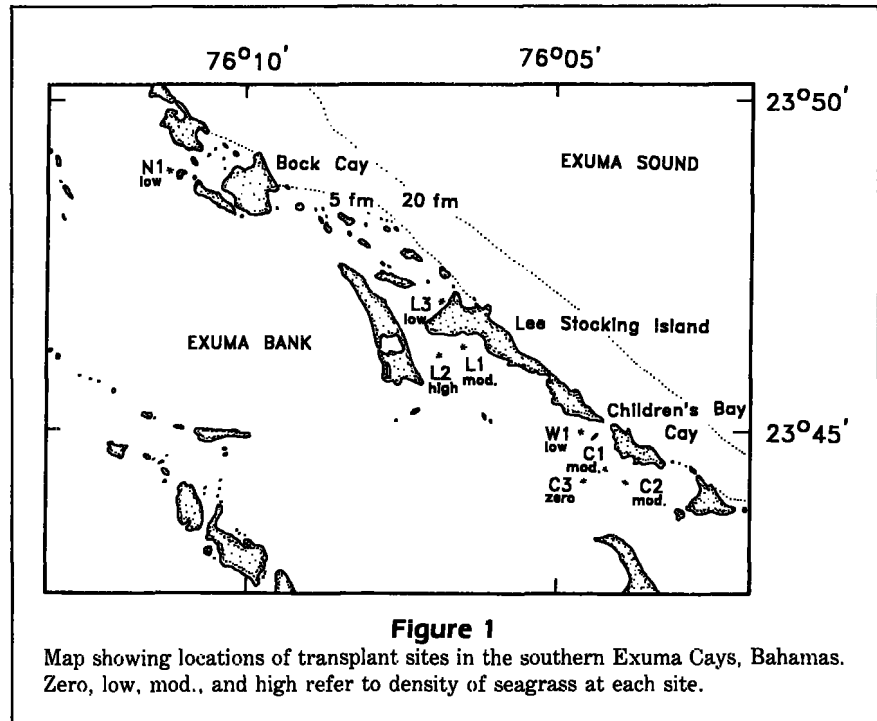


Figure 2
Standing crop of *Thalassia testudinum* and macrodetritus at sites where juvenile queen conch were transplanted. Histograms are mean values found in enclosures at the beginning and end of the experiment. Error bars are \pm standard deviation. Note the change of scale for macrodetritus at station L2. Asterisks indicate stations with resident conch. Station C3 (not shown) had zero macrophyte biomass.

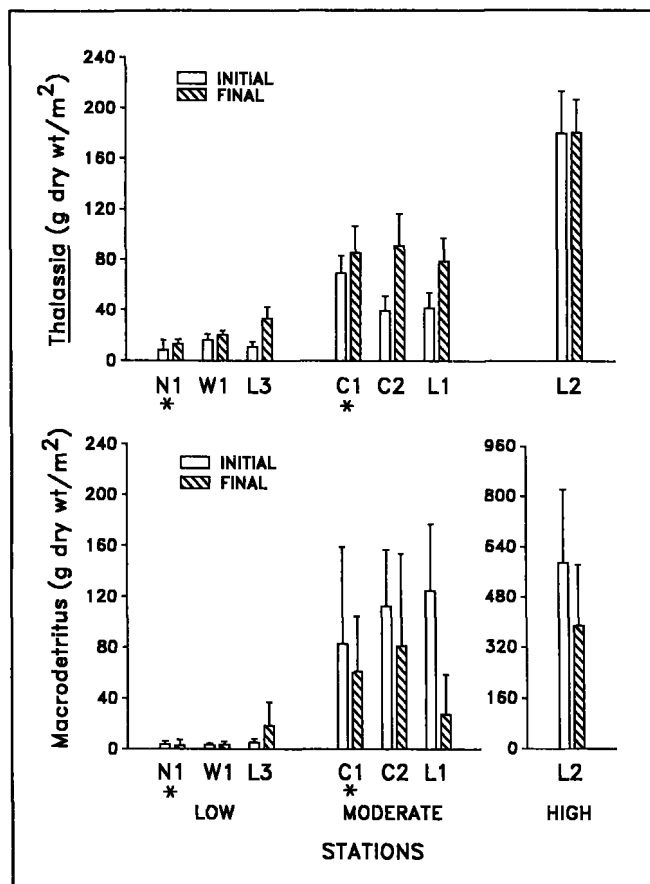


Table 1

Habitat characteristics of eight sites where juvenile queen conch were transplanted. Depth is the mean at low water. Values for sediments are mean \pm standard deviation ($n = 2$). Asterisks and plus signs indicate mean values which are not different statistically (ANOVA and Neuman-Keuls test; $P < 0.05$).

Site	Resident conch	Seagrass biomass	Depth (m)	Sediment grain-size (ϕ)	Sediment sorting (ϕ)	Sediment organics (%)
C3	No	Zero	1.3	1.50 \pm 0.02*	0.84 \pm 0.10*	2.38 \pm 0.33*
N1	Yes	Low	2.3	1.52 \pm 0.10*	1.14 \pm 0.06*	2.68 \pm 0.14**
L3	No	Low	2.2	2.02 \pm 0.30*	1.08 \pm 0.20*	3.66 \pm 0.33*
W1	No	Low	2.0	1.82 \pm 0.20*	1.47 \pm 0.28*	3.83 \pm 0.47*
C1	Yes	Moderate	3.6	2.56 \pm 0.29*	1.39 \pm 0.22*	3.76 \pm 0.33*
C2	No	Moderate	3.7	1.15 \pm 0.11*	1.62 \pm 0.19*	2.80 \pm 0.33**
L1	No	Moderate	3.4	2.26 \pm 0.23*	1.40 \pm 0.23*	2.92 \pm 0.32**
L2	No	High	3.7	2.40 \pm 0.19*	1.04 \pm 0.07*	5.36 \pm 0.48

cages were 30 cm high, 5 m in diameter, and pushed into the sediment approximately 2.0 cm to prevent loss of animals. Exact positions of the cages were chosen to provide uniformity in macrophyte cover at each site, and to insure that sites selected for similar characteristics (C1, C2, L1 and N1, L3, W1) had equivalent seagrass and detrital cover as well as sediment quality (Table 1, Fig. 2).

Previous experiments with the same cage design at Children's Bay Cay site 1 showed that the cages did not effect sediment grain-size, sediment chlorophyll, or accumulation of detritus. Enclosed animals had growth rates equivalent to individuals tagged and released in the field surrounding the enclosures (Stoner 1989a).

Animals used in this experiment were 1-year-old *Strombus gigas* collected from the sand bank near Children's Bay Cay. At the beginning of the experiment, all of the conch were between 82 and 105 mm total shell length. Mean lengths in individual treatments were not different at the beginning of the experiment (ANOVA, $F = 1.90$, $P > 0.05$), ranging from 92.0 to 94.3 mm. After measuring habitat characteristics (see below) and clearing all noticeable macroinvertebrates from the 16 enclosures, 24 individually tagged and measured conch were placed in each cage (1.2 conch/m²), yielding a density equivalent to mean summer population density at C1 and N1. Dead or lost conch were replaced to maintain the population density within cages (Table 2). Replacements were of a size similar to the mean conch size in a particular treatment at the replacement time. Conch were marked with vinyl spaghetti tags (Floy Tag & Mfg., Inc.) tied around the shell spire.

All transplants were made by 26 April 1988, and measurements of total shell length (spire to siphonal

canal) were taken with calipers at 35, 75, and 120 days. Growth rate was determined on the basis of mm shell growth per day. Each enclosure was examined at approximately 2-week intervals to determine mortality rates over time, to replace dead conch, and to remove invading invertebrates. One of the cages at C3 was destroyed by wave action in June 1988, and all of the enclosed animals were lost. This cage was rebuilt and new animals were introduced on 23 June.

At the end of the experiment, soft tissue weight of individual conch was determined by drawing the animal from its shell after freezing and subsequent thawing. Wet weight was measured after washing away feces and light blotting of the tissues. Body condition was determined by the ratio of wet weight:shell length.

Living macrophytes and macroscopic detritus were collected from each enclosure at the beginning and end of the experiment. Four replicates were taken from 25 \times 25 cm quadrats into nylon bags (3.0 mm mesh) for determination of aboveground biomass. Individual samples were divided into green *Thalassia testudinum* blades and detritus (senescent blades and blade fragments). The only other macrophytes collected were the seagrasses *Syringodium filiforme* and *Halodule wrightii* found in very small amounts, and an occasional calcareous green alga *Rhypocephalus phoenix*. The aboveground fractions were dried at 80°C to constant weight. *Rhypocephalus phoenix* was not included in analysis of macrophytes because of the large bias created in dry weight and because the alga is not consumed by juvenile conch.

Sediments to 5 cm depth were sampled with a 3.5 cm diameter core tube, one sample per enclosure. These samples were frozen until laboratory analyses were performed. Sediment organic content was determined by drying a subsample of approximately 50 g wet

Table 2

Summary of replacements made for loss or mortality of juvenile queen conch in enclosures, by date, site, and cage number. Twenty-four animals were maintained per cage, 26 April–25 August 1988.

Site	Cage	Resident conch	Seagrass biomass	11 May	31 May	21 June	11 July	1 August	Total
C3	1	No	Zero	1	2	5	1	Terminated	9
	2	No	Zero	1	0	5	4	Terminated	10
N1	1	Yes	Low	0	0	0	0	0	0
	2	Yes	Low	0	0	0	0	0	0
L3	1	No	Low	4	2	11	3	11	31
	2	No	Low	1	9	3	4	1	18
W1	1	No	Low	0	0	1	0	0	1
	2	No	Low	0	0	3	8	20	31
C1	1	Yes	Moderate	0	0	0	0	0	0
	2	Yes	Moderate	0	0	0	0	0	0
C2	1	No	Moderate	1	0	2	0	1	4
	2*	No	Moderate	1	3	1	0	0	5
L1	1	No	Moderate	0	4	4	0	2	10
	2	No	Moderate	2	4	0	0	2	8
L2	1	No	High	6	7	9	3	1	26
	2	No	High	2	4	5	6	4	21

*This cage was rebuilt and all animals were replaced on 23 June 1988.

weight at 80°C to constant weight and incineration at 500°C for 4 hours. Organic content was quantified as the percent difference between dry weight and ash-free dry weight. Another subsample of approximately 50 g was analyzed for granulometric properties. The sample was washed to remove salts and to extract the silt-clay fraction (<62 μ m) which was analyzed with standard pipette procedures (Galehouse 1971). The sand fraction (>62 μ m) was analyzed with standard sieve fractionation procedures (Folk 1966). Product-moment statistics were generated for mean grain-size and sortedness (McBride 1971).

Analysis-of-variance techniques were applied according to Sokal and Rohlf (1969), with log₁₀ transformations where Bartlett's test indicated heterogeneity of variances (macrophyte data). Conch growth data proved to be heterogeneous in variance in most cases, as indicated by Bartlett's test and plots of means versus variances. Heterogeneity was improved little by log-transformation. Additionally, necessary replacement of conch during the transplant experiment produced a violation in independence in the growth data. For these reasons, Kruskal-Wallis analysis of variance was followed by nonparametric Mann-Whitney U-tests for multiple comparison of growth rates.

Results

Changes in habitat characteristics

Juvenile conch were transplanted to four different habitat types based upon macrophyte biomass: zero, low-, moderate-, and high-biomass habitats (Table 1). Sediment grain-size varied from 1.15 to 2.56 ϕ at the eight sites; however, there were no significant differences in mean values (ANOVA, F 2.26, P >0.05), and all are classified as fine to medium sand. Similarly, there were no differences in sediment sorting coefficients (F 2.09, P >0.05), with all sites except the bare sand (C3) in the poorly sorted range. Significant differences occurred in sediment organic content (F 15.97, P <0.001) with highest values at the high-biomass site (L2) and lowest at the sand site (Table 1). There were no significant differences in sediment organics among the sites with low or moderate biomass.

At the beginning of the experiment there were no significant differences in biomass of either seagrass or macrodetritus between the two cages at any site (Student's t -test, P >0.05). Analysis of variance indicated that macrodetritus varied significantly (F 76.48, P <0.001) among the eight sites, but there were no significant differences in mean values for the three low-biomass stations (N1, L3, W1) or for the three moderate biomass sites (C1, C2, L1) (Neuman-Keuls test, P >0.05). Macrodetritus was more abundant at the

high-biomass site (L2) than at any other site ($P < 0.05$), and zero at the sand site (C3) (Fig. 2). The same pattern occurred with living seagrass biomass, except that site C1 had significantly higher biomass than the other moderate-biomass sites, but less than that found at the high-biomass location (L2) (ANOVA, F 58.12, $P < 0.001$; Neuman-Keuls test, $P < 0.05$).

For analysis of seagrass and macrodetritus standing crops at the beginning and end of the experiment, paired-comparison analysis of variance was conducted, where differences between cages and the effect of time were examined. Significant difference between cages occurred only at N1 where enclosure 2 had a higher biomass of living seagrass than enclosure 1 (F 7.46, $P < 0.05$). Paired cages had similar amounts of macrodetritus at all sites ($P > 0.05$). Significant differences with time were found at L1 where detritus decreased (F 13.22, $P < 0.005$), while living seagrass increased with time (F 20.15, $P < 0.001$). Seagrass increased also at C2 (F 23.12, $P < 0.001$) and at L3 (F 34.89, $P < 0.001$). No other significant time effects occurred for either macrodetritus or seagrass biomass.

Mortality

Mortality at experimental sites with natural populations of conch was low, ranging from zero at site C1 to a total of only four individuals during the last three weeks of the experiment at site N1 (Fig. 3). Total mortality at the sites with moderate seagrass density and no resident conch was also low: nine individuals at station C2 and 19 at L1. At both of these sites, mortality rates decreased with time. Mortality was high at all other sites, with either a constant (sites L2 and L3) or accelerating rate (C3 and W1). By the end of the experiment, 61 animals had died at the high-biomass site (L2) and 61 had died at one of the low-biomass sites (L3). At the sand site (C3), the transplant experiment was terminated after 95 days because of rapidly accelerating mortality.

Kruskal-Wallis test was insufficiently powerful to distinguish mortality differences among the sites (H_{adj} . 13.37, P 0.064) despite mortality rates ranging from 0 to 129% of the original number of conch transplanted. This is related to the low number of degrees of freedom in the design (2).

Growth

Growth rates decreased over the three experimental periods at most of the stations, but the decrease was variable among stations, and most extreme at W1 (Fig. 4). Because of station-time interaction in growth rates, Kruskal-Wallis analyses were performed for each growth period to test for station effects. In all cases

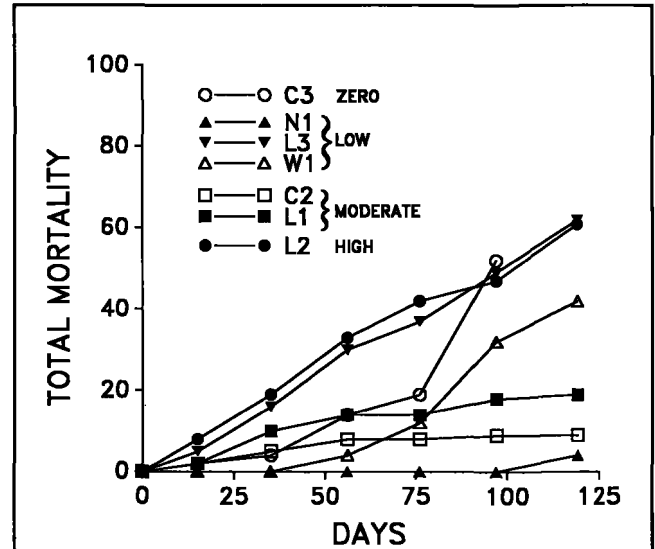


Figure 3

Total mortality of juvenile queen conch shown as a function of time at eight transplant sites near Lee Stocking I. Values are direct counts where 48 conch were transplanted to each site at the beginning of the experiment and replaced upon death. There was zero mortality at station C1 (not shown). Conch were resident at stations C1 and N1.

the effect of site was highly significant (H_{adj} . 164, $P < 0.001$ for period 1; H_{adj} . 234, $P < 0.001$ for period 2; and H_{adj} . 209, $P < 0.001$ for period 3).

During the first growth period, there were no significant differences between growth rates at low-biomass site W1 and moderate biomass site C2 (Mann-Whitney U-test, U 993, P 0.441), between moderate-biomass sites C1 and L1 (U 858, P 0.297), or between sites N1 and L2 (U 825, P 0.572). Growth rates at W1 and C2 were higher than all other sites ($P < 0.05$). Rates at sites L3 and C3 were different from all other sites ($P < 0.05$). During this period there were no significant differences in growth rates between paired cages ($P > 0.05$).

During period 2, growth rates at C1, C2, and N1 were higher than those at the five other stations ($P < 0.05$) and different from one another ($P < 0.05$). Despite negative growth (shell erosion) at L2 and L3, growth rates at L2, L3, C3, and W1 were not different ($P > 0.05$). A significant difference in growth rates between cages at C3 (U 371, P 0.001) was the result of new animals being introduced in the rebuilt cage 1 during this period; however, growth rates were low in both cages.

As in period 2, highest growth rate during period 3 was observed at the moderate-biomass site C2 where there was no resident conch population. Rates at W1,

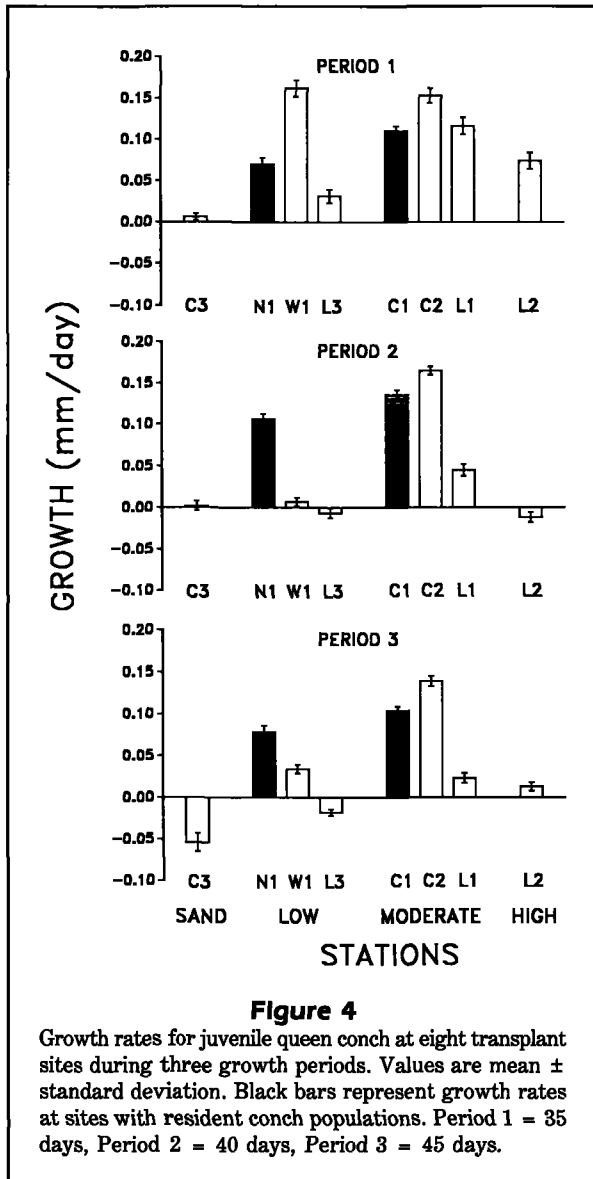


Figure 4

Growth rates for juvenile queen conch at eight transplant sites during three growth periods. Values are mean \pm standard deviation. Black bars represent growth rates at sites with resident conch populations. Period 1 = 35 days, Period 2 = 40 days, Period 3 = 45 days.

L1, and L2 were low and not different ($P > 0.05$). Growth rates at all other sites were different, and strongly negative growth rates occurred at station C3 and L3. There were no significant cage differences at any of the sites during this period ($P > 0.05$).

High growth rates at sites C2 and C1 were associated with high body condition (Table 3). Predictably, condition was low in the bare-sand habitat and other sites where survivorship was low (e.g., L3, W1), and there were various site differences (Kruskal-Wallis test, $H_{adj.} 57.38$, $P < 0.001$) (Table 3). Despite high mortality and low growth rate at the high-biomass site (L2), condition factor at that site was not significantly different from site N1, a natural conch habitat.

Table 3

Condition factor of juvenile queen conch transplanted to eight different sites. Values are mean \pm standard deviation ($n = 15$). Vertical bars indicate sites for which medians were not different (Mann-Whitney U-tests, $P > 0.05$).

Site	Resident conch	Seagrass biomass	Condition factor
C2	No	Moderate	0.257 ± 0.030
C1	Yes	Moderate	0.246 ± 0.031
N1	Yes	Low	0.227 ± 0.031
L2	No	High	0.216 ± 0.036
L1	No	Moderate	0.208 ± 0.025
L3	No	Low	0.188 ± 0.034
W1	No	Low	0.180 ± 0.030
C3	No	Zero	0.165 ± 0.020

Comparing rates of mortality and growth, a pattern emerges: low growth occurred with high mortality at sites C3 and L2. Accelerating mortality and rapidly declining growth rates were found at W1 and L3, while mortality remained low and growth rates high at C1, C2, and N1. At L1, mortality was low but growth declined from a high rate in the first period.

Discussion

Growth rates found in the natural conch habitats (C1 and N1), between 0.1 and 0.2 mm/day, were similar to those determined for free-ranging juveniles at C1 during summer 1985 (0.12 mm/day) (Wicklund et al. 1988), and summer 1987 (0.10–0.15 mm/day) (Stoner 1989a). The rates reported here are also similar to those reported from Los Roques, Venezuela, where growth curves give mean growth rates of 0.16 mm/day for tagged conch between 85 and 105 mm in shell length (Laughlin and Weil 1982), and 0.14 mm/day for 90 mm conch (Brownell 1977). These results suggest that enclosures used in this experiment did not inhibit growth in the test animals.

So that the numbers of conch in the enclosures remained constant, dead conch were replaced with new individuals which, in the less optimal sites, grew at a rate slightly higher than conch enclosed earlier. Replacement, therefore, results in overestimation of growth rate (and probably survivorship) in the poor-quality habitats and conservative separation of sites. Differences in shell length among the experimental sites by the second and third growth periods, and slight differences in growth rates of conch between 90 and 120 mm (Brownell 1977) would have only a minor in-

fluence on site differences. Despite these limitations, high mortality rates and low or negative growth rates provide clear evidence that five of the sites without resident conch (except site C2) were poor habitats for juvenile queen conch.

Stoner and Waite (1990) showed that 1- and 2-year-old conch actively select areas with intermediate seagrass biomass over areas with high and low biomass. Additionally, it was shown that seagrass shoot density and biomass were good predictors of juvenile conch distribution within nursery habitats. Among the sites which were known to serve as natural habitats for queen conch (C1, C3, N1) there was a direct relationship between seagrass biomass and habitat quality, as measured by conch growth. On the larger scale of this study, however, seagrass density was not a good predictor for conch success, and other variables—probably trophic factors—need to be examined.

Adult and subadult queen conch are generally considered to be herbivores (Robertson 1961, Randall 1964, Hesse 1976), but recent data on juvenile conch living in seagrass beds show that seagrass detritus is consumed in large quantities, and macroalgae such as *Batophora oerstedii* and *Laurencia poitei* are primary sources of nutrition (Stoner and Waite 1991). Field experiments have shown that juvenile conch can have a major influence on detritus and other characteristics of the benthic environment, with much of the benthic productivity being removed by grazing (Stoner 1989a,b). The observed depletion of detrital biomass followed by decreasing conch growth rates at the moderate biomass site L1 suggests trophic limitation at that station.

Abundance of macrophytes does not necessarily provide superior habitat. Site L2 had a thick accumulation of detritus and high seagrass biomass, but conch transplanted to that site had high mortality and low growth rates. Randall (1964) noted that young conch may not be able to move readily through dense seagrass stands, and are rarely found in that habitat type.

No attempt is made here to equate mortality rates in the transplants with natural mortality because of potential density-dependent effects on predation rate, partial exclusion of predators by cages, and uncertainty in the sources of mortality. Observations of potential queen conch predators in the enclosures were rare. The tulip snail *Fasciolaria tulipa* was seen attacking conch three different times, and in a few instances the giant hermit crab *Petrochirus diogenes* was found in empty shells; both of these species are known predators on queen conch (Randall 1964, Jory 1982). The apple murex *Murex pomum* and hermit crabs *Paguristes* sp. were observed occasionally in the enclosures, but both

are thought to be scavengers (Jory and Iversen 1983, Iversen et al. 1986). Lack of broken shells, low body condition, and low shell growth rates lead us to conclude that much of the mortality in "poor" habitats was a result of inadequate food resources. On the other hand, large differences in mortality rate between the two enclosures at two of the sites suggest that heavy predation may have occurred in some cages.

The fact that one site with no resident juvenile conch (C2) produced high growth rates and survivorship suggests that queen conch do not occupy all suitable habitats. Several explanations are plausible: Pelagic larvae may not be dispersed to the area, settlement may not occur, or early-juvenile stages may suffer high mortality rates at the site. It is also possible that, historically, site C2 has been a nursery site for queen conch. Macroscopic conch shell fragments at the site were found in a density of 3.0 fragments/m²; this is lower than the density at site C1 (6.8/m²), but considerably higher than that in other non-conch areas (e.g., density at L1 was 0.05 fragments/m²) (Stoner and Yoshioka, unpubl. data).

Presence or absence of juvenile queen conch in seagrass meadows appears to be mediated by site-specific characteristics. Habitat quality, as measured by growth rate, was related directly to seagrass biomass in natural conch sites; however, the hypothesis that habitats with similar depth, sediments, and macrophyte biomass have equivalent qualities as nurseries for juvenile conch is clearly rejected. Until the distributional ecology of queen conch is understood, small-scale transplanting will be a valuable tool in manipulations designed to test the significance of other environmental variables, and as a means of testing habitats where enhancement of stocks is proposed.

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