Distribution of Two Mesogastropods, the Queen Conch, Strombus Gigas Linnaeus, and the Milk Conch, Strombus Costatus Gmelin, in La Parguera, Lajas, Puerto Rico

Zelma A. Torres Rosado
University of Puerto Rico, Mayaguez Campus, 1987

DISTRIBUTION OF TWO MESOGASTROPODS, THE QUEEN CONCH, STROMBUS GIGAS LINNAEUS, AND THE MILK CONCH, STROMBUS COSTATUS GMELIN, IN LA PARGUERA, LAJAS, PUERTO RICO

by

Zelma A. Torres Rosado

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Committee Member, Chairman	11/2/87 Date
Paul M. Y... Committee Member	Nov 2, 1987 Date
Committee Member	Nov 3, 1987 Date
Representative Graduate Studies	Nov 3, 1987 Date
Director Department of Marine Sciences	11/3/87 Date
Director Graduate Studies	Nov. 12/87 Date

This thesis is dedicated to my

mother, Margarita Rosado

Cruz, with all my love.

COMPENDIO

La distribución y preferencias en habitáculos por el carrucho rosado Strombus gigas Linnaeus y el carrucho de leche Strombus costatus Gmelin fue estudiada en La Parguera, Puerto Rico. La densidad promedio del carrucho rosado fue 0.0811 por 100 m^2 (2.04 carruchos por transecto), con mayor abundancia en cascajo calcáreo (carricoche) a profundidades intermedias desde 6 a 18 metros. Los adultos del carrucho rosado fueron también comunes en plena arena. Los carruchos de leche estuvieron presente a una densidad de 0.1340 por 100 m^2 (3.37 carruchos por transecto), fueron más abundantes en arena, pero al igual que el carrucho rosado, su densidad fue mayor en cascajo calcáreo. Estos estaban en aguas relativamente más profundas que los carruchos rosados (10 a 28 metros).

La temporada de reproducción del carrucho rosado no pudo ser determinada, pero dos hembras fueron observadas desovando durante principios de octubre. Para los carruchos de leche la temporada de reproducción se maximizó entre finales de marzo hasta principios de mayo y con otra máxima a mediados de Julio. La actividad reproductiva fue predominante en las planicies de arena.

Asociación positiva fue encontrada entre carruchos a larga escala, basados en presencia/ausencia de data usando tablas de contingencia. Estos fueron también positivamente asociados a pequena escala, en carricoche ($p = 0.0127$, prueba exacta

Fisher), arena gruesa con fragmentos de coral ($p < 0.001$, prueba del cuadrado de Chi). y en planicies de arena ($p < 0.025$, prueba Chi¯square). En una prueba ANOVA, las densidades de Strombus gigas y Strombus costatus fueron comparadas entre los siete tipos de habitículos. No se encontró diferencia entre especies. Sin embargo, diferencias entre habitículos y la interacción especies-habitáculo fueron significantes ($p < 0.005$ y $p < 0.001$ respectivamente, prueba ANOVA). No hubo diferencia intraespecífica significativas entre el carrucho rosado o el de leche en las distancias entre individuos en secuencia ($p > 0.05$, prueba U de Mann-Whitney). La distancia interespecífica fue significativamente mayor que las distancias intraespecíficas para ambas especies ($p < 0.01$, prueba U de Mann-Whitney). Esto indica una asociación negativa en una escala fins, p.ej. dentro de transectos.

La escala usada para examinar esta asociación es un factor muy importante. Las asociaciones negativas y positivas podrían indicar una competencia por espacio o alimento dentro del habitáculo, y preferencia por el mismo habitáculo, respectivamente.

La sobre pesca del carrucho rosado podría eliminar esta especie y ayudar a incrementar la abundancia y distribución del carrucho de leche.

ABSTRACT

The distribution and habitat preference of the queen conch Strombus gigas Linnaeus and the milk conch Strombus costatus Gmelin was studied at La Parguera, Puerto Rico. Mean queen conch density was 0.0811 per 100 m^2 (2.04 conchs per transect), with greatest abundance in rubble at depths from 6 to 18 meters. Adult queen conchs were also common on plain sand. Milk conchs were present at a density of 0.1340 per 100 m^2 (3.37 conchs per transect), were most abundant in sand, but had a high density on rubble. They were in relatively deeper water than queen conchs (10 to 28 meters).

The reproductive season for queen conchs could not be determined but two females were observed laying eggs during early October. For milk conchs the reproductive season peaks between late March to early May with another peak in mid July. The reproductive activity was predominant on sand flats.

Positive association was found between conchs on a large scale, based on presence/absence data of transects made using a contingency table. On a small scale, comparison within habitat types indicated positive association within rubble (p - 0.0127, Fisher exact test), coarse sand ($p < 0.001$, Chi—square test) and sand plains ($p < 0.025$, Chi—square test). In an ANOVA test, the densities of Strombus gigas and Strombus costatus were compared among the seven habitat types. No difference between species was found. However, differences among habitats and the species—habitat interaction were significant ($p < 0.005$ and $p < 0.001$ respectively, ANOVA). No significant difference was found between queen and milk conchs in conspecific distances between individuals in sequence ($p > 0.05$, Mann—Whitney U—test). Interspecific distance was significantly greater than intraspecific distances for both species ($p < 0.01$, Mann—Whitney U—test). This indicates a negative association on

a fine scale, i.e. within the transects.

The spatial scale used to examine association is a very important factor. The negative and positive associations may indicate a competition for space or food within habitat, and preference for the same habitat, respectively.

The over—fishing of queen conch could eliminate this species and help to increase the abundance and distribution of milk conch.

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My committee consisted of Dr. Richard S. Appeldoorn, Dr. Paul Yoshioka, and Prof. Ricardo Cortés. Dr. Appeldoorn designed part of the study and provided necessary equipment and materials for the research. He helped at all time to execute my thesis. Dr. Yoshioka critically reviewed the thesis. Special thanks to Professor Cortés who at a critical moment at the end of this work helped kindly accepted to become a member of my committee; I will remember this for the rest of my life. I wish to thank all of them for their time, suggestions, advice, and assistance. I was lucky to have good professors who care about the quality of theses, the reputation of the university, and their students, indiscriminately, without prejudgments. Professors like these give the university high standing and make the student feel proud to be part of that institution.

For diving assistance I thank Jerry González, Javier Colley, Shawna Reed, Félix Grana, and again Dr. Appeldoorn for those hours of travel out to the study site in all types of weather.

Special thanks go to my friends Denise DeVore and Graciela García¯Moliner who helped review some drafts and inspired me to finish this research. Thanks to Vance Vicente who helped make the slides for my defense.

Finally, I thank two persons who aided me financially, one way or the other, providing funds for my studies: Dr. Appeldoorn and especially my mother.

Good job!

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INTRODUCTION

The gastropod family Strombidae has five species in the Caribbean Sea of which, _Strombus gigas_ Linnaeus, the queen conch, and _Strombus costatus_ Gmelin, the milk conch, are the largest and heaviest respectively. _Strombus gigas_ ranges from South Florida and Bermuda to the Caribbean sea, and _Strombus costatus_ from Southeast Florida and Bermuda to Brazil.

The queen conch is commercially the most valuable gastropod in many Caribbean islands. Principal studies on various aspects of queen conch biology were carried out by Randall (1964), Alcolado (1976), Berg (1976), Brownell (1977), and Hesse (1979). These studies concentrated on _Strombus gigas,_ principally because of its commercial importance and the recent decline in populations due to over—fishing. The milk conch is neither as large nor as abundant as queen conch, but plays a minor role in the conch fisheries of Los Roques Archipelago (Brownell, 1977), Bermuda Islands (Burnett—Herkes, 1981), and Quintana Roo, Mexico (Torre Alegria, 1984).

Many studies compare queen conch and milk conch in various aspects of morphology (Randall, 1964; Berg, 1975; Warmke and Abbott, 1975; Alcolado, 1976; Appeldoorn, 1984), growth (Brownell, 1977; Wefer and Killingley, 1980; Ballantine and Appeldoorn, 1983; Appeldoorn and Sanders, 1984; Appeldoorn, 1985), reproduction (Robertson, 1959; Randall, 1964; Brownell, 1977; Ballantine and Appeldoorn, 1983), mortality (Appeldoorn and Ballantine, 1983; Appeldoorn, 1984; Appeldoorn, 1985), habitat (Newell et al., 1959; Robertson, 1961; Randall, 1964; Percharde, 1968; Brownell, 1977; Hesse 1979; Berg, 1981; Brownell and Stevely, 1981; Jurnett-Herkes, 1981; Percharde, 1982), behavior (Berg, 1974; Brownell, 1977; Appeldoorn and Ballantine, 1983; Iversen et al., 1986), burial (Randall, 1964; Appeldoorn, 1985), movement (Berg, 1974; Appeldoorn, 1985), and preferred food (Robertson, 1961; Berg, 1975; Alcolado, 1976; Woon, 1983).

Some studies have assumed both species to have similar developmental characteristics and behave similarly in culture (Ballantine and Appeldoorn, 1983). Although there are differences between the species, their biological similarities indicate a potential for significant competition. If competition does exist the removal of one may allow the other species to have more ecological space and access to food and other resources.

Some workers report differences in habitat preference between species and others do not. Newell et al. (1959) described the habitat of Strombus gigas (Strombus samba) as unstable sand bottom with sparse vegetation, mainly Thalassia, while the habitat of Strombus costatus as stable sandy bottom moderately covered with seagrass and algae. Burnett-Herkes (1981) indicated that Strombus gigas preferred the sandy areas adjacent to offshore seagrass beds, while Strombus costatus was restricted to the inshore harbors and bays. In contrast, Brownell (1977) associated both species with seagrass beds, and Robertson (1961) observed these species co-occurring at the same localities. The reported distributions for each species are broad, occurring on sandy areas, seagrass beds (turtle and/or manatee grass), gravel, coral rubble, and smooth hard coral or rock bottom (Robertson, 1961; Randall, 1964; Berg, 1981; Brownell and Stevely, 1981); but in general conchs have been found to inhabit sandy bottoms that are stable enough to support the growth of numerous species of algae and seagrass (Robertson, 1961; Randall, 1964; Hesse, 1979; Brownell and Stevely, 1981). Appeldoorn (personal communication) observed both species to have broad and overlapping habitats, although he felt Strombus costatus preferred areas of softer sediment. However, Strombus costatus has not been found in areas where there is only mud or 50% mud and sand (Percharde, 1968). Strombus costatus was described to be usually in shallower waters than Strombus sigas (Percharde, 1968), but in subsequent studies Percharde (1982) found a very large colony of Strombus costatus in 37 — 40 meters. No specific studies have been done on association between species.

The objective of this research is to find how Strombus costatus and Strombus gigas are distributed within and between habitats and to find if there is an association (positive or negative) between species and, if so, what is the scale of this association and its underlying cause. The association among Strombus gigas, Strombus costatus and environment, and to each other was investigated in this research in the area of La Parguera, Puerto Rico.

METHODS AND MATERIALS

1. Study Site

The study site covered from Bahia Sucia, Cabo Rojo (67°10'W) to Punta Jorobado, Guánica (66°55'W), and from the shoreline to the shelf edge off La Parguera, Puerto Rico (Figure 1). The area spanned approximately 25 by 11 km (13.5 by 6 nautical miles), covered depths from two to thirty meters, and included various types of environmental regimes (seagrass beds, coral reef, mud bottoms, mangrove lagoons, sand flats, algal plains, or a combination of these). The duration of this research was from May 1985 to April 1986.

2. Station Selection

Station locations were chosen by placing a grid, drawn at 0.1 minute of latitude and longitude, over a map of the study site. Intersections on the grid were numbered and eighty-one stations were selected at random (Figure 1), taking numbers from a random number table (Sokal and Rohlf, 1981, Table 10). Each station was located taking compass bearings from landmarks. Two transects were made at each station.

3. Data Collection

Distribution data for both species and habitat type were recorded using strip transects (Eberhardt, 1978). Each transect was 10 meters wide, with a diver attached by a 5-meter line to either side of a

Figure 1. Approximate position of the 81 stations in the study site covered during a one year survey in La Parguera, Puerto Rico from May 1985 through April 1986.

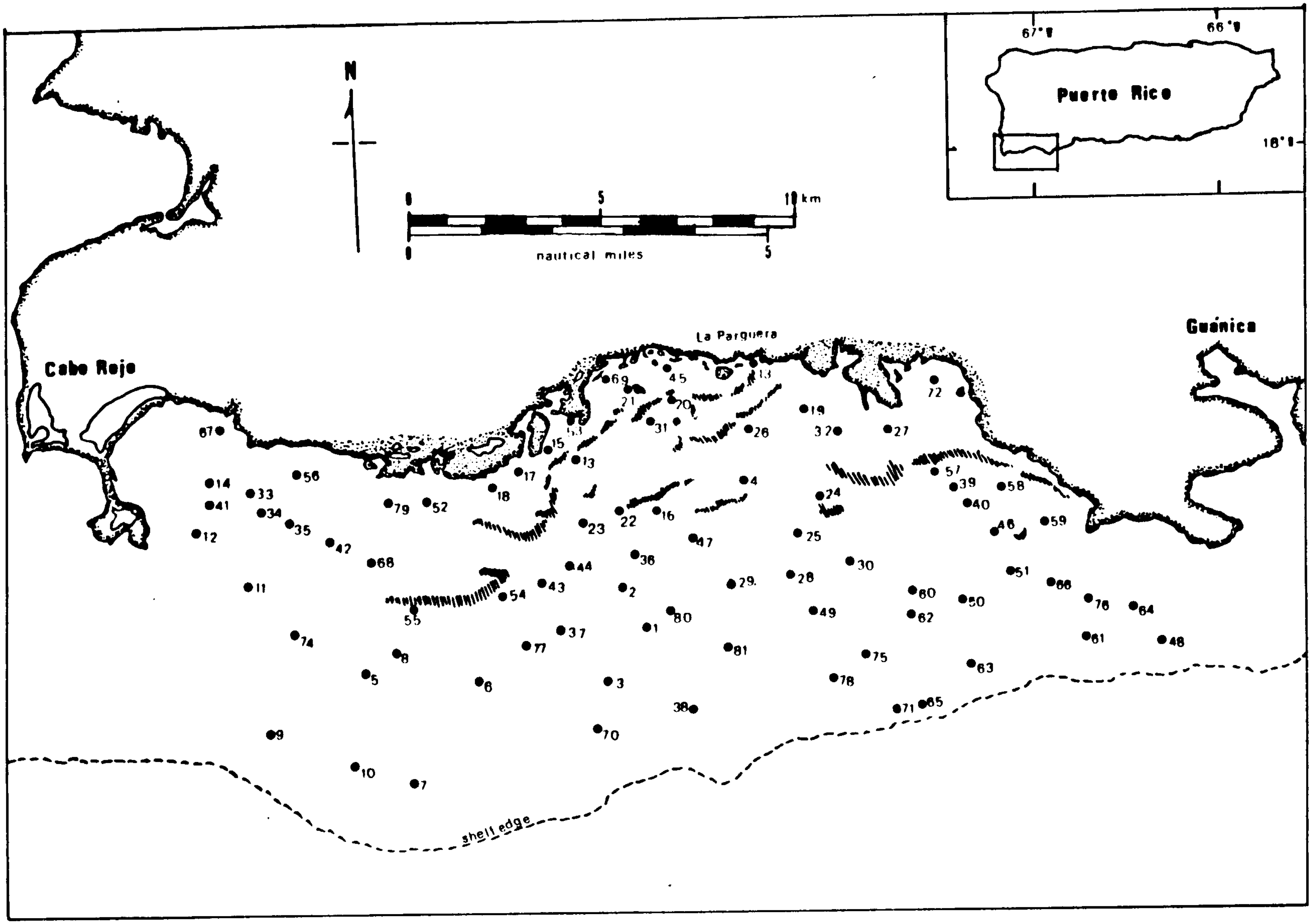

N
0
5
10 km
0
nautical miles
5
67°W
66°W
Puerto Rico
18°N
Cabo Rojo
La Parguera
Guánica
shelf edge

Figure 2. Plexiglass slate used for recording data during the survey, with attached flowmeter and compass. (*Figure not included, ed.*)

diver in the middle. Lateral divers signalled the middle diver of the presence of either species. The middle diver was in charge of maintaining course and recording the number of conchs, change of habitat, behavior, distance covered, and any anomalous observations.

Length of each transect depended on the depth and population density of the conchs and was recorded using a flowmeter (Figure 2). Time ranged from no more than 26 minutes in shallow waters to no less than 7 minutes in deep areas as a safety factor (19 transects were made at depths more than 20 meters). The first transect on each station ran between 110° and 150° (SE) depending on the bottom current, the second ran between 290° and 330° (NW). At two stations, 4 and 68, the direction was reversed. To avoid covering the same area on the second transect, at each station were separated by running perpendicular to the first for one or two minutes before initiating the second. Distance traveled was recorded.

Presence of both species was recorded in the order in which they were encountered. Juvenile and adult conchs of both species were reported. Adults were identified as those conchs with a developed flared lip. Position of each queen conch was estimated using the flowmeter. After the 26th station, the position of each milk conch was also recorded.

Information on habitat, behavior, depth, and bottom type where each conch was found was recorded. Each occurrence of a particular substrate type was treated as replicate for subsequent within-habitat analyses. The number of replicates depended on how many changes of habitat occurred. Substrates were qualitatively classified into seven categories based on the following descriptions:

a) Rubble: brownish sand with coralline grains and usually conch—size rocks, covered by numerous macroalgae.

b) Coarse sand: sand with gravel and small fragments of shell and coral covered with live algae. Algae are relatively less abundant than in the rubble habitat.

c) Sand: sand with medium grain size to small grain size. The sand was mainly clean, with sparse live algal cover. On some transects, the sand was fine with a dirty color and more algae than on the typical transects.

d) Mud: silt mud, sometimes mixed with dirty fine sand. Halimeda, Udotea, Penicillus are the most abundant algae in this habitat. Dictyota, Caulerpa, Acetabularia were present in less abundance. On some transects this habitat was mixed with calcareous grit and seagrass.

e) Patch reef: reefs mostly covered with living hard coral especially Montastrea, Acropora, and gorgonians with sponges and some macroalgae. On some transects small patches were of dead coral (Acropora and Porites were the most abundant genus). Patch reefs were relatively small and elevated off a bottom of differing substrate.

f) Hard bottom: has typically the appearance as a large flat area of rock covered with a thin coat of sand, hard on the bottom, with some macroalgae of small size, few rocks and sparse gorgonians.

g) Seagrass: the seagrasses Thalassia testudinum and Syringodium filiforme were mostly found. This habitat varied from dense beds of Thalassia to sparse and mixed beds of both species associated with clean sand and coarse sand bottoms.

4. Calibration

The flowmeter was calibrated to distance by running a measured transect of 100 m length eight times, four times in each direction (std. dev. = 9.11 m; std. Error

= 3.22 m). Directions of the runs were similar to survey transects: 120° (SE) one way and 300° (NW) the other.

5. Statistical Analyses

There were seven statistical analyses used, described as follows.

a) 2 X 2 contingency table. The first analysis tested association on a broad scale using presence—absence data for each species on each transect. The resulting 2 X 2 contingency table was analyzed using a Chi—square statistic (Pielou, 1977). The same approach was used to test for association between species within habitats, using data from the 544 replicates found in the whole survey. When transects were broken—down into the seven habitats, Fisher's exact probabilities in the 2 X 2 table were used to test for independence instead of Chi—square in those habitats where a value of expected frequency for a cell in the table was less than 1, and/or 80% of expected frequency was less than 5.

b) Correlation. Densities between species of juveniles and adults on the different habitat types were compared using Pearson's Product—Moment Correlation Coefficient, r (Sokal and Rohlf, 1981).

c) ANOVA. Another analysis examining densities of queen conch and milk conch on different habitat types was made with a Two-Way, Model I, Analysis of Variance (ANOVA) with unequal sample size.

d) Mann-Whitney U-test. A Mann-Whitney U-test was used to test two sets of data: first, relative density per 100 m^2 between species within habitat; second, nearest neighbor distances (in meters) between and within species.

e) Nearest neighbor. Spatial pattern in one dimension was evaluated by comparing the average expected distance from an individual to its nearest neighbor in a random distribution (inverse of conchs per unit area multiplied by two), r_E, against the measured mean distance, r_A (Clark and Evans, 1979). Most of the measured distances from conch to conch were taken within aggregated conch-groups and/or transects with the highest number of conchs. The significance of departure from randomness was tested by the normal curve (Clark and Evans, 1954).

f) Kolmogorov-Smirnov. Finally, a Kolmogorov-Smirnov test was used to compare frequency distributions (number of individuals found per transect) between species.

g) GT2-method. A multiple unplanned comparisons among pairs of means based on unequal sample sizes using GT2-method proposed by Gabriel in 1978 (Sokal and Rohlf, 1981) was made to determine significance in depth distribution among habitat types.

RESULTS

Total distance covered on the 162 transects was 40810.27 m, distributed in seven habitats as shown in Table 1. During the survey, 544 replicates were recorded, distributed among the seven types of habitat encountered. A total of 331 queen conchs and 547 milk conchs were recorded in the 162 transects. Queen conchs had a mean of 2.04 and milk conchs a mean of 3.37 conchs per transect. Out of the total, 67.7% of queen conchs (224 conchs) and 1.6% of milk conchs (9 conchs) were juveniles.

1. **Behavior**

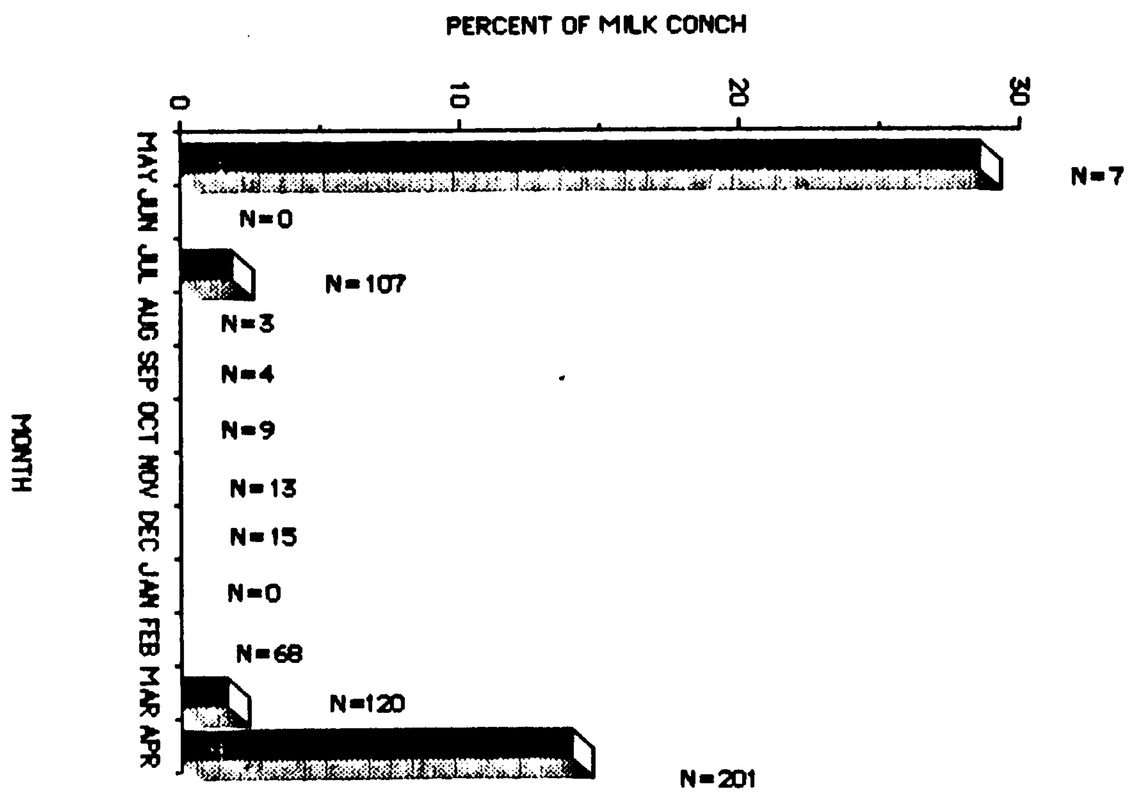
For both species, reproductive activity occurred on sand flats. Of 36 reproductively active conchs encountered, 34 were milk conchs (6.3% of adults) and 2 were queen conchs (1.9% of adults). The two queen conchs were laying eggs on sand early in October. The number of milk conchs in reproductive activity was predominant from late March to early July (Figure 3). The percentages of reproductively active milk conchs during the months of March, April, May and July were, respectively, 1.67%, 13.9%, 28.6%, and 1.87%. Fourteen milk conchs were pairing (2.6% of adults) on plain sand. Four milk conchs were copulating (0.7% of adults), two on rubble and two on the sand-flat habitat. Sixteen milk conchs were laying eggs (3.0% of adults), one on rubble, one on coarse sand, one on hard bottom, and 13 were found on plain sand. In all cases eggs were deposited on sand within the habitat previously mentioned.

Table 1

Frequency of habitat type in 544 replicates in the 162 transects studied, distance covered per habitat, the abundance of juveniles (JUV), adults (ADL), and total (TOL) nuler of queen and milk conchs, the mean of replicates, and percent of abundance, and density per 100 m of juvenile (JUV) and adults
(ADL) of each species in the specific habitat-type found. N is the number of replicates. RBL - Rubble; COS - Coarse sand; SND - Sand; MUD = Mud; PTH = Patch reef; HDB = Hard bottom; GRS = Seagrass.

HAB. TYPE	N	DISTANCE (Meters)	QUEEN CONCHS							MILK CONCHS						
			ABUNDANCE			Mean	%	DENSITY		ABUNDANCE			Mean	%	DENSITY	
			JUV	ADL	TOL			JUV	ADL	JUV	ADL	TOL			JUV	ADL
RBL	39	2228.03	105	32	137	3.51	41.4	0.4713	0.1436	0	90	90	2.31	16.4	0.0000	0.4039
COS	68	4088.35	50	12	62	0.91	18.7	0.1223	0.0293	4	128	132	1.94	24.1	0.0098	0.3131
SND	173	10442.70	30	41	71	0.41	0.3	0.0287	0.0393	0	201	201	1.16	0.2	0.0000	0.1925
MUD	37	4397.24	1	0	1	0.03	3.6	0.0023	0.0000	0	6	6	0.16	6.9	0.0000	0.0136
PTH	116	5546.07	1	0	1	0.01	0.3	0.0018	0.0000	1	0	1	0.01	1.1	0.0000	0.0018
HDB	48	4281.96	8	4	12	0.25	21.4	0.0187	0.0093	2	36	38	0.79	36.7	0.0046	0.0841
GRS	63	9825.73	29	18	47	0.75	14.2	0.0295	0.0183	3	76	79	1.25	1.2	0.0030	0.0773
TOL	544	40810.27	224	107	331	0.60	100.0			9	538	547	1.01	100.0		

Figure 3. Percent of milk conchs reproductively active (pairing, laying eggs, copulation)' from May 1985 through April 1986 in La Parguera, Puerto Rico, and number of conchs found per month (N).
MAY = May; JUN June; JUL July; AUG = August; SEP = September; OCT = October; NOV = November; DEC = December; JAN = January; FEB = February; MAR March; APR = April.


PERCENT OF MILK CONCH
0
10
20
30
MONTH
MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR
N=7
N=0
N=107
N=3
N=4
N=9
N=13
N=15
N=0
N=68
N=120
N=201

Three queen conchs were found actively feeding (with pieces of algae in the mouth), one on coarse sand, one on seagrass bed and the other on sand plain bottom. Dictyota and Laurencia were found around those queen conchs. Five conchs were moving inside the transect while we were running the transect, two queen conchs (one on rubble and one on coarse sand) and three milk conchs (two on rubble and one on plain sand).

Eighteen conchs were found half buried; of these, eleven (3.3%) were queen conchs (5 juveniles and 6 adults) and seven (1.3%) were adult milk conchs. Both species were found buried mostly on coarse sand and sand plain (Figure 4). The number of conchs observed per habitat (Table 1) and conchs buried vat correlated on milk conchs at 0.01 level ($r = 0.878$; $N = 7$), but no significant correlation was found on queen conchs ($p > 0.05$).

2. **Association between species, among and within habitats**

Association between species, regardless habitat type, was determined using a Chi-square contingency table for the whole survey. Both species were present on 37 transects, on 35 transects only queen conchs were found, on 24 transects only milk conchs were found, and on 66 transects both were absent. Association was significant ($X^2_1 = 9.60$) at the 0.001 level (Table 2). The same test was used for the 544 replicates found along the survey. The observed value of $X^2_1 = 32.74$ was significant, showing high association between conchs ($p << 0.001$) (Table 2).

Transects were then broken down into seven habitat types. On

Figure 4. Comparison of number of conchs buried on different habitat types. RBL = rubble; COS = coarse sand; SND = sand; MUD = mud; PTH = patch reef; HDB = hard bottom; GRS = seagrass.

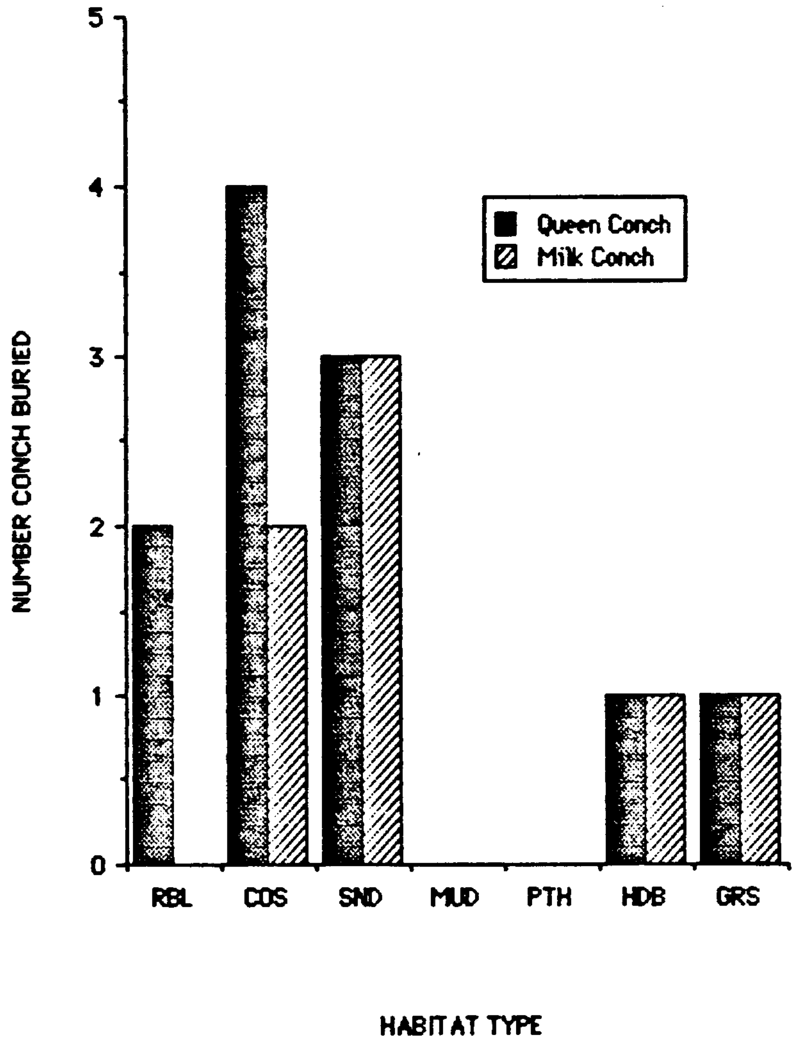

NUMBER CONCH BURIED
5
4
3
2
1
0
Queen Conch
Milk Conch
RBL
COS
SND
MUD
PTH
HDB
GRS
HABITAT TYPE

Table 2

Presence/absence data for contingency table analysis and results, using specific habitat—type on the 544 replicates in the 162 transects. HAB TYP Habitat Type; ASSOC = Association; POS = Positive; RDM = Random; RBL = Rubble; COS = Coarse sand; SND = Sand; MUD = Mud; PTH = Patch reef; HDB = Hard bottom; GRS = Seagrass; REPLI = Replicates; TRANS = Transects.

HAB TYP	Both Species Present	Queen Conch Only	Milk Conch Only	Both Species Absent	Test Used	Results	ASSOC
	Obs(Exp)	Obs(Exp)	Obs(Exp)	Obs(Exp)			
RBL	6(3)	10(13)	1(4)	22(19)	Fisher	0.0127*	POS
COS	15(8)	9(16)	8(15)	36(29)	X^2_1	11.72***	POS
SND	11(6)	19(24)	21(26)	122(117)	X^2_1	5.17**	POS
MUD	0(0)	1(1)	3(3)	33(33)	Fisher	0.92NS	RDM
PTH	0(0)	1(1)	1(1)	114(114)	Fisher	0.99NS	RDM
HDB	1(1)	5(5)	8(8)	34(34)	Fisher	0.69NS	RDM
GRS	6(5)	13(14)	11(12)	33(32)	X^2_1	0.10NS	RDM
REPLI.	39(16)	58(81)	53(76)	394(371)	X^2_1	32.74***	POS
TRANS.	37(27)	35(45)	24(34)	66(56)	X^2_1	9.90***	POS

NS = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

rubble, Fisher's exact test showed a significant positive association ($p = 0.0127$). Chi-square tests (using Yates' correction) showed high association on coarse sand at 0.10% level, and on sand plain at 2.5% level. The test was not significant at the 5% level on patch reef, hard bottom, mud, and seagrass bed habitats (Table 2).

The densities of juvenile and adults of queen and milk conchs (based on number of conch per 100 m^2) within habitats are summarized in Table 1. Densities were positively correlated on both species on the different habitat types, the correlation was significant at 5% level ($r = 0.8427$; $N = 7$).

In a Model I, Two-way (species, habitat) ANOVA (Table 3), densities of Strombus gigas and Strombus costatus did not differ significantly between the two species ($p > 0.99$; F ratio = 0.03223), but differed among habitat type ($p < 0.005$; F ratio = 17.03). Also, the species - habitat type interaction was significant ($p << 0.001$; F ratio = 9.17) as shown in Table 3.

Relative densities (per 100 m^2) of both species are given in Figures 5 and 6. A Mann-Whitney U-test comparing relative densities between species within each habitat showed queen conchs have a significantly higher density only on rubble (t_s = 2.028, $p = 0.02$).

Seven hundred ninety-four of nearest neighbor distances between conchs were taken, based on one dimension (i.e. distance along the transect center lines). Tests for inter- and intraspecific nearest neighbor distances did not include individuals found alone in transects. Two hundred thirty-seven nearest neighbor distances were measured between queen conchs. The mean distance was 8.61 meters.

Table 3

Two‾way Model I Anova of abundance of queen and milk conchs in the different habitat types.

SOURCE	SS	df	MS	F ratio
Among	0.0157801	13	0.0012139	
Conch species	0.0000047	1	0.0000047	0.03223NS
Habitats	0.0149007	6	0.0024835	17.03361***
Interaction	0.0008747	6	0.0001458	9.16981****
Error	0.1208614	1074	0.0000159	
Total	0.1366415	1087		

NS, $p > 0.05$; ***, $p < 0.005$, ****, $p < 0.001$

Figure 5. Relative densities of juveniles and adults of both species in 100 m^2 on the seven habitat types.
RBL = rubble; COS = coarse sand; SND = sand; MUD = mud; PTH = patch reef; HDB = hard bottom; GRS = seagrass.

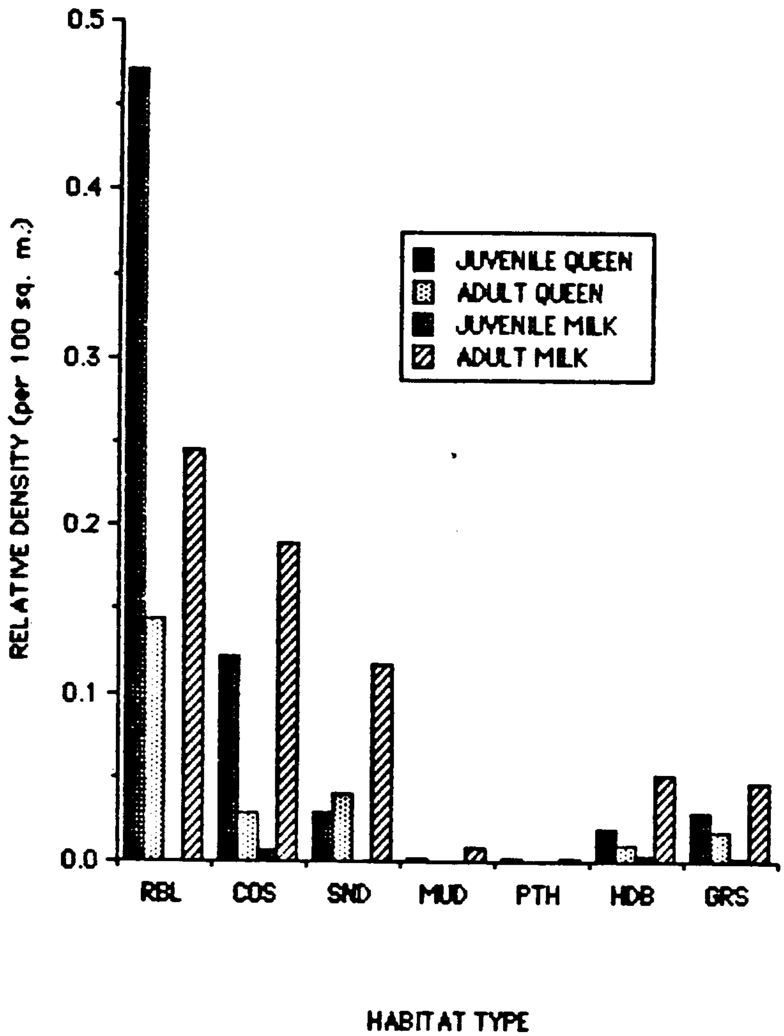
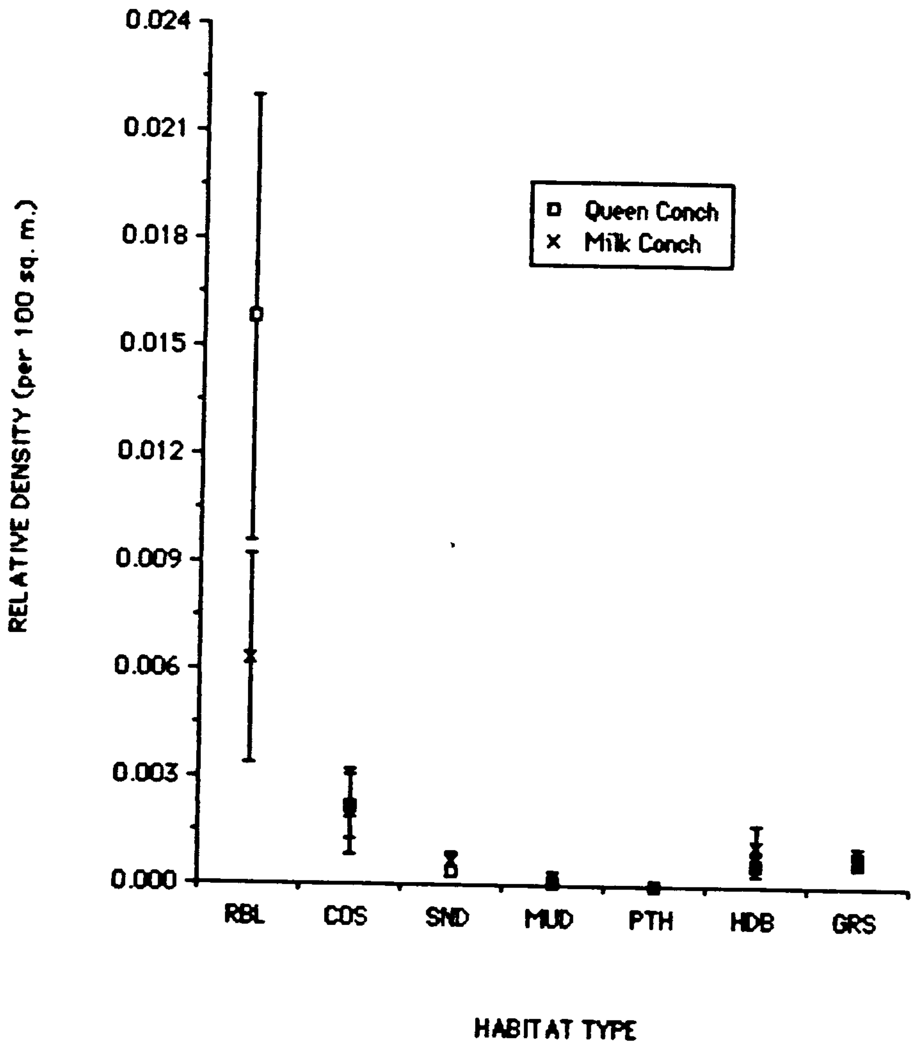

0.5
0.4
0.3
0.2
0.1
0.0
RELATIVE DENSITY (per 100 sq. m.)
JUVENILE QUEEN
ADULT QUEEN
JUVENILE MILK
ADULT MILK
RBL
COS
SND
MUD
PTH
HDB
GRS
HABITAT TYPE

Figure 6. Mean and standard error (vertical lines) of the relative densities of both species in 100 m^2 on the seven habitat types.
RBL = rubble (N = 39); COS = coarse sand (N = 68); SND = sand (N = 173); MUD = mud (N = 37); PTH = patch reef (N = 116); HDB = hard bottom (N = 48); GRS = seagrass (N = 63).


0.024
0.021
0.018
0.015
0.012
0.009
0.006
0.003
0.000
RELATIVE DENSITY (per 100 sq. m.)
Queen Conch
Milk Conch
RBL
COS
SND
MUD
PTH
HDB
GRS
HABITAT TYPE

Four hundred and fifty‾six distances were measured between two milk conchs. The mean distance was 7.29 meters. This difference in intraspecific distances was analyzed with a Mann-Whitney U-test. No significant difference was obtained ($p > 0.05$; $t_s = 1.851$).

One hundred-one measurements were taken between a queen conch and milk conch. The mean of these was 21.42 meters. This interspecific distance was significantly different, at the 0.1% and 1% levels, respectively, from the intraspecific distances found between just queen conchs or milk conchs separately ($t_s = 4.447$ and $t_s = 2.670$, respectively).

Spatial distribution pattern was tested for each species using the five transects having the highest number of conchs or clumps, respectively (Table 4). On 7 transects (4 for queen conchs, 3 for milk conchs) the measured mean distance (r_A) was greater than the average expected distance from an individual to its nearest conspecific neighbor in a random distribution (r_E) (i.e. ratio $R = r_A/r_E > 1.0$, indicating a trend toward uniform distribution), and on 3 transects r_E was greater than r_A (i.e. $R < 1.0$, indicating aggregation). Departures from randomness were significant for all but just one transect for milk conchs.

Finally differences in the frequency distribution for each species (i.e., the number of conchs of each species found per transect versus frequency, in the 162 transects) was tested to examine if both species come from population with the same distribution of abundance using a Kolmogorov-Smirnov test, with no significant difference obtained (Figure 7).

Table 4

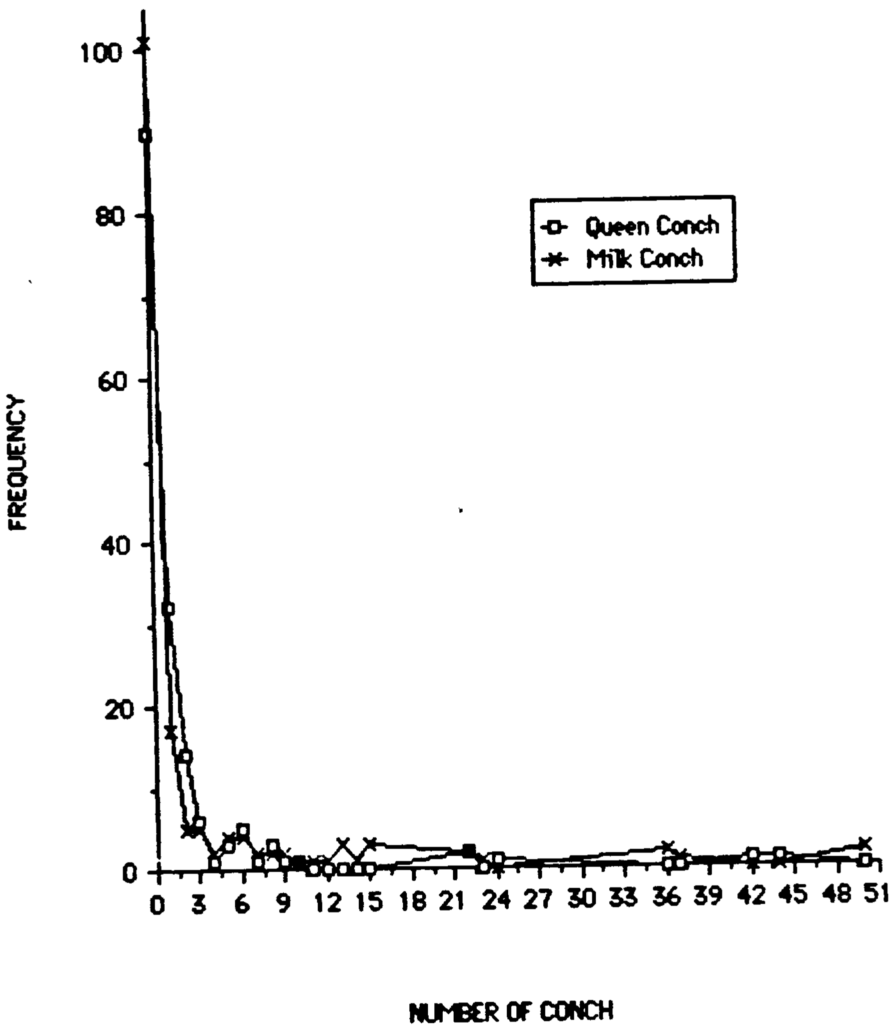
Results of the analysis of spatial pattern in conchs taking the five transects of highest number of conchs for each species. Average expected distance from an individual to its nearest neighbor in a random distribution (r_E) is compared against the measured mean distance (r_A). R (r_A/r_E) is the test statistic and is compared to the z statistic of a normal distribution.

Number conchs	Length (meters)	r_E (meters)	r_A (meters)	R ratio	Spatial Pattern	z	p
			Queen conchs				
10	134.11	6.70	13.41	2.00	E	3.16	****
22	60.43	1.37	2.01	1.47	E	2.19	*
44	65.33	0.74	1.48	1.99	E	6.60	****
22	196.08	4.46	7.24	1.62	E	2.93	***
24	183.09	3.81	0.92	0.24	A	3.71	****
			Milk conchs				
36	319.02	4.43	8.86	2.00	E	6.00	****
50	208.62	2.09	1.33	0.64	A	2.52	**
9	233.77	12.99	7.43	0.57	A	1.22	NS
36	143.90	2.00	3.69	1.84	E	4.97	****
15	28.45	0.95	1.90	2.00	E	3.74	****

NS, p>0.05; *, p<0.05; **, p<0.02; ***, p<0.01; ****, p<0.001

Spatial pattern: E = even; A = aggregated.

Figure 7. Comparison between species of number of individuals found per transect versus frequency, in the 162 transects.

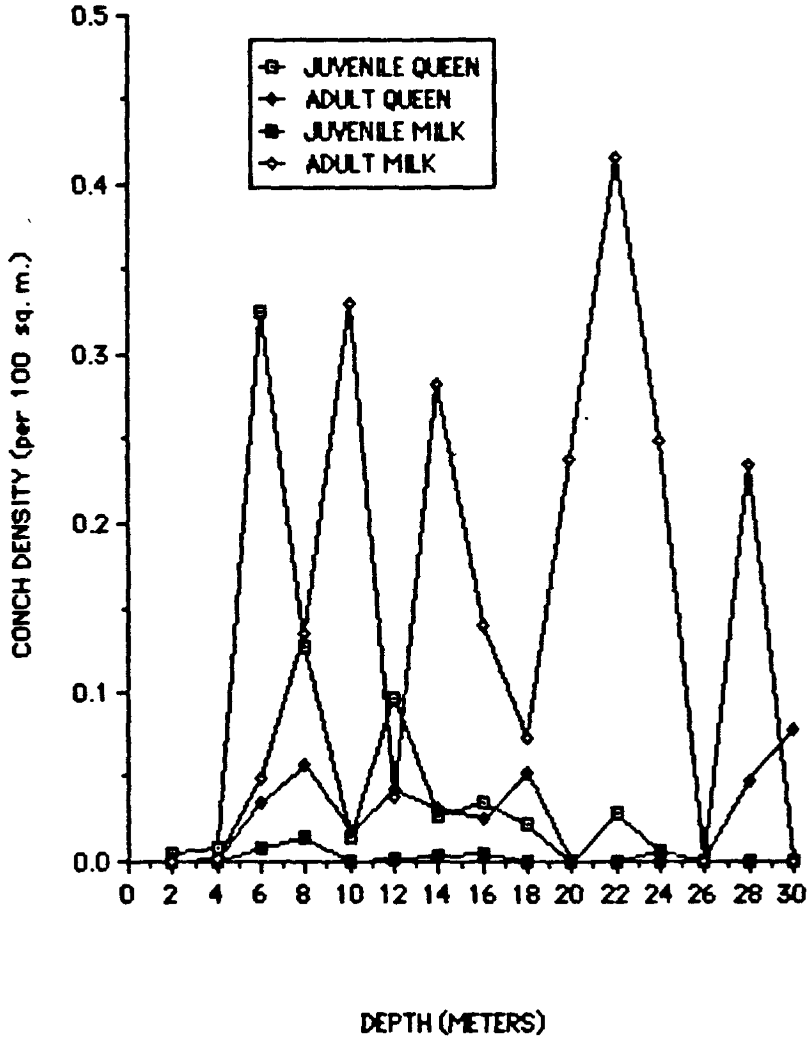


100
80
60
40
20
0
FREQUENCY
Queen Conch
Milk Conch
0 3 6 9 12 15 18 21 24 27 30 33 36 39 42 45 48 51
NUMBER OF CONCH

Densities of age classes of both species was compared to depth (at depth intervals of 2 meter). An interesting feature indicated in Figure 8 is an apparent reverse oscillation pattern between species densities with depth; the increase of one species is mirrored by the decrease in density of the other. However, no significant correlation was found at 0.05 level for total density (r = 0.0716), but the queen conchs (juvenile and adult) were positive correlated (r = 0.5654; N = 15) as were juveniles of both species (r = 0.6156; N = 15) at 0.05 level. To reduce these oscillations, depth was subdivided in 6 categories, and a tendency of milk conchs toward deeper waters was observed (Figure 9). Scaled at 5-meter intervals, again, no significant difference in total density of both species was obtained. This observation is amplified in Figure 10, showing the number of conchs per 100 m^2 versus depth scaled at 10 meters. However, scaled at every 10 meters a negative correlation was found between juvenile queen conchs and adult milk conchs (r = - 0.9998; N = 3) at 0.05 level (Figure 10).

Multiple unplanned comparisons using GT2-method indicated no significant differences between habitat-types with respect to depth distribution, except for seagrass. Seagrass showed differences in depth distribution from all habitats (i.e., its interval does not overlap those of other habitat-types) except rubble (Figure 11).

Figure 8. Density per 100 m^2 of juvenile and adult conchs of both species at 2 meter depth intervals.



JUVENILE QUEEN
ADULT QUEEN
JUVENILE MILK
ADULT MILK
CONCH DENSITY (per 100 sq. m.)
0.0
0.1
0.2
0.3
0.4
0.5
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
DEPTH (METERS)

Figure 9. Density per 100'm^2 of juvenile and adult conchs of both species studied relative to the water depth at 5 meters intervals.

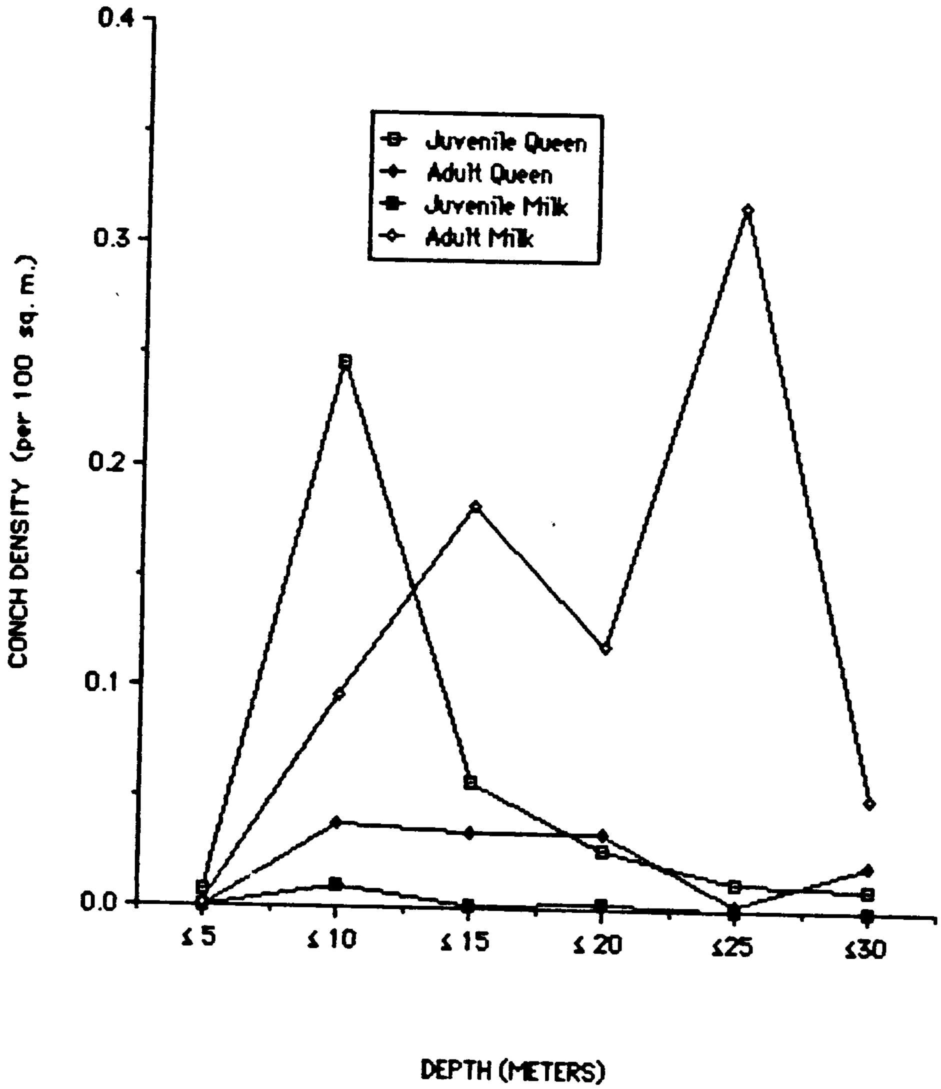
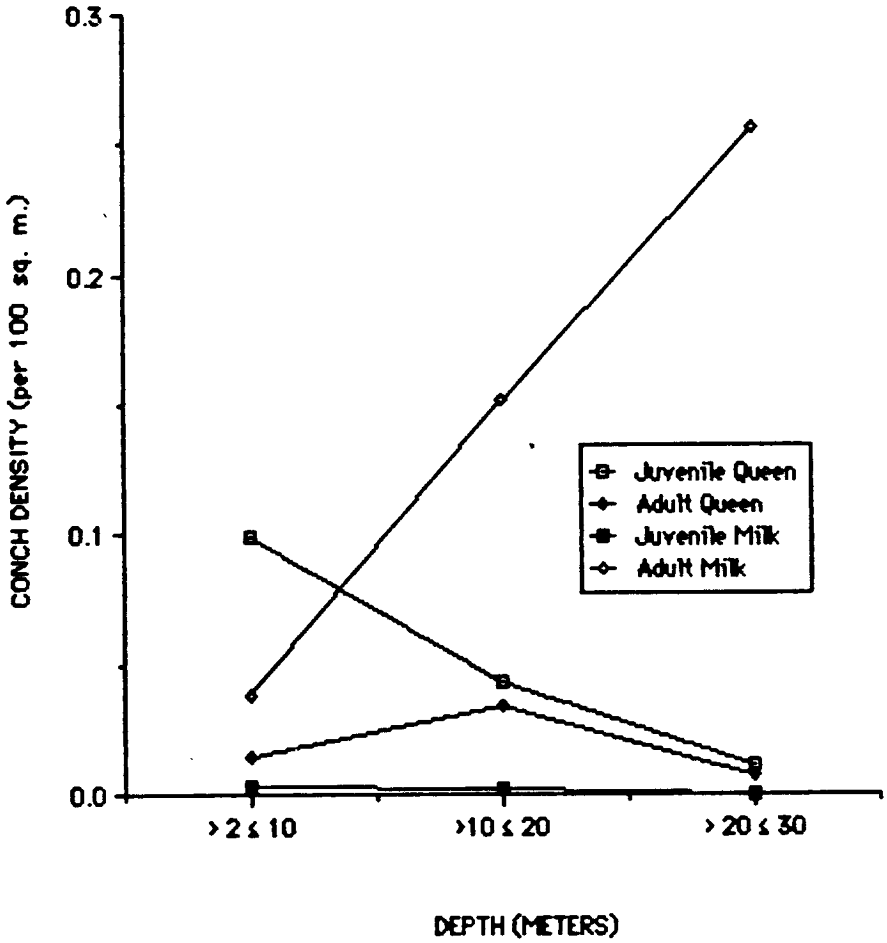
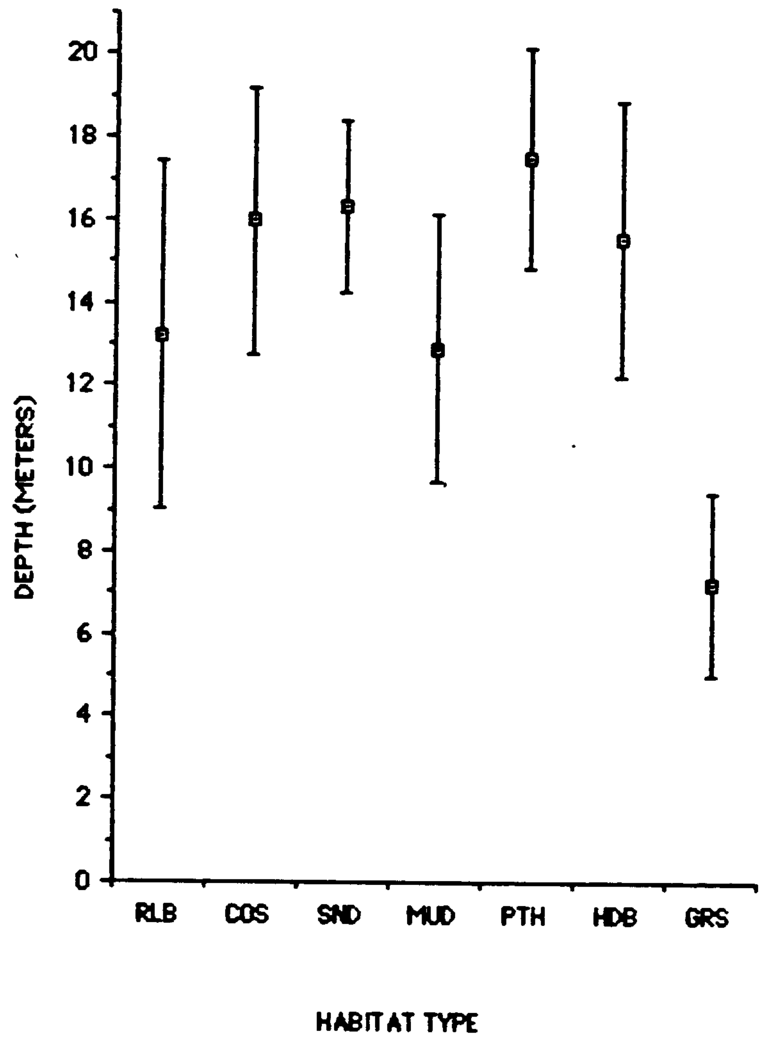

0.4
0.3
0.2
0.1
0.0
CONCH DENSITY (per 100 sq. m.)
Juvenile Queen
Adult Queen
Juvenile Milk
Adult Milk
≤ 5
≤ 10
≤ 15
≤ 20
≤25
≤30
DEPTH (METERS)

Figure 10. Density per 100 m^2 of juvenile and adult conchs of both species studied relative to the water depth at 10 meters intervals.



0.3
0.2
0.1
0.0
CONCH DENSITY (per 100 sq. m.)
Juvenile Queen
Adult Queen
Juvenile Milk
Adult Milk
> 2 ≤ 10
>10 ≤ 20
> 20 ≤ 30
DEPTH (METERS)

Figure 11. Multiple unplanned comparison among pairs of means of depth distribution based on unequal sample sizes of habitat types using GT2-method.


20
18
16
14
12
10
8
6
4
2
0
DEPTH (METERS)
RLB
COS
SND
MUD
PTH
HDB
GRS
HABITAT TYPE

DISCUSSION

Strombus costatus has been fished lightly in most places in contrast to _Strombus gigas._ The high levels of fishing pressure on queen conch threaten its future as a commercially viable resource. Studies on the mariculture potential of queen conch are currently in progress. Field studies seek, in part, to determine the optimal habitat for field release and growth. Much less is known about the milk conch. However, even with the disadvantage of its heavier shell and smaller size, the milk conch can be seen to have fishery potential as a substitute or supplement to the queen conch. Thus, habitat preferences and distribution patterns between and within species are important to know.

In the present study the percent of adult queen conchs (32.3%) compared with adult milk conchs (98.4%) was quite low, which could be due to high fishing pressure. This should be kept in mind when interpreting results. This difference, though, could also represent differential sampling—efficiency due to milk conch juveniles' smaller size and their greater tendency to remain buried (Appeldoorn 1984; 1985).

Because of the way the survey was designed, conchs that were completely buried were not recorded, just conchs showing part of the shell were recognized and counted. Both species showed a tendency to bury on sand and coarse sand habitat. These observations are consistent with those made by Randall (1964), who found juvenile _Strombus gigas_ buried in sand or gravel during the day and presumed that juvenile _Strombus costatus_ live in the same manner as _Strombus gigas._ But, both species also were seen buried on hard bottom (in small patches of sand inside of this habitat, not much larger than the conch), seagrass beds, and two queen conchs on rubble habitat.

The abundance and density of queen conchs (Table 1) indicated a predominance of juveniles in almost all habitats. No significant difference was obtained between species comparing the frequency of number of conchs per transect (Figure 7). This data suggest the two species come from populations with low densities and similar distribution of abundance.

Contingency table analysis based on presence/absence data among transects showed a high association between conchs, but the number of transects without conchs was high (66 transects or 39%). Thus, at this large scale, significance could be due to (1) mutualism, (2) independent preference for similar habitats, (3) one species preferring to be with the other, or (4) the large number of negative transects. Breaking down transects by habitat removed large-scale effects of mutual absence in some types of habitats. Significant association was still found on rubble, coarse sand, and on sand (Table 2). It should be noted that these were also the most densely populated habitats. Lack of significant association in other habitats could have been due to small sample size.

Apparently, adults of both species have a tendency to be found on sand bottom. However, although the highest total abundance of milk conchs and adult queen conchs were found on sand, the highest densities for both species were on rubble (Table 1). Distance covered in rubble habitats was less, but the density of conchs in this habitat was higher than the other habitat. Coarse sand and sand were second in terms of habitat preference (Figure 5). Conchs were less abundant on hard bottom, seagrass beds, mud, and patch reefs.

Both species have the same percent of abundance (14%) on seagrass beds, and comparing the densities in 100 m^2, milk conchs showed a higher density in this habitat. On sand, the milk conch had a higher relative density (0.11165 conchs per 100 m^2) than queen conch (0.0680 conchs per 100 m^2).

Analyses of densities using ANOVA showed no difference between Strombus gigas and Strombus costatus, and the high correlation observed between species suggest association between the species. There was a significant difference among habitat type in the ANOVA, thus indicating the same overall habitat preference. However, the significant interaction term indicates that a given habitat type appears to affect the two species in different ways, which may reflect the slight preference of one species toward specific habitats relative to the other species. This conclusion is supported by the queen conch's greater preference for rubble habitat (Figure 6). Thus, on a large scale both species preferred to be on similar habitats, but on a smaller scale milk conchs preferred to be on fine—sediment areas while queen conchs preferred rubble areas.

Intraspecific distances between conchs showed no differences between species, but were shorter in contrast with those distances observed between the two different species. This negative association at a fine scale may be due to habitat type, and our categories may still be too coarse and broad. However, this may represent a true effect, with conchs preferring conspecifics at this scale.

The spatial pattern analysis showed queen conchs to be spaced more evenly within clumps (high density transects), at a fine scale, suggesting possible interindividual interaction that may be due to competitive for limited resources such as food. For milk conchs, two transects showed aggregations within clumps, and three were evenly spaced. The intensity of the pattern (density varied from place to place) was high, departing from randomness in both species.

There were no significant differences observed in depth distribution scaled at 2 meters. Mostly, both species overlapped greatly at all depths studied in this survey. This contrasts with studies of Percharde (1966) in Trinidad and Tobago who describes Strombus costatus as usually in shallower water compared with Strombus gigas. Juvenile queen conchs range in depth from 6 to 18 meters with fluctuations and a peak at 6 meters, while adult queen conchs range from 6 to 30 meters with less oscillations and a peak at 30 meters. Juvenile milk conchs had a low abundance, so cannot be compared with adults, but they showed a slight tendency to range from 6 to 16 meters like juvenile queen conchs. Adult milk conchs had a range slightly deeper (from 10 to 28 meters) with a peak at 22 meters. Comparison between juvenile queen conchs and adult milk conchs at 10¯meter scale resulted in a significant negative correlation. This indicates a predominance of juvenile queen conchs in shallow waters (less than 20 meters) and adult milk conchs in waters deeper than 20 meters. Adult queen conchs showed a bell¯shaped distribution curve with predominance in intermediate waters (10 to 20 meters). These observations were consistent among habitat types. Habitat types with higher density of conchs (i.e. rubble, coarse sand, and sand) overlapped among depth range. Overfishing is, no doubt, disturbing the queen conch population and pattern of distribution, and this curve may not represent their real preference. However, the generally greater abundance of adults, both of queen and milk conchs, in deeper waters relative to juveniles is expected since it is well known that conchs' undergo a progressive migration to deeper waters with age (Hesse, 1979).

In summary, these results showed that there is an association between Strombus gigas and Strombus costatus. When comparing densities in those transects that had both species, as one species increased, so did the other species. They were positively associated among habitats and within rubble, coarse sand, and sand habitats. While their habitat ranges were broad and generally similar, species¯specific habitat preferences were noted. Association was not evidenced at fine scales, as intraspecific distances were less than interspecific distances.

The queen conch is described as being bigger, solid but lighter than milk conch (Warmke and Abbott, 1975; Appeldoorn, 1984), and as being more active than milk conch (Appeldoorn, 1985). This combination of behavioral and morphological characteristics may give Strombus gigas competitive advantage with respect to their habitat preference. The removal of Strombus gigas due to heavy fishing may have opened ecological space to Strombus costatus, providing access to more food and area, resulting in an increase in its abundance. As suggested the negative association between species and the repulsion of individuals within intraspecific clumps, at a fine scale, inter and intraspecific density‾dependent processes may be active. Indeed in culture both species have shown progressively reduced growth with increasing density (Appeldoorn and Sanders 1984; Sidall, 1984). Thus, with higher queen conch densities milk conchs may become more restricted in habitat use, being forced into areas not preferred by queen conchs (i.e. mud or patch reefs).

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