Seasonality in reproductive activity and larval abundance of queen conch *Strombus gigas*

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Abstract.–Reproductive behavior and larval abundance of queen conch *Strombus gigas* L. were investigated near Lee Stocking Island, Bahamas, with the primary purpose of determining relationships between physical variables, spawning frequency, and larval abundance. Monthly observations made by divers at the offshore spawning site showed that copulation increased as a linear function of bottom water temperature from April until the end of July, when maximum summer temperature was reached. Pairing, copulation, and egg-laying were all positively correlated with photoperiod throughout the study period. The last pairing and copulating conch were observed in the middle of the warmest period in August suggesting that stimuli other than temperature, such as declining photoperiod, induce the end of reproductive activity. The last egg mass was found in early October.

There was a significant correlation between spawning activity at the offshore reproductive site and larval abundance in the adjacent downcurrent inlet. The first conch veligers were found in plankton tows made in early June, five weeks after the first egg masses were observed at the end of April. High larval density was confined to July and August. Advanced-stage larvae, close to metamorphosis, were found only in the vicinity of a shallow, benthic nursery habitat. Comparison of reproductive season in queen conch populations of the Caribbean region showed no latitudinal trend. In all areas, reproduction was associated with long days and warm temperatures. Production of conch larvae at the time of high water temperature and steady trade wind conditions may promote rapid larval development and facilitate transport of the veligers to inshore nursery habitats.

Manuscript accepted 31 January 1992.
Fishery Bulletin, U.S. 90:161–170 (1992).

The queen conch *Strombus gigas* L. is the second most important fisheries species in the Caribbean region, after spiny lobster *Panulirus argus* (Brownell and Stevely 1981). Consequently, its general life history is well known (Randall 1964, Brownell and Stevely 1981, Berg and Olsen 1989). Sexes are separate and sexual maturity occurs at about 3½ years of age, a few months after the flared lip is formed (Egan 1985, Wilkins et al. 1987, Appeldoorn 1990). Fertilization is internal and copulation may precede spawning by several weeks (D'Asaro 1965). An individual female may spawn six to eight times during a single reproductive season (Davis and Hesse 1983). An egg mass, usually laid on clean, coral sand, takes 24–36 hours to produce and consists of a single continuous egg-filled tube folded upon itself to form a kidney-shaped aggregate of eggs and sand about 15 cm in length. Robertson (1959) estimated that between 385,000 and 430,000 eggs were laid in a single egg mass. Eggs hatch after 5–6 days; pelagic veligers remain in the water column for 18–40 days prior to metamorphosis (Randall 1964, D'Asaro 1965, Brownell 1977, Davis et al. 1987, Boidron-Metairon 1988, Mianmanus 1988).

Reproductive seasonality in queen conch has been reported for different sites within the Caribbean region (see Fig. 6), but the mechanisms which regulate reproductive behavior are poorly known. In this study, we provide the first report on abundance and seasonality of queen conch veligers in the field, and examine relationships between adult habitat, reproductive activity, temperature, photoperiod, and larval abundance.

Methods and materials

Study site

This study was conducted near Lee Stocking Island (southern Exuma Cays), Bahamas, an area known for high abundance of queen conch (Fig. 1). The islands and cays of the Exuma chain are bordered on the west by the shallow Great Bahama Bank (mean depth ~3 m) and on the east by the deep Exuma Sound. Waters from the Exuma Sound flow onto the Bank through numerous passes on the flood tide and are mixed with Bank water by wind-driven circulation. Surface drogue studies (N.P. Smith, Harbor Branch Oceanogr. Inst., Fort Pierce, FL 34946, unpubl. data) indicate that at the north end of Lee Stocking Island, water flows through Adderley Cay cut toward Shark Rock. At the south end of the Island, water flows through Rat Cay cut to the west between Barraterre Island and Children's Bay Cay. Most juvenile queen conch are located in shallow seagrass habitats on the Exuma Bank; largest populations are found near Shark Rock and southwest of Children's Bay Cay.

In Exuma Sound, approximately 1 km to the east of Lee Stocking

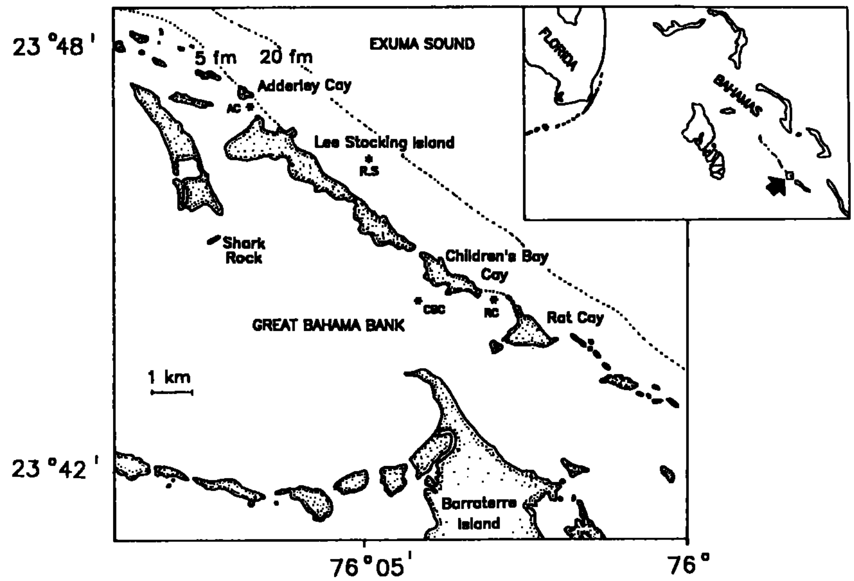

Figure 1
Map of the Lee Stocking Island, Bahamas, study site showing plankton sampling stations (*). RS = location of the Reproductive Site, where observations and plankton collections were made; RC = Rat Cay cut; AC = Adderley Cay cut; CBC = Children's Bay Cay nursery site.

Island, there is a coral ledge at which depths increase rapidly from 10 to 18m. Beyond the ledge is a 1km-wide platform with a gradual slope from 18 to 24m. Seaward from the platform, depth increases rapidly to the deep basin of Exuma Sound. This geomorphology is typical of the western side of the Exuma Sound. Highest number and density of adult *S. gigas* occur on the 18m-deep platform, which is beyond the normal free-diving range of conch fishermen. In this area, more than 99% of the conch are sexually mature (Stoner and Sandt 1992). In the colder months, the conch are found on algae-covered hardbottom; they move to sand for mating and egg-laying in the summer.

A study site of approximately 12 ha surface area on the 18m platform was chosen for the investigation of reproductive behavior and habitat association in adult conch (Fig. 2). The particular location, north of the 10m coral ledge, was selected because of an abundance of adult conch and close proximity of feeding and spawning habitats (Stoner and Sandt 1992). A scale map of the site was constructed from compass bearings and distances measured by scuba divers along the sides of primary habitat features or boundaries. Figure 2 shows all prominent features between the coral ledge and the 23m isobath.

Observations on reproductive behavior were made in three habitat types (1) Five hard-bottom domes (called "mounds"), each surrounded completely by bare sand, were examined. All of the mounds (designated with the letter "M" in Fig. 2) were located at depths of 18m at the base with tops between depths of 12 and 14m. (2) Sand habitats were divided into two major regions. S1 is the extensive sand flat between the 10m reef front and the mound zone. S2 is the sand area within the mound zone. (3) Rubble and boulder areas are found at the base of the 10m reef in a narrow band, with an extensive boulder field (B1) at the southeast end of the study site. The mounds and rubble, particularly in the B1 area, are covered with a turf of green algae (primarily *Cladophoropsis* spp.), plus abundant erect forms such as *Halimeda* spp. An area of mixed hardground, sand, and coral heads (H1) extends to the north and east of the study site.

Reproductive activity

Reproductive behavior was surveyed for 14 months, on a monthly basis during the period of highest activity (March–October 1988) and at 6–8 week intervals during January–February 1988 and November 1988–February 1989. Longer sampling intervals were used in the winter because preliminary observations near Lee Stocking Island in previous years indicated that no reproductive behavior occurs between November and March. During each survey, spanning 5–15 days, a scuba diver search for adult conch was made on mounds M1, M3, M4, and M5, in the boulder area (B1), in the rubble area (at the base of the coral ledge), and in both sand zones S1 and S2. During each survey period, all conch were counted on each of the mounds and at least one-half of the B1 area was examined. Very few conch were found on M2 and this mound was abandoned early in the study. After determining that most reproductive activity occurred on sand and not on hardground or rubble (Table 1), the sampling protocol was modified to locate at least 100 individuals on sand for each survey. During winter months, less than 100 conch were located on sand in several days searching; however, 100–300 animals were observed per month during most of the reproductive season.

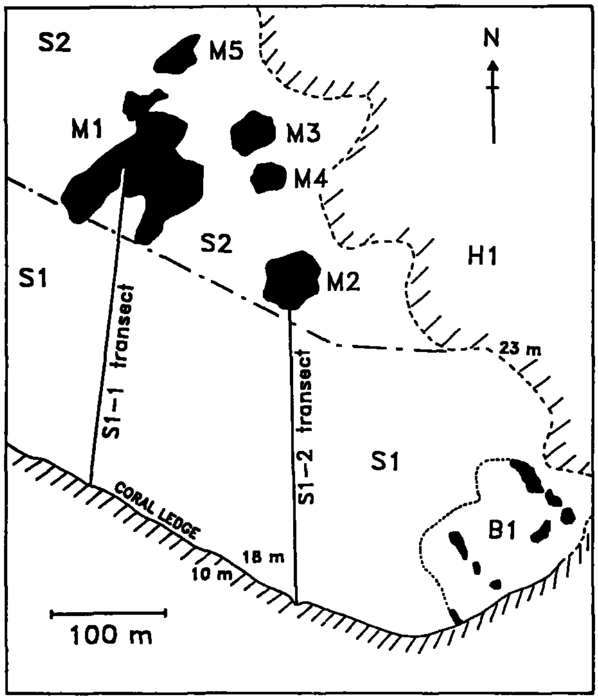

Figure 2
Map of the Reproductive Site (see Fig. 1) showing elevated Mounds (M), sand habitat (S1 and S2), boulder area (B1), and area of mixed hardground and sand (H1). S1-1 and S1-2 are transects over which density of conch were determined.

Table 1
Numbers and (percentages) of queen conch engaged in reproductive activity on three substratum types near Lee Stocking Island, Bahamas, 1988. Values for pairing and copulating represent number of male/female pairs.

	Behavioral type		
Substratum	Pairing	Copulating	Egg-laying
Sand	51 (94.4)	28 (84.4)	148 (99.3)
Rubble	0 (0.0)	2 (6.1)	0 (0.0)
Hardground	3 (5.6)	3 (9.1)	1 (0.7)

Each individual conch was classified in one of the following reproductive categories. (1) Pairing: Two conch were aligned, with the anterior part of the shell of one animal overlapping the posterior part of the shell of the other; but copulation was not observed. (2) Copulating: Animals were engaged in copulation, with the verge of the male beneath the mantle of the female. (3) Egg-laying: A female was actively laying an egg mass. (4) Non-reproductive: Conch was not engaged in reproductive behavior.

Seasonality in reproductive behavior was quantified by recording the percentage of total animals on sand in each behavioral category. Notes were made on the locations and substratum types (sand, rubble, hardground) where pairing, copulating, and egg-laying conch were found. Conch were measured for total shell length (spire to siphonal groove) and greatest shell lip thickness (approximately two-thirds of the distance posterior from the siphonal groove). Shell measurements were made to the nearest mm.

To estimate seasonal abundance of conch on sand, two quantitative transects across the S1 sand area (transects S1-1 and S1-2; Fig. 2) were examined each survey period. The transect surveys were made by a scuba diver who counted all adult conch within a known range while being towed 5 m above the sediment. High water transparency resulted in a mean transect width of 29 m (SD 6; range 20–40 m), which was measured with a tape on each survey date. The total survey area for each transect was calculated on the basis of horizontal visibility and the fixed distance of each transect line. For additional information on the abundance of queen conch on sand during the reproductive season, all adult conch were counted in circles of 20 m radii at locations of highest conch density in August 1987 (*n* 7 circles), and in June (*n* 2) and July 1988 (*n* 2).

Physical measurements

To provide information on sediment grain-size and organic content in the spawning habitat, sediment samples were taken from the surface adjacent to females laying eggs in August. Only eight samples were collected; however, the sediment in sand areas S1 and S2 appeared to be of uniform grain size. An effort was made to collect sediment samples from throughout the study site. Sediments were frozen until laboratory analysis. Organic content was determined by drying a subsample (~100 g wet wt) at 80°C to constant weight and incinerating at 500°C for 4 hours. Organic content was quantified as the percent difference between dry weight and ash-free dry weight. Another subsample (~50 g wet wt) was examined for granulometric properties. The sample was washed to remove salts and extract the silt-clay fraction (<62 μm). Silt-clay was analyzed with standard pipette procedures (Galehouse 1971), and the sand fraction with standard dry sieve procedures (Folk 1966).

Bottom-water temperature was recorded with a Ryan Instruments Temp Mentor placed at 17 m depth, near the base of the coral ledge. The thermograph recorded temperature with a precision of 0.2°C every

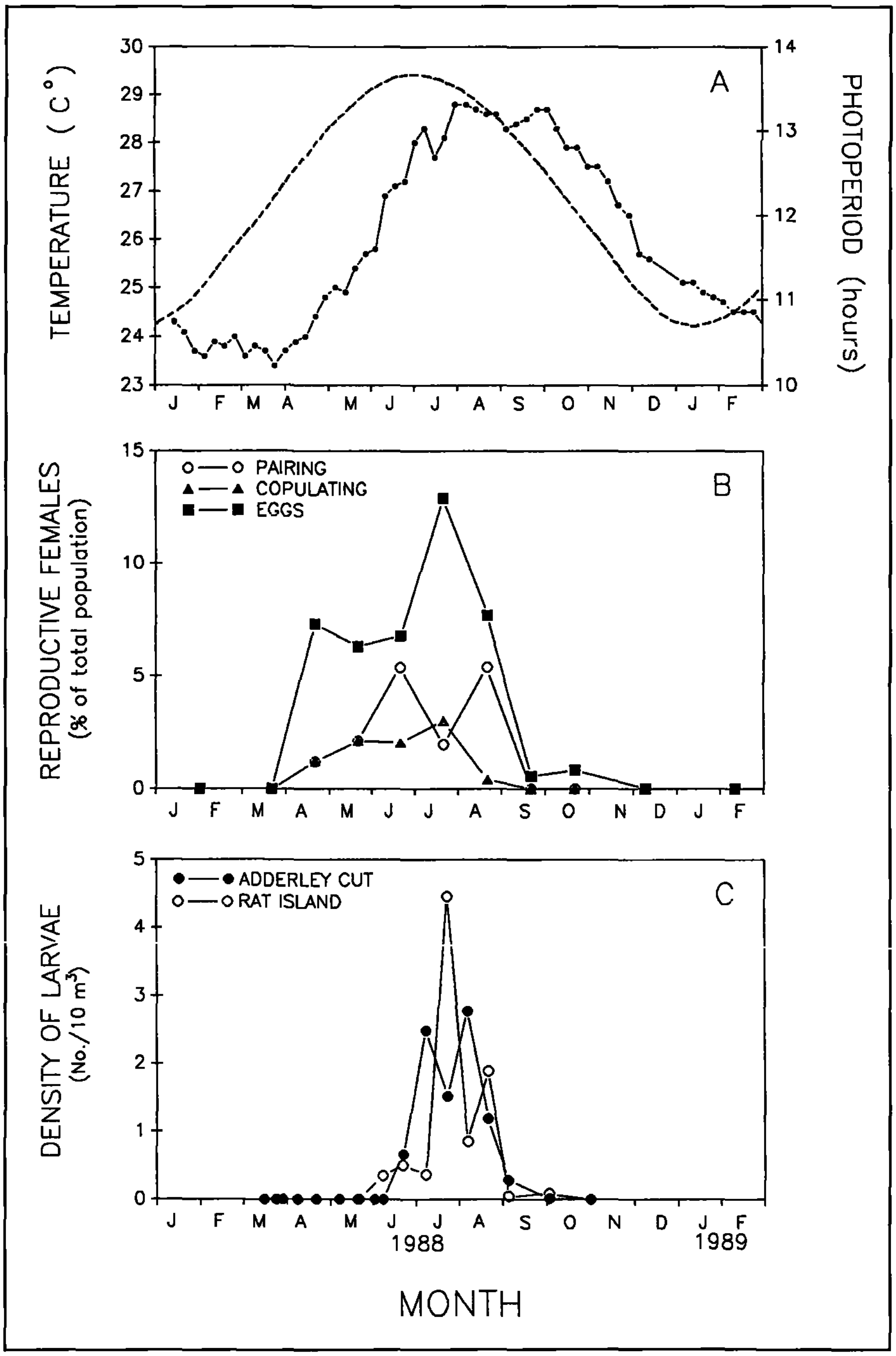

Figure 3
(A) Bottom-water temperature at 17 m depth with 7-day averages (solid line) and photoperiod in number of hours between sunrise and sunset (dashed line). (B) Number of queen conch *Strombus gigas* females on sand engaged in various reproductive activities. (C) Number of conch larvae in Rat Cay and Adderley Cay passes, January 1988–February 1989.

30 minutes; 7-day averages were generated and plotted (Fig. 3A). Surface-water temperature and weather conditions were recorded each time that plankton was collected.

To examine potential correlation between reproductive seasonality and photoperiod, a yearlong photoperiod curve (Fig. 3A) was constructed for the study site. Numbers of hours and minutes between sunrise and sunset were calculated for local latitude at 9-day intervals using the Nautical Almanac.

Plankton collections

Daytime plankton collections were made for queen conch veligers from mid-March to October 1988. For seasonal analysis of larval abundance, collections were made every 2 to 3 weeks in the pass between Lee Stocking Island and Adderley Cay (Adderley Cay cut) and in the pass between Rat Cay and Children's Bay Cay (Rat Cay cut) (Fig. 1). Additionally, collections were made over the area surveyed for reproductive activity (Reproductive Site) with the primary purpose of detecting low densities of conch larvae at the onset and end of the reproductive season. Collections were not made at the Reproductive Site during peak reproduction, between July and mid-August. To examine densities and size-frequency of larvae on Exuma Bank, four collections were made over a known nursery for *S. gigas*, west of Children's Bay Cay (Fig. 1). This site is approximately 3.4 m deep and vegetated with the seagrass *Thalassia testudinum*.

In the passes, plankton were sampled during the first 2 hours of the flood tide; on the bank, tows were scheduled during the last 2 hours of flood tide. Plankton collections were made by towing a 0.5 m diameter conical net, 5 m long, with 202 μm mesh. Two tows were made at each site. Because the location of larvae in the water column was unknown, collections at the Reproductive Site were made by towing the net at 9 m depth (midwater column) for 10 minutes, then raised near the surface at 1.5 m depth for another 10 minutes. At the other three sites where there was considerable vertical mixing and shallow depth, the net was towed for 20 minutes in the upper 1.5 m of the water column. Water volume sampled was calculated using a calibrated General Oceanics flowmeter, and larval abundance was expressed in numbers of veligers per 10 m^3.

To identify larvae, samples were refrigerated, sorted live (within 4 hours), and compared with laboratory-cultured larvae of the two most abundant *Strombus* spp. in the central Bahamas, *S. gigas* and *S. costatus*. Two other strombids occur in the Lee Stocking Island area (*S. gallus* and *S. raninus*); however, both are very rare relative to *S. gigas* and neither has been observed on the windward side of the island or in the inlets. Shell length, shell width, and shape of the shell tip were the principle criteria used to identify early-stage larvae. Number and shape of shell whorls and other shell characteristics were used to identify advanced larval stages. Measurement of shell length, from apex to siphonal edge, was made with an ocular micrometer and reported in microns for all intact shells.

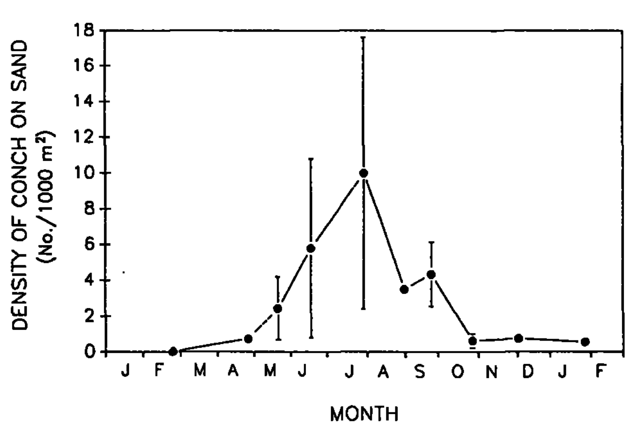

Figure 4

Density of queen conch *Strombus gigas* on sand at the Reproductive Site, off Lee Stocking Island, Bahamas, January 1988–February 1989. Values are mean ±SE for two transects.

Results

Conch reproduction

The reproductive season for *Strombus gigas* at Lee Stocking Island extended from mid-April to early October. The beginning of the season was marked by a massive migration of conch from hardground (mounds, rubble, and boulder areas) to sand habitats (Fig. 4) where first copulation, pairing, and spawning were observed on 14, 15, and 25 April 1988, respectively. In subsequent months, virtually all reproductive behavior occurred on sand (see later). The number of females engaged in reproductive activity increased gradually from April (9.7% of total sampled population) to July (18%) (Fig. 3B). In August, 13.8% of the population were reproductively active females; the percentage declined to less than 1.0% in September and October. Last copulation and pairing were seen in August, but egg-laying was observed through September. The last egg mass was discovered on 5 October 1988.

The number of reproductive conch increased with conch density on sand (Fig. 4) from January and February (0 conch/1000 m^2) to July (10 conch/1000 m^2). Density decreased after the beginning of August and was 0.61 conch/1000 m^2 in October. Conch were aggregated on some dates and not distributed evenly along the transect lines. Large error bars in Figure 4 show that the two transect lines frequently had different densities of conch during the primary reproductive season. In August 1987, measurements in areas with high conch densities ranged from 11.1 to 20.7 conch/1000 m^2. Values as high as 29.7 conch/1000 m^2 (SE 2.0) were found in June 1988.

Low bottom-water temperatures were observed from early March to early April 1988 (near 23.6°C) (Fig. 3A). First pairing and copulating conch were seen at a temperature of 24°C in mid-April, and the first egg-laying female was found at 24.5°C. The number of copulating females increased as a linear function of bottom water temperature until the reproductive maximum (r 0.916, F 15.726, p 0.029; March through July 1988). There was no significant correlation between egg-laying and temperature (p 0.061) and pairing and temperature (p 0.285). Bottom temperature was relatively constant (28.3–28.8°C) from the end of July through September; the last pairing and copulating conch were observed during this period. Temperature decreased rapidly after September, and the last egg mass was found on 5 October. Water temperature was 26.5°C by late November 1988, decreasing to 25.1°C in late December.

All pairing and copulation were confined to the season with photoperiod greater than 12 hours, while egg-laying was observed until day length declined to 11 hours (Fig. 3A,B). Highest correlation occurred between length of day and copulation (r 0.870, F 24.838, p 0.001), but significant correlations were also found between photoperiod and both pairing (r 0.709, F 8.064, p 0.022) and egg-laying (r 0.838, F 18.896, p 0.002).

A few conch were buried partially in sand in mid-October 1987 and again in January and early February 1988. Burrowing was not seen again until mid-September 1988. In November, a few conch were buried

Table 2
Density of queen conch larvae at the Reproductive Site offshore from Lee Stocking Island, Bahamas, and at the nursery site near Children's Bay Cay on Exuma Bank, 1988. Values are numbers of conch larvae/10m³ ± SD (*n* 2).

	Location	
Date	Reproductive Site	Children's Bay Cay
15 March	0±0	–
28 March	0±0	–
7 April	0±0	–
20 April	0±0	–
19 May	0±0	–
2 June	0.26±0.11	–
6 June	0.04±0.03	–
16 June	0.99±0.25	–
29 June	0.30±0.09	–
13 July	–	0.82±0.23
28 July	–	1.35±0.47
12 August	–	0.77±0.41
23 August	0.77±0.32	–
14 September	–	0.17±0.10
23 September	0±0	–
6 October	0±0	–

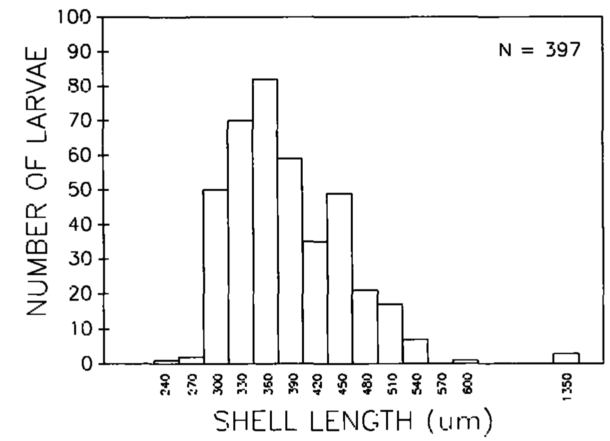

Figure 5
Length-frequency distribution for veligers collected near Lee Stocking Island, Bahamas, May–September 1988 (*n* 397).

in sand-filled depressions on the mounds. Some were almost entirely covered with sand and the shells were devoid of algae. It is possible that conch in the sand habitat were underestimated during winter months because of burial behavior; however, tag return data (Stoner and Sandt 1992) suggest that most adult conch move to hardground or rubble for the winter months.

The mean shell length of pairing, copulating, and egg-laying females ($\bar{x}$ 226mm, SD 23.6, *n* 180) was 2.3% larger than that for males in reproductive behavior ($\bar{x}$ 221mm, SD 17.4, *n* 180). However, pairwise ANOVA, using female-male pairs as statistical blocks, indicated no significant differences in shell length among pairs (F 1.155, p 0.358), or between females and males (F 0.847, p 0.366). Results were similar in the case of copulating conch (among pairs, F 1.105, p 0.430; between females and males, F 0.112, p 0.743).

Reproductive activity in *Strombus gigas* was rare on hardbottom substrata (i.e., mounds, rubble and boulder areas). Ninety-four percent of the pairing conch were observed on sand, none were observed on rubble, and only 5.6% were found on hardbottom (Table 1). Eighty-five percent of copulating conch were found on sand, with small percentages found on rubble and hardbottom.

A total of 149 egg-laying females were observed between April and October 1988; except for one female found laying eggs on hardbottom in area B1, all were found spawning on sand (Table 1). Nine observations of simultaneous pairing and egg-laying were made; only one simultaneous copulation and egg-laying was observed. All 148 females on sand were oriented perpendicular to sand waves, with the anterior end of the shell elevated near the crest of the wave and the egg mass near the trough. Mean grain size of sediments collected immediately adjacent to egg-laying females was 0.389 θ (774μm) (SD 0.248, *n* 8), which is in the coarse-sand classification. Sediments were poorly sorted as indicated by a mean sorting coefficient of 0.967 θ (SD 0.302, *n* 8). Organic content was 3.45% of dry weight (SD 0.69, *n* 8).

Larval abundance

Conch larvae were first collected at the Reproductive Site on 2 June 1988 at a density of 0.26 larvae/10m³ (Table 2), 5 weeks after the first egg mass was discovered (Fig. 3B). Surface- and bottom-water temperatures were 27.5°C and 25.8°C, respectively. Veliger density at the Reproductive Site ranged from 0.04 larvae/10m³ on 6 June to 0.99 larvae/10m³ on 16 June. No plankton collections were made at this site between 29 June (0.30 larvae/10m³) and 23 August (0.77/10m³); during this interval, emphasis was shifted to the Children's Bay Cay site on Exuma Bank.

Larvae were not found until 6 June in Rat Cay cut and 20 June in Adderley Cay cut (Fig. 3C). By the end of June, surface-water temperature was near maximum (29.5°C and 29°C) in the two inlets. Highest density in the tidal passes was 4.46 larvae/10m³ on 21 July at the Rat Cay cut, concurrent with maximum egg-laying frequency (13%) and surface and bottom temperatures

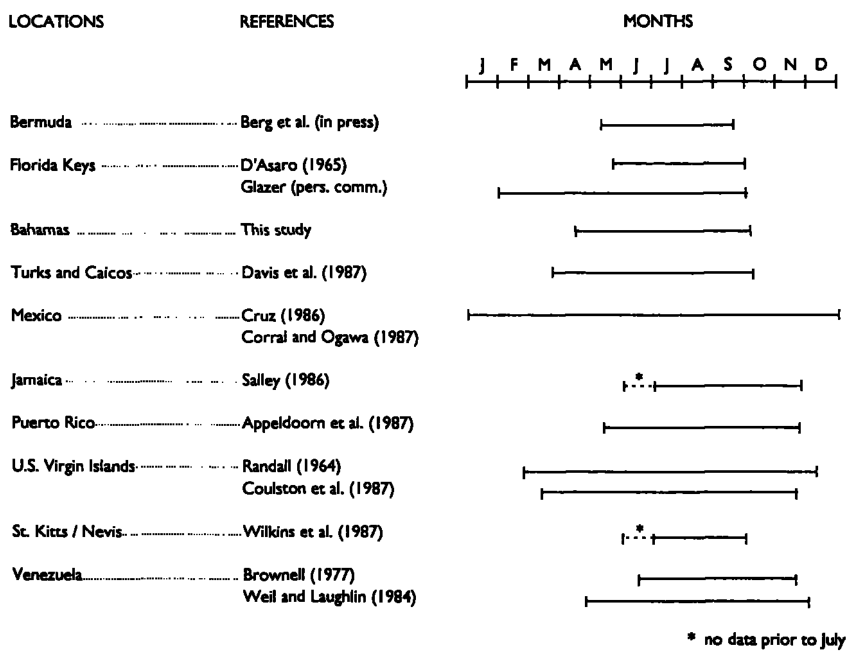

Figure 6

Reproductive seasons reported for *Strombus gigas* in the Caribbean region. Seasonality refers to any observations of reproductive behavior (copulating or egg-laying), and does not include histological results (see text). Locations are arranged in order of latitude from north (top) to south (bottom). Data for Mexico are for Banco Chinchorro on the Caribbean coast.

density was 0.82/10 m^3 (Table 2) and surface-water temperature was 31°C. Highest density at this site (1.35 larvae/10 m^3) occurred on 28 July, when numbers of copulating and spawning females were highest at the Reproductive Site. On 12 August, larval density declined to 0.77 larvae/10m^3, concurrent with declines in reproductive activity. Larvae were last collected over the nursery area on 14 September at a density of 0.17 larvae/10 m^3; at this time, surface-water temperature on the Exuma Bank was 30°C and reproductive activity was near zero.

During the reproductive season, all but three of the conch veligers collected were between 340 and 600 µm in shell length ($\bar{x}$ 384 µm, SD 64, n 394) (Fig. 5). The largest three larvae (1350 µm) were removed alive from samples collected at the bank site in mid-July. Metamorphosis occurred within 24 hours in all three larvae.

of 29.8°C and 28.1°C, respectively. Larvae continued to be found at the pass sites until the end of September, but were not present at the Reproductive Site after 23 August. No veligers were collected at any of the sites in October, concurrent with observation of the last egg mass. At this time, surface-water temperature had declined to 27.2°C and bottom temperature was 27.5°C.

Density of larvae at the Adderley Cay cut site showed a direct correlation with the percentage of females copulating (r 0.952, F 68.312, $p<0.0001$) and egg-laying (r 0.860, F 19.889, p 0.003). Densities of larvae at the Reproductive Site and the Rat Cay cut site were not correlated with copulation or egg-laying ($p>0.05$). Maxima in larval abundance occurred during months with highest water temperature, but there was no significant correlation between abundance of larvae and surface-water temperature at Adderley Cay cut (F 5.232, p 0.056) or Rat Cay cut (F 0.514, p 0.494) during the reproductive season (June–October). Log-transformation of the data did not improve the correlation coefficients.

Plankton collections over the nursery area, west of Children's Bay Cay, were begun on 13 July 1988; larval

Discussion

At Lee Stocking Island, the reproductive season for queen conch began in April and ended in early October. Although differences by a few months were found in the occurrence of reproductive behavior, there was no apparent trend related to latitude in beginning, end, or length of reproductive season in queen conch from Bermuda to Venezuela (Fig. 6).* The longest reproductive season was reported for the Caribbean coast of Mexico (Banco Chinchorro) (Cruz 1986, Corral and Ogawa 1987), where egg masses were found year-round. One of the shortest reproductive seasons was reported by D'Asaro (1965) for the Florida Keys, but more recent, intensive observations have shown that queen conch may spawn over at least a 9-month period in Florida (R. Glazer, Dep. Nat. Resour., Marathon, FL 33050, pers. commun., Sept. 1990).

* For geographic comparison, "reproductive seasonality" refers to any reported observation of pairing, copulation, or egg-laying in queen conch, except where noted in the text. Histological data are not included.

Geographic comparisons of seasonality in reproduction must be interpreted cautiously due to different methods, frequency and number of observations, annual variation, and different habitat types. For example, Brownell (1977) found that egg-laying in Los Roques, Venezuela, extended later into the season in deep water than in shallow water. Quantitative measures of reproductive activity provide a basis for examining mechanisms of seasonality, which is more useful than records of reproductive occurrence. In all studies that present seasonal curves for reproductive behavior or numbers of egg masses (e.g., Davis et al. 1984, Weil and Laughlin 1984, Corral and Ogawa 1987, and this study), maximum reproductive activity was reported during the warmest months of the year.

Control of gametogenesis and the physiology of egg production are still unknown for *S. gigas*, but histological studies of queen conch from Belize showed that mature eggs and sperm were in the gonads year-round (Egan 1985). External factors, therefore, are likely to mediate seasonality in the intensity of reproductive behavior and egg-laying.

Emphasis in the past has been placed on the potential role of water temperature in reproductive activity. Similar to observations in Los Roques, Venezuela (Brownell 1977, Weil and Laughlin 1984), reproductive activity at Lee Stocking Island began with rise in temperature. At both locations, reproductive activity intensified with increasing temperature to reach its maximum during the warmest period. Brownell (1977) suggested that a sharp temperature decline of 1.1°C from November to December was responsible for the termination of queen conch egg-laying in Los Roques. Similarly, egg-laying at Lee Stocking Island ended as bottom-water temperature began to decline steadily from 28.6°C in late September to 25.1°C in December. On the other hand, pairing, copulation, and egg-laying all decreased suddenly between August and September, during a period of high and relatively-stable water temperature, near 28.5°C.

Unlike the partial (early summer) correlation between reproductive behavior and temperature, pairing, copulation, and egg laying were all positively correlated with length of day throughout the year. Photoperiod, therefore, may be one of the important environmental variables which mediates the timing and length of reproductive season. Synergistic interaction between photoperiod and water temperature is possible.

In addition to decreasing length of day in late summer, increasing frequency and intensity of winds from the northeast produce a surge reaching the bottom at the Lee Stocking Island study site in the fall (Caribb. Mar. Res. Cent., Vero Beach, FL 32963, unpubl. data). The significance of wave disturbance is suggested by our own anecdotal observations of short-term decreases in reproductive activity concurrent with 1–2 day periods of reduced temperature and increased surge which occurred during the survey periods in early summer. Reductions in reproductive activity with increasing water turbulence have been noted for queen conch in the Caicos Islands (Davis et al. 1984) and for milk conch *Strombus costatus* in Puerto Rico (R.S. Appeldoorn, Dep. Mar. Sci., Univ. Puerto Rico, Mayaguez, PR 00709, pers. commun., May 1990).

As with temperature, photoperiod may influence the production of mature gametes or have a direct effect on the behavior of conch. It is likely that the combination of increasing water temperature, coupled with increasing length of day, triggers the mass migration of adult conch from hardground to sand habitats and to search for mates. Decreasing length of day and increasing wave surge appear to provide the best explanation for termination of the reproductive season, as pairing and copulation ended while bottom-water temperature was high. Experimental analysis will be required to determine the mechanisms involved in seasonal reproductive rates. Temperature, rates of temperature change, photoperiod, physical turbulence, and other seasonally variable environmental factors will need to be considered.

Similar to the findings of several others (D'Asaro 1965, Robertson 1959, Brownell 1977), egg-laying occurred primarily on clean coral sand with coarse grain size. Davis et al. (1984) noted that this type substrate may be critical for reproductive activity. Copulation and spawning stopped when they placed conch on a bottom type other than coral sand. At Lee Stocking Island, mating on hardbottom was observed, but was rare. Given that only one egg mass was found on substrate other than coral sand, it is clear that this is the preferred, if not critical, substrate for egg-laying.

This study provides the first report on abundance and distribution of queen conch veligers in the field. Veligers were present in the water column from 2 June to the end of September, in concordance with relatively constant rates of egg-laying from April through August. Despite a spawning season spanning 7 months, high numbers of larvae were present in the two inlets only during a 2-month period (July and August).

Although mechanisms involved in seasonality of larval production and survival are unknown as yet, it is clear that larvae were most abundant during the period of warmest water conditions. Summer spawning in Exuma Sound has adaptive significance. First, high temperatures are associated with higher developmental rates in pelagic larvae (Thorson 1950, McEdwards 1985, Boidron-Metairon 1987), decreasing the time larvae spend in the plankton and probably reducing larval mortality (Strathmann 1980). However, increase in temperature needs to be coupled with a food supply sufficient to provide for higher feeding and metabolic rates (Scheltema and Williams 1982). Second, midsummer months are characterized by prevailing tradewind conditions (i.e., relatively constant winds and moderate seas from the southeast) in the Exuma Cays. General circulation over the reproductive site during this period was to the northwest, parallel to the Exuma island chain (N.P. Smith, Harbor Branch Oceanogr. Inst., Fort Pierce, FL 34946, unpubl. data). This would facilitate transport of pelagic larvae past the numerous inlets which veligers must enter to reach primary nursery habitats on Exuma Bank. As veligers are carried alongshore on the island shelf, they would readily be drawn through the inlets on flood tides. Northwest drift over the reproductive site may, in fact, explain the close correlation between larval abundance in Adderley Cay cut and reproductive activity occurring upcurrent. Winter weather patterns, with frequent passage of cold fronts and shifting winds and currents, would be less favorable for transport of conch larvae to the Exuma Bank nurseries.

On the basis of laboratory growth curves (Boidron-Metairon, unpubl. data), all but the three largest larvae collected in this study were less than approximately 2 weeks old in a larval life stage near 30 days. There are several possible explanations for the scarcity of advanced stage larvae: Late stages occupy habitats different from those of early-stage larvae (on or near the bottom), the abundance of older stages in the water column is reduced due to natural mortality, and/or the late stages are advected to different locations. Virtually nothing is known about transport or behavior of queen conch larvae in the field. Given the great significance of recruitment processes to management of this rapidly depleted fishery species, future research should include studies of larval transport and settlement.

In summary, highest reproductive activity occurred near Lee Stocking Island at a time of stable circulation patterns, high temperature (28–30°C), and long photoperiod. Maximum larval abundance in July and August placed high numbers of veligers in the water column at a time favorable for both high rates of development and transport to nursery habitats. Proximal mechanisms affecting short-term and seasonal variation in reproduction in queen conch may include temperature, rates of temperature change, photoperiod, wave-induced turbulence, and other variables associated primarily with season.

Acknowledgments

This research was supported by a grant from the Undersea Research Program of the National Oceanic and Atmospheric Administration (U.S. Department of Commerce) to the Caribbean Marine Research Center. We thank R.I. Wicklund, Director of the Caribbean Marine Research Center, for providing bottom-water temperature data for the reproductive site. Thanks to P. Bergman, N. Christie, K. McCarthy, O. Monterrosa and E. Wishinski for assistance in the field. R. Appeldoorn, P. Colin, L. Jones, J. Shenker, J.-P. Thonney, and anonymous reviewers provided helpful comments on the manuscript.

Citations

Appledoorn, R.S.
1990 Fishing pressure and reproductive potential in strombid conchs: Is there a critical stock density for reproduction? Mem. Soc. Cienc. Nat. La Salle (In press).

Appeldoorn, R.S., G.D. Dennis, and O. Monterrosa Lopez
1987 Review of shared demersal resources of Puerto Rico and the Lesser Antilles region. *In* Mahon, R. (ed.), Report and proceedings of the expert consultation on shared Fishery resources of the Lesser Antilles region. FAO Fish. Rep. 383: 36–57.

Berg, C.J. Jr., and D.A. Olsen
1989 Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. *In* Caddy, J.F. (ed.), Marine invertebrate fisheries: Their assessment and management, p. 421–442. Wiley, NY.

Berg, C.J. Jr., J. Ward, B. Luckhurst, K. Nisbet, and F. Couper
In press Observations of breeding aggregations of the queen conch, *Strombus gigas*, in Bermuda. Proc. Gulf Caribb. Fish. Inst.

Boidron-Metairon, I.F.
1987 Effet de la temperature sur la duree des periodes larvaires de quatre especes d'Echinides des Caraibes. Bull. Soc. Sci. Nat. Ouest Fr. H.S:75–79.
1988 A new approach to comparative studies of *Strombus gigas* L. (Gastropoda: Strombidae) larvae at the developmental and nutritional levels. Proc. Gulf Caribb. Fish. Inst. (In press).

Brownell, W.N.
1977 Reproduction, laboratory culture and growth of *Strombus gigas*, *S. costatus*, and *S. pugilis* in Los Roques, Venezuela. Bull. Mar. Sci. 27:668–680.

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.

Corral, J.L., and J. Ogawa
1987 Cultivo masivo de larva de caracol *Strombus gigas* en estanques de concreto. Proc. Gulf Caribb. Fish. Inst. 38: 345–352.

Coulston, M.L., R.W. Berey, A.C. Dempsey, and P. Odum
1987 Assessment of 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.

Cruz, R.S.
1986 Avances en la experimentacion de produccion massiva de caracol en Quintana Roo, Mexico. Proc. Gulf Caribb. Fish. Inst. 37:12–20.

D'Asaro, C.N.
1965 Organogenesis, development and metamorphosis in the queen conch, *Strombus gigas*, with notes on breeding habits. Bull. Mar. Sci. 15:359–416.

Davis, M., and C. Hesse
1983 Third world level conch mariculture in the Turks and Caicos Islands. Proc. Gulf Caribb. Fish. Inst. 35:73–82.

Davis, M., B.A. Mitchell, and J.L. Brown
1984 Breeding behavior of the queen conch *Strombus gigas* Linne, held in a natural enclosed habitat. J. Shellfish Res. 4:17–21.

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

Egan, B.D.
1985 Aspects of the reproductive biology of *Strombus gigas*. M.S. thesis, Univ. British Columbia, Vancouver, 147 p.

Folk, R.L.
1966 A review of grain-size parameters. Sedimentology 6: 73–93.

Galehouse, J.S.
1971 Sediment analysis. *In* Carver, R.E. (ed.), Procedures in sedimentology petrology, p. 69–94. Wiley, NY.

McEdwards, L.R.
1985 Effects of temperature on the body form, growth, electron transport system activity, and development rate of an echinopluteus. J. Exp. Mar. Biol. Ecol. 93:169–181.

Mianmanus, R.T.
1988 Induction of settlement and metamorphosis in larvae of *Aplysia brasiliana* and *Strombus gigas* (Mollusca: Gastropoda). Ph.D. diss., Univ. Miami, Coral Gables, 171 p.

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

Robertson, R.
1959 Observations on the spawn and veligers of conchs (*Strombus*) in the Bahamas. Proc. Malacol. Soc. 33:164–171.

Salley, S.
1986 Development of the statocyst of the queen conch larva, *Strombus gigas* L. (Gastropoda: Prosobranchia). M.S. thesis, McGill Univ., Montreal, 116 p.

Scheltema, R.S., and I.P. Williams
1982 Significance of temperature to larval survival and length of development in *Balanus eburneus* (Crustacea: Cirripedia). Mar. Ecol. Prog. Ser. 9:43–49.

Stoner, A.W., and V.J. Sandt
1992 Population structure and seasonal movements in deepwater queen conch, *Strombus gigas*. Bull. Mar. Sci. 51 (In press).

Strathmann, R.R.
1980 Why does a larva swim so long? Paleobiology 6:373–376.

Thorson, G.
1950 Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25:1–45.

Weil, E., and R. Laughlin
1984 Biology, population dynamics, and reproduction of the queen conch, *Strombus gigas* Linne, in the Archipielago de Los Roques National Park. J. Shellfish Res. 4:45–62.

Wilkins, R.M., M.H. Goodwin, and D.M. Reid
1987 Research applied to conch resource management in St. Kitts/Nevis. Proc. Gulf Caribb. Fish. Inst. 38:370–375.