Notes on the Reproductive Biology and Behavior of the West Indian Fighting Conch, *Strombus pugilis* Linnaeus in Barbados, with Evidence of Male Guarding

BY

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(1 Text figure)

INTRODUCTION

EXISTING INFORMATION on the reproductive biology and behavior of the West Indian fighting conch, *Strombus pugilis* Linnaeus, 1758, is limited. PERCHARDE (1970) reported that in Trinidadian waters three colonies of fighting conchs moved downslope and buried themselves, with apparent sex segregation, in November 1967. They did not return to normal feeding and behavioral patterns until March/April 1968. Then the males emerged and commenced feeding but the females, all of which were solitary, simultaneously engaged in egglaying before emerging to feed. He suggested that copulation, which had not been witnessed, and fertilization occur within a short time period and might be lunar related. BROWNELL (1977) in Venezuela found from diving observations, which averaged twice per month from July 1975 to June 1976, that *S. pugilis* spawned from March to May. He also noted that all egglaying females were solitary. However, both RANDALL (1964) in the U.S. Virgin Islands, and Brownell have reported that ovipositing females of *Strombus gigas,* the queen conch, were often accompanied by one to three males, sometimes with concurrent copulation.

This study reports in detail on the reproductive behavior of *Strombus pugilis* in Barbadian waters. Additional information on their fecundity and apparent spawning cycle is supplied, with new evidence supportive of combative tendencies in the males. All research was carried out in Barbados, West Indies, at the Bellairs Research Institute of McGill University during the period May 1979 - October 1980.

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DESCRIPTION AND LOCATION OF STUDY SITES

The principal study site was located 200 m offshore and 50 m north of the mouth of the Holetown River, St. James Parish, Barbados. The colony inhabited an area of sandy-mud in 5-8 m of water, where the bottom sloped to sea-

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ward at an angle of approximately 10°. Two secondary sites were also established on the west coast in 8-10 m water depths. One colony was approximately 600 m north of the principal site and separated from it by two coral reefs. The other was several kilometers to the north at Speightstown, St. Peter. Both secondary sites had sandy-mud bottoms with no appreciable slope.

MATERIALS AND METHODS

Field Materials and Methods

On November 1, 1979, divers at the principal site measured, sexed, tagged and released 33 adult conchs *in situ*. These tagged conchs constituted a sub-sample from a large colony of approximately 500 individuals inhabiting a surveyed grid area of 300 m^2. This site was visited 17 times from November 1 to December 16, 1979. During each visit the entire grid plus an additional 5 m on the periphery were surveyed for tagged animals. When conchs were encountered their exact location in relation to the grid was determined, their ongoing behavior recorded and the main activity of the entire colony noted. In the periods May-September 1979 and January-October 1980, only the main activity of the colony was noted. Temperature and salinity of the bottom waters at this site were monitored October 1979-October 1980.

Untagged colonies at the secondary sites were visited occasionally from May to December 1979.

Laboratory Materials and Methods

In July 1979, a cement water table (3 m x 1 m x 26 cm) was filled to a depth of 6 cm with sediment from areas in the field inhabited by *Strombus pugilis*. This muddy sand was then overlain with 1 cm of beach sand to help maintain water clarity. The water table was supplied with running seawater averaging 28.1° C pumped directly from an intake 25 m offshore. On July 17, 35 adult *S. pugilis* were collected by divers from the bay at Holetown. Four of the 20 females collected were in the process of egg-laying.

All conchs were maintained overnight in three 40 L aquaria supplied with running seawater. Measurements and sex determinations were made the next day. The animals were then tagged with numbered squares of buoyant polyethylene tied to 6 cm lengths of dental floss. These were attached to the conch shells between two dorsal spines on the penultimate whorl (Barbadian *Strombus pugilis* lack spines on the body whorl) with a rapid-drying adhesive. These conchs, plus 10 others from the Speightstown site which had been treated similarly 3 weeks previously and exhibited no harmful side-effects, were then placed in the prepared water table for observation over a period of 4 months. Various algal species scraped from hard surfaces in the intertidal zone were added periodically to the water table and were accepted by the conchs as food items.

The laboratory population density of approximately 14 conchs per square meter was similar to densities obtained in censuses of field colonies actively engaged in reproduction or feeding, or both. The laboratory population was 58% female, which was similar to the composition obtained in field studies.

LABORATORY RESULTS AND OBSERVATIONS

Egglaying, Copulation and Associated Pairs

The laboratory colony was observed July 18-November 15, 1979. The first egg mass was produced on July 19 at 1400 h by a female accompanied by a male positioned posteriorly and on her right side. Their shells formed an angle of approximately 60°, with the male's propodium touching the shell lip of the female. The male remained inactive while the female deposited the egg strand. As the egg mass increased in length, it was occasionally pushed away to the right of the female by her propodium; a behavioral pattern similar to that described for *Strombus costatus* (Berg, 1974). Thus, the two partners remained stationary as the egg mass was produced. (This behavior is contrary to that observed by Percharde; *i.e.*, buried, solitary, egglaying females in Trinidad, 1970). This association of the male and female continued undisturbed until sometime after 1845 h when they were last observed together. The female finished the egg mass sometime between 2030-2230 h. It is not known whether she was alone during the last few hours of ovipositing. Copulation prior to this egglaying was not observed and may have occurred in the laboratory and/or in nature. The eggs of this female and those subsequently laid by all other females in the laboratory produced viable embryos which hatched within 3 to 5 days. During that same day, several solitary females were observed laying eggs.

A brief period (5 days) of intense reproductive activity ensued in the laboratory colony. Copulation with non-egglaying females was observed 15 times and with ovipositing females 6 times, and 12 associated pairs were studied. All conchs remained on the sand surface until 2100-2230 h on July 23 when 5 conchs buried themselves. By 1900 h on July 24, 44 of the 45 tagged animals were completely buried with only their eyestalks and some spine tips visible. Thirty-one of the 34 egg masses produced were ascribed to 20 specific females, therefore averaging a minimum of 1.6 egg masses per female in a 5-day reproductively-active period. Records were not kept of the percentage of egglaying time that ovipositing females were solitary.

Male Guarding and Fighting

Initially it was thought that the male attending an ovipositing female might be protecting her from predation while she was fully exposed and stationary on the substrate surface. However, on July 22 at 1050 h the significance of this guarding behavior of the male *Strombus pugilis* became apparent.

A female was engaged in egglaying and two males were positioned with their anterior ends close to the female's flared shell lip. Neither male was engaged in copulation but one was touching the outside of the female's shell lip with his propodium. The males began to 'spar' with each other using the radulae and jaws on their extended proboscises. When one retracted his proboscis, the more aggressive conch (in this case, the conch not touching the female) jabbed under the shell of the other with his proboscis at the eye and tentacle region of the retracted conch. After receiving several of these jabs, the less aggressive conch, with its soft parts retracted under its shell, moved off of the female, became quiescent for several minutes, then moved away. The victor then copulated with the female and assumed what apparently is the guarding stance of touching her shell lip with his propodium. Within a few minutes of copulation the new male guard successfully defended his position in similar fashion from take-over by a new male. Males that actively attempted to copulate with a guarded female or to displace her male guard are referred to here as 'primary' suitors (Figure 1). During this entire sequence of events, the female continued to lay eggs uninterruptedly.

This behavior pattern was subsequently observed several times in other groups in the water table. These groups were composed of two to four conchs: one egglaying female, her male guard and usually one but sometimes two primary suitors. Occasionally a third or fourth male, here designated as 'secondary' suitors, was present. These secondary suitors had no physical contact with the female nor with her male guard but would remain very close to a mated pair, albeit inactive, for long periods. They displayed no other behavior that could be described as a form of active pursuit of the female.

When two or more females were ovipositing close to each other, larger aggregates of conchs resulted and the activity level amongst the males was high. One such grouping consisted of 19 conchs, which were either touching or within one conch-length of another individual. Aggregates of this type of up to 30 conchs were also observed in the field colonies. The exact sexual makeup of these aggregates was not recorded in any observation; however, in the laboratory aggregates every ovipositing female was guarded and several primary suitors were seen moving

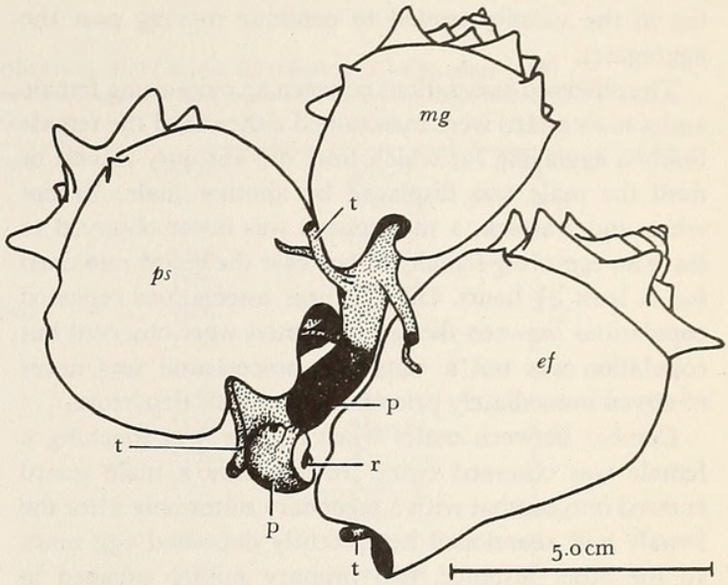

Figure 1

CONCH FIGHTING

Two male *Strombus pugilis* fight – one to remain and the other to become the male guard of the egglaying female. (The emerging egg mass is not shown, but would be along her right side, on the sediment surface.) mg – male guard; ps – primary suitor (see text); ef – egglaying female; p – proboscis; r – radula; t – tentacle-bearing eyestalk

within the large groupings. Non-egglaying females feeding in the vicinity tended to continue moving past the aggregates.

The observed associations between an ovipositing female and a male guard were maintained either until the female finished egglaying (at which time she abruptly leaves) or until the male was displaced by another male. Except when under attack, a male guard was never observed to leave an egglaying female. In one case the guard remained for at least 8½ hours. During these associations repeated copulations between the same partners were observed but copulation was not a continual process and was never observed immediately prior to the female's departure.

Combat between males when neither was touching a female was observed twice. In one case a male guard entered into combat with a secondary suitor only after the female had abandoned her recently deposited egg mass. In the other instance, two primary suitors engaged in combat while near a male guard copulating with his ovipositing female.

Females did not engage in combat. Often a feeding female approached a guarded ovipositing female but no aggression was noted on either the part of the male guard or of the females; nor did the male guard abandon the ovipositing female to pursue the passing female.

Copulation with non-egglaying females occurred frequently in the laboratory population but no fighting over these females was observed. In one instance a non-egglaying female was seen with the verges of two males inserted under her shell lip, one anteriorly and the other from the more usual 60° angle. No fight resulted between these two males.

Seven fights were observed before 99% of the conchs buried themselves on July 24.

Attenuation of Activity in the Laboratory Colony

Two additional periods of intense reproductive activity occurred in the laboratory colony within the next two weeks; one of 4 days duration from July 26 to 29 and the other of 2 days on August 7 and 8. In total, 32 egg masses were produced and 17 copulations with non-egglaying females, 13 with egglaying females, 15 associated pairs and 5 fights were observed. After August 8, the laboratory conchs remained buried most of the time except when fresh algae were added to the water table. Only one reproductive act was observed between August 8 and November 15 (when all observations were terminated) and that was a single copulation involving a non-egglaying female on August 26; the female did not subsequently oviposit. Perron (1978) reported a similar reduction of surface activity as the length of time retained in the laboratory increased for specimens of *Aporrhais occidentalis* (Superfamily Strombacea).

FIELD RESULTS AND OBSERVATIONS

Egg masses were seen at at least one of the three sites each month from May 1979 to October 1980, except March 1980 at which time only the tagged colony was under observation. At times of intense reproductive activity all sites revealed groups of conchs varying in number from 2-30 individuals, as well as some solitary egglaying females. No correlation of their reproductive, burying or feeding activities with lunar phases was evident.

The tagged colony showed some evidence of a cyclic behavior pattern, however, with individuals alternating between buried and surface-active periods. Table 1 lists the main ongoing behaviors of the Holetown colony at each visit. In early October 1979, the colony exhibited a period of intense reproductive activity. By late October individuals were more dispersed and actively feeding on the sediment surface. By mid-November very few were feeding, minimal reproductive activity was noted and many were buried. This condition remained extremely stable through to mid-December as shown by one tagged individual which was found in exactly the same location for three consecutive weeks, feeding on the sediment surface while buried. By late December more individuals were emerged and feeding and the presence of one egg mass was noted. No further observations were made until January 26, 1980, when most animals were actively feeding and a few females were laying eggs. Intense reproductive activity was observed on the 1ST and 23RD February. No conchs were seen on the surface on March 1, nor were any tags visible. Heavy seas which stirred up the bottom sediments on February 28 and 29 may have caused this disappearance of the colony. It is presumed that they were in the grid area but buried with their tags covered by the settled sand and silt because their previous greatest migration from the grid site had been 25 m and this additional distance was searched on March 1 without locating them. On April 12, they were again feeding within the grid area but by April 29 intense reproductive activity was evident. Feeding, egglaying and copulating were the main activities observed on the May to October 1980 dives except on July 12 when many buried conchs were noted.

Two conch fights involving male *Strombus pugilis* were seen *in situ* in the tagged colony. These fights were similar to those observed in the laboratory.

Table 1

Main activity of the *Strombus pugilis* colony at Holetown, Barbados, October 1979-October 1980

Year	Time	Date	Main activity	Year	Time	Date	Main activity
1979	1100	Oct. 2	F, (M)	1979	1030	Dec. 7	B
	1100	Oct. 3	E		1100	Dec. 10	B, (F)
	1300	Oct. 5	F, M		1100	Dec. 11	B, F
	1400	Oct. 6	F, M		1100	Dec. 13	B, F
	1100	Oct. 9	F, (M)		1100	Dec. 16	B, F
	1400	Oct. 10	F	1980	1100	Jan. 26	F, (E)
	1400	Oct. 13	F, (E)		1100	Feb. 1	E
	1500	Oct. 28	F, (M)		1100	Feb. 23	E, M
	1200	[1]Nov. 1	F		1100	Mar. 1	B presumed[2]
	1400	Nov. 8	B		1100	Mar. 24	F, B
	1300	Nov. 9	B		1100	Apr. 12	F
	1000	Nov. 12	B		1100	Apr. 29	E
	1300	Nov. 17	B		1100	May 13	F, M
	1400	Nov. 18	B		1100	May 30	E
	1100	Nov. 20	B		1100	June 28	E, F
	1100	Nov. 24	B		1100	July 12	F, B, M
	1030	Nov. 27	B		1100	July 28	E, M
	1430	Dec. 1	B, (F)		1100	Aug. 10	F, E, M
	1630	Dec. 5	B		1100	Sept. 25	E, M
	0830	Dec. 6	B		1100	Oct. 23	E, M

[1] = tagged *in situ*

[2] = see text for explanation

B = buried conchs; F = feeding conchs, exposed on the sediment surface; E = egglaying activities, with fresh egg masses on the sediment surface; M = abandoned egg masses on the sediment surface; ( ) = this activity noticeable but not a main activity of the colony.

Sex segregation in burying was not apparent nor was there any appreciable migration up- or downslope as had been observed by Percharde in Trinidad. However, there was evidence of migration of the colony north and south along the 5-7 m depth contour in October, November 1979 and February, May, July, August and September 1980. The migration range was approximately 60 m; the greatest distance covered by the colony between successive observations was 30 m.

During a period of very heavy rainfall and freshwater inundation of the principal site's surface waters in November-December 1979, bottom temperatures did not fluctuate by more than 0.5° C and bottom salinity was stable to within 0.5‰ of the annual mean of 34.7‰. Mean annual bottom temperature was 27.6° C. In view of this apparent stability even during periods of heavy run-off, local rainfall was not further considered as having a direct influence on the conchs' behavior.

DISCUSSION

Surface Activity Cycle

The field and laboratory observations indicate that *Strombus pugilis* in Barbados engage in reproductive activity, to some extent, on a year-round basis. In addition, they have an apparently cyclic behavior affecting reproduction which seems to consist of the following generalized stages in order: (i) burying, with highly localized feeding; (ii) emergence, with feeding on the sediment surface over greater distances; (iii) one or more periods of intense reproductive activity in pairs or aggregates; (iv) dispersal into the surface feeding pattern, followed by either (i) or (iii).

The greatest numbers of conchs were seen on the surface in August-September of 1979 and 1980 and the least numbers in November 1979 and March 1980; the number

on the surface at other times varied between these two extremes. Therefore, for much of the year this activity cycle may not be followed rigorously by all members of the population at any one time.

The attenuation of reproductive activity of the laboratory population indicates that the control(s) over levels of surface activity of these animals is (are) exogenous.

An Interpretation of the Male Guarding and Fighting Behaviors

The observance of male guarding and conch fighting in the wild colony indicates that the behaviors are elements of the natural behavioral repertoire of *Strombus pugilis* and not artifacts induced by laboratory confinement. These behaviors can be interpreted as tactics of the male reproductive strategy. To assure paternity, the male *S. pugilis* may (i) copulate with any available female even if she is not ovipositing; (ii) copulate with an ovipositing solitary female and then guard her as she continues to deposit her eggs; (iii) attempt to displace a male guard and if successful, immediately copulate with the female, remaining with her until ovipositing is completed or until he is in turn displaced; (iv) engage in multiple inseminations with the female he is guarding. Of these 4 tactics, the 3 which involve male guarding and fighting tend to limit female promiscuity and may confer an advantage towards successful paternity for the male guard.

Male guarding behavior is not new to the animal kingdom but it is reported here for the first time for *Strombus pugilis* Linnaeus. It was very appropriate, therefore, that this animal was so named. Literally translated, *Strombus pugilis* means 'boxing spire' and was intended as a description of the animal's active nature when handled (Dodge, 1956; 1959). It is fitting then, that this is the first species of this genus for which combative tendencies have been recorded.

Although analagous behavior has not been observed in any other member of the Superfamily Strombacea, its members are noted for their similarity in other behaviors (notably leaping, escape response and normal locomotion) and morphology (Berg, 1974). Furthermore, it has been noted that members of the *Strombus* genus generally congregate in large colonies to spawn (Abbott, 1960) and *S. gigas* has been observed spawning in groups consisting of 1 female and 2 to 3 males (Randall, 1964), as does *S. pugilis*. Future careful observation of other species may reveal the widespread occurrence of male guarding and fighting behaviors within the genus and perhaps within the Superfamily.

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