Gulf and Caribbean Research

Volume 7 | Issue 1

January 1981

Morphometrics of the Burrowing Clam *Diplothyra smithii* Tryon

Alfred P. Chestnut
Gulf Coast Research Laboratory

Recommended Citation

Chestnut, A. P. 1981. Morphometrics of the Burrowing Clam *Diplothyra smithii* Tryon. Gulf Research Reports 7 (1): 1-11.
Retrieved from https://aquila.usm.edu/gcr/vol7/iss1/1
DOI: https://doi.org/10.18785/grr.0701.01

Gulf Research Reports, Vol. 7, No. 1, 1–11, 1981.

MORPHOMETRICS OF THE BURROWING CLAM *DIPLOTHYRA SMITHII* TRYON[1]

ALFRED P. CHESTNUT[2]
Gulf Coast Research Laboratory, Ocean Springs, Mississippi 39564

ABSTRACT *Diplothyra smithii* Tryon, a small bivalve mollusk, is a common inhabitant of the calcareous shell material of the American oyster, *Crassostrea virginica* Gmelin. Large populations of this clam are found on commercial oyster reefs in the western portion of Mississippi Sound. Several aspects of the population of *D. smithii* in Mississippi Sound were examined.

On the Pass Marianne Reef, 71% of the live oysters and 44% of the dead shells were infested with *D. smithii*. The mean number of clams removed from valves of live oysters was 22.1 ± 1.7 (range, 1–109; N = 146). Infested dead shells had a mean number of 23.7 ± 2.6 (range, 1–103; N = 75) clams per shell.

Clams from live and dead shells indicated monthly variations in morphological stages. During January through April, clams were predominantly immature. In late spring and early summer, clams matured morphologically. In May and June, the majority of clams were mature. Immature clams from early and midsummer spawnings appeared in July and August.

Mean lengths and heights of clams with and without a callum and the monthly changes in those dimensions were determined for clams from live and dead shells. All clams from live oysters had greater mean dimensions and size ranges than clams from dead shells. Female clams were significantly larger than nonfemale clams from live oyster shells; females from dead shells were significantly larger than nonfemale clams in length only.

INTRODUCTION

Information on population dynamics of invertebrate organisms is essential to adequately appraise the role of specific organisms within an estuarine ecosystem. Although numerous population studies have been conducted on burrowing bivalve species from sand or mud substrata (Fraser 1967, Moore and Lopez 1969, Holland and Dean 1977), few have been conducted on rock- or shell-burrowing bivalves.

Diplothyra smithii Tryon is a small bivalve mollusk specialized for burrowing into calcareous shell material, particularly the American oyster, *Crassostrea virginica* Gmelin. Despite the high incidence of *D. smithii* in oysters on the northern coast of the Gulf of Mexico, very little information concerning the percentage of shells infested, the density of clams per shell, or the morphology, size, or sex of those clams is available. Collier ([unpublished] cited by Hopkins 1949) attempted to survey the *D. smithii* population in Texas; however, only a few unpublished reports were available.

Most surveys have reported only the prevalence of *D. smithii* and have made observations on oyster-shell damage (Moore 1899, Cary 1906, Galtsoff et al. 1935, Higgins 1940, Federighi and Collier [unpublished] cited by Hopkins 1949). Higgins (1940), Menzel (1950), Galtsoff (1964), and Harry (1976) reported densities of *D. smithii* within single oyster valves. Information on the size of *D. smithii* can be found in the original description (Tryon 1862), in taxonomic monographs (Bartsch and Rehder 1945, Turner 1955), and in numerous guides to marine mollusks (Abbott 1974, Andrews 1977). None of those reports presented series of measurements.

Diplothyra smithii is characterized by a change in shell morphology as it develops from an immature to a mature form. Turner (1954) described the morphological stages and their characteristic behavioral, structural, and functional patterns for pholads in general. Specific information on the morphological stages of *D. smithii* has not been reported.

The objective of this study was to obtain information on the oyster shell as a substratum inhabited by *D. smithii*, the percentage of shells infested (prevalence), densities of clams within oyster shells, and information on the morphological stages, sizes, and sex of *D. smithii*.

MATERIALS AND METHODS

Field Sampling

Samples of live and dead oyster shells containing *D. smithii* were dredged monthly from January through August 1976, and infrequently during 1975, 1977, and 1978, from Pass Marianne Reef. This reef is located 2 miles due south of Pass Christian, Mississippi, in the vicinity of navigation marker 7M in Mississippi Sound. Surface salinity and temperature were also recorded on each sampling date.

Laboratory Procedures: Percentages of Shells Infested

The percentage of live and dead oyster shells infested with *D. smithii* was determined by placing individual live oysters and dead shells in a large fiberglass trough of sea water which was heated to approximately 30°C to drive off oxygen. This forced the clams to extend their siphons and facilitated identification of infested shells.

Oyster Shell Measurements

To adequately describe the substrata inhabited by

[1]This paper is part of a dissertation submitted to the Graduate School of the University of Southern Mississippi.

[2]Present address: Department of Biology, Belhaven College, Jackson, Mississippi 39202.

Manuscript received July 30, 1980; accepted October 15, 1980.

D. smithii, live and dead shells were examined. Ten live oysters were arbitrarily selected and shucked. Measurements were made with vernier calipers of left and right valves for height and length (to the nearest 1.0 mm), and thickness in the umbo region and at the ventral margin (to the nearest 0.1 mm). Heights and lengths of ten dead shells also were measured. Because of the eroded nature of dead shells, only a single measurement of thickness was made midway between the dorsal and ventral margins.

Number of Diplothyra smithii per Oyster Valve

From the infested shells, ten live oysters and ten dead shells were arbitrarily selected to determine the densities of burrowing clams within the shells. The numbers of siphon holes in a given dead valve were counted. Each valve of live shells was divided into four quadrants through the dorso-ventral and anterio-posterior midpoints, and the number of siphon holes within each quadrant was counted. Quadrant densities were examined to relate the number of clams to thickness, i.e., age, of the shell. The procedure that was followed and the orientation of the quadrants were basically those described by Galtsoff (1964).

Cross products of shell heights and lengths were used to compute relative shell areas which were correlated with the number of clams present. This was determined to be the most feasible method for computing area, since the actual shell areas were not calculated prior to destruction of shell valves to obtain *D. smithii.*

Burrowing clams were collected from oyster shells cracked open with a hammer. All clams visible to the naked eye were removed by successively breaking and picking through the shell fragments.

Morphological Stages of Diplothyra smithii

Clams were separated into three stages of morphological maturity based on callum development to determine relationships between the season and the stage of maturity. Clams **without a callum** were morphologically immature and in the active burrowing stage. These were characterized by the presence of a wide pedal gape through which the foot protruded, unprotected by a shell covering. Clams **with a partial callum** varied from those with a thin shell just beginning to grow over the pedal gape to those having a thin, pliable callum almost completed but still allowing valve articulation about the umbonal-ventral axis. The mature stage was characterized by **a complete callum.** At that stage, the pedal gape was completely covered by shell material with no valve articulation.

Sizes of Diplothyra smithii

Lengths and heights of all clams were measured to relate size to substratum, to morphological stage, and to sex. Length was the greatest anterior-posterior dimension of the shell. Height was the length of the umbonal-ventral sulcus, a line from the umbo to the ventral shell margin (Evans 1968). Clams were measured to the nearest 0.1 mm using an ocular micrometer and a steroscopic binocular microscope.To determine the monthly population structure, length-frequencies for all clams from a given month were plotted to indicate the percentage of clams within 2 mm size classes.

Sex: Mature Females

Numbers and sizes of mature females in each monthly sample were compared with numbers and sizes of all other clams. Only ovigerous females were recorded because they were recognized easily by the presence of pink gonadal material.

Statistical Notation

Numerical and size measurements in text and tables herein are represented as mean ± one standard error of the mean. The sample size is given in parentheses. All tests of significance were done using Analysis of Variance (ANOVA). Only probability levels exceeding 95% were reported.

RESULTS

Oyster Shell Measurements

From live shells, the mean height of left valves, 83 ± 1.5 mm (73), was significantly larger than the mean height of right valves, 77 ± 1.4 mm (73). The mean length of left valves, 64 ± 1.1 mm (73), also was significantly larger than the mean length of right valves, 59 ± 1.0 mm (73). There was no significant difference between the thickness of left valves, umbo: 8.9 ± 0.2 mm (73), mid-ventral: 2.6 ± 0.1 mm (73); and right valves, umbo: 8.8 ± 0.3 mm (71), mid-ventral: 2.6 ± 0.1 mm (71). Dead shells had a mean height of 82 ± 2.5 mm (76), a mean length of 49 ± 1.0 mm (76), and a mean shell thickness of 5.7 ± 0.2 mm (75).

Percentage of Shells Infested with Diplothyra smithii

Seventy-one percent of the live oysters and 44% of the dead shells were infested with *D. smithii* (Table 1).

Density of Diplothyra smithii per Infested Oyster Valve

There was no significant difference between the mean densities of clams in the left and right valves of live oysters, left: 22.6 ± 2.5 mm (73); right: 21.6 ± 2.2 mm (73); combined: 22.1 ± 1.7 mm (146). The maximum density was 109 clams per shell. Fifty-seven percent of the live shells examined contained between 1 and 20 clams. There were significantly greater numbers of clams near the umbo in the dorsal quadrants of live shells. Anterior quadrants had mean densities of 9 clams per quadrant compared with mean densities of 2 clams per quadrant in the ventral quadrants (Table 2).

Dead shells had a mean density of 23.7 ± 2.6 clams per valve, and a maximum number of 103 clams per valve. Fifty-one percent of the dead shells had between 1 and 20 clams present.

TABLE 1.

Numbers and percentages of live oysters and dead shells infested with *Diplothyra smithii* from Pass Marianne Reef, 1976 and 1977.

Month	Live Oysters			Dead Shells		
	With *D. smithii*	Without *D. smithii*	Total	With *D. smithii*	Without *D. smithii*	Total
February 1976	140	13	153	–	–	–
April	45	22	67	77	98	175
May	–	–	–	38	148	186
June	9	46	55	–	–	–
July	–	–	39	118	146	264
August	–	–	43	82	62	144
September	–	–	22	149	86	235
February 1977	15	6	21	53	108	161
Total	209	87	400	517	648	1165
Mean	52	22	57	86	108	194
Range	9–140	6–46	21–153	38–149	62–148	148–264
Percentage	71	29	–	44	56	–

TABLE 2.

Number of *Diplothyra smithii* located within each of four quadrants of live oyster shells from Pass Marianne Reef.

Quadrant	Mean Number Removed	(N)	Range
Dorsal Anterior	9.3 ± 0.8	(136)	0–53
Dorsal Posterior	8.9 ± 0.7	(136)	0–41
Ventral Anterior	2.2 ± 0.3	(136)	0–20
Ventral Posterior	2.2 ± 0.2	(136)	0–11

The mean densities of clams per infested valve were similar for both live and dead shells, and the proportion of valves containing equivalent numbers of clams also was similar for both live and dead shells. There was a positive correlation between the number of clams and the size of the shell for both live shells ($r^2 = 0.1084$; N = 146) (Figure 1), and for dead shells ($r^2 = 0.2215$; N = 75) (Figure 2).

Morphological Stages of Diplothyra smithii

Monthly frequencies for the presence of morphological stages of *D. smithii* were similar from both live and dead shells except during July and August (Figures 3 and 4). During the first four months of 1976, 60 to 90% of the clams were present in the immature stage in both live and dead shells. Live shells had 10 to 20% more immature clams than dead shells. In April, there was an increase in the number of mature clams in both live and dead shells, and in May and June, 70 to 90% of the clams examined had a callum. In July and August, differences were found between the morphological stages present in live and dead shells. In live shells 70% of the clams had a callum present; however, in dead shells 80% were without a callum.

Sizes of Diplothyra smithii

Clams from live shells were larger than clams from dead shells (Tables 3–6). Clams from live shells also had wider ranges for both length and height measurements. Mean lengths for clams with a callum were larger than the mean lengths for clams without a callum from both shell types (Figures 5 and 6).

Mean lengths and heights for each morphological stage are given for each month (January through August 1976) in Tables 3 and 4 for clams removed from live shells, and in Tables 5 and 6 for clams removed from dead shells. Clams removed from live shells had a total mean length of 6.8 ± 0.4 mm (1,567) for clams with a callum, and a total mean length of 3.9 ± 0.0 mm (1,451) for clams without a callum (Table 3). Clams removed from dead shells had a total mean length of 5.5 ± 0.1 mm (724) for clams with a callum, and a total mean length of 3.0 ± 0.0 mm (917) for clams without a callum (Table 5). The greatest recorded length was 11.4 mm (Table 5).

*Diplothyra smithii: **Length-Frequencies***

Changes in length-frequencies of the sample population of *D. smithii* throughout an 8-month period from live and dead shells are shown in Figures 7 and 8. There was a progressive shift in increasing length of clams from January through June for clams from both live and dead shells. With recruitment of young individuals during July and August, an increase in the percentage of clams was observed in the smaller length intervals. Changes in length-frequency were more pronounced for clams removed from dead shells than for clams removed from live shells.

Sex: Mature Females

Means and ranges for lengths and heights of females from live and dead shells, both with and without a callum,

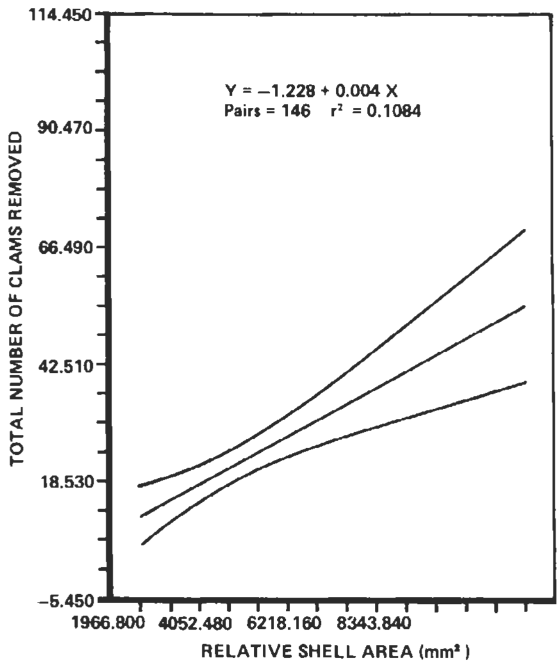

Figure 1. Relative area (length X height) of live shells compared with the number of *D. smithii* removed from the shells.

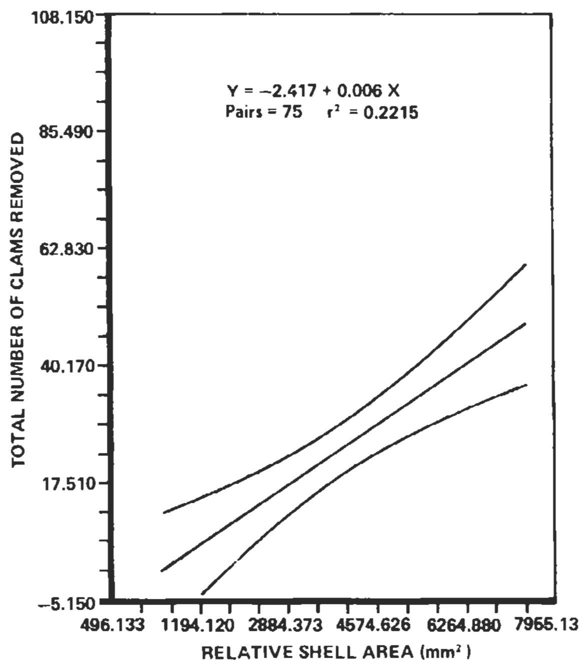

Figure 2. Relative area (length X height) of dead shells compared with the number of *D. smithii* removed from the shells.

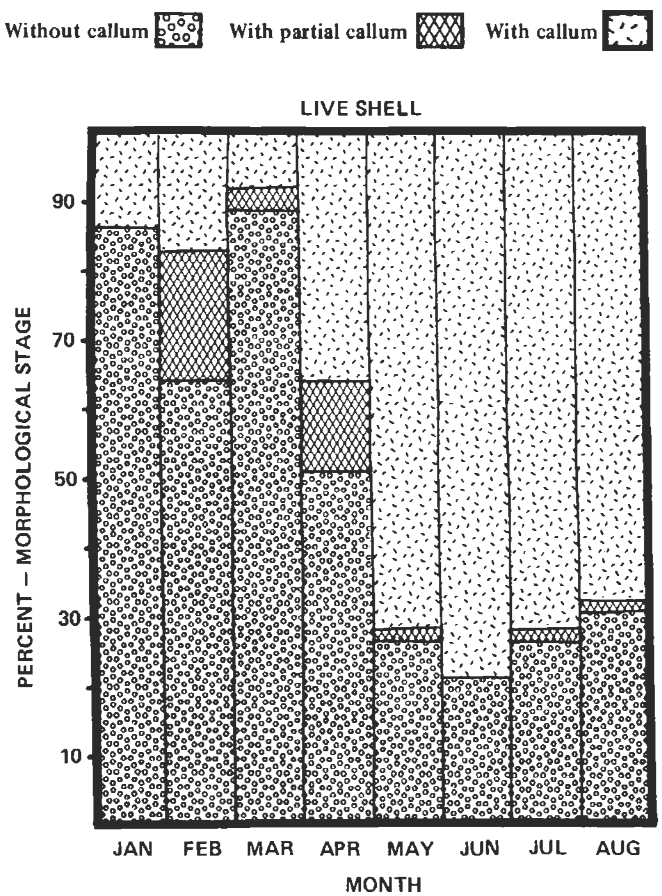

Figure 3. Percentage of clams present in each of three morphological stages for clams examined monthly, January–August 1976, from live shells.

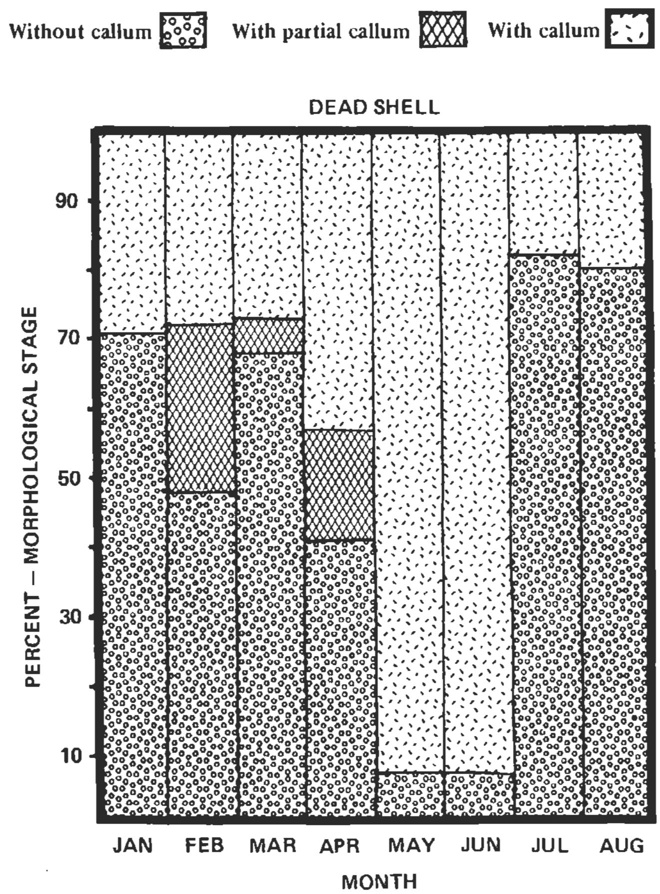

Figure 4. Percentage of clams present in each of three morphological stages for clams examined monthly, January–August 1976, from dead shells.

TABLE 3.

Mean lengths for each of three morphological stages of *Diplothyra smithii* removed from live shells monthly, January–August 1976.

Month	With Callum			With Partial Callum			Without Callum		
January	6.3 ± 0.2	(3.2– 9.5)	40*		0		3.8 ± 0.1	(1.4–9.2)	249
February	5.7 ± 0.3	(1.2–11.0)	57	6.5 ± 0.2	(3.1–8.7)	62	3.9 ± 0.1	(1.2–9.7)	207
March	6.2 ± 0.3	(2.9– 8.7)	29	6.5 ± 0.5	(4.0–8.7)	9	4.4 ± 0.1	(1.4–8.7)	310
April	6.0 ± 0.1	(2.4– 9.7)	150	6.1 ± 0.2	(3.5–8.7)	56	4.1 ± 0.1	(1.4–8.8)	210
May	6.5 ± 0.1	(3.2–10.5)	292	5.7 ± 0.9	(3.8–8.0)	4	4.0 ± 0.1	(1.6–8.0)	107
June	7.0 ± 0.1	(3.1–10.7)	299	6.1 ± 0.2	(3.9–9.1)	43	4.8 ± 0.1	(2.7–9.2)	77
July	6.7 ± 0.1	(2.9–11.0)	276	6.8 ± 1.0	(3.9–8.6)	4	2.7 ± 0.2	(0.8–7.1)	103
August	7.3 ± 0.1	(3.2–11.0)	424	8.1 ± 0.4	(6.6–8.9)	6	3.0 ± 0.1	(1.0–8.4)	194
Total	6.8 ± 0.0	(1.2–11.0)	1567	6.3 ± 0.1	(3.1–9.1)	184	3.9 ± 0.0	(0.8–9.7)	1457

*Mean (mm) ± 1 standard error (range), N.

TABLE 4.

Mean heights for each of three morphological stages of *Diplothyra smithii* removed from live shells monthly, January–August 1976.

Month	With Callum			With Partial Callum			Without Callum		
January	4.6 ± 0.2	(1.9–6.8)	40*		0		2.7 ± 0.1	(1.0–6.6)	249
February	3.9 ± 0.2	(1.0–7.1)	57	4.4 ± 0.1	(1.9–6.0)	62	2.8 ± 0.1	(1.0–6.7)	207
March	4.1 ± 0.2	(2.4–5.9)	29	4.7 ± 0.3	(3.0–6.0)	9	3.4 ± 0.1	(1.0–7.0)	310
April	4.1 ± 0.1	(1.6–6.6)	150	4.3 ± 0.1	(2.3–6.0)	56	3.1 ± 0.1	(1.2–7.8)	210
May	4.4 ± 0.0	(1.8–7.1)	292	4.1 ± 0.5	(3.1–5.5)	4	3.1 ± 0.1	(1.4–5.3)	107
June	4.5 ± 0.0	(2.0–6.6)	299	4.1 ± 0.1	(2.1–5.8)	43	3.7 ± 0.1	(1.7–6.1)	77
July	4.4 ± 0.0	(1.9–7.3)	276	4.4 ± 0.5	(3.0–5.3)	4	2.1 ± 0.1	(0.5–5.0)	103
August	4.8 ± 0.0	(2.1–7.6)	424	5.5 ± 0.2	(5.1–6.5)	6	2.3 ± 0.1	(1.0–6.3)	194
Total	4.5 ± 0.0	(1.0–7.6)	1567	4.3 ± 0.1	(1.9–6.5)	184	2.9 ± 0.0	(0.5–7.8)	1457

*Mean (mm) ± 1 standard error (range), N.

TABLE 5.

Mean lengths for each of three morphological stages of *Diplothyra smithii* removed from dead shells monthly, January–August 1976.

Month	With Callum			With Partial Callum			Without Callum		
January	3.6 ± 0.3	(3.3– 3.9)	2*		0		3.7 ± 0.2	(1.9–6.0)	50
February	5.3 ± 0.2	(2.0– 9.1)	66	5.5 ± 0.2	(2.9–8.2)	56	3.5 ± 0.1	(1.3–8.4)	110
March	5.0 ± 0.1	(1.9– 7.0)	62	4.5 ± 0.4	(2.9–6.9)	11	3.7 ± 0.1	(1.4–9.2)	154
April	5.3 ± 0.1	(2.2– 8.0)	103	4.9 ± 0.2	(1.6–7.4)	40	3.3 ± 0.1	(1.4–7.4)	99
May	5.7 ± 0.1	(3.0– 9.4)	221		0		3.7 ± 0.3	(1.6–5.1)	16
June	6.1 ± 0.1	(2.3–11.4)	160		0		4.2 ± 0.4	(2.0–6.1)	10
July	4.8 ± 0.2	(1.9–10.0)	70	5.4 ± 0.0	(5.4–5.4)	1	2.3 ± 0.0	(0.8–6.6)	314
August	4.8 ± 0.3	(1.9– 8.9)	40		0		2.7 ± 0.1	(1.2–6.2)	164
Total	5.5 ± 0.1	(1.9–11.4)	724	5.2 ± 0.1	(1.6–8.2)	108	3.0 ± 0.0	(0.8–9.2)	917

*Mean (mm) ± 1 standard error (range), N.

TABLE 6.

Mean heights for each of three morphological stages of *Diplothyra smithii* removed from dead shells monthly, January–August 1976.

Month	With Callum			With Partial Callum			Without Callum		
January	2.4 ± 0.0	(2.4–2.4)	2*	0			2.6 ± 0.1	(1.4–4.3)	50
February	3.6 ± 0.1	(1.4–6.0)	66	4.0 ± 0.1	(1.9–6.2)	56	2.6 ± 0.1	(1.0–5.2)	110
March	3.2 ± 0.1	(1.4–4.8)	62	2.9 ± 0.2	(2.0–3.9)	11	2.7 ± 0.1	(1.2–6.3)	154
April	3.3 ± 0.1	(1.6–6.3)	103	3.2 ± 0.1	(1.1–4.4)	40	2.5 ± 0.1	(1.4–5.6)	99
May	3.7 ± 0.1	(1.7–6.5)	221	0			2.9 ± 0.2	(1.2–4.4)	16
June	3.8 ± 0.1	(1.4–6.8)	160	0			3.0 ± 0.3	(1.3–4.8)	10
July	3.1 ± 0.1	(1.3–6.2)	70	3.7 ± 0.0	(3.7–3.7)	1	1.8 ± 0.0	(0.7–4.0)	314
August	3.0 ± 0.2	(1.3–5.6)	40	0			2.1 ± 0.0	(0.9–4.6)	164
Total	3.5 ± 0.0	(1.3–6.8)	724	3.6 ± 0.1	(1.1–6.2)	108	2.2 ± 0.0	(0.7–6.3)	917

*Mean (mm) ± 1 standard error (range), N.

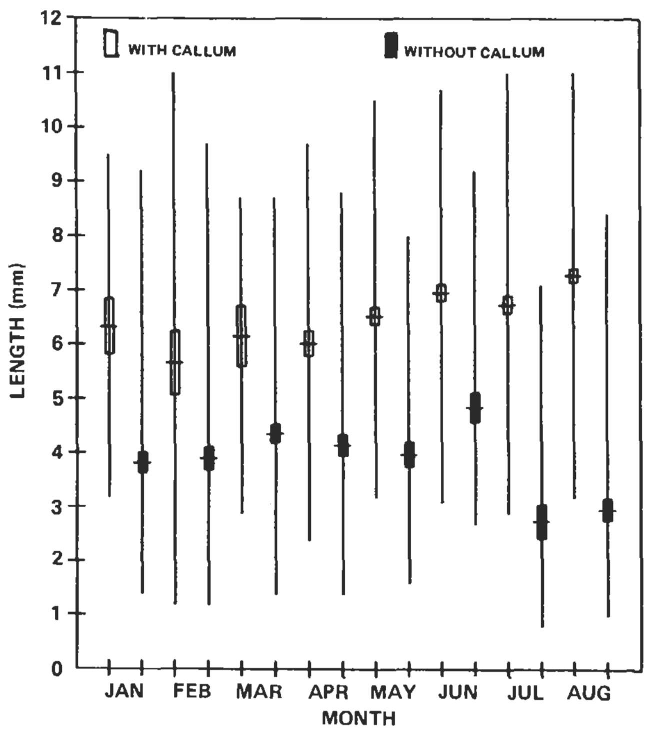

Figure 5. Mean length (horizontal line), one standard error of the mean (box), and size range (vertical line) of *D. smithii* with a callum (open box) and without a callum (solid box) removed from live shells: January–August 1976.

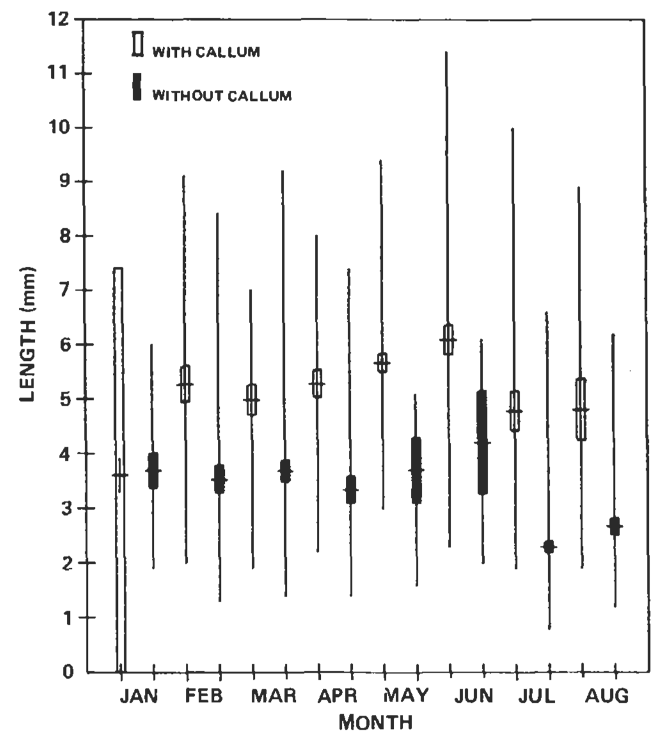

Figure 6. Mean length (horizontal line), one standard error of the mean (box), and size range (vertical line) of *D. smithii* with a callum (open box) and without a callum (solid box) removed from dead shells: January–August 1976.

are given in Tables 7 and 8. Female clams removed from live shells had significantly greater mean lengths and heights than females removed from dead shells.

Females removed from live shells had significantly greater mean lengths and heights when compared with mean lengths and heights of nonfemales of the same morphological stages (Table 7). There was a significant difference between the lengths of all females and nonfemales removed from dead shells (Table 8). Also there was a significant difference between the heights of females without a callum and nonfemales without a callum removed from dead shells; however, there was no significant difference between the heights of females with a callum and nonfemales with a callum removed from dead shells (Table 8).

DISCUSSION

Oyster Shell Measurements

Oyster shells are the primary substratum for *D. smithii* in Mississippi Sound. Several characteristics of oyster shells, including the nature of the shell material (living or dead), the surface area available for setting, and the age and

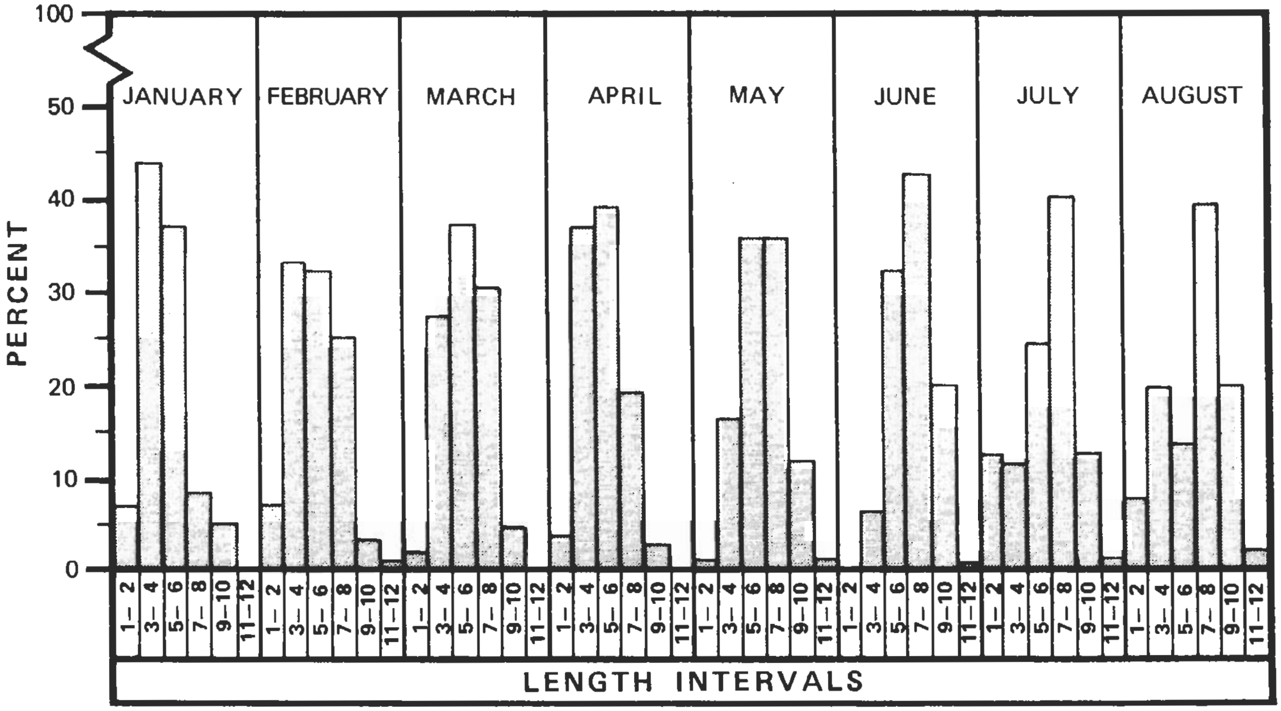

Figure 7. Length-frequency histograms for the composition of monthly samples of the population of *D. smithii* removed from live shells at Pass Marianne Reef.

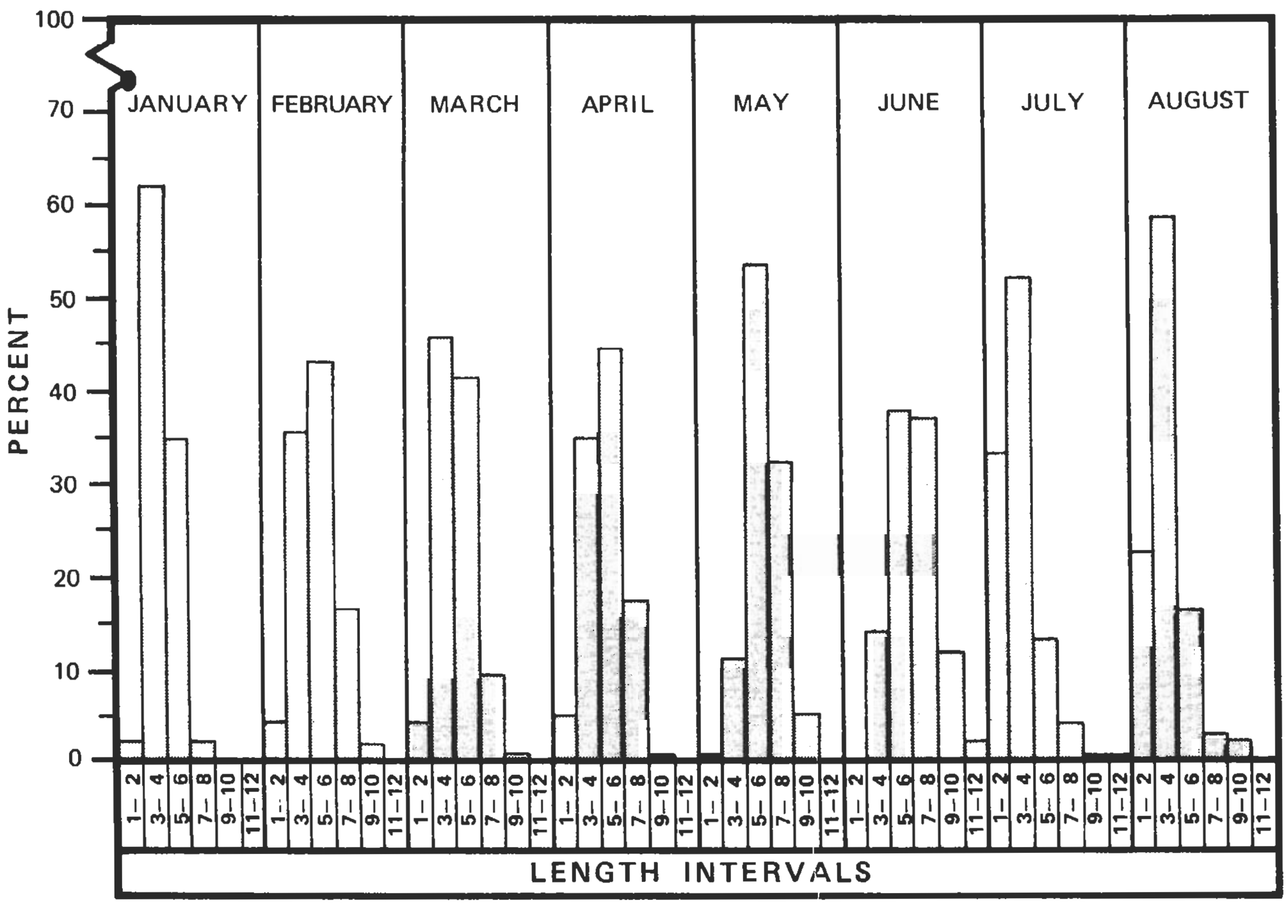

Figure 8. Length-frequency histograms for the composition of monthly samples of the population of *D. smithii* removed from dead shells at Pass Marianne Reef.

TABLE 7.

Comparison of lengths (A) and heights (B) of ovigerous female clams with and without a callum, and nonfemale clams with and without a callum, from live shells.

Month	Ovigerous Females: With Callum	Ovigerous Females: Without Callum	Nonfemale: With Callum	Nonfemale: Without Callum
		LENGTH (A)		
April	6.4 ± 0.3 (4.9– 7.5) 11*	0	6.0 ± 0.1 (2.4– 9.7) 139	4.1 ± 0.1 (1.4–8.8) 210
July	7.0 ± 0.2 (4.3–10.9) 56	0	6.7 ± 0.1 (2.9–11.0) 220	2.7 ± 0.2 (0.8–7.1) 103
August	7.3 ± 0.1 (3.2–10.6) 161	4.7 ± 0.4 (2.1–8.4) 15	7.2 ± 0.1 (3.6–11.0) 262	2.8 ± 0.1 (1.0–7.9) 179
Total	7.2 ± 0.1 (3.2–10.9) 228	4.7 ± 0.4 (2.1–8.4) 15	6.7 ± 0.1 (2.4–11.0) 621	3.4 ± 0.1 (0.8–8.8) 492
		HEIGHT (B)		
April	4.2 ± 0.2 (3.4– 5.2) 11	0	4.0 ± 0.1 (1.6– 6.6) 139	3.1 ± 0.1 (1.2–7.8) 210
July	4.5 ± 0.1 (2.3– 7.3) 56	0	4.3 ± 0.1 (1.9– 6.4) 220	2.1 ± 0.1 (0.5–5.0) 103
August	4.8 ± 0.1 (2.1– 6.7) 161	3.5 ± 0.3 (1.4–6.2) 15	4.7 ± 0.0 (2.3– 7.6) 262	2.2 ± 0.1 (1.0–6.3) 179
Total	4.7 ± 0.1 (2.1– 7.3) 228	3.5 ± 0.3 (1.4–6.2) 15	4.4 ± 0.0 (1.6– 7.6) 621	2.6 ± 0.0 (0.5–7.8) 492

*Mean (mm) ± 1 standard error (range), N.

TABLE 8.

Comparison of lengths (A) and heights (B) of ovigerous female clams with and without a callum, and nonfemale clams with and without a callum, from dead shells.

Month	Ovigerous Females: With Callum	Ovigerous Females: Without Callum	Nonfemale: With Callum	Nonfemale: Without Callum
		LENGTH (A)		
March	5.5 ± 0.9 (4.6– 6.4) 2*	0	5.0 ± 1.4 (1.9– 7.0) 60	3.7 ± 0.1 (1.4–9.2) 154
April	5.6 ± 0.2 (3.6– 8.0) 35	5.6 ± 0.0 (5.6–5.6) 1	5.1 ± 0.2 (2.2– 7.8) 68	3.3 ± 0.1 (1.4–7.4) 98
May	5.8 ± 0.1 (2.0– 5.8) 93	0	5.9 ± 0.1 (3.0– 9.4) 128	3.7 ± 0.3 (1.6–5.1) 16
July	4.9 ± 0.3 (1.9–10.0) 33	3.1 ± 0.1 (1.9–4.6) 46	4.7 ± 0.2 (2.4– 7.8) 37	2.1 ± 0.0 (0.8–6.6) 268
August	4.4 ± 0.4 (2.1– 8.2) 15	4.4 ± 0.2 (3.4–5.5) 9	5.1 ± 0.4 (1.9– 8.9) 25	2.6 ± 0.1 (1.2–6.2) 155
Total	5.5 ± 0.1 (1.9–10.0) 178	3.4 ± 0.1 (1.9–5.6) 56	5.2 ± 0.1 (1.9– 9.4) 318	2.8 ± 0.0 (0.8–9.2) 691
		HEIGHT (B)		
March	3.2 ± 1.0 (2.3– 4.2) 2	0	3.2 ± 0.1 (1.4– 4.8) 60	2.7 ± 0.1 (1.2–6.3) 154
April	3.4 ± 0.1 (2.0– 4.5) 35	4.0 ± 0.0 (4.0–4.0) 1	3.3 ± 0.1 (1.6– 6.3) 68	2.5 ± 0.1 (1.4–5.6) 98
May	3.8 ± 0.1 (2.0– 5.8) 93	0	3.7 ± 0.1 (1.7– 6.5) 128	2.9 ± 0.2 (1.2–4.4) 16
July	3.1 ± 0.2 (1.3– 6.2) 33	2.4 ± 0.1 (1.2–4.0) 46	3.0 ± 0.1 (1.5– 5.6) 37	1.7 ± 0.0 (0.7–3.2) 268
August	2.8 ± 0.2 (1.4– 4.6) 15	3.3 ± 0.2 (2.7–4.2) 9	3.2 ± 0.2 (1.3– 5.6) 25	2.0 ± 0.0 (0.9–4.6) 155
Total	3.5 ± 0.1 (1.3– 6.2) 178	2.6 ± 0.1 (1.2–4.2) 56	3.4 ± 0.0 (1.3– 6.5) 318	2.1 ± 0.0 (0.7–6.3) 691

*Mean (mm) ± 1 standard error (range), N.

thickness of specific shell regions may affect setting, density of infestation, growth rates, and morphological development of *D. smithii*.

Oyster thickness had the greatest effect on clam size and morphological maturity (see discussion on ***Morphological Stages and Sizes***). Live shells had regions of greater thickness than dead shells. Dead shells varied less in overall thickness because of wear at both the umbo and ventral edges. Shell thickness may be related to the presence of burrowing organisms. Gunter (1953) suggested that the oyster may secrete additional shell material as a response to burrowing organisms. Thick shells may be an adaptive feature which prevents penetration by burrowers.

Percentage of Shells Infested

At Pass Marianne Reef, 71% of the live shells were infested with *D. smithii*. The prevalence of infestation in live shells could lead the reader to draw misleading conclusions. Prevalence of infestation does not indicate a preference of clams for live shells, rather it reflects the unsuitability of dead shells for either initial or continued infestation. Whereas live oysters must be at least partially exposed, dead shells may be either exposed or buried, a factor which would affect initial infestation. Infested shells could be buried by dredge activities which would kill burrowing clams. Constant movement of the substratum by wave action also may prevent otherwise suitable dead shells from becoming infested (Gunter 1979).

The prevalence of infestation of live shells in this study (Table 1) was consistent with high values reported for the northern coast of the Gulf of Mexico (Galtsoff et al. 1935, Federighi and Collier [unpublished] cited by Hopkins 1949). Varying conditions affect the population of oysters present from year to year, as well as the numbers of burrowing clams. During the same time that the prevalence of *D. smithii* infestation increased on Pass Marianne Reef (1976–1978), the number of live oysters declined (Table 1). If fewer numbers of oysters were available for setting, a higher percentage may have been infested by the burrowing clam.

Density of Diplothyra smithii

Density of *D. smithii* was influenced by shell area and thickness, i.e., age of the oyster. The number of clams increased with an increase in shell area for both live and dead oysters (Figures 1 and 2). More clams were found in the dorsal quadrants of live shells than in other regions. Hofstetter (R. P. Hofstetter, Texas Parks and Wildlife Department, personal communication) also noted that heavy concentrations of clams were more common near the hinge (dorsal portion). This is the oldest region of the oyster and thus has been available for setting clams longer than other parts. Danglade (1917) noted that burrowing clams were present primarily in larger and older shells. Densities of burrowing clams per oyster shell reported in this study are lower than those reported in previous studies (Higgins 1940, Collier [unpublished] cited by Hopkins 1949, Menzel 1950, Galtsoff 1964).

Morphological Stages of Diplothyra smithii

The proportion of burrowing clams in each morphological stage followed an annual pattern consistent with seasonal changes in water temperature. Undoubtedly water temperatures affected the rates of growth and burrowing, and the rate at which substratum limits were reached, at which time metamorphosis occurred and growth stopped. Seasonal changes in morphological stages are shown in Figures 3 and 4, and temperature and salinity changes are recorded in Figure 9. Clams spawned during the summer or fall of 1975 were predominantly immature during the first four months of 1976. Clams remained immature during the months when water temperatures were below 15°C.

Clams were found in the transition stage with partial callums from February through April. The presence of a partial callum indicated changes in morphological stage. These changes were most pronounced when water temperatures increased in March and April.

In May and June, callums had developed in most clams. Along with increased water temperatures, the ratio of immature to mature clams changed dramatically during May when the majority of clams from the 1975 spawning season

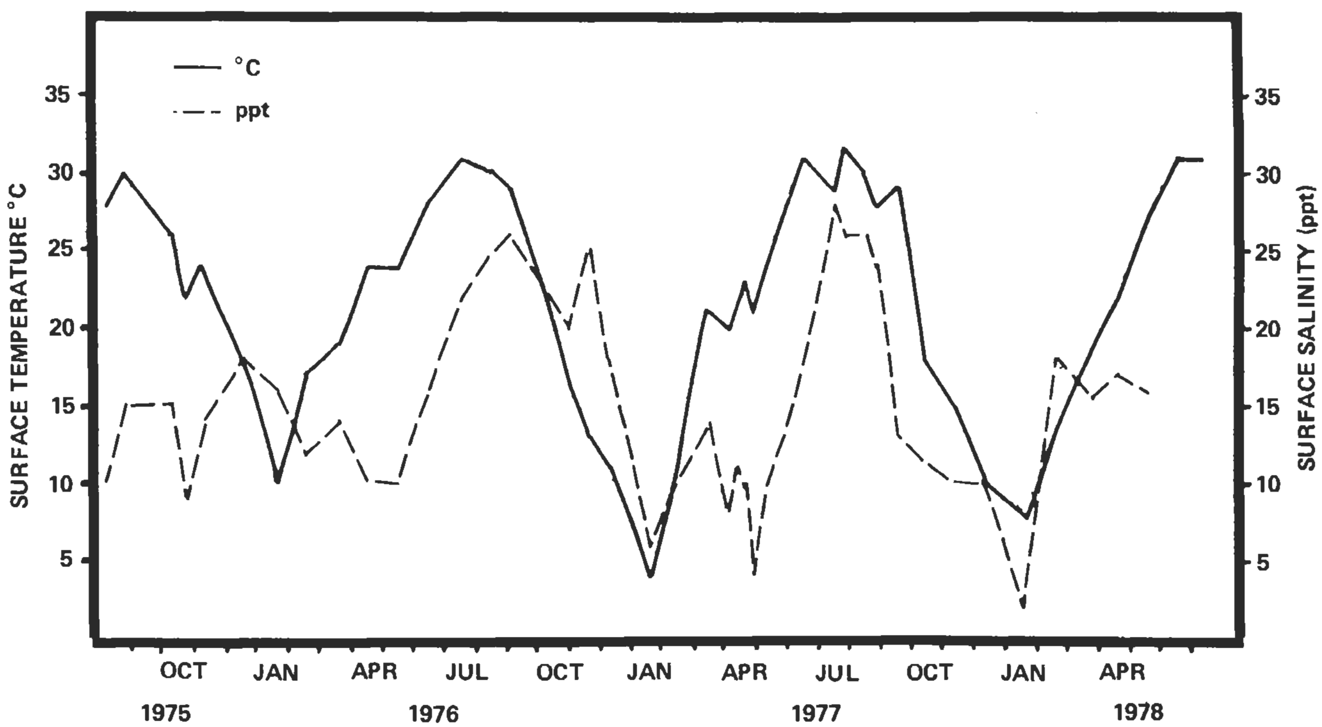

Figure 9. Surface salinity and temperature measurements from Pass Marianne Reef, August 1975 through July 1978.

reached substratum limits, metamorphosed, and matured. In July and August, recruitment of juvenile clams resulted in increased numbers of immature clams in dead shells. In live oysters the ratio of immature clams to mature clams remained approximately the same throughout the summer.

Although there were no differences between mean densities for live and dead oysters, there were differences in morphological maturation. Clams in thinner, dead shells reached the substratum limits faster than clams in live shells, and metamorphosed at smaller sizes (Tables 3 and 5). The larger percentage of mature clams observed in dead shells throughout 1976 may be related to the thinner valves of dead oysters.

Prior to this study, the attainment of a critical size (Evans 1968), crowding (Turner 1954), and substratum thickness (Smith 1969) were the only agents known to influence the production of a callum in the subfamily Martesiinae. This study indicated that, in addition to those factors, metamorphosis in *D. smithii* is induced also by seasonal temperature changes either directly or indirectly. There was a yearly cycle during which clams set in the summer or early fall and reached morphological maturity during the following spring and summer.

Sizes of Diplothyra smithii

Since growth ceases at metamorphosis (Turner 1954), factors which affect the onset of metamorphosis directly influence the size reached by *D. smithii.* Hence, mature clams vary in size depending on the thickness of the shell substratum which affects the onset of metamorphosis, and on environmental conditions which affect the rate of growth.

The mean lengths of mature clams removed from live and dead shells in this study were below the values reported by Tryon (1862), Turner (1955), Abbott (1974), and Andrews (1977). Although the largest clam from this study was comparable with that reported by Turner (1955), mature clams from Mississippi Sound were shorter than those reported in the literature. The umbonal-ventral sulcus dimensions recorded in this study were not comparable to the height measurements of previous investigators.

Although the clam may be oriented in the oyster shell at almost any angle, the majority of clams burrowed approximately perpendicular to the shell surface. The mean length of mature clams from live oysters (6.8 mm) can be related to the greater shell thickness at the dorsal margin (8.8 mm). The mean length of clams removed from dead shells (5.5 mm) also can be related to the thickness of those shells (5.7 mm).

Mean sizes from each month for clams from both live and dead shells (Figures 5 and 6) can be related to the monthly percentage of clams in given morphological stages (Figures 3 and 4). The size increase for clams with a callum, which began in March in dead shells (Figure 6) and in April in live shells (Figure 5), and continued through June, is not an indication for growth of mature clams. A callum indicates that a clam is mature, and has terminated growth (Turner 1954). The increase in size resulted from the larger-sized, immature clams undergoing metamorphosis. The results in Figures 3 and 4 indicate that the number of mature clams increased slightly in April, then sharply in May and June. The change in size of mature clams during the same period (Figures 5 and 6) has been related to the maturation of immature clams.

The mean size of immature clams remained fairly constant from January through May, as larger, immature clams metamorphosed into mature clams. In July and August, decreases in mean length of immature clams resulted from summer spawning and the subsequent recruitment of small, postlarval clams in live and dead shells. Also in some dead shells, immature clams burrowed completely out of the shell, thus limiting both the number and size of immature and mature clams.

The length-frequency histograms (Figures 7 and 8) suggest a seasonal pattern of mid- to late-summer setting. From March through June, clams in smaller size classes from both shell types gradually decreased in number. With the onset of spawning in June, July, and August, numbers of clams in the 1- to 2-mm size class increased. In August, the numbers in the 3- to 4-mm size class increased, an indication of growth of clams which set during the months of June and July. Dead shells had a much lower frequency of clams in the larger size classes, particularly during July and August, probably related to shell thickness.

Sexually Mature Females

The size difference noted between females and nonfemales of *D. smithii* (Tables 7 and 8) may be evidence of sexual dimorphism. Among mollusks, particularly bivalves, sexual dimorphism is rarely obvious. Galtsoff (1964) found that in *Crassostrea virginica*, the sexual identity of the organism was influenced by size. He stated that oysters which were larger or were able to respond more quickly to favorable changes in the environment may develop into females first.

Several females from both shell types developed sexual maturity without a callum but developed only a small quantity of gonadal material. The presence of a completed callum was not a prerequisite for sexual maturity.

ACKNOWLEDGMENTS

I thank the Gulf Coast Research Laboratory for providing support during this study, and the Computer Section for the statistical analysis of the data. Dr. Edwin W. Cake, Jr., Gulf Coast Research Laboratory, and my graduate committee at the University of Southern Mississippi provided many helpful suggestions and comments. I also thank Dr. A. F. Chestnut, University of North Carolina Institute of Marine Sciences, for his critical review of the manuscript.

REFERENCES CITED

Abbott, R. Tucker. 1974. *American Seashells.* Van Nostrand Reinhold Company, New York. 663 pp.

Andrews, Jean. 1977. *Shells and Shores of Texas.* University of Texas Press, Austin, Texas. 365 pp.

Bartsch, P. & H. A. Rehder. 1945. The west Atlantic boring mollusks of the genus *Martesia. Smithson. Misc. Collect.* 104:1–16.

Cary, L. R. 1906. The conditions for oyster culture in the waters of Vermilion and Iberia parishes, Louisiana. *Gulf Biol. Sta. Bull.* 4:1–27.

Danglade, Ernest. 1917. Condition and extent of natural oyster beds and barren bottoms in the vicinity of Apalachicola, Florida. *U.S. Bur. Fish., Rept. U.S. Comm. Fish.* (1916) App. V:1–68.

Evans, John W. 1968. Factors modifying the morphology of the rock-boring clam, *Penitella penita* (Conrad, 1837). *Proc. Malacol. Soc. Lond.* 38:111–119.

Fraser, Thomas H. 1967. Contributions to the biology of *Tagelus divisus* (Tellinacea: Pelecypoda) in Biscayne Bay, Florida. *Bull. Mar. Sci.* 17:111–132.

Galtsoff, Paul S. 1964. The American oyster, *Crassostrea virginica* Gmelin. *U.S. Fish Wildl. Serv. Fish. Bull.* 64:1–480.

Galtsoff, P. S., H. F. Prytherch, R. O. Smith & V. Koehring. 1935. Effects of crude oil pollution on oysters in Louisiana waters. *U.S. Fish Wildl. Serv. Fish. Bull.* 48:143–210.

Gunter, Gordon. 1953. The relationship of the Bonnet Carre spillway to oyster beds in Mississippi Sound and the "Louisiana Marsh," with a report on the 1950 opening. *Publ. Inst. Mar. Sci. Univ. Tex.* 3:17–71.

______ . 1979. The grit principle and the morphology of oyster reefs. *Proc. Natl. Shellfish. Assoc.* 69:1–5.

Harry, Harold W. 1976. Correlation of benthic Mollusca with substrate composition in lower Galveston Bay, Texas. *Veliger* 19: 135–152.

Higgins, Elmer. 1940. Progress in biological inquiries for 1939. *U.S. Bur. Fish., Rept. U.S. Comm. Fish.* (1940) App. I:1–96.

Holland, A. F. & J. M. Dean. 1977. The biology of the stout razor clam, *Tagelus plebeius*: I. Animal–sediment relationships, feeding mechanism, and community biology. *Chesapeake Sci.* 18:58–66.

Hopkins, Sewell H. 1949. Preliminary survey of the literature on the boring clam, *Martesia.* Texas A&M Research Foundation Project 9 (mimeo). 16 pp.

Menzel, R. W. 1950. Report on oyster studies in Lake Felicity and Bayou Bas Bleu, Terrebonne Parish, Louisiana. Texas A&M Research Foundation Project 9 (mimeo). 69 pp.

Moore, H. F. 1899. Report on the oyster beds of Louisiana. *U.S. Bur. Fish., Rept. U.S. Comm. Fish.* (1898) 24:49–100.

Moore, H. B. & N. N. Lopez. 1969. The ecology of *Chione cancellata. Bull. Mar. Sci.* 19:131–148.

Smith, E. 1969. Functional morphology of *Penitella conradi* relative to shell penetration. *Am. Zool.* 9:869–880.

Tryon, George W. 1862. Description of a new genus and species of Pholadidae. *Proc. Acad. Nat. Sci. Phila.* 14:449–450.

Turner, R. D. 1954. The family Pholadidae in the Western Atlantic and Eastern Pacific. I. Pholadinae. *Johnsonia* 3:1–63.

______ . 1955. The family Pholadidae in the Western Atlantic and Eastern Pacific. II. Martesiinae, Jouannetiinae, and Xylophaginae. *Johnsonia* 3:65–160.