The Veliger 28(1):37–51 (July 1, 1985)

THE VELIGER

Aspects of Reproduction, Larval Development, and Morphometrics in the Pyramidellid *Boonea impressa* (=*Odostomia impressa*) (Gastropoda: Opisthobranchia)

by

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Abstract. *Boonea impressa* is an important ectoparasite of the American oyster, *Crassostrea virginica*. Here, the reproductive and larval life history, intraspecific variation in certain shell characters, and the internal anatomy of the feeding apparatus are described for populations of *B. impressa* from the western Gulf of Mexico (Texas) and, for the latter two subjects, the western Atlantic (North Carolina). Larval development in the Pyramidellidae is reviewed. The life-span of *B. impressa* was approximately one year. Reproduction occurred throughout the year, but peaked in mid-summer. Eggs (182–238 μm diameter) were deposited in numbers of 20–250 per egg mass. Larval development from oviposition to hatched veliger required 3.3–4.8 days. Two days after hatching, the veligers became negatively phototaxic. Metamorphosis occurred within one week of hatching. The developmental mode of *B. impressa* fits that designated as Type II-lecithotrophic, and agrees with that expected for an opisthobranch with a stable food source. The short pelagic life-span may facilitate dispersal for a species with a non-mobile, but patchy host. Recently metamorphosed *B. impressa* often attached near the aperture of an adult. This behavior may protect the young snail from predation and increase access to its food supply. The internal anatomy of the feeding apparatus differed from European odostomians in the absence of a well developed first buccal pump. Shell sculpture (number of cords per whorl) was most dependent on the length of the whorl. Adult snail size, whorl length, whorl width, and the number of spiral cords varied significantly between populations collected from Texas and from North Carolina. Egg size, size of the components of the feeding apparatus, whorl length-width ratio, and protoconch size differed less. These latter characters might be employed advantageously in the study of interspecific differences among odostomians where, heretofore, characters with greater intraspecific variability typically were used.

INTRODUCTION

PYRAMIDELLID GASTROPODS ARE important components of many shallow-water benthic communities (SANDERS, 1958; WELLS *et al.*, 1961; FRANZ, 1976). Presumably, all are parasitic (FRETTER & GRAHAM, 1949). As such, their impact on host population dynamics and subsequent changes in community structure may be important. Little is known, however, about pyramidellid life histories or their impact on host populations.

The pyramidellid *Boonea impressa* (=*Odostomia impressa*) is a frequent component of oyster reef communities on the east and Gulf coasts of the United States. ROBERTSON & MAU-LASTOVICKA (1979) found that *B. impressa* can feed on 36 different gastropod and bivalve species. The predominant host, however, was the oyster *Crassostrea virginica*. WHITE *et al.* (1984) showed that the growth rate of juvenile oysters was reduced significantly at a parasite level of 10 *Boonea impressa* per oyster. Numbers as high as 100 per oyster occurred on the Texas Coast (WHITE *et al.*, 1984). WHITE *et al.* (1984) concluded that *B. impressa* may have a significant impact on oyster populations and oyster population dynamics.

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ROBERTSON (1978) found that *Boonea impressa,* like all other American odostomians* studied, utilize spermatophores for sperm transfer, whereas European species use penial copulation (FRETTER, 1951, 1953; MAAS, 1964). Data of WELLS (1959), ROBERTSON (1978), and WHITE *et al.* (1984) indicated that reproduction occurs throughout the year, but peaks during early summer. ROBERTSON (1978) also noted that spermatophores are larger in Texas populations of *B. impressa* than in North Carolina populations. Additional morphometric data for North Carolina populations were reported by PORTER (1976) and PORTER *et al.* (1979).

In view of the potential impact of *Boonea impressa* parasitism on oyster populations and the limited data available on the reproductive life history of *B. impressa,* we undertook a study of its reproductive cycle and larval life history. In addition, we review the available data on other pyramidellids to elucidate whether the general trends in larval development described for other opisthobranchs are also applicable to the ectoparasitic Pyramidellidae.

Taxonomic and ecologic studies on the Pyramidellidae have been hindered by a poor understanding of intraspecific variation within the group. Species distinctions and species descriptions tend to rely on highly variable characters. Species identifications often are difficult. ROBERTSON's (1978) work is notable for the use of anatomical criteria beyond shell characters to confirm taxonomic distinctions. Intraspecific variability in anatomical characters still is documented poorly in the Pyramidellidae, however. The degree of variability in shell characters between populations also is little known. POWELL (1981) found whorl width to be highly variable between populations in some *Turbonilla,* for example, thus limiting its taxonomic usefulness. Here, we also report data on some aspects of morphometrics, both of shell characters and internal anatomy, in North Carolina and Texas populations of *B. impressa* with particular emphasis on a comparison of the variability present in the internal anatomy of the feeding apparatus vis-à-vis that observed in shell morphology.

MATERIALS AND METHODS

Oyster clumps were collected from Big Slough on Harbor Island near Port Aransas, Texas, and kept in a running seawater system with adult *Boonea impressa.* Approximately every 3 or 4 days, these clumps were examined for the presence of egg masses. Egg masses were removed with forceps and placed in small dishes of filtered seawater (24–26°C) to which penicillin G and streptomycin sulfate were added to control bacterial growth (BONAR & HADFIELD, 1974). Development from oviposition through metamorphosis was studied by examining these egg masses under a microscope at hourly intervals. Additionally, daily observations were made of oyster clumps with attached egg masses that were kept in large bowls under the same conditions.

Specimens of *Boonea impressa* were collected every other month from a relatively undisturbed reef located off the south side of Mud Island near Port Aransas, Texas. Clumps of oysters were shaken vigorously in a bucket of seawater to remove all *B. impressa.* A careful visual check was done and the process repeated until no more snails were found. Snails were separated from debris by using a 500-μm sieve and preserved in formalin. For shell morphometrics, the following measurements were taken using an ocular micrometer: shell length, shell width, number of whorls, length, width and number of cords of the second and sixth whorl, and the width of the larval shell. Shell length was determined by measuring the length from the apex to the abapical end of the shell. Only those shells with an intact protoconch were used. Shell width was determined by measuring the width of the largest whorl with the aperture facing upwards. These measurements also were recorded for specimens of *B. impressa* from North Carolina generously loaned by H. Porter. Collections were made at Virginia Creek near Topsail Sound and at Williston Creek. PORTER (1976) and PORTER *et al.* (1979) gave additional information on these specimens.

Specimens from Big Slough (Texas) and from North Carolina were dissected while living. The feeding apparatus including the proboscis, stylet apparatus, buccal pump, and salivary glands were removed and measured. Occasional staining with 0.5% toluidine blue or methylene blue during the dissection proved to be efficacious (DAVIS, (1967). The longest dimension of eggs taken from egg masses laid by both groups of snails also was measured.

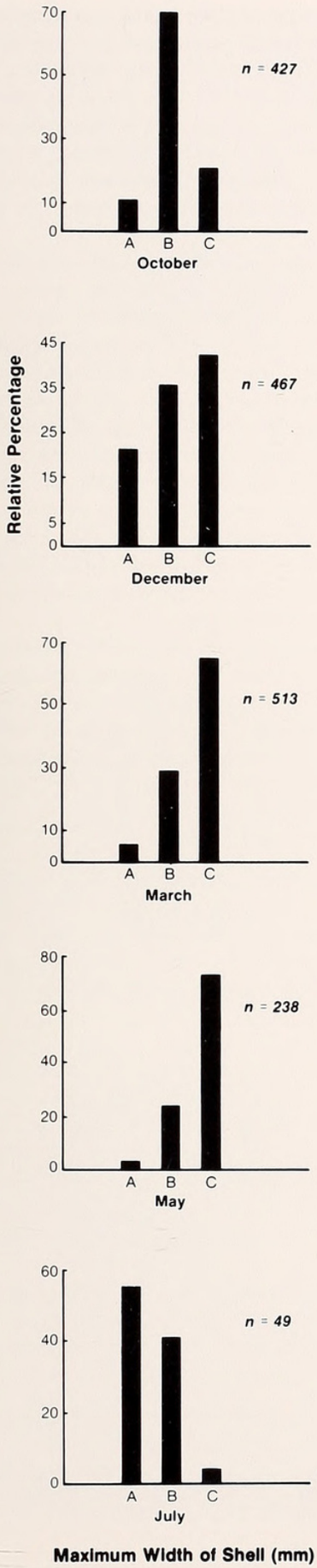
Boonea impressa specimens from each sample taken at Mud Island were decalcified using 0.5 M EDTA (ethylene diamine tetraacetic acid) and subsequently embedded in a paraffin medium and sectioned at 6 μm. Sections were stained for one hour with toluidine blue (method of PREECE, 1972, modified by using colloidinization during the rehydration step to ensure further that sections would remain on the slides). The sections were examined for the presence of sperm, as well as the number and size of the oocytes.

RESULTS

Larval Development and Population Dynamics

The mean size of *Boonea impressa* in the population from Mud Island increased from October to May (Figure 1). The population's size-frequency distribution changed significantly (Chi-square test, $P < 0.05$) between all sampling periods except March and May ($P < 0.10$ for the latter two).

* The term odostomian is used here for species usually referred to the genus *Odostomia* prior to ROBERTSON (1978) (*e.g.,* ABBOTT, 1974; DALL & BARTSCH, 1909).



Recruits (specimens 0.5–1.00 mm in width) were observed in all samples, but recruitment in December (22% of the population sampled were new recruits) was noticeably higher than in October (10%), March (5%), or May (3%). The largest recruitment of juvenile snails was in July (55% of the population sampled were new recruits). Just prior to the July sampling, an extremely low tide and high temperature caused extensive mortality among the intertidal oysters. Although the population of *B. impressa* sampled was subtidal, the population structure for July may not be indicative of the normal summer condition.

Mean oocyte size did not differ significantly among the October, March, and May collections (Duncan's multiple range test, $P < 0.05$) (oocyte diameters in μm for October, March, and May were 17 ± 2, 15 ± 4 and 17 ± 3 respectively). Significantly more oocytes were found in the snails collected in May than in those collected in either March or October (Kruskal-Wallis test, $P < 0.05$) (Table 1). The latter two months' collections were not significantly different. No oocytes were found in any specimen collected in December, and oocytes were found in only a single specimen collected in July. Sperm were present in most or all specimens examined in every collection period.

The eggs (Figure 2a) of *Boonea impressa* were laid in clear, irregular, gelatinous masses (Figure 3a) often deposited in crevices near the edge of the oyster shell. The number of eggs in an egg mass varied from approximately 20 to 250 under laboratory conditions. Egg diameter (maximum dimension) ranged from 182 to 238 μm. Significant differences were present in mean egg size between egg masses (Table 2). The range in egg size within an egg mass was always less than the range in egg size among all the egg masses measured. Eggs in a single egg mass tended to be of similar size so that some egg masses consisted almost exclusively of small eggs, whereas others consisted almost exclusively of large eggs. No difference was apparent, however, between the North Carolina and Texas populations.

The early embryological development of *Boonea impressa* followed the typical pattern for opisthobranch mollusks by exhibiting spiral cleavage and asynchronous cell division (RAVEN, 1958, 1964). Total developmental time required from oviposition to hatched veliger was 80–114 h (Table 3). The first cleavage of eggs occurred 2 h after oviposition, the second and third divisions (8 cells) after 4–6 h (Figure 2b). After 26–30 h, a gastrula had formed (Figures 2c–e).

Further development was divided into three stages: ear-

←

Figure 1

Size-frequency distributions for the *Boonea impressa* population at the Mud Island reef during Fall 1981 to Summer 1982. Shell widths of A, B, and C are 0.50–1.00 mm, 1.01–1.66 mm, ≥1.67 mm respectively.

Table 1

The mean, standard deviation, and range of the number of oocytes observed in the stained sections of *Boonea impressa* gonad. The snails were collected from the Mud Island reef.

Sampling period	Mean ± SD	Range
October	53.25 ± 5.38	48–60
December	0	0
March	50.25 ± 20.02	33–75
May	140.00 ± 27.12	102–160
July	2.25 ± 4.5	0–9

ly-, mid- and late-veliger. The early-veliger stage, reached 32–36 h after oviposition, was characterized by the first noticeable movement of the embryo and the beginnings of velum development; however, neither shell nor statocysts were present and a bipartite velum was not observed. The mid-veliger stage, reached 50–54 h after oviposition, was characterized by the presence of statocysts, a bipartite velum, and a partially developed shell. The shell, however, did not extend down to the level of the statocysts, but covered only the upper part of the visceral mass (Figure 2f). The capability of retraction into the shell was not present nor was the velum completely developed. In particular, although the velum was ciliated, the long cilia characteristic of the velum of the hatched veliger were not present. Movement within the egg was most rapid at this stage and slowed noticeably thereafter. Between this stage and the late-veliger stage, reached 56–60 h after oviposition, the embryo grew rapidly from a size roughly one-half of the egg volume to a size nearly filling the entire egg volume. Prior to this, development had not markedly increased embryo size. The late-veliger stage was characterized by a fully developed velum and a completely developed shell extending down below the level of the statocysts. The long cilia characteristic of the velum of a planktonic larva were fully formed only at this stage. Additionally, the embryo first showed the capability of retraction into the shell at this stage.

Hatching occurred 80–114 h after oviposition (Figure 3b). After hatching, veligers frequently were caught at the air-water interface by surface tension. Strands, probably the remnants of the "mucus string" that bound the eggs together (RASMUSSEN, 1944), often connected as many as 20 floating larvae together. Trapped veligers did not seem to be capable of submerging and subsequently died at the surface, unless the surface water was actively disturbed. Submerged veligers immediately demonstrated rapid movement both horizontally and vertically. During the first two days, movement was positively phototaxic and rapid. Afterwards, the veligers became negatively phototaxic and movement slowed considerably. For lengthy periods of greater than 1 h, the veligers often remained retracted into the shell or were stationary on algae or the bottom.

Many larvae metamorphosed in the large bowls in which oyster clumps were present; however, only a single individual was observed to metamorphose under the microscope. This occurred seven days after hatching. In an attempt to get more larvae to metamorphose, various possible metamorphosis inducing factors such as oyster shells, living oysters, algae typically found on oyster shells, and adult *Boonea impressa* were placed separately in bowls with apparently competent larvae (in the sense of CHIA, 1978), but without success. Larvae probably were competent to metamorphose, however, when negative phototaxis was observed, about two days post-hatching. Thus, seven days is probably an overestimate of the average larval life span in this species.

Newly metamorphosed snails were observed crawling freely, but most often they attached just outside the aperture on the outer lip of an adult *Boonea impressa* (Figures 3c, d). Juvenile *B. impressa* up to two teleoconch whorls frequently were observed demonstrating this behavior.

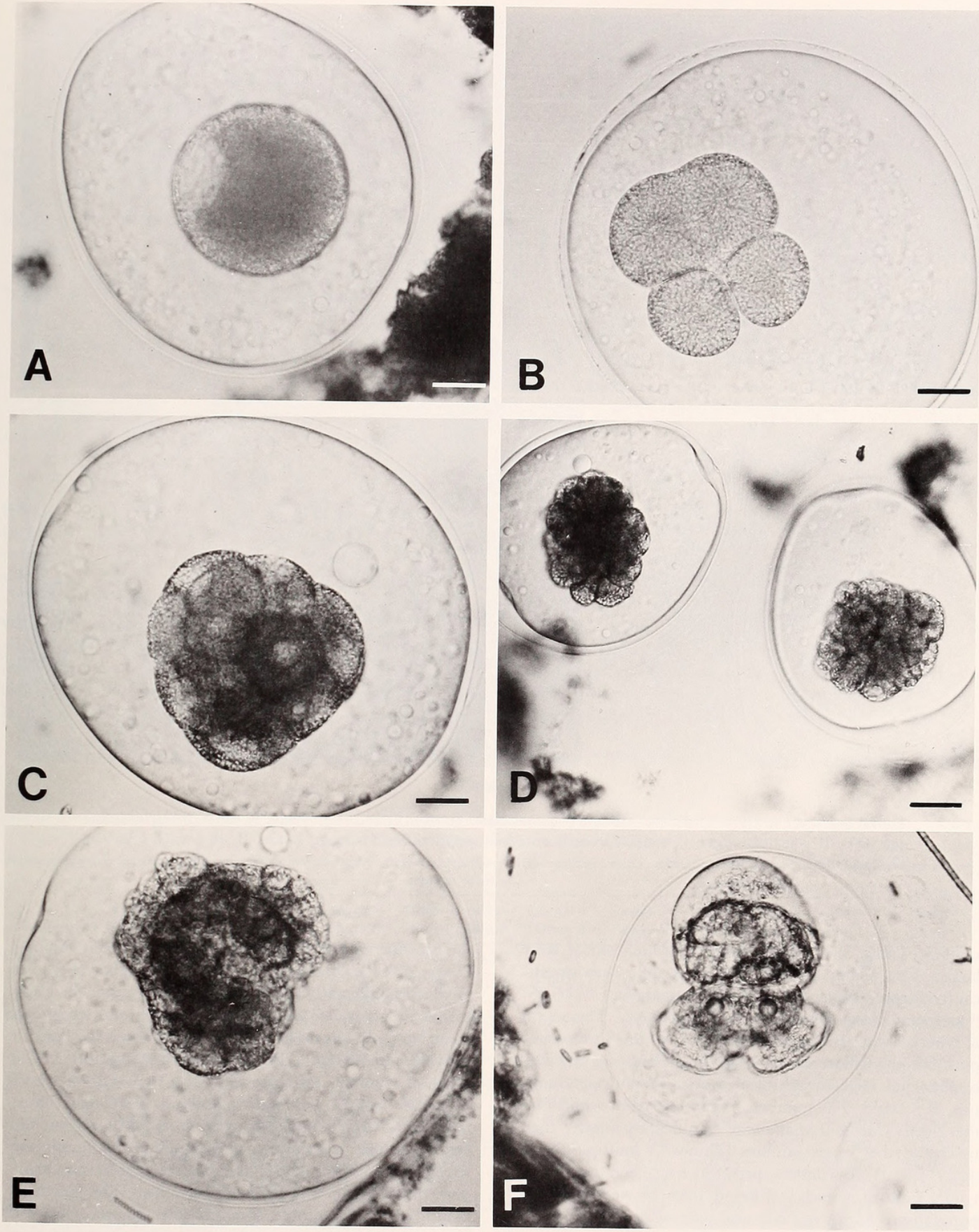
Shell Morphometrics

The mean length, width, and length-width ratio of whorls 2 and 6 of snails from Mud Island, Texas, were similar in each of the five collecting periods (Table 4). The number of spiral cords in whorl 2 was not significantly different for any of these samples (Duncan's multiple range test) either, averaging about three. The number of spiral cords in whorl 6 varied considerably more. Snails collected in May had significantly fewer cords than in any other month but October (Duncan's multiple range test, $P < 0.05$). The October, December, March, and July samples did not differ significantly, nor did October samples differ significantly from May ($P > 0.05$). The width of the protoconch varied only slightly, ranging from 234 to 240 μm. This variation was considerably less than noted for egg size.

The two populations of North Carolina snails were not significantly different except for the number of spiral cords and length of whorl 6; thus, they were treated as one

Figure 2 →

Developmental stages of *Boonea impressa* from the Mud Island reef, Texas. A, egg. B, 4-celled stage. C, multicelled stage. D, blastula. E, gastrula. F, mid-veliger stage. Scale bars: A, 40 μm; B, 24 μm; C, 23.6 μm; D, 57.5 μm; E, 21.5 μm; F, 38.8 μm.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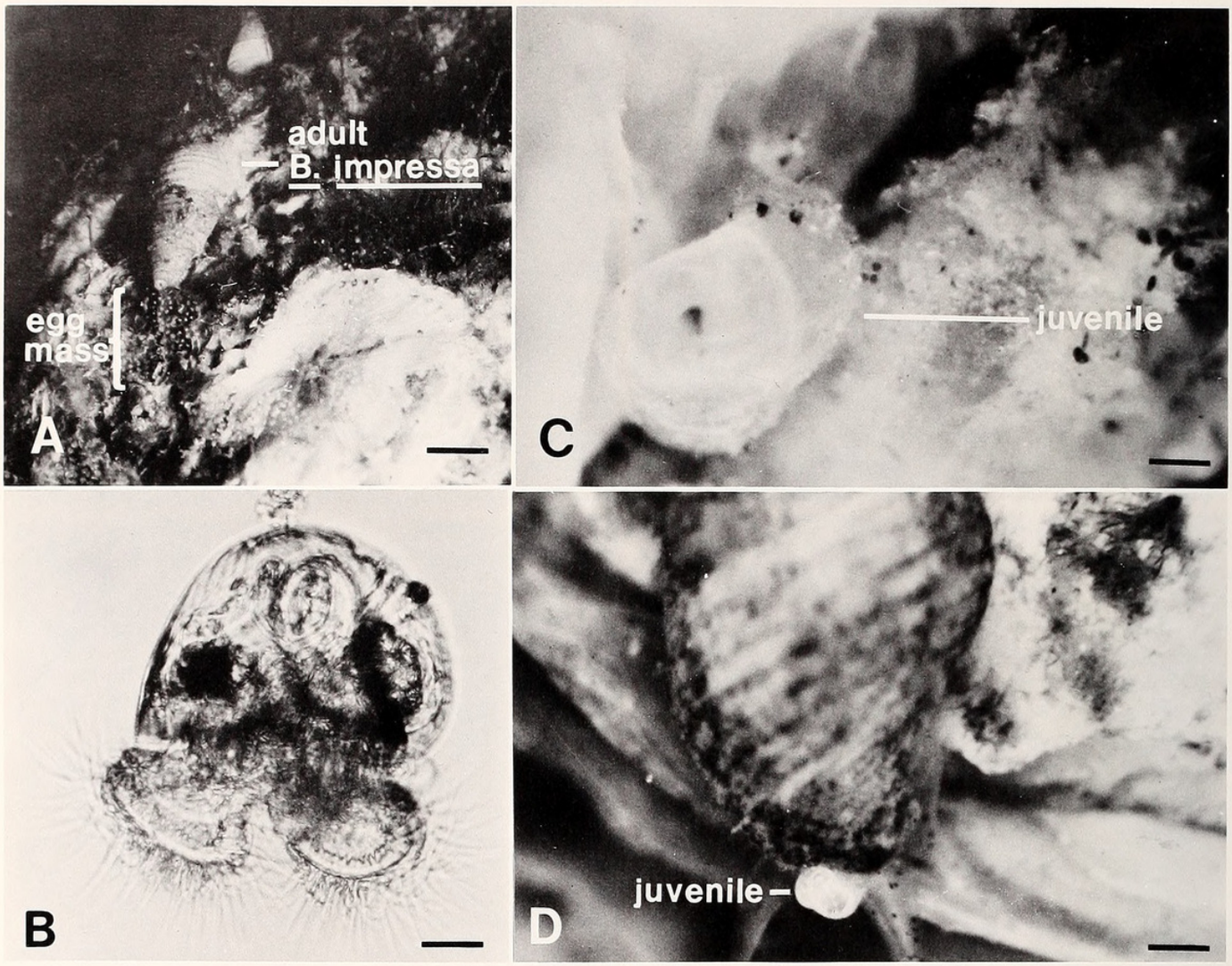

Figure 3

Larval and juvenile stages of *Boonea impressa* collected from the Mud Island reef, Texas. A, adult *B. impressa* and egg mass. B, hatched veliger. C and D, juvenile on adult aperture. Scale bars: A, 2 mm; B, 48 μm; C, 68.5 μm; D, 240 μm.

sample (Table 5). Overall, North Carolina snails were larger. The width of whorl 6, for example, was significantly larger (Duncan's multiple range test, $P < 0.05$) than in any of the Texas samples, except May. The length of whorl 6 was also larger than in any of the Texas samples, but the difference was significant only for the December and October samples (Duncan's multiple range test, $P < 0.05$). The number of spiral cords in whorl 6 in the North Carolina snails was significantly higher than in any of the Texas samples (Duncan's multiple range test, $P < 0.05$). In contrast, protoconch size and the length-width ratio of whorl 6 differed little between the two populations. Mean egg size also was very similar (Table 2).

A Pearson product-moment correlation test based on all shell measurements was conducted on the Texas samples (Table 6). The shell length, width, and number of whorls all were significantly correlated with each other for every month. In most samples, the whorl width and length for whorl 6 were correlated with both the total shell width and total shell length. This was not true for whorl 2. The width of whorl 2 was correlated with the width of whorl 6, but the lengths were not consistently correlated. Thus, the rate of whorl expansion was more constant than the rate of whorl translation. Consequently, although the length and width of whorl 6 were correlated in most samples, the correlation coefficients were low. The length of whorl 6 and the number of spiral cords in whorl 6 were also correlated in most samples, but width of whorl 6 was correlated less well with spiral cord number than was the

Table 2

Mean and range of the sizes of eggs in each *Boonea impressa* mass. Seven egg masses were measured: five from snails collected at Big Slough, Texas (No. 1, 2, 3, 4, 7) and two from North Carolina (No. 5, 6). n is the number of eggs measured. A, B, and C indicate results of Duncan's multiple range tests ($\alpha = 0.05$) where mean egg size for egg masses with the same letter are not significantly different.

Egg mass	Mean (μm)	Range (μm)	n	Significance ($\alpha = 0.05$)
1	218	214–238	8	A
2	209	198–222	15	B
3	207	198–222	9	B
4	205	214–222	12	B
5	205	190–222	12	B
6	192	190–206	12	C
7	189	182–190	10	C

Table 3

Development time for the embryonic stages of *Boonea impressa*.

Larval stage	Time from oviposition to when stage was first observed
Two cells	2 h
Four cells	4–6 h
Gastrula	26–30 h
Early-veliger	32–36 h
Mid-veliger	50–54 h
Late-veliger	56–60 h
Hatched veliger	80–114 h
Veliger negatively phototaxic	~ 6 day (2 day post-hatch)
Metamorphosis	~11 day (7 day post-hatch*)

* Probably a maximum.

length. The number of spiral cords in whorl 2 was poorly correlated with any other shell feature. Larval shell width was poorly correlated with any other character except the width of whorl 2.

In order to determine whether the number of cords in whorl 6 was influenced by any other shell feature besides whorl length, a stepwise regression test (maximum R^2 improvement) was conducted. This procedure (for all samples—Texas and North Carolina) showed that the length of whorl 6 was the best one-variable model for determining the cords in whorl 6. The R^2 values, however, were only 0.04, 0.13, 0.18, 0.18, and 0.24 (October, December, March, May, and North Carolina respectively). For the Texas populations, addition of shell width, width of whorl 6, and the number of whorls improved the correlation only marginally (corresponding $R^2 = 0.05$, 0.19, 0.25, 0.20). In contrast, the same procedures improved the correlation considerably for the North Carolina population. By adding the width of whorl 6, R^2 increased from 0.24 to 0.45, and then to 0.54, by adding the number of whorls and shell width.

Table 4

Mean and standard deviation of shell characters (in mm) of the samples of *Boonea impressa* from the Mud Island, Texas reef. Number measured is in parentheses.

				Length-width				Length-width				
Sample	Shell length	Shell width	Number of whorls	Length—whorl 6	Width—whorl 6	ratio—whorl 6	Cords—whorl 6	Length—whorl 2	Width—whorl 2	ratio—whorl 2	Cords—whorl 2	Width larval shell
October	3.44	1.47	5.99	0.71	1.43	0.50	3.92	0.23	0.48	0.48	3.00	0.234
	±0.96	±0.27	±1.15	±0.05	±0.09		±0.34	±0.02	±0.03		±0.03	±0.01
	(293)	(400)	(293)	(231)	(231)		(231)	(293)	(293)		(293)	(293)
December	2.97	1.42	5.53	0.74	1.42	0.52	3.99	0.23	0.48	0.48	2.99	0.236
	±1.40	±0.41	±1.52	±0.07	±0.09		±0.43	±0.01	±0.02		±0.08	±0.02
	(331)	(462)	(331)	(143)	(143)		(143)	(331)	(331)		(331)	(331)
March	3.75	1.65	6.20	0.77	1.48	0.52	4.09	0.24	0.49	0.49	3.01	0.238
	±1.35	±0.32	±1.31	±0.07	±0.12		±0.49	±0.01	±0.03		±0.18	±0.01
	(280)	(537)	(280)	(170)	(170)		(170)	(280)	(280)		(280)	(280)
May	4.05	1.78	6.39	0.76	1.51	0.50	3.76	0.24	0.49	0.49	3.00	0.239
	±1.23	±0.33	±1.22	±0.07	±0.13		±0.51	±0.01	±0.03		±0.00	±0.01
	(133)	(237)	(133)	(104)	(104)		(104)	(133)	(133)		(133)	(133)
July	2.06	1.03	4.14	0.76	1.44	0.53	4.00	0.24	0.50	0.48	3.00	0.240
	±0.94	±0.31	±1.27	±0.07	±0.14		±0.00	±0.02	±0.04		±0.00	±0.00
	(49)	(49)	(49)	(8)	(8)		(8)	(49)	(49)		(49)	(49)

Table 5

Mean and standard deviation of shell characters (in mm) of samples of *Boonea impressa* from North Carolina.

Character	Williston Creek (n = 22)	Virginia Creek (n = 9)	Combined
Number of whorls	6.98 ± 0.32	7.00 ± 0.65	6.99 ± 0.43
Width of shell	1.73 ± 0.11	1.75 ± 0.16	1.74 ± 0.12
Length—whorl 6	0.80 ± 0.05	0.75 ± 0.03	0.79 ± 0.05
Width—whorl 6	1.56 ± 0.10	1.51 ± 0.09	1.55 ± 0.10
Cords—whorl 6	4.55 ± 0.65	4.06 ± 0.17	4.40 ± 0.60
Width—larval shell	0.24	0.24	0.24
Length-width ratio—whorl 6	0.51	0.50	0.51

Feeding Apparatus

The proboscis and associated feeding structures of *Boonea impressa* were similar to other odostomians described by MAAS (1965). Here, we use the terminology of FRETTER & GRAHAM (1949) and cross-reference it to that of MAAS (1965) as much as possible. Rather than repeating the detailed descriptions of MAAS (1965), we emphasize only the differences observed. The feeding apparatus of *B. impressa* consisted of a buccal pump (*Pumpbulbus II* of MAAS, 1965) to which the esophagus and salivary glands attached at its proximal end, a long tubular structure homologous to the first buccal pump (*Pumpbulbus I*) described by MAAS (1965), the stylet and associated structures, and the proboscis (Figure 4). The first buccal pump, well developed in the European odostomians described by MAAS (1965), ANKEL (1949a, b), and FRETTER & GRAHAM (1949), was poorly developed. In its place was a long tubular structure connecting the buccal pump to the stylet tube. This long tube thickened gradually but noticeably over the last 25% or so of its length at the end where it connected with the buccal pump. Possibly this thicker portion functions as the first buccal pump does in European odostomians.

The salivary glands consisted of four sections: a proximal section containing about 2 or 3 small linearly arranged, circular rings of cells; a larger, wider middle section with 5 or 6 linearly arranged, circular groups of cells; a second but usually narrower middle section with 15–17 circular groups of small cells; and a very narrow distal region that might function as a storage compartment for the salivary cells' products (FRETTER & GRAHAM, 1949; MAAS, 1965). Serial sections were not studied; cell numbers were determined by staining during dissection. Thus, the variability in the number of cells observed within each group might be an artifact of preparation rather than true variability. Considerable variation was present in the width of the salivary glands so that, on occasion, the salivary glands were nearly cylindical in shape, as opposed to the more common appearance depicted in Figure 4. Even when cylindrical, however, the four groups of cells were readily distinguishable. The salivary glands closely resembled those described by MAAS (1965) and ANKEL (1949b) from *Odostomia plicata* and by FRETTER & GRAHAM (1949) from *O. unidentata,* except that the proximal group of small cells is absent in *O. plicata.* Differences in shape observed by MAAS (1965) for *O. eulimoides,* however, which are similar to differences described above for *Boonea impressa,* and the hypothesized cell cycle whereby new cells originate near the middle of the gland and move proximally as they grow (ANKEL, 1949b; FRETTER & GRAHAM, 1949) suggest that salivary gland morphology may be variable from snail to snail. Thus, the significance of the similarities and differences noted by MAAS (1965) and us as taxonomic criteria remains unclear.

Approximate sizes for the various components of the feeding apparatus are given in Table 7. Except for the two cuticularized structures, the stylet (*Stachel* of MAAS, 1965) and the stylet tooth (*Stempel* of MAAS, 1965), the sizes varied considerably in different preparations due to relaxation or contraction and should be considered as rough estimates only. No significant difference in the sizes of any component was found between the North Carolina and Texas populations.

DISCUSSION

Reproduction and Growth

Our results agree with those of WELLS (1959) from North Carolina that the life-span of *Boonea impressa* is approximately one year and that reproduction and recruitment to the population occurs more or less continuously. Reproduction and recruitment rates are not constant, however. Although sperm were present in all adult specimens in all months sampled, marked differences in oocyte numbers were found. In May, approximately 38% more oocytes were found than during any other sampling period. No oocytes were found in December; this could possibly be correlated with the cold water temperatures encountered at that time. WELLS & WELLS (1961) suggested that reproduction in *B. seminuda* was directly related to water temperature. The absence of oocytes in most of the specimens in July probably was due to the young age of the majority of the specimens collected.

Growth rates also were comparable between the Texas population studied here and the North Carolina population examined by WELLS (1959). In both populations, the large summer set reached adult size in early spring of the following calendar year. Both populations consisted of predominately juvenile individuals in mid-summer and predominately adult individuals in late spring. Thus, reproduction and recruitment, although continuous, are markedly higher in early summer (May–July). This more or less coincides with the peak period of oyster reproduction in the study area (GUNTER, 1941; COPELAND & HOESE, 1966). Adults of *Boonea impressa* were most abun-

Table 6

Shell sculpture characters of *Boonea impressa* which were correlated significantly ($\alpha = 0.05$). Numbers 1, 2, 3, 4, and 5 represent samples from October, December, March, May, and July respectively. Correlation coefficients for significant correlations are given in the mirror image left and below of the diagonal midline. For example, width of whorl 6 was significantly correlated with shell lengths in months 1, 2, 3, 4 with $r = 0.62, 0.46, 0.37$, and 0.29 respectively.

	Shell length	Shell width	Number of whorls	Length—whorl 2	Width—whorl 2	Cords—whorl 2	Length—whorl 6	Width—whorl 6	Cords—whorl 6	Width larval shell
Shell length	*	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3	2, 3	1	1, 2, 3, 4	1, 2, 3, 4	2, 3, 4	—
Shell width	0.96, 0.93, 0.95, 0.96, 0.97	*	1, 2, 3, 4, 5	1, 2, 3	2, 3	1	1, 2, 3, 4	1, 2, 3, 4, 5	3, 4	—
Number of whorls	0.96, 0.97, 0.96, 0.93, 0.97	0.92, 0.92, 0.94, 0.92, 0.94	*	1, 2	2	1	2, 3, 4	1, 2, 3	2, 3, 4	—
Length—whorl 2	0.23, 0.18, 0.18	0.22, 0.17, 0.16	0.15, 0.16	*	1, 3, 5	2	1, 3	1	3	1
Width—whorl 2	0.17, 0.12	0.11, 0.16	0.12	0.28, 0.19, 0.75	*	—	1, 2, 3	1, 2, 3, 4	1, 2	1, 2, 4
Cords—whorl 2	0.13	0.13	0.13	0.12	—	*	—	—	—	—
Length—whorl 6	0.54, 0.50, 0.61, 0.67	0.57, 0.22, 0.48, 0.67	0.33, 0.40, 0.38	0.46, 0.28	0.28, 0.25, 0.31	—	*	2, 3, 4	1, 2, 3, 4	1
Width—whorl 6	0.62, 0.46, 0.37, 0.29	0.77, 0.32, 0.60, 0.47, 0.80	0.23, 0.28, 0.24	0.34	0.27, 0.43, 0.39, 0.39	—	0.33, 0.34, 0.38	*	2, 3, 4	1
Cords—whorl 6	0.39, 0.42, 0.28	0.31, 0.25	0.29, 0.39, 0.23	0.19	0.17, 0.17	—	0.13, 0.36, 0.42, 0.42	0.27, 0.22, 0.19	*	—
Width larval shell	—	—	—	0.22	0.23, 0.13, 0.17	—	0.23	0.29	—	*

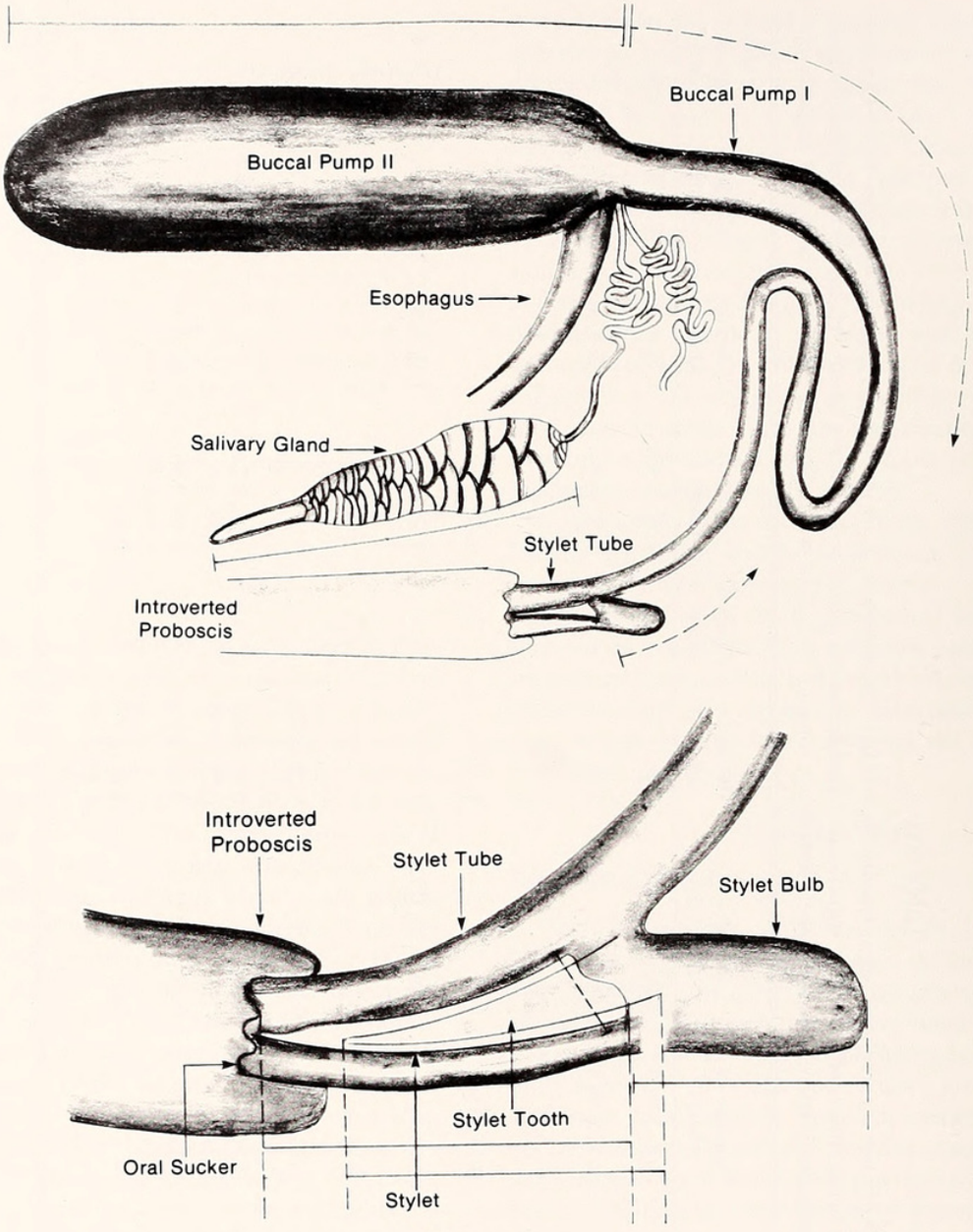

Figure 4

The internal anatomy of the feeding apparatus. Bars indicate the method of measurement for dimensions reported in Table 7. Above, the entire feeding apparatus excluding the proximal portion of the proboscis. Below, an enlargement of the stylet tube.

dant during the spring when oyster gonadal development and spawning occurred, and juveniles of *B. impressa* were most abundant in the summer and fall when oyster spat were also most common.

Larval Development—*Boonea impressa*

THOMPSON (1967) classified the larval development of opisthobranchs into three categories: Type I-planktotrophic larvae with small ova (40–170 μm), a short embryonic period (2–28 days), and a free-swimming veliger stage usually of >3 days duration; Type II-lecithotrophic larvae with larger eggs (110–250 μm), a longer embryonic development (4–42 days), and a free-swimming veliger stage usually of <3 days duration; and Type III-direct development with even larger ova (205–400 μm), an even longer embryonic period (13–50 days), and hatching at the post-larval stage. Type II includes THORSON's (1950) planktonic larvae with a short pelagic life-span. Development in pyramidellids fits more or less into THOMPSON's (1967) scheme. In Table 8, we compare our data on *Boonea impressa* with other data available on pyramidellids where both egg size and embryonic development time are

Table 7

Measurements of components of the feeding apparatus of *Boonea impressa*. Terminology of MAAS (1965) appears in parentheses. Measurements were made as shown by the bars in Figure 2.

Structure	Population	Mean (μm)	Range (μm)	n	Mean (μm/μm)	Range (μm/μm)
Maximum width of shell	NC	1920	1840–2000	6		
	TX	1856	1760–1920	5		
Buccal pump, length	NC	1497	1310–1736	6	0.781	0.616–0.904
(*Pumpbulbus* II)	TX	1616	1499–1767	5	0.873	0.781–0.960
Buccal pump connecting	NC	3834	2761–4418	5	1.990	1.381–2.301
tube, length	TX	3676	3077–4181	5	1.984	1.603–2.186
(*Pumpbulbus* I)						
Salivary glands, length	NC	861	757–994	9	0.447	0.395–0.540
	TX	921	742–1136	8	0.500	0.386–0.617
Stylet bulb, length	NC	152	136–174	3	0.077	0.068–0.091
(blind sack)	TX	131	124–143	4	0.070	0.067–0.074
Stylet length (*Stachel*)	NC	218	202–233	5	0.113	0.101–0.127
	TX	207	182–225	5	0.112	0.095–0.128
Stylet width	NC	45	39–47	4	0.023	0.020–0.024
	TX	44	39–47	5	0.023	0.022–0.026
Stylet tooth, length	NC	199	174–221	5	0.103	0.087–0.120
(*Stempel*)	TX	196	174–233	5	0.106	0.091–0.132
Stylet opening, length	NC	47	39–54	5	0.024	0.020–0.029
(*Stachelöffnung*)	TX	40	39–43	4	0.022	0.020–0.023

known. *Boonea impressa* is Type II. Egg size and development time from oviposition to hatching are well within the range suggested by Thompson. Larval life-span is somewhat longer than Thompson's range for other Type II larvae; however, if the advent of negative phototaxic behavior marks the initial competence for metamorphosis, then the minimum planktonic life-span would be about 3 days rather than 7. This is close to THOMPSON's (1967) range for Type II life-spans. Furthermore, *B. impressa* does not show significant growth during the planktonic phase. Egg size and hatched veliger size are no less than 80% of size at metamorphosis. Egg sizes range up to 238 μm and protoconch size as measured on the adult was also in this range. Thus, feeding, if it occurs, probably is relatively unimportant in the planktonic stage.

Overall, development in *Boonea impressa* most closely resembles that described for the form of *Brachystomia rissoides* with a planktonic larva (RASMUSSEN, 1944) and *Odostomia eulimoides* (FRETTER & GRAHAM, 1949), both of which also are Type II. Egg size is similar, as are de-

Table 8

Comparison of egg size, development time, and larval life-span in the Pyramidellidae.

Species	Egg size	Development time: oviposition to hatching	Larval life-span	Authority
Boonea impressa	182–238 μm	>3 to <5 days	7 days (probably 3–7)	our data
Brachystomia rissoides	300–650 μm	25 days	none	RASMUSSEN (1951)
Brachystomia rissoides	~200 μm	6.5 days	?	RASMUSSEN (1944, 1951) THORSON (1946)
Eulimella nitidissima	~100 μm	5 days	long	RASMUSSEN (1944)
Odostomia eulimoides	~160 μm	10–12 days	3–4 days	FRETTER & GRAHAM (1949) LEBOUR (1932)
Chrysallida cincta	300–340 μm	22–27 days	none	LAFOLLETTE (1977, 1979)
Odostomia omaensis	120–150 μm	8 days	?	AMIO (1963)
Odostomia desimana	130–160 μm	14 days	?	AMIO (1963)

velopment time and larval life-span (Table 8). The longer development times for *O. eulimoides* and *Brachystomia rissoides* probably are due to a lower temperature regime (see SPIGHT, 1975). On the other hand, RASMUSSEN (1944) found that the shell and statocysts of *Brachystomia rissoides* with a planktonic larva developed prior to formation of a bipartite velum, and observed first movement only after 100 h. In *Boonea impressa,* the statocysts and a bipartite velum were present prior to complete formation of the shell. First movement was observed at 32–36 h, prior to shell formation or the development of a bipartite velum. In fact, in this regard, *Boonea impressa* more closely resembles *Eulimella nitidissima* for which movement was observed at 53 h, prior to the development of a bipartite velum or statocysts (RASMUSSEN, 1944). Additionally, the 75 h embryo is similar to our mid-veliger stage reached at 50–54 h in that shell formation is incomplete: the shell covers only the visceral mass somewhat above the level of the statocysts. *Eulimella nitidissima,* however, has a Type I-planktotrophic larva. Egg size is considerably smaller than in *Boonea impressa* and the larva more than triples in size during the planktonic phase (RASMUSSEN, 1944). Thus, although the larval development of *Boonea impressa* is best described as Type II overall, certain aspects of its embryonic development more closely resemble that of *E. nitidissima* which results in a Type I larva.

Larval Development—Pyramidellidae

Some information is available for a number of other pyramidellid species. *Parthenia decussata,* which grows considerably during its planktonic life-span and has a small egg size (90–120 μm) (LEBOUR, 1936), also can be considered Type I. At the other extreme, *Chrysallida cincta* and one form of *Brachystomia rissoides* have direct development (Type III of THOMPSON, 1967) (RASMUSSEN, 1951; LAFOLLETE, 1977, 1979). ROBERTSON & ORR (1961) suggested that *Odostomia chitonicola* also may have direct development. AMIO (1963) discussed two additional *Odostomia* species with egg sizes and development similar to *Boonea impressa.* Thus, all three types of larval development described by THOMPSON (1967) are present in pyramidellids, with each larval type represented by at least two of the seven species for which some data are currently available.

Apparently, ectoparasitism has produced no obvious universal modification to the opisthobranch developmental plan. This suggests that factors determining developmental mode in opisthobranchs generally might apply to the Pyramidellidae also. CLARK & GOETZFRIED (1978) suggested that trophic stability was an important factor. Direct development would be favored when the food source was stable or predictable, a planktonic larva when the food source was unstable or unpredictable. The pyramidellid species listed in Table 8 having either direct development (Type III) or a lecithotrophic larva (Type II) usually parasitize organisms with long life-spans or organisms that are components of persistent (in the sense of BOESCH *et al.,* 1976) communities. *Chrysallida cincta* has direct development and parasitizes gastropods such as *Haliotis corrugata* and *Tegula eiseni* whose life-spans probably exceed 10 yr (LAFOLLETTE, 1977). Similarly, hosts for *Brachystomia rissoides* and *Odostomia eulimoides* live 10–20 yr (FRETTER & GRAHAM, 1949; COMFORT, 1957; ANKEL & CHRISTENSEN, 1963). The host of *Boonea impressa* is the keystone species of a particularly persistent community, the oyster reef, so that food supply and location is dependable year to year. In contrast, although the host of *Eulimella nitidissima* is unknown, the planktotrophic larva of *E. nitidissima* suggests that the host's population will be temporally less stable than in the above species.

Although adult snails frequently move from one host to another (ANKEL & CHRISTENSEN, 1963; WHITE *et al.,* 1984), movement by adults between host populations probably is rare. A short pelagic life-span of the type demonstrated by *Boonea impressa* might be expected, particularly when the host species is immobile, even though trophic stability might favor direct development. Both gene flow and dispersal between host populations would be facilitated. Of the three species with uniformly only Type II or Type III development, both species (*B. impressa* and *Odostomia eulimoides*) which primarily parasitize immobile hosts (bivalves in these cases) have larvae with a short pelagic phase. In contrast, the one species with only direct development, *Chrysallida cincta,* parasitizes gastropods, all of which have at least some mobility that might facilitate adult dispersal.

The few data available suggest that development time increases with increasing egg size in pyramidellids, as was suggested for other gastropods (*e.g.,* SPIGHT, 1975; STRATHMANN, 1977). The shorter time for *Boonea impressa* relative to other species of the same egg size probably can be attributed to the higher temperature regime of Texas bay waters. There appears to be little relationship between development mode and taxonomic status. Disparate modes are found in one species, *Brachystomia rissoides,* and very similar modes in clearly distinct genera (*e.g., Boonea* and European *Odostomia*).

Juvenile Behavior

The behavior of the young *Boonea impressa* veligers was positively phototaxic the first two days but then became negatively phototaxic. THORSON (1950) suggested that positive phototaxis allowed young larvae to stay near the surface where currents might aid their dispersal, whereas negative phototaxis in older larvae that were ready to metamorphose increased the time spent near the bottom and, thus, increased their chances of finding a suitable substrate for settlement.

The frequent observations of juvenile *Boonea impressa* attached near or at the aperture on the outer lip of the shell of adult *B. impressa* are too frequent to be simply

accidental, but suggest a behavioral mode that might increase juvenile survival. Several advantages are possible. (1) Predation might be decreased, particularly by predators that are too small to attack an adult snail. Small predators, such as polychaetes and juvenile crabs, are common on oyster reefs. Movement over the host might be accomplished more safely by hitching a ride because fewer potential predators would be encountered. (2) Small *B. impressa* may be unable to approach the oyster's mantle closely enough for feeding or to maintain a stable foothold on the oyster shell because the proboscis and foot are small and the edge of the oyster shell tends to be ragged. Adult *B. impressa* may provide a more stable substrate. (3) In fact, one cannot rule out the possibility that juveniles actually might feed on the adults for a short time until a size is reached that allows feeding on the oyster host. It seems unlikely that the outer mantle fold of the oyster can be fed upon because newly formed periostracum would interfere (see GALTSOFF, 1964; WALLER, 1980), and the remainder of the mantle might be difficult to reach with the short proboscis of a juvenile. Juvenile gastropods frequently utilize food resources not used by adults (KITTING, 1984). *Boonea impressa* certainly is capable of feeding on a variety of species, some of which may be more easily utilized by juveniles than are oysters.

Morphometrics—Shell Characters

LOPES (1958), WHARTON (1976), PORTER (1976), PORTER *et al.* (1979), POWELL (1981), and others discussed the intraspecific variability in certain shell characters often used for taxonomic identification in pyramidellids. Some, such as axial rib number and spiral cord number, are particularly variable. The North Carolina and Texas populations differed considerably in some respects. Snails from the North Carolina population were larger, and they had a greater width and length at whorl 6 than the Texas snails. Mean width of whorl 6, for example, ranged from 1.42 to 1.51 mm among the Texas samples, but was 1.55 mm in the North Carolina snails. In addition, the number of cords in whorl 6 was significantly greater in the North Carolina specimens than in any sample from the Texas population. The number of populations sampled was too few to suggest a regional difference in size or cord number. The data do indicate, however, that significant inter-population differences are present in shell sculpture and size. POWELL (1981), PORTER (1976), and PORTER *et al.* (1979) described similar variability in other pyramidellid species. Unfortunately, both shell sculpture and size are often used as taxonomic characters for identification.

In *Boonea impressa,* certain characters are much less variable. North Carolina and Texas specimens had very similar length-width ratios at whorl 6. Egg size and protoconch size were nearly identical. The size and shape of the feeding apparatus, including stylet, buccal pump and salivary glands, also were very similar. POWELL (1981) found that both length-width ratios and protoconch size were less variable between populations of several *Turbonilla* (*Pyrgiscus*) species than other shell characters, and suggested their taxonomic usefulness in the Pyramidellidae. Our data support this conclusion.

The number of cords at whorl 6 was more closely correlated to whorl 6 length than any other parameter. Certainly, the larger lengths of whorl 6 in the North Carolina snails explain the larger number of cords observed. Whorl 6 length alone, however, cannot explain all of the variation observed. The significant differences in cord number for whorl 6 between some collections from the Texas population (*e.g.,* the May and March collections), for example, cannot be explained easily by differences in whorl 6 length or in any other shell character measured. Thus, seasonal or other environmental changes also may influence cord number.

The size of the protoconch was correlated with only one other shell feature, the width of whorl 2. Interestingly, the widths of whorls 2 and 6 were correlated much better than the lengths of the same two whorls. POWELL (1981) pointed out that the length-width ratio and the sculpture of early whorls frequently differ considerably from those of the later adult whorls in pyramidellids. That is, both shell sculpture and growth form often change dramatically with age (see also LAWS, 1937). Increased variability with age is an important taxonomic problem in the Pyramidellidae where species frequently are described from juvenile individuals. Our data suggest that, for *Boonea impressa,* whorl width and the rate of whorl expansion are determined to a larger extent by factors also determining protoconch size than are the whorl length and the rate of whorl translation. Additionally, the number of cords in whorl 2 was not correlated with any other shell feature, unlike whorl 6 where a good correlation with whorl length was present. In fact, there was almost no variability in cord number in whorl 2, and this number was less than that typically given in descriptions of the species (*i.e.,* three rather than four cords).

Morphometrics—Feeding Apparatus

ROBERTSON (1978) distinguished American and European odostomians based on several features including the method of sperm transfer. European odostomians used penial copulation, whereas spermatophores were present in American species. The feeding apparatus of *Boonea impressa* exhibits another striking difference between *Boonea* and European odostomians. In all European odostomians studied, the first buccal pump is well developed (MAAS, 1965; FRETTER & GRAHAM, 1949) and attaches closely to the stylet tube. In *B. impressa,* the first buccal pump is very poorly developed and attaches by way of a long tube (over twice as long as the second buccal pump) to the stylet tube. This reinforces ROBERTSON's (1978) suggestion that American odostomians are deserving of a separate generic status from their European counterparts

and suggests that anatomical studies may provide important information for species and generic determinations.

Descriptions by FRETTER & GRAHAM (1949), FRETTER (1953), and MAAS (1965) all suggest that stylet length and size of the salivary glands and buccal pump may be good taxonomic characters, but measurements relative to shell size for comparison to *Boonea impressa* are unavailable. Nevertheless, the similarity between populations in the feeding apparatus (and in the size of the larval shell) sharply contrast to the differences present in many shell characters normally used for species distinctions. Characters with limited inter-population variability should be highly useful taxonomic characters when species specific differences are present. The evidence suggests that detailed studies of the feeding apparatus in the Pyramidellidae may provide useful comparative data when shell morphological criteria are too variable to provide unambiguous results, just as internal anatomical characteristics have in other groups of small, taxonomically abstruse groups of snails (DAVIS, 1967; DAVIS & CARNEY, 1973).

ACKNOWLEDGMENTS

Special thanks go to Hugh Porter who sent us snails from his collection and who collected living snails and sent them to us for the dissections. We thank B. Rogers for assistance in collecting Texas snails. We thank Drs. S. Ray, J. Brooks, and Mr. J. Parrack for helpful comments on the manuscript, and D. Lang for typing the manuscript and tables. The research was funded by a Texas A&M University mini-grant and an institutional grant #NA83AA-D-0061 to Texas A&M University by the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce to EP, and by the University of Texas Research Institute and C. Kleberg Foundation (CK).

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