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Title: Early Life History of the Giant Clams

Tridacna crocea Lamarck, *Tridacna maxima* (Röding),

and *Hippopus hippopus* (Linnaeus)

Approved: MASASHI YAMAGUCHI, Chairman, Thesis Committee

Giant clams may be stimulated to spawn by the addition of macerated gonad to the water. *Tridacna maxima* collected at Anae Island, Guam were spawned during November to March. *Hippopus hippopus* spawned in June and *Tridacna crocea* in July on Palau.

T. crocea, *T. maxima*, and *H. hippopus* displayed a stereotyped development pattern in morphogenesis and rate of development. Fertilized eggs of *T. crocea*, *T. maxima*, and *H. hippopus* had a mean diameter of 93.1, 101.5, and 130.0 μ, respectively. The day 2 straight-hinge veligers of *T. crocea*, *T. maxima*, and *H. hippopus* had mean shell lengths of 158.0, 168.0, and 176.4 μ, respectively. Settlement occurred 12, 11, and 9 days after fertilization at a mean shell length of [illegible], 195.0, and 202.0 μ for *T. crocea*, *T. maxima*, and *H. hippopus*, respectively. Metamorphosis was basically complete about one day after settlement. Juveniles first acquire zooxanthellae for *T. crocea*, *T. maxima*, and *H. hippopus* after 19, 21, and 25 days, respectively. Growth rates increase sharply after the acquisition of zooxanthellae. Calcification of juvenile shells begins after 47 days for *T. maxima* and after 50 days for *H. hippopus*.

The short pelagic larval period of the giant clams studied makes the outlook for mass aquaculture favorable. At this stage, the development of a suitable substrate for spat collection is the crucial problem.

EARLY LIFE HISTORY OF THE GIANT CLAMS

TRIDACNA CROCEA Lamarck, TRIDACNA MAXIMA (RÖDING),

AND HIPPOPUS HIPPOPUS (LINNAEUS)

by

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TO THE GRADUATE SCHOOL:

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INTRODUCTION

The motive behind investigating the early life history of the giant clam is twofold. First, giant clams are being subjected to an ever increasing fishing pressure because of their food and shell value. Early life history information would help alleviate some of this pressure by providing conservationists the necessary information for efficient population management. Second, understanding the early life history of the giant clam would determine the possibility and feasibility of a large-scale aquaculture of the animal as a food product by providing the required basic knowledge.

On Guam, research was conducted on Tridacna maxima at the University of Guam Marine Laboratory from September, 1979 to March, 1980. Research was carried out on Tridacna maxima, Tridacna derasa, Tridacna gigas, and Hippopus hippopus in Palau at the Micronesia Mariculture Demonstration Center (MMDC) from June 7 to August 15, 1980.

MATERIAL AND METHODS

On Guam, specimens of *T. maxima* were collected exclusively at Anae Island at depths from 3-10 meters. This species is usually found embedded in the substrate and was removed by chipping away the surrounding substrate with a hammer and chisel, then cutting the byssus clean with a thin-bladded fillet knife. This method was preferred as it did not injure the animal.

Specimens of *T. hippopus* and *T. derasa* were collected in Palau at Ngeruktabel Island at depths of 6-10 meters. Specimens of *T. crocea* were collected from the reef at the MBDC dock at a depth of 1-4 meters using the same methods as described for *T. maxima*. Specimens of *T. gigas* were collected near the Ngkabal Passage light house at a depth of about 3 meters by attaching a nylon sling to the clam and hoisting it to the bottom of the boat. Then, under slow speed, the clams were towed back to MBDC underwater.

Four to twelve individuals of *T. maxima* were collected monthly at Anae Island, Guam, from November, 1973 to March, 1975, except for the months of December, 1973, and October, 1974. They were subjected to spawning stimulus (excised gonad) the day after collection. If no eggs were spawned, the animals were dissected and the gonads were inspected microscopically. In spawning experiments only clams greater than 130 mm in shell length were used, as *T. maxima* does not attain sexual maturity, i.e. develop the female phase, until it attains a shell length of 110-130 mm. The tridacnid clams are protandric functional hermaphrodites (Wada, 1952; 1952). Gonad conditions

were judged using Stephenson (1934) as a basic reference. Gonad specimens were preserved in 70% isopropyl alcohol.

The fecundity of I. nasuta was estimated from eight clams collected in February, 1975. The number of eggs spawned by each of the individuals in separate containers was counted by volumetric estimate.

These clams were stimulated to spawn, using a 5-10 ml of excised gonad, and allowed to spawn until the water was very dense with sperm. They were transferred repeatedly to new containers until the spawning of eggs occurred. Five to ten ml of seawater containing sperm were added to the container to fertilize the eggs. The eggs were then isolated by using a net-system of a 210 μ nylon mesh over an 80 μ nylon mesh, which caught large detritus on the top net, the eggs on the bottom net, and allowed the sperm and water to pass through. The eggs from the bottom net were then gently washed into a 5-liter glass container using filtered seawater. The number of eggs was then adjusted, so that only one layer of eggs covered the bottom after settling occurred. Eggs were then washed three times using a settling and decanting technique and placed in several 500-liter tanks, at a concentration of about 10,000 eggs per tank. A prolonged washing period decreased survivorship, so fertilized eggs were washed only three times before being placed in a large tank. The 500-liter holding tanks contained seawater filtered through an 80 μ nylon mesh to remove large detritus and potential predators. Larval and juvenile I. nasuta were raised in the 500-liter rearing tanks. No additional nutrients were added to those present naturally in the seawater. The water in the rearing tanks for juveniles was changed once a week.

Various substrates (live rocks, rocks covered with coralline algae, glass, shells, and dead coral) were used as spat collectors during the settlement of T. maxima, to test substrate preference. Substrates were suspended in the tanks from a series of monofilament slings attached to sticks which were placed across the tops of the rearing tanks.

On Palau, suspended glass petri dishes, some with a sand bottom and others without, were used as spat collectors for H. hippopus. Suspended glass petri dishes, some with a sand bottom and others with an added coral bottom, were used as spat collectors for T. crocea.

After settlement, some juveniles of T. crocea and H. hippopus which had settled on petri dishes were placed in a 6x4x2 foot cement subsoiling pool with a running seawater flow, and others were left in the rearing tanks. The water in the rearing tanks was changed every two days.

The percent survivorship of T. crocea, T. maxima, and H. hippopus from the trochophore stage to the straight-hinge veliger stage was determined by placing 100 trochophores in each of six 1,800 ml beakers of filtered seawater. After the transition from trochophore to straight-hinge veliger, the number of veligers in each beaker was counted. To determine the percent survivorship from the straight-hinge veliger stage to the juvenile stage, the total number of straight-hinge veligers in the culture was estimated visually and the number of juveniles surviving was determined by direct count.

RESULTS

Spawning and Gonad Condition

After the addition of excised gonad, the clams would usually spawn immediately up to three minutes. The spawning of sperm continued for as long as six hours or more and exhibited variation in duration among individuals. For a detailed description of the spawning reaction see Wada (1954). After the spawning of sperm, the spawning of eggs will proceed, if the gonad is fully ripe. If the gonad is not fully ripe, only the spawning of sperm will occur.

The results from monitoring the gonad condition of *I. nasuta* at Anae Island are given in Table 1. Field collected animals stimulated by excised gonad spawned eggs in November, 1973; in January, February, and December, 1974; and in February, 1975. During no other months could *I. nasuta* at Anae Island be stimulated to spawn eggs. Spent gonads were found in dissected specimens during the months of December, 1973; March, September, and November, 1974; and January, 1975. From April through August, specimens in varying degrees of ripeness were observed.

The number of eggs spawned by *I. nasuta* varied with the size of the individual (Fig. 1) and can be expressed by the equation

$$F = .00743L^{4.03}$$

where F is the number of eggs spawned and L is the shell length.

H. hirsuta spawned sperm and eggs on June 12 in Pohue. A clam 260 mm in length released approximately 25 million eggs. Later in

Table 1. Monthly data on the gonad condition of a population of *Tridacna maxima* at Anae Island, Guam, monitored from November, 1973 to April, 1975.

Gonad Condition	1973 Nov	Dec	1974 Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	1975 Jan	Feb
Ripe	1		3	8										3		7
9/10 Ripe	3			1		2	2		1	3	1			1	1	
7/10 Ripe	1					2	3	1	2	2				1	3	
1/2 Ripe	3		1		3	3	2	4	3				1	1	1	
Spent	4				2						5		3		1	

Ripe: Spawned eggs after stimulus.

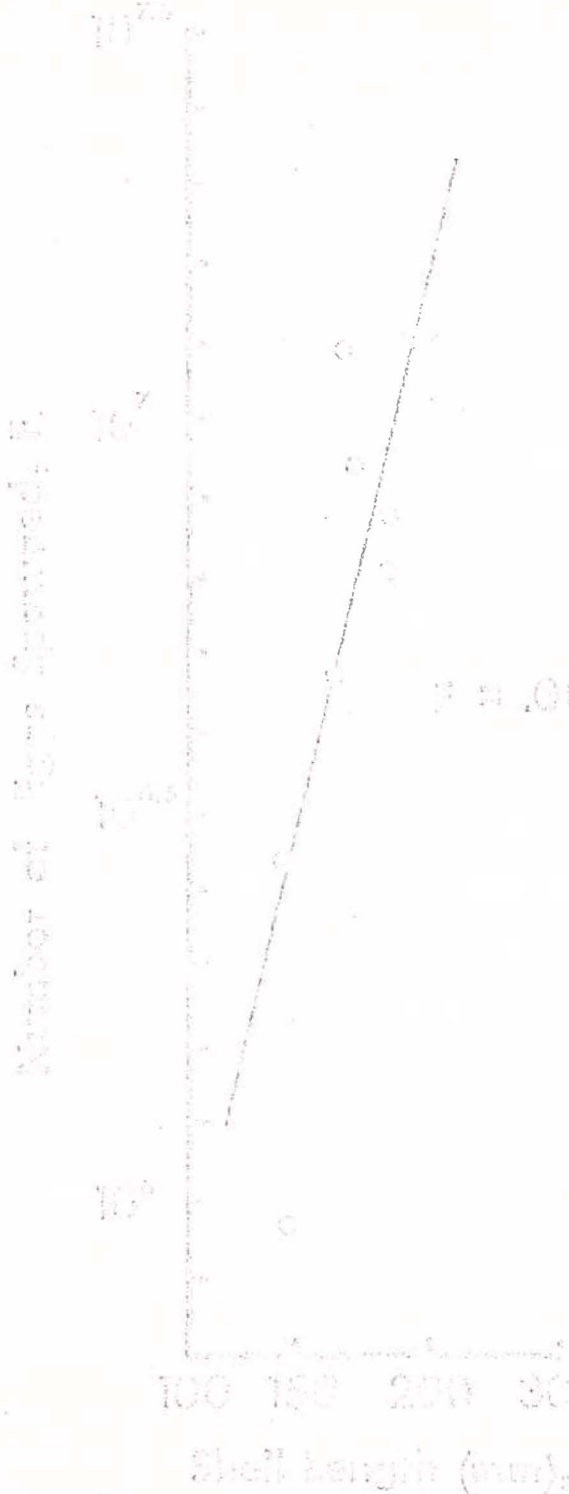
9/10 Ripe: Egg size between 100-150 μ. Gonad very large and white in color.

7/10 Ripe: Egg size between 80-130 μ. Gonad large and white in color.

1/2 Ripe: Egg size between 30-100 μ. Gonad small and white in color.

Spent: Very few to no eggs present. Gonad small and brown to olive drab in color.

Figure 1. Number of eggs spawned in relation to shell length of *Tridacna maxima* at Anse Lafond, Guam, a logarithmic plot.



August an H. hippopus 200 mm in length, was dissected and found to be in a half ripe condition. T. crocea spawned sperm and eggs on July 7. However, more than thirty clams were subjected to spawning stimulus before two finally spawned eggs.

Specimens of T. derasa 390 and 410 mm in shell length were subjected to spawning stimulus on July 3, 1974 and no spawning occurred. The specimens were then dissected and were found to be spent. Two T. gigas, 530 and 560 mm in shell length, on July 26, 1974, were found to be still in the male phase.

Early Life Chronology

The early life chronologies of T. crocea, T. maxima, and H. hippopus are presented in Table 2. T. maxima was cultured on four different occasions with fertilization occurring December 12, 1973; January 3rd, February 14, and February 22, 1974. The early life chronology is a composite of the above cultures.

T. crocea, T. maxima, and H. hippopus displayed a stereotyped developmental pattern (Figs. 3, 6, 9) which is considered to be typical for bivalves in general. Development times and size at a particular stage exhibit much individual variation (Tables 2, 3, 4, 5). In general, the three species observed exhibit similar development times when the great range of individual variation in these times is considered.

Embryonic and Larval Development

After fertilization, first cleavage produces two unequal blastomeres. Further spiral cleavages proceed in a manner typical of

Table 2. The early life chronology of the giant clams Tridacna crocea, Tridacna maxima, and Hippopus hippopus. Means are in parenthesis unless otherwise specified. All times given since cleavage are rounded off to the nearest hour, and all times mentioned are from time of fertilization. The times listed for development, unless otherwise specified, are when approximately 50 percent of the individuals observed from the cultures had reached that stage.

	T. crocea	T. maxima	H. hippopus
Culture temperature range	27.5-33.1° C	28.0-29.6° C	27.5-33.1° C
1st Cleavage	30 min.	60 min.	55 min.
Ciliated gastrula	7 hr.	7 hr.	8 hr.
Trochophore	15 hr.	16 hr.	17 hr.
Straight-hinge veliger	20 hr.	20 hr.	20 hr.
Pediveliger	10(9-17) days	9(8-10) days	7(6-15) days
Settlement	12(11-17) days	11(10-19) days	9(8-15) days
Metamorphosis	13(12-18) days	12(11-20) days	10(9-16) days
1st Juvenile w/zooxan.	19 days (190 u)	21 days (250 u)	28 days (300 u)
Smallest juv. w/zooxan.	190 u (19 days)	210 u (20 days)	300 u (27 days)
1st Juvenile w/calcification	-	47 days (440 u)	50 days (435 u)
Smallest juv. w/calcification	-	440 u (47 days)	435 u (50 days)

meridian the micromeres divide faster than the macromeres. A spherical blastula results. The rotating ciliated gastrulae may be observed 7 hours after fertilization for I. crocea and I. mayina and after 8 hours for H. hippopus.

The transition from a ciliated gastrula to the top-shaped trochophore is gradual. The anterior region develops a prototroch and apical flagella, and the posterior region develops a telotroch. The longitudinal axis elongates, and the anterior region becomes broader than the posterior. The trochophore stage (Figs. 3a, 6a, 9a) is reached for I. crocea, I. mayina, and H. hippopus, 15, 16, and 17 hours after fertilization, respectively. The outer layer of cells in the trochophore are thicker near the apical region (Fig. 3a). Trochophores exhibit negative geotaxis and swarm in the upper layers of the water.

As the prodissoconch I (PDI) shell forms, the body of the larva becomes laterally compressed. Straight-hinge veligers (day 2) (Figs. 4a, 7a, 10a) possess fully functional larval retractor muscles and anterior adductor muscles. All three species observed have their own characteristic arrangement of retractor muscles (Figs. 4a, 7a, 9a). Tridacna squamosa raised by Lab-Ybora (in press) had the same basic arrangement of retractor muscles as I. crocea. The velum, which has a peripheral ring of cilia, is used for swimming and gathering food. Straight-hinge veligers swimming near the surface exhibit negative geotaxis and positive phototaxis. The mouth is located ventrally on the posterior side of the velum. The esophagus and sac-like stomach are open and ciliated. The stomach leads posteriorly to an intestine which is without a lumen. By day 3 the

intestine becomes holler and the straight-hinge veligers actively feed. Food is gathered by the preoral cilia of the velum and passes through the esophagus to the stomach. Food is kept in motion by cilia in the stomach. At all times the digestive gland is either dark brown or gold in color. All three species feed primarily on a flagellate which is round in shape and about 5 μ in diameter. The day 2 PDL shells of I. crocea and I. maxima are similar in shape. The day 2 PDL shell of I. hiangsis, has a less steeply sloping posterior shoulder than those of I. crocea and I. maxima (Figs. 4a, 7a, 10a).

Pediveligers have developed for I. crocea, I. maxima, and I. hiangsis by day 10, 9, and 7, respectively. Pediveligers (Figs. 4b, 7b, 10b) possess a velum and a functional and active foot. The shell has begun to lose its definite straight-hinge appearance because of the slight growth of the umbo (Figs. 3c, 6c, 9d), and has increased in length. The stomach is now 2 chambered with a slight constriction separating the style sac from the anterior stomach chamber. The anterior stomach chamber is less ciliated than the posterior style sac. The esophagus opens into the stomach and has decreased in diameter. The stomach chamber also has openings coming from the digestive gland and an opening to the style sac. The style sac leads to the intestine which opens posteriorly as an anus. The anterior-adductor is present. The foot contains a byssus gland located towards the base of the foot (Fig. 6f). Cilia are present at the tip of the foot and smaller cilia run down the length of the foot to the byssus gland. Cilia are present only at the tip and on the side of the foot where the byssus gland is located. Pediveligers alternately swim about and crawl on

the bottom. Crawling is accomplished by attaching the tip of the foot to the substrate and then pulling the rest of the body forward (Fig. 6e). Another form of locomotion was a gliding movement which was accomplished by extending the foot and using the cilia on the tip of the foot to produce a gliding effect or continuous pull. A more bizarre form of locomotion was exhibited by a young juvenile that was attached to a filamentous alga. After slight movement of the alga, the young clam propelled itself through the water to another filament by rapidly contracting its valves. Upon arrival, it immediately attached to the new filament using its foot.

Settlement and Metamorphosis

Settlement and metamorphosis are gradual processes. The appearance of an active foot signifies that the time for settlement is near and that the process of metamorphosis is beginning. Pediveligers with a functional velum and foot alternately swim about and crawl on the bottom and possess a recently developed posterior adductor muscle and kidney. When swimming, most are confined to the lower half of the culture tank because of the increase in shell weight and reduction in size of the velum. After a period of alternately swimming, crawling, and making temporary attachments to the substrate, the pediveliger becomes increasingly sedentary in its habits. The velum gradually degenerates confining the clam to the substrate while functional gills develop (Figs. 5, 8, 11). Also at this time, a statocyst located at the base of the foot (Figs. 5, 11) was first observed in *T. crocea* and *H. hippopus*. This basically indicates completion of metamorphosis. Settlement is 50 percent complete for

I. crocea, I. maxima, and H. hippopus by day 12, 11, and 9, respectively. About 50 percent of the clams observed from culture bed completed metamorphosis by day 13, 12, and 10 for I. crocea, I. maxima, and H. hippopus, respectively. The times of settlement and metamorphosis exhibit much individual variation (Table 2).

After metamorphosis juveniles continue to crawl until a suitable place to attach by means of the byssus gland is found. Experiments using different substrates seem to indicate that juveniles prefer a permanent settling spot which can protect them from as many different angles as possible. For example, four crawling juveniles of I. crocea were introduced into a rectangular holding tank continually supplied with fresh seawater. The juveniles took, as their preference for permanent settling sites, the corners of the tank. Later, more juveniles were introduced. They took as their preference for permanent settling sites the edges of the tank, since the corners were already filled. Apparently, maximum protection governs the site of permanent settlement. This seems warranted as smaller individuals appear to be more susceptable to predation in their early life. Preliminary experiments, using juveniles ranging in length from 600 μ to 3 cm, demonstrated that only clams over 1 cm in length survived predation after being introduced into a natural situation. The boring species seem to be more demanding in their substrate requirement than the nonboring species.

Juvenile Development

The acquisition of zooxanthellae in the mantle of juvenile I. crocea, I. maxima, and H. hippopus occurred between 19-25, 21-40, and 25-27 days, respectively. The smallest juvenile with zooxanthellae

for T. crocea, T. maxima, and H. hippopus was 190, 210, and 200 μ in shell length, respectively. In general, the three species acquire zooxanthellae soon after metamorphosis. The shell of juveniles with zooxanthellae has a definite umbo (Fig. 6f), least pronounced in T. crocea. The stomach which previously only contained small flagellates now also has zooxanthellae rotating in it. The anterior and posterior adductor muscles are present.

Calcification of juvenile shells was observed for T. maxima on day 47 and for H. hippopus on day 50. Juveniles without signs of calcification could still be observed for T. maxima on day 91 and for H. hippopus on day 58. The shell length of the smallest juvenile with first signs of calcification was 440 μ for T. maxima and 435 μ for H. hippopus. In general, the time and smallest size at which T. maxima and H. hippopus first begin calcification are relatively similar. The majority of calcification usually begins in the ventral region. However, minor patches in other various locations were also noticed. The shell of juveniles beginning calcification is heart-shaped in appearance and the mantle is packed with zooxanthellae (Figs. 6g, 6e). Mantle extensions (Fig. 6h), which may be sensory in function and have small terminal bristles, are also developed on T. maxima and H. hippopus. Labial palps are present and active. An extended exhalent siphon is evident in T. maxima at this time (Fig. 6h). The heart was first observed beating on day 47 in a specimen of T. maxima which had a shell length of 360 μ. The rate of heart beat is very irregular and ranges from 19-31 beats per minute.

Growth and Survivorship

Mean sizes in length, ranges, and standard deviations for the different stages of T. crocea, T. maxima, and H. hippopus are presented in Tables 3, 4, and 5. Mean length in relation to time for the three species is plotted in Fig. 2 for comparison.

The growth curves for the three species exhibit similar basic characteristics. The growth rate from fertilized eggs to straight-hinge veligers (day 2) is high. The growth rate of pelagic larvae is low (1.2 μ/day for T. crocea, 2.7 μ/day for T. maxima, 3.6 μ/day for H. hippopus). Growth rates after settlement and metamorphosis until day 30 for T. crocea, day 40 for T. maxima, and day 27 for H. hippopus are also low (2.5 μ/day for T. crocea, 2.3 μ/day for T. maxima, 0.9 μ/day for H. hippopus). After day 40 (T. maxima) and day 27 (H. hippopus), growth rate increases sharply (6.5 μ/day for T. maxima, 13.9 μ/day for H. hippopus). This corresponds to the time by which the majority of juveniles had acquired zooxanthellae. Low growth rates from day 2 to the acquisition of zooxanthellae are probably because energy is channeled for various developmental changes, leaving less available for growth in size. Increased growth rates after the acquisition of zooxanthellae are probably brought about in a large part by the zooxanthellae themselves, which according to Goreau et al. (1973), supply T. maxima with energy from photosynthates and by digestion of older algal cells.

The survivorship from the trochophore stage to the straight-hinge veliger stage for T. crocea, T. maxima, and H. hippopus was determined to be 100 percent. Survivorship from the straight-hinge veliger stage

Table 3. Growth in length and height with respect to time for Iridaea cordata. Standard deviations are followed by ranges in parentheses.

Stage	Time	No.	Length (μ)	Height (μ)
Fertilized eggs	0	8	93.1±3.1(90-97)	
Straight-hinge veliger	Day 2	7	155.0±4.7(150-160)	130.0±4.1(125-135)
Straight-hinge length	Day 2	5	85.0±5.0(80-90)	
Pediveliger	Day 10	5	173.0±2.7(170-175)	
Settlement	Day 12	5	168.0±2.7(165-170)	146.0±4.2(140-150)
Juvenile	Day 17	5	182.0±5.7(175-190)	
Juvenile	Day 25	9	207.7±29.4(165-250)	
Juvenile	Day 35	8	228.3±62.5(185-300)	

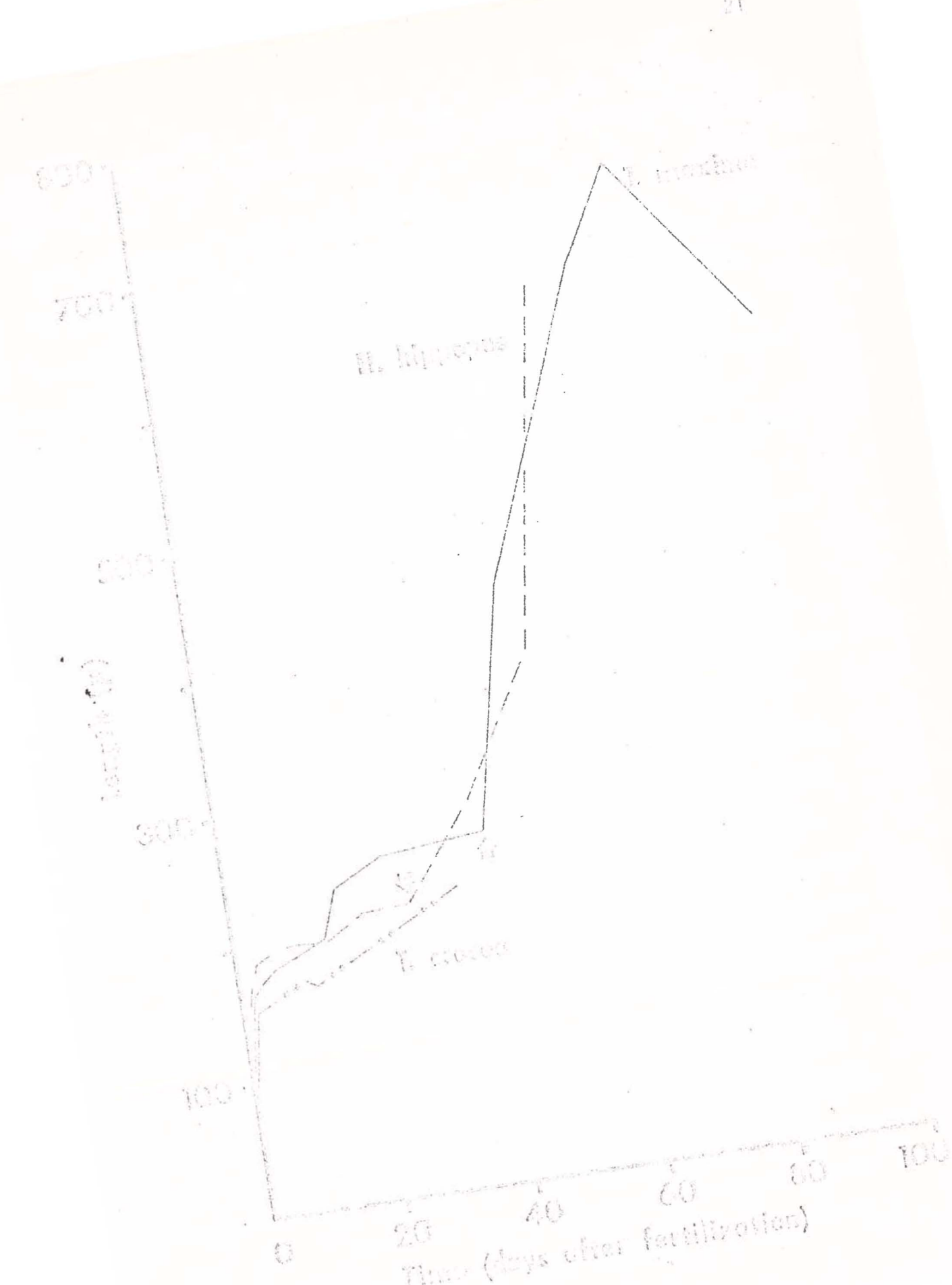
Table 4. Growth in length and height with respect to time for *Iridaea papillosa*. Standard deviations are followed by ranges in parentheses.

Stage	Time	No.	Length (μ)	Height (μ)
Fertilized eggs	0	10	104.5±5.5(100-115)	
Straight-hinge veliger	Day 2	6	168.0±4.5(160-170)	140.0±0(140-140)
Straight-hinge length	Day 2	4	91.3±2.5(90-95)	
Veliger	Day 4	3	173.3±5.2(170-180)	
Veliger	Day 6	6	184.2±4.3(180-190)	
Pediveliger	Day 9	7	192.1±9.1(180-200)	
Settlement	Day 11	7	185.0±8.7(180-205)	168.5±4.8(160-180)
Juvenile	Day 14	11	208.0±5.3(200-215)	
Juvenile	Day 16	4	207.5±12.3(200-230)	
Juvenile	Day 24	8	250.7±24.5(200-325)	
Juvenile	Day 40	5	264.0±53.2(220-350)	
Juvenile	Day 47	6	444.2±106.4(280-550)	
Juvenile	Day 64	5	572.0±58.1(505-630)	
Juvenile	Day 72	3	745.0±101.5(635-835)	
Juvenile	Day 97	8	617.5±191.1(400-835)	

Table 5. Growth in length and height with respect to time for *Mimachlamys hinnanus*. Standard deviations are followed by ranges in parentheses.

Stage	Time		No.	Length (μ)	Height (μ)
Fertilized eggs		0	6	130.0±6.3(120-140)	
Straight-hinge veliger	Day	2	9	174.4±12.4(150-190)	146.6±7.1(130-150)
Straight-hinge length	Day	2	5	100.0±8.4(100-120)	
Veliger	Day	3	6	191.6±4.1(190-200)	
Pediveliger	Day	7	5	200.0±0(200-200)	
Settlement	Day	9	5	202.0±2.7(200-205)	165.0±2.2(165-170)
Juvenile	Day	14	5	200.0±3.5(195-205)	
Juvenile	Day	20	12	216.6±10.6(205-240)	
Juvenile	Day	27	6	219.1±17.7(200-235)	
Juvenile	Day	38	3	283.3±48.6(235-330)	
Juvenile	Day	50	6	391.6±62.5(300-500)	
Juvenile	Day	58	9	556.7±39.6(535-635)	

Figure 2. Growth in length of Tridacna crocea, Tridacna maxima, and Hippopus hippopus. Only mean values are plotted for clarity. See Tables 3, 4, and 5 for ranges and standard deviations. Arrows indicate the time when the majority of the culture had acquired zooxanthellae.


600
700
500
300
100
0
20
40
60
80
100
Time (days after fertilization)

to day 91 for *I. unicus* was about 0.04 percent. For *T. crocea*, survivorship from the straight-hinge veliger stage to day 25 was about 0.075 percent, and for *H. binoyus* the survivorship from straight-hinge veliger stage to day 58 was about 3.0 percent.

DISCUSSION

Observations of the gonad condition of a population of T. maxima at Anae Island indicate that the winter months of November to March are the most promising for spawning. The height of the spawning period seems to be in the month of February. It appears that the majority of the population is in the process of recovering from winter spawning between the months of March and August. Some individuals with a high degree of maturity were observed at this time and some spawning may occur but probably only to a small extent. Spawning seems to increase in frequency around August or September and peak again in February.

Stephenson (1934) reported that H. hippopus spawn in the austral summer months of December to March on the reef-flat at Low Isles, Great Barrier Reef. She suggests high temperatures during two hot spells as the stimulus for spawning. The first hot spell was from December 7 to the end of the month with temperatures ranging from 29.0-30.7° C. The second hot spell lasted from January 12-30 with temperatures ranging from 29.0-32.0° C. This as a factor in stimulating spawning may be valid for reef-flat animals which are exposed to temperature fluctuations.

It is doubtful that temperature plays any role in the spawning period of T. maxima at Anae Island because the annual temperature range for oceanic surface water around Guam is 26.5-29.0° C. Deeper waters have insignificant annual temperature fluctuations; giant clams living in deeper waters are probably influenced in their

spawning activities by some other factor. Evidence suggests that temperature is not a factor in determing the spawning period of subtidal populations. Populations in relatively constant temperature environments may be genetically disposed to synchronize their spawning behavior to a characteristic environmental stimulus that may be unique to each population location.

It is also interesting to point out that in Australia and Palau, H. hippopus spawned in the summer months, and in Guam and Fiji, T. maxima spawned in their respective winter months. The same species may spawn during the same season of the year regardless of geographical location. Further investigation is needed into this question.

Many temperature shifting experiments similar in style to those used in spawning temperate water bivalves (Galtsoff, 1938) were carried out, using various temperatures and different periods of exposure. None of these procedures stimulated spawning; in some cases they made the animal sick, or even killed it. In the study of tropical bivalves one should consider the different environmental conditions to which tropical coral reef organisms are exposed to and not expect to find the same reproductive processes or strategies which are common to temperate water species.

Adding excised gonad to seawater containing giant clams seems to be the easiest and most efficient way to stimulate spawning. Wada (1954) contends that the active principle that stimulates spawning comes from both the eggs and the primordial ovogonia or other ovarian tissue cells. The active principle seems to be species specific in effect, as T. maxima would not react to stimulation using T. squamosa

eggs and vice versa (LaBarbera, in press), nor would I. squamosa react to stimulation using H. hippopus or T. derasa eggs, or T. derasa would not react to stimulation using I. squamosa or H. hippopus eggs (Wada, 1954).

In Guam, complete spawning was stimulated when 22 I. maxima were transferred from a 500-liter holding tank at 26.1° C to a 1,000-liter holding tank which was being filled, and at the time had only 6 inches of water in it. The water being added caused a circular flow in the tank and was at 29.7° C. Once the tank was filled the water cooled to 28.5° C and several clams spawned. Previous experiments designed to stimulate spawning by changing the temperature failed. This may lend support to the idea that spawning in nature is stimulated by water movement. In Guam, during the months of September to January, rougher than average sea states occur as a result of large swells generated by the trade winds, which are strongest at this time. At Anae Island continuous large swells during one or several winter months, causing very strong currents underwater, are common. The coincidence of strong underwater currents during the spawning period at Anae Island may further support this idea. LaBarbera (in press) notes the apparent effect of the changing tide in the stimulating the spawning of clams in Fiji.

In spawning giant clams for culture, it is essential that the spawning of eggs occurs in seawater with a low density of sperm. Spawned eggs with an excess of sperm in the surrounding jelly-coat do not develop normally. This problem was also observed by LaBarbera (in press).

The pelagic larval period of the three species observed is short (12 days for T. crocea, 11 days for T. maxima, 9 days for H. hippopus) and under better culture conditions can probably be shortened further. Lallmahare (in press) also observed similar short pelagic periods in the culture of T. maxima and T. squamosa in Fiji. This is definitely a favorable characteristic in considering the giant clams for mass aquaculture because food supplements, environmental quality and contamination do not have to be dealt with for long periods.

Larvae can be cultured adequately in a stagnant system but a food supplement and bacteriostat (Davis and Calabrese, 1969) should be added. Phytoplankton smaller than the esophagus diameter of about 8 μ should be considered. Monochrysis lutheri or Isochrysis galbana might be suitable.

The development of a suitable substrate for spat collection is crucial if mass aquaculture is to be considered. After settlement and metamorphosis, juveniles seek a suitable permanent settling spot which will give them maximum protection. If juveniles are to be maintained in a particular area after settlement, a suitable substrate must be available to them otherwise they will leave their original settling spot and be lost. For nonboring species a container with a sand bottom is adequate. For the boring species a spat collector that can give juveniles protection from as many angles as possible is preferred. Some nontoxic material with crevices or pits in it must be supplied.

After settlement, juveniles attached to spat collectors should be removed from the stagnant rearing system which contains much decaying matter and benthic bacteria and be transferred to a system

with a current of fresh seawater running through it. Juveniles should be raised to about 3-4 cm in length in the laboratory before being introduced into the field to grow in natural ecosystems. Any size below this is very susceptable to predation.

Several factors should be considered in choosing the most suitable giant clam species for commercial aquaculture. The ideal species should be hardy, easy to provide suitable substrates for, grow rapidly to market size on easily-procured food sources, and satisfy the food preferences of purchasers. No one species meets all of these criteria.

T. crocea is the preferred giant clam by island people because of its flavor and small size. However, it is a boring clam, and settling substrates would be critical for its successful culture. The nonboring clams would be the easiest to raise as their substrate requirement is less critical. These species raised only to a small size would provide the best marketability in the shortest time and be the easiest to culture. From personal experience, it seems T. squamosa is the hardiest of the nonboring giant clams because of its abundance on the coral reef and might be the prime candidate for a large scale aquaculture.

CONCLUSION

The outlook for the possible establishment of a large scale aquaculture of giant clams appears favorable. The short pelagic life of the giant clams studied and the probability that development times can be shortened and growth and survivorship increased with a more favorable culture environment support this opinion.

At this stage, the development of a suitable substrate for spat collection is the crucial problem, with the investigation of larval food preference also needed. With the advent of information on the survivorship of cultured juveniles which are introduced back into the field to grow, the aquaculture of giant clams will be basically established and further improvements will be only a matter of applied technology.

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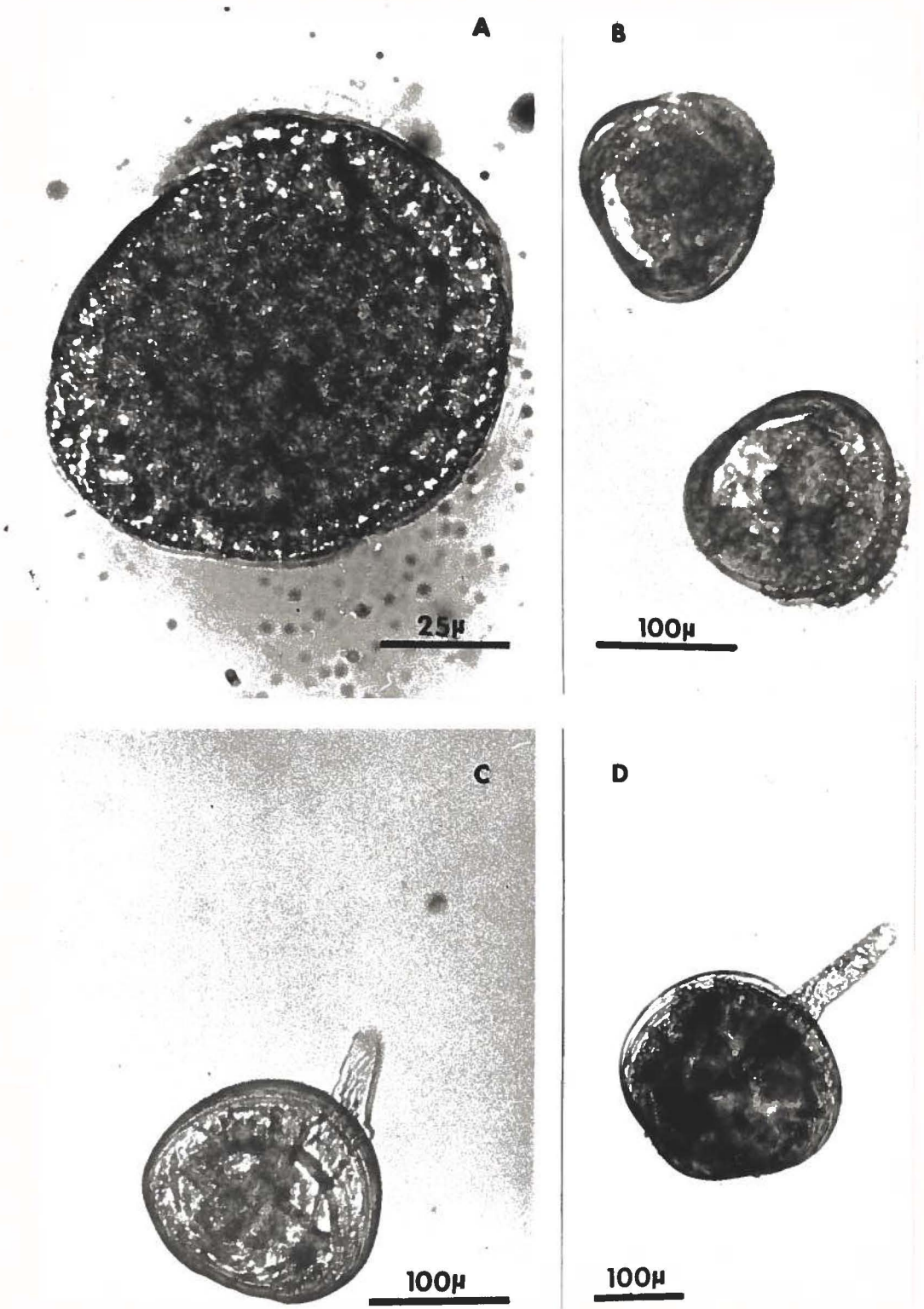
Figure 3. Larval and juvenile Tridacna crocea. A. Trochophore. B. Day 3 veligers. C. Day 10 pediveliger. D. Day 25 juvenile.


A
25µ
B
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C
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D
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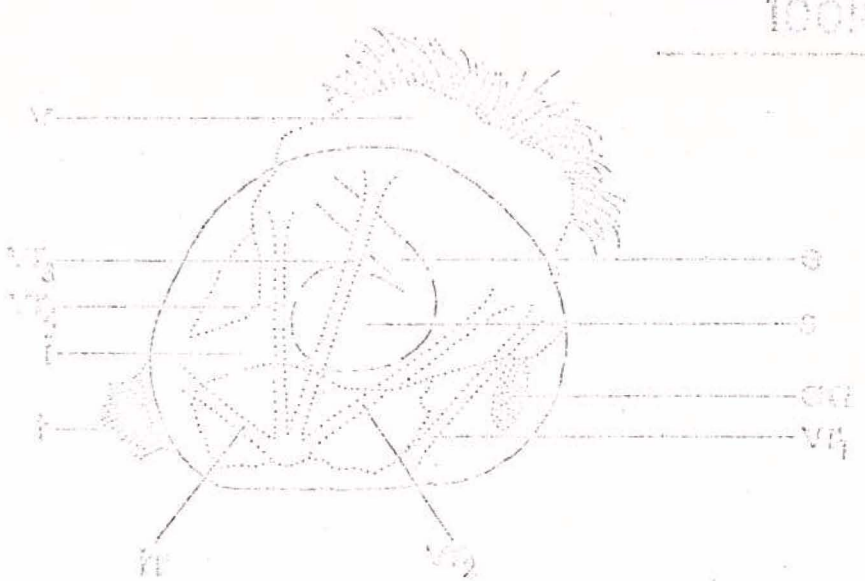
Figure 4. Internal anatomy of larval Tridacna crocea. A. Day 2 veliger. B. Pediveliger.

A



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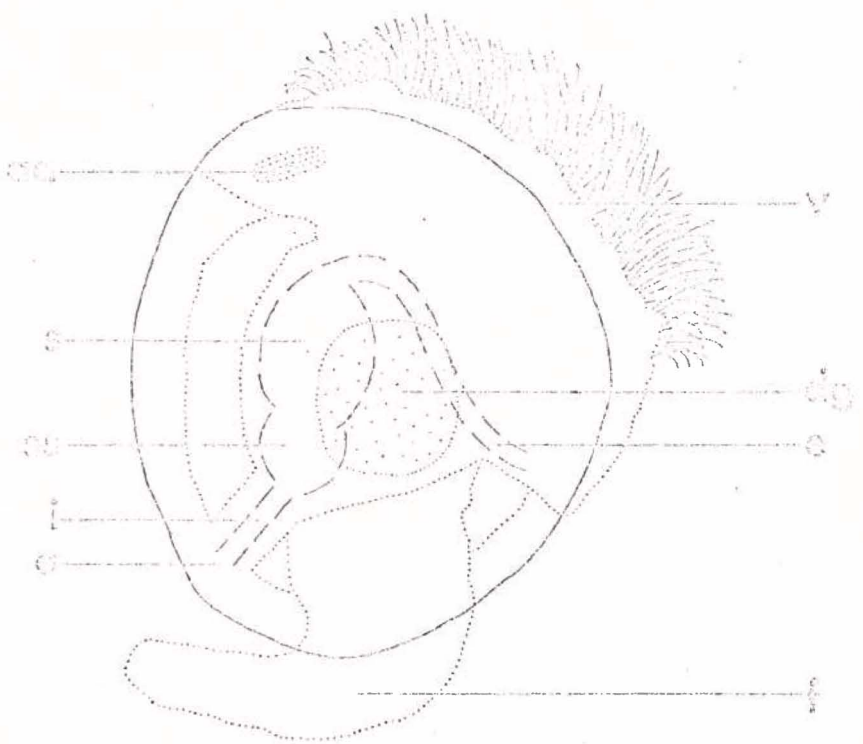


Figure 5. Internal anatomy of juvenile Iridaea cornea (day 25).

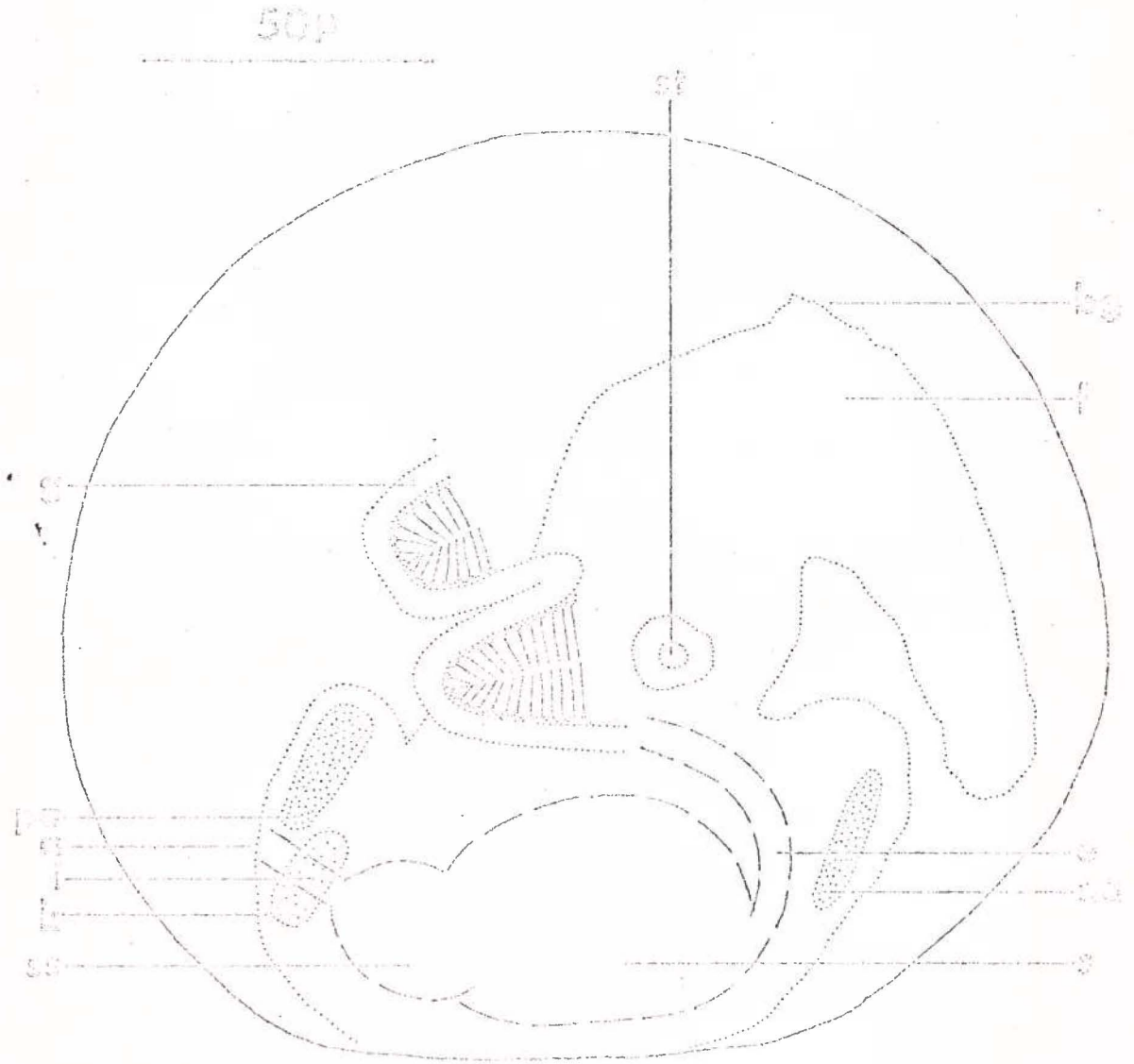
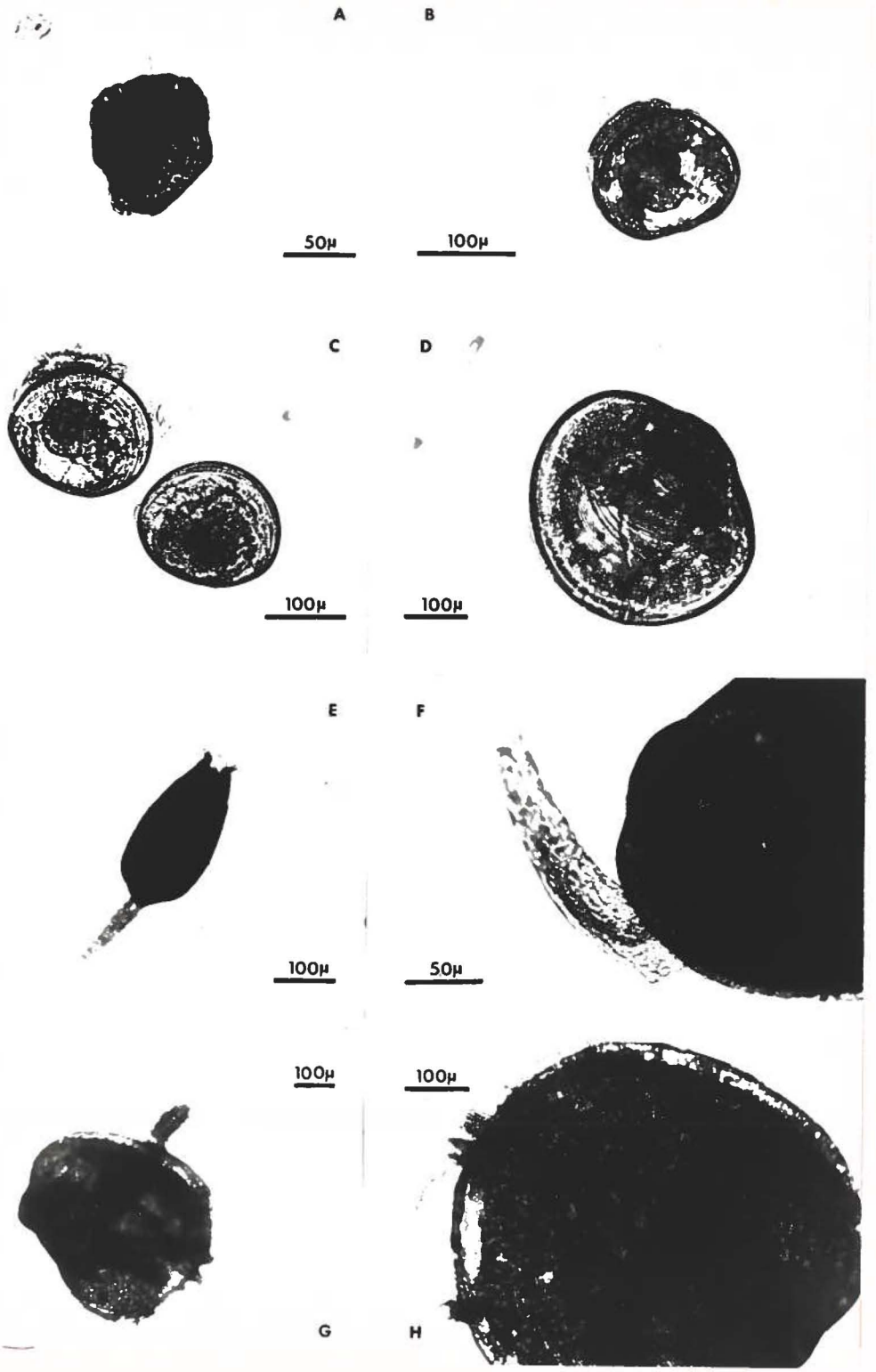

50µ

Figure 6. Larval and juvenile Tridacna maxima. A. Trochophore. B. Day 4 veliger. C. Day 9 pediveligers. D. Juvenile with first zooxanthellae. E. Crawling juvenile. F. Byssus gland. G. Day 64 juvenile. H. Exhalent siphon, mantle extensions, and abundant zooxanthellae in day 64 juvenile.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B
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C
D
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E
F
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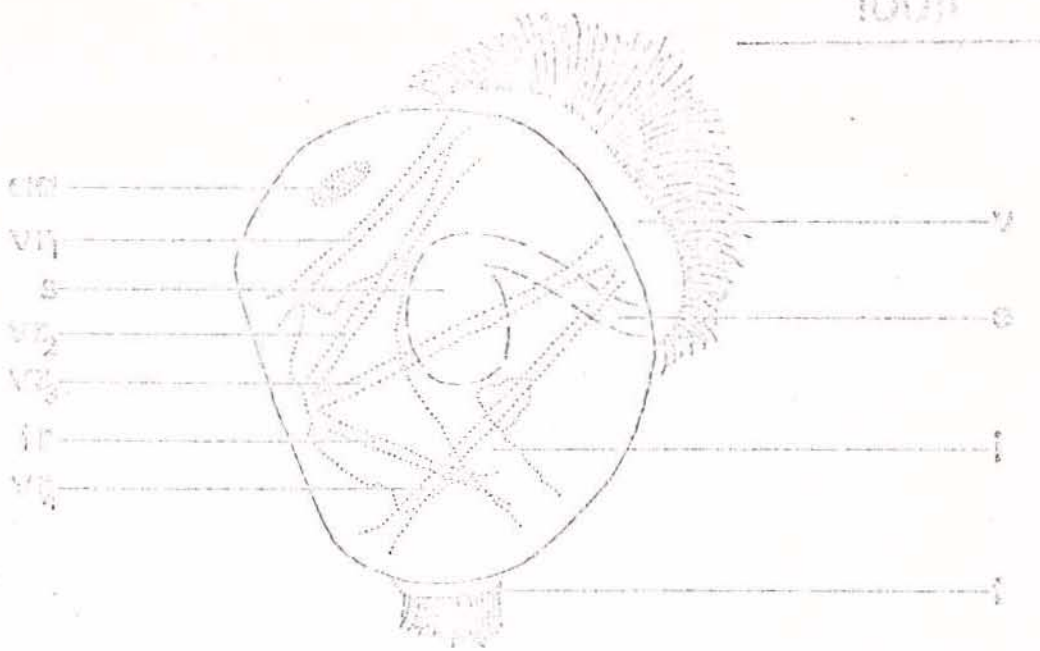
G
H

Figure 7. Internal anatomy of larval Tridacna maxima. A. Day 2 veliger. B. Pediveliger.

A



B

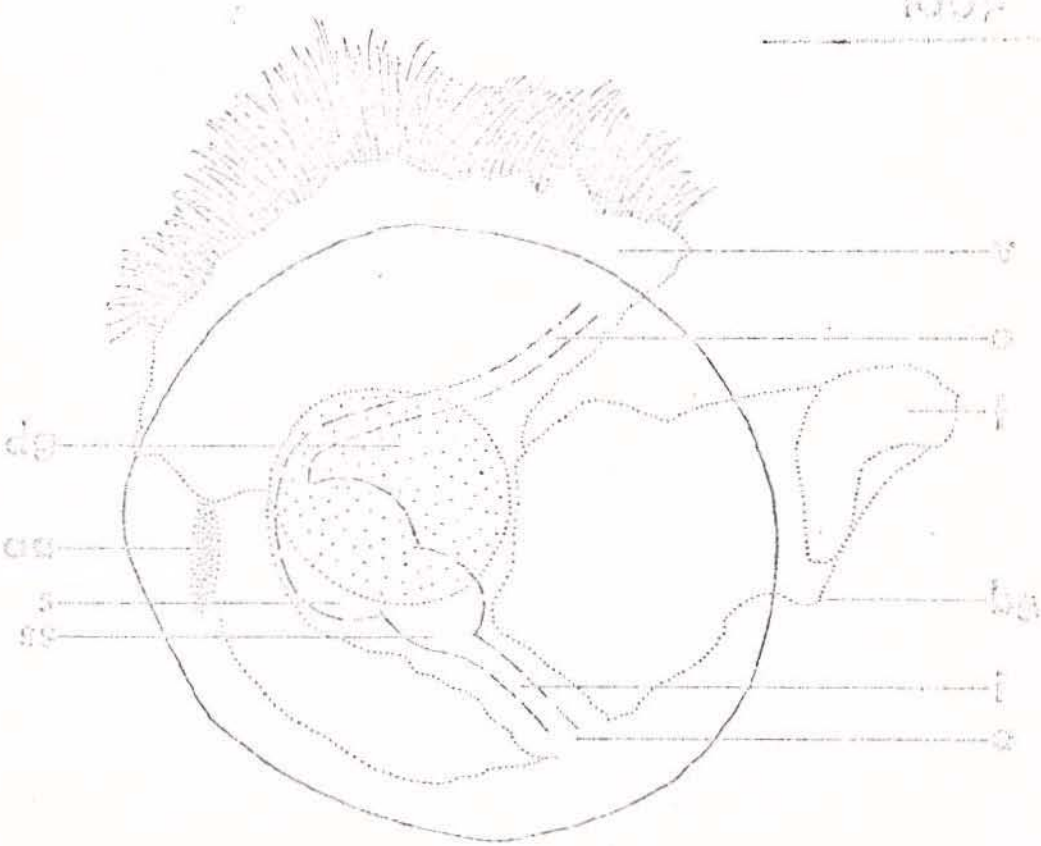


Figure 8. Internal anatomy of juvenile Tridacna maxima (day 47).

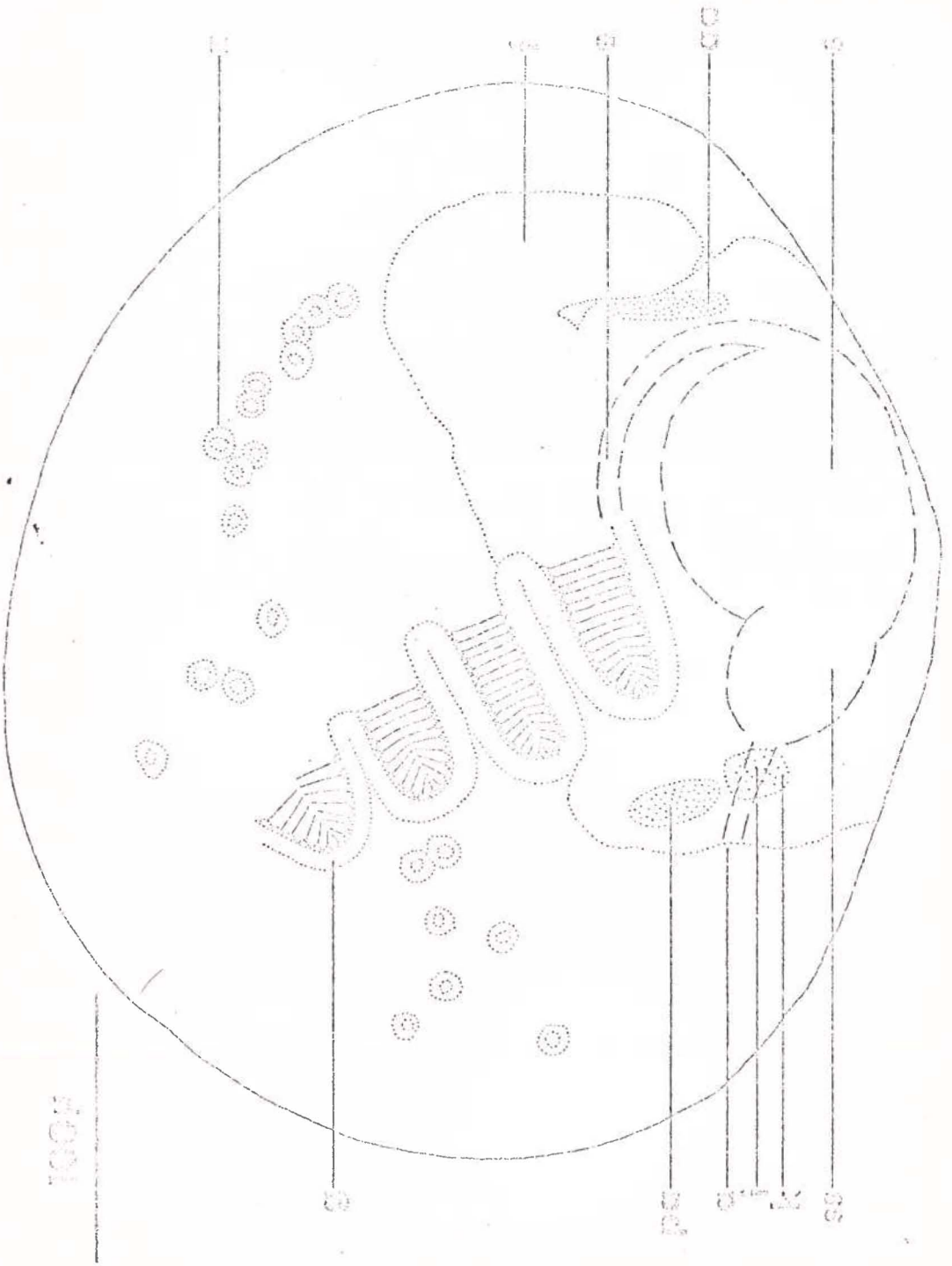
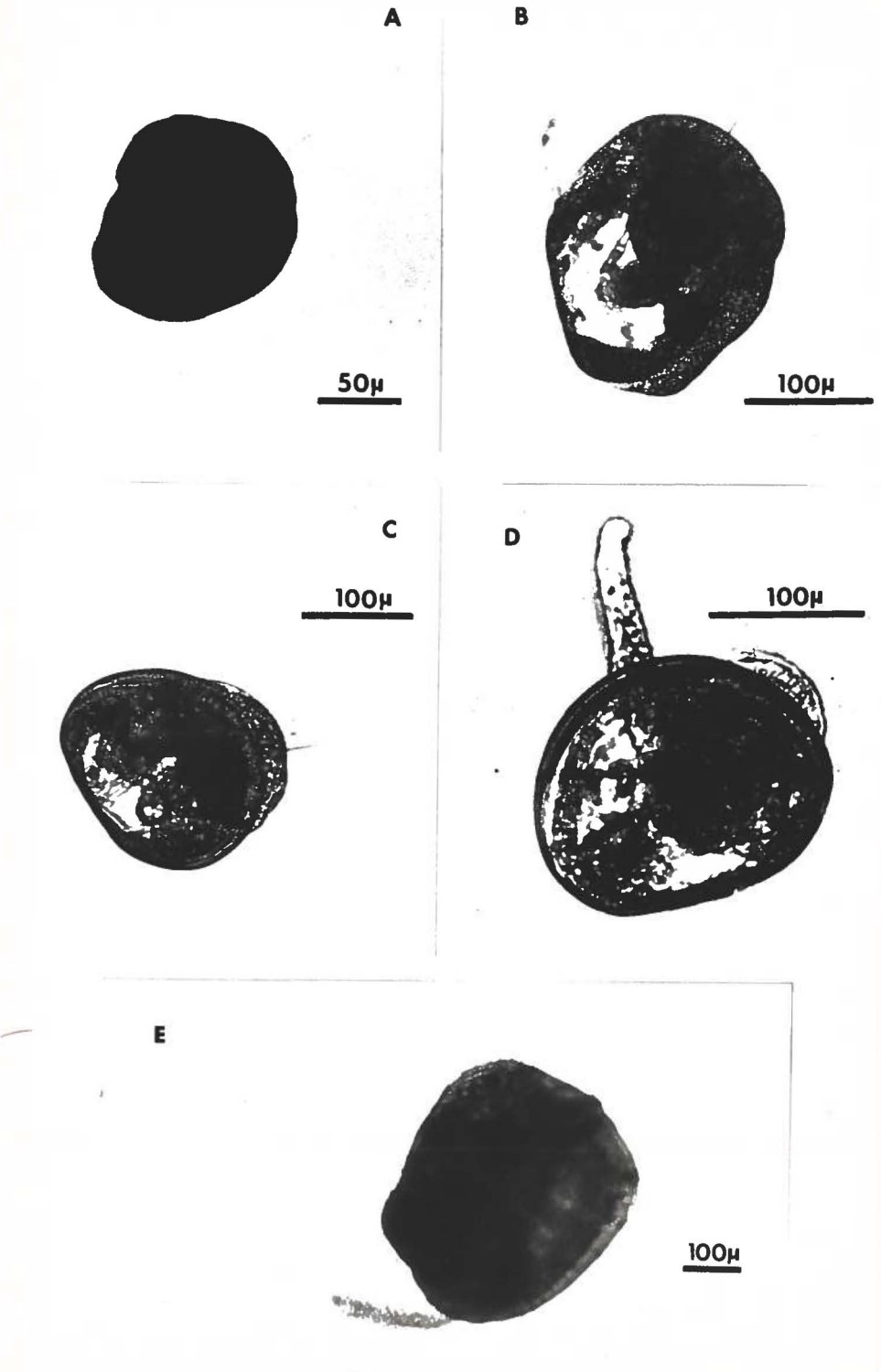


Figure 9. Larval and juvenile Hippeutis hippeus. A. Trochophore. B. Trochophore-veliger transition stage. C. Day 4 veliger. D. Day 11 pediveliger. E. Day 58 juvenile.


A
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C
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E
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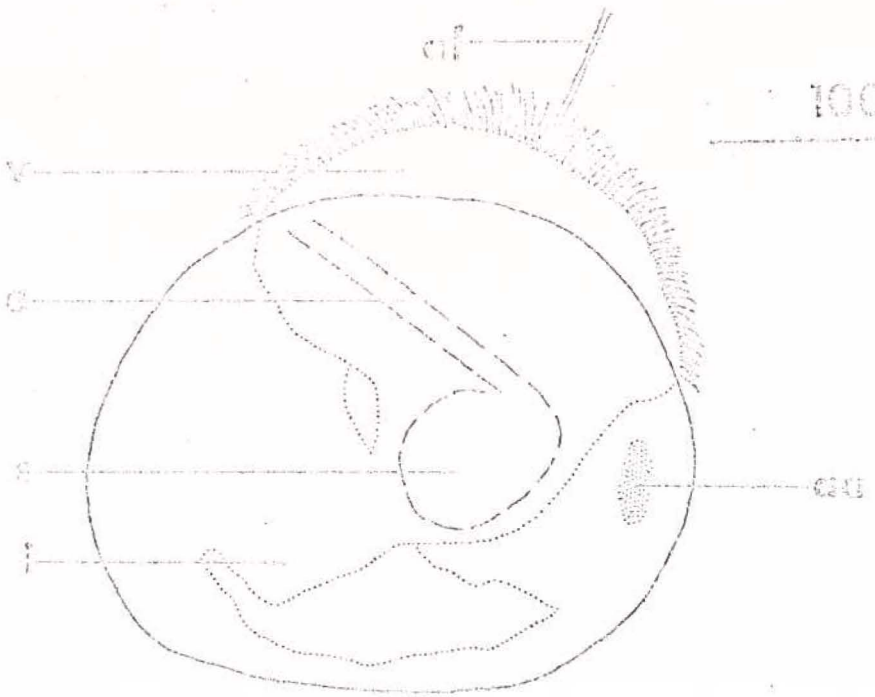
Figure 10. Internal anatomy of larval Hippopus hippopus. A. Day 7 veliger (see Fig. 9c for arrangement of retractor muscles). B. Pediveliger.

A



B

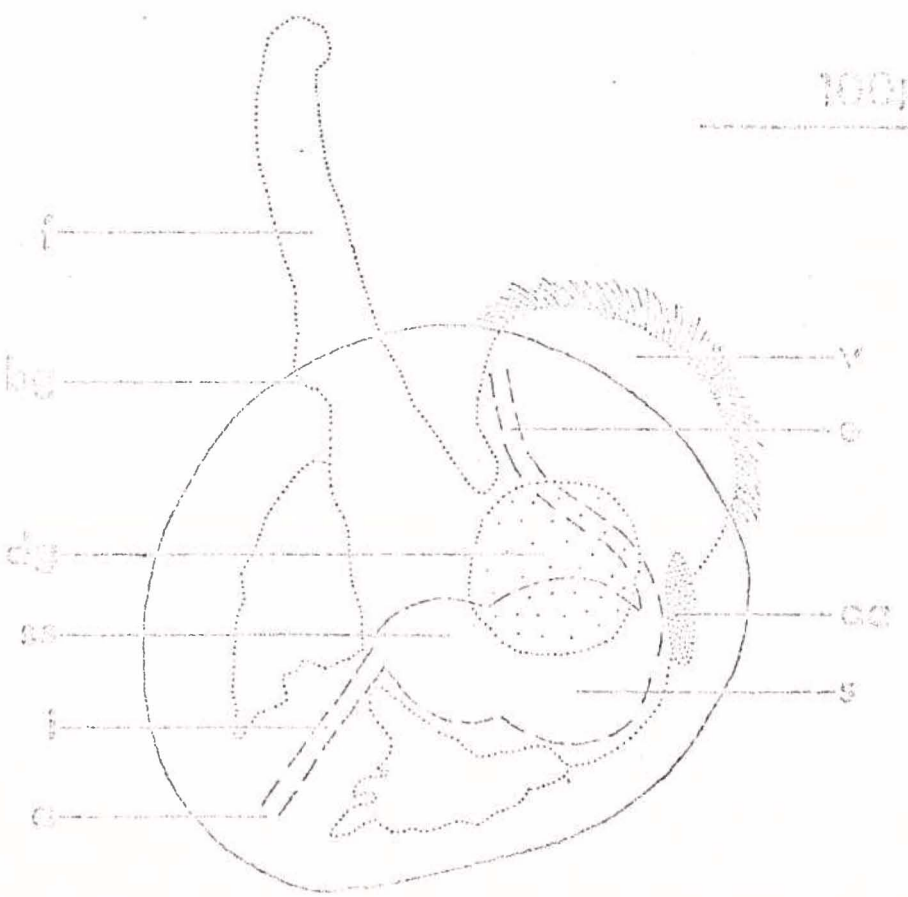
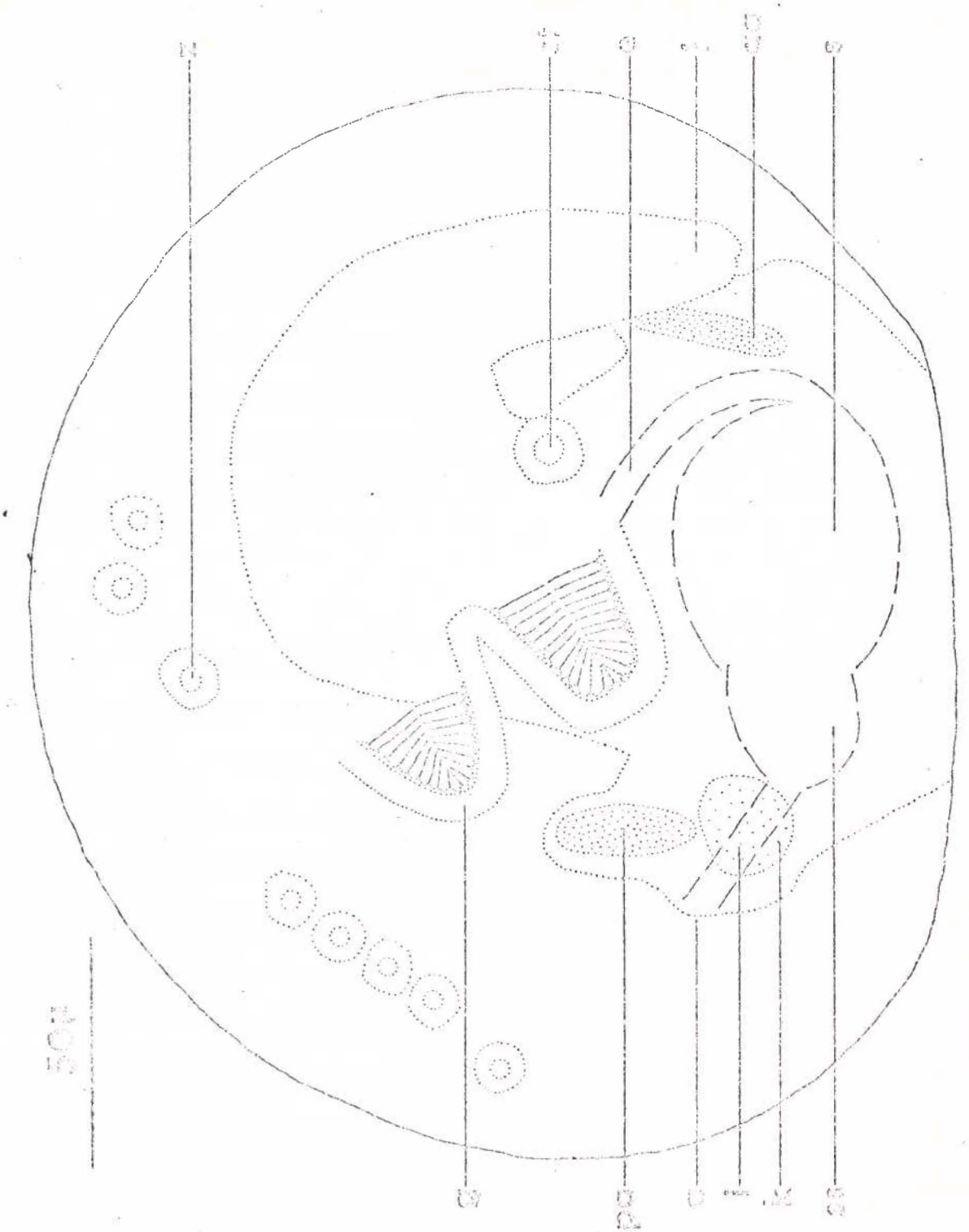


Figure 11. Internal anatomy of juvenile Hippopus hippopus (day 27).



KEY TO FIGURE ABBREVIATIONS

a	anus
aa	anterior adductor
af	apical flagella
bg	byssus gland
dg	digestive gland
e	esophagus
es	exhalent siphon
f	foot
g	gill
i	intestine
k	kidney
pa	posterior adductor
s	stomach
ss	style sac
st	statocyst
t	telotroch
tr	telotrochal retractor
v	velum
vr	velar retractors (numbered)
z	zooxanthellae