Studies on Spawning Behavior, Egg Masses, and Larval Development in the Gastropod Genus *Conus*, Part I Observations on Nine Species in Hawaii[1]

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THIS REPORT deals chiefly with the characteristics of egg masses and the course of larval development of gastropod mollusks of the genus *Conus*, based on material collected in the Hawaiian Islands during 1954–56, while the author was at the Hawaii Marine Laboratory. Some information has been obtained on 9 of the 33 species of *Conus* known to occur in the Hawaiian archipelago (Kohn, 1959*a*).

Bergh stated (1895: 100), "Ueber Paarung, Eilegen und Laich der Coniden ist ... absolut nichts bekannt."

The only reference prior to that date which has come to the attention of the present writer is an extremely brief description of the oöthecae or egg capsules of *C. capitaneus* Linnaeus by Adams and Adams (1853: 5). Cooke (1895) and Hornell (1922) figured egg capsules of unidentified species of *Conus*, but Lamy (1928), in an extensive study of prosobranch egg capsules, noted their similarity to those of other genera. These early figures cannot be assigned with certainty to *Conus*, and Bergh's statement remained essentially correct until Petit and Risbec (1929) and Risbec (1931, 1932) described the egg masses and development of four species of *Conus* from New Caledonia. Subsequently, similar information on six additional species has been reported by Thorson (1940), Persian Gulf; Lebour (1945), Bermuda; Knudsen (1950), West Africa; Natarajan (1957), India. More recently Lewis (1960) has provided additional information on the egg capsules and larvae of *C. mus* Hwass *in* Bruguière, a species discussed also by Lebour (1945).

Ostergaard (1950) described the spawning and development of six species of *Conus* in Hawaii. The present paper provides information on five additional species and notes on development in one species mentioned by Ostergaard but not studied in detail by him.

Most of the material was collected on coral reefs which fringe much of the Hawaiian coastline and provide suitable spawning sites for a number of species of *Conus* (Kohn, 1959*b*). Bouin's solution and 10 per cent sea water formalin were used as fixatives. Except where stated otherwise, all material was collected by the author, and the numbers used to identify specimens are those of the author. The preserved egg capsules and embryological material have been deposited in the University Zoological Museum, Copenhagen.

GENERAL CHARACTERISTICS OF SPAWNING AND EGG MASSES

As is typical of the higher prosobranch gastropods, the sexes are separate and fertilization is internal. The prominent penis of the male is a flattened muscular tube which arises from the right side of the dorsolateral body wall just behind the head and is rounded or pointed at the tip (Bergh, 1895: 97, figs. 4, 5, 76, 149, 159).

In copulation, it is inserted into the vagina of the female, which is located anteriorly at the extreme right edge of the mantle cavity, where the mantle joins the body wall, and adjacent to the anus (unpublished observations). A detailed account of the genital apparatus of prosobranchs has been given by Fretter (1941, 1946).

Although the process of oviposition in *Conus* has not been studied closely, it is essentially similar to that first described in other higher prosobranchs (Order Neogastropoda) by Cunningham (1899) and later amplified by Ankel (1929), MacGinitie (1931), and Ino (1950). Eggs surrounded by albuminous, probably nu-

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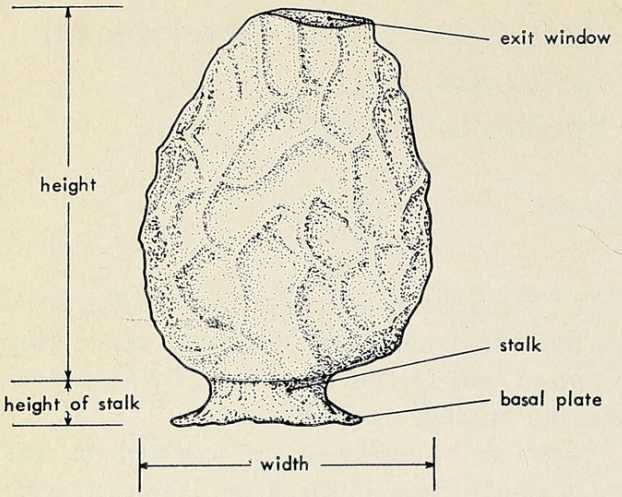


FIG. 1. Generalized egg capsule of *Conus*, with terms used in presentation of dimensions.

tritive, material are passed out of the genital aperture of the female downward through a temporary groove on the side of the foot to the egg capsule gland, which is situated on the anterior portion of the sole. The fluid mass of eggs passes into the aperture of the gland, in which horny egg capsules are produced. This method of egg capsule formation is characteristic of the Neogastropoda, in contrast to the Mesogastropoda in which the capsule is secreted in the genital ducts and only moulded and hardened by the egg capsule gland (Ankel, 1929; Fretter, 1941).

The general shape of the capsules (see Fig. 1) is "like a flattened pouch or flask" (Knudsen, 1950). As will be shown below and in a forthcoming paper (Kohn, MS), there is a moderate degree of interspecific variation in the form of the egg capsules and, in some species, considerable intraspecific variation. It is usually not possible to determine the species to which an egg mass belongs in the absence of the parent. This is in marked contrast to the egg capsules of some other prosobranch genera, e.g., *Murex* and *Nassa*, which are highly species-specific (Thorson, 1959).

The capsule is typically white or straw-colored and is presumably constructed of conchyolin, a scleroprotein. The capsules are deposited in clusters which frequently consist of several short rows of a few capsules each. A cluster of egg capsules is referred to as an egg mass, following Thorson (1940, *et seq.*) and others. The number of capsules deposited in a cluster and the number of eggs per capsule are variable. In the material collected in Hawaii, the number of capsules per cluster ranged from 1 to 68 (Table 1) and the number of eggs per capsule from 80 to about 10,000 (Table 2).

In most species, each capsule is attached to the substratum, usually the underside of a rock, by an adhesive basal plate (Fig. 1). There is a narrow, short stalk, above which is the capsule proper. Its walls are thin, nonrigid, and translucent, and they usually bear ridges on the flat surfaces. The lateral edges are typically convex, and there is a preformed exit window along the straight, uppermost part of the capsule. It is covered by a hyaline membrane or operculum, which is never very thick and appears to become thinner and more transparent as development proceeds. The hatching process has not been studied closely, but it appears that the entire membrane dissolves prior to escape of the larvae. This is in contrast to the family Muricidae, in which the egg capsule is closed by a thick operculum which is lost intact at hatching (Ankel, 1937; Hancock, 1956). Dissolution of the operculum may be due to an enzyme liberated by the larvae just prior to hatching (Ankel, 1937). The larvae of *Conus* do not occupy the entire capsule before hatching.

DEVELOPMENT WITHIN EGG CAPSULE

To study the course of larval development, egg masses were kept in constantly aerated running sea water in finger bowls or wide-mouth 4-l. jars. Following hatching, the larvae were kept in the larger jars in aerated, but not circulating, sea water. In some cases, sand and coral rocks from the normal habitat were placed on the bottom of the vessel in an effort to induce settling of the larvae, but this was generally unsuccessful. Details of embryonic development are described below for those species in which they could be determined, and present knowledge of development in *Conus* is reviewed in the section, Discussion.

Conus abbreviatus Reeve

A cluster of 33 egg capsules was found attached to the underside of a metal refuse can

TABLE 1

COLLECTION RECORDS AND CHARACTERISTICS OF EGG MASSES OF *Conus* IN HAWAII

SPECIES	LOCALITY[1]	DATE OF COLLECTION	SPECIMEN NUMBER	NO. OF CAPSULES IN CLUSTER	HEIGHT × MAXIMUM BREADTH OF CAPSULES (mm.)
abbreviatus	Waikiki	15 III 1923	(Ostergaard, 1950)	12	10 × 8
abbreviatus	Diamond Head	10 III 1956	1382	33	9 × 7–7.5
catus	Waikiki	12 VI 1922	(Ostergaard, 1950)	19	12 × 9
catus	Paia, Maui	5 VIII 1956	2180	1	12 × 10
catus	Koko Head	22 VIII 1956	2299	3[2]	11–12 × 10
catus	Koko Head	22 VIII 1956	——	4	10–11 × 8.5–9.5
ebraeus	Waikiki	22 III 1921	(Ostergaard, 1950)	—	10 × 10
imperialis	Diamond Head	6 VII 1956	1983	6[3]	18–20 × 12–13
leopardus	Kaneohe Bay	25 IV 1956	——	19	49–58 × 34–37
lividus (?)	Maile	7 II 1956	1264	36, 30	10.5–12 × 10–12; 9–10 × 8.5–10
pennaceus[4]	Waikiki	19 V 1921	(Ostergaard, 1950)	34	11 × 8
pennaceus[4]	Waikiki	25 V 1922	(Ostergaard, 1950)	—	——
pennaceus	Waikiki	26 VII 1954	156	20	8.5 × 7.5
pennaceus	Waikiki	4 VIII 1955	——	38	——
pennaceus	Diamond Head	13 VIII 1955	401–404	68, 50, 25, 9	——
pennaceus	Hauula	9 VI 1956	1811	34	9–10.5 × 7–8
pennaceus	Mahie Point	9 VI 1956	1810	58	9.5–11 × 7.5–9
pennaceus	Diamond Head	10 VI 1956	——	68	12–13 × 9–10
pennaceus	Diamond Head	4 VII 1956	1962	10	9–11 × 8
quercinus	Kaneohe Bay	9 II 1956	——	40	19–26 × 17–22
quercinus	Kaneohe Bay	9 II 1956	——	3	17–19 × 18–20
rattus	Waikiki	4 VIII 1921	(Ostergaard, 1950)	22	15 × 11
rattus (?)	Waikiki	21 III 1956	——	31	12–14 × 11–14
vexillum[5]	Waikiki	16 V 1921	(Ostergaard, 1950)	34	20 × 13
vitulinus	Ala Moana	7 VII 1956	2020	11	23 × 16–17
vitulinus	Diamond Head	VII 1957	——	—	——

[1] All from the island of Oahu unless otherwise indicated.
[2] Oviposition possibly interrupted by collector.
[3] Oviposition definitely interrupted by collector.
[4] This species is referred to as *C. omaria* Hwass by Ostergaard (1950).
[5] This species is referred to as *C. sumatrensis* Hwass by Ostergaard (1950).

cover in 1 m. of water on the reef at Diamond Head, Oahu, 10 March 1956. The capsules (Fig. 2) were affixed to their substratum in three rows of 12, 17, and 14. Two adult *C. abbreviatus* (no. 1382, ♀, 29 × 21 mm.; no. 1383, sex undet., 32 × 21 mm.) were found about 1 m. from the can lid, which appeared to be the nearest available protected site for oviposition, since all nearby coral rocks were buried to a depth below the oxidized surface layer of sand. This egg mass is tentatively assigned to *C. abbreviatus* because of the proximity of the adults and the close similarity with the egg capsules of that species described by Ostergaard (1950).

The shape of the capsules is typical of the genus. They are slightly higher than broad and are affixed to the substratum by a short stalk and broad basal plate. The capsular walls are smooth except for peripheral ridges on one side (Fig. 2*b*) and two ridges extending downward from near the upper corners on the opposite side (Fig. 2*c*). Both lateral edges of the capsule are convex. The characteristics of the egg mass are summarized and compared with that studied by Ostergaard (1950) in Tables 1 and 2.

In order to study the course of development, the egg mass was placed in aerated circulating sea water. One egg capsule was removed from the cluster and its contents examined on the day of collection. The embryos, which were pink in color when viewed through the translucent capsular wall, were found to be in the blastula

stage, with the four macromeres and many micromeres distinctly visible. It is likely that the embryos were 1–2 days old. They were oval in shape, measured 175–200 × 165–175 μ, and were slowly motile when released from the capsule into sea water. The blastula is the earliest stage at which activity is observed in *Conus* embryos (Ostergaard, 1950).

An egg capsule opened on the second day after collection contained motile embryos which resembled early trochophores (Fig. 3*a*). The resemblance of this stage to typical trochophore larvae is somewhat closer in *C. abbreviatus* than in other species of *Conus* (see below and Ostergaard, 1950) in which the trochophore stage is suppressed. This is typical of gastropods in which this stage is passed within an egg capsule or brood pouch (Raven, 1958).

The trochophore-like embryos of *C. abbreviatus* measured 270 × 170 μ and retained the pink color of the previous stage. On the fourth day after collection, the first traces of shell were visible (Fig. 3*b*). Two days later, velar lobes were beginning to form (Fig. 3*c*) and the embryos, which now measured 255 × 150–165 μ, swam actively when released from the capsule. On the 9th day after collection the velar lobes and larval shell appeared to be fully developed (Fig. 3*d–f*). The pink color persisted, and the shells were transparent and bore numerous fine nodules (Fig. 3*d, e*). Otocysts, eyes, heart, foot, and operculum were easily visible. The maximum dimension of the shell was 270 μ, and the breadth of the velar lobes was about 250 μ. The veligers were motile within the capsule and swam actively when released from it into sea water. No further development was detected on the 11th day after collection. On the 13th day after collection, presumably the 14th or 15th day after oviposition, some veligers hatched from egg capsules following apparent dissolution of the exit window. The hatched veliger larvae closely resembled those in Figure 3 *d–f* but measured 275–300 μ in maximum shell dimension. They swam freely in the container and were colorless except for a row of green pigment spots inside the margins of the velar lobes (Fig. 3*e, f*). Unhatched veligers within the capsule retained the pink color in the visceral mass.

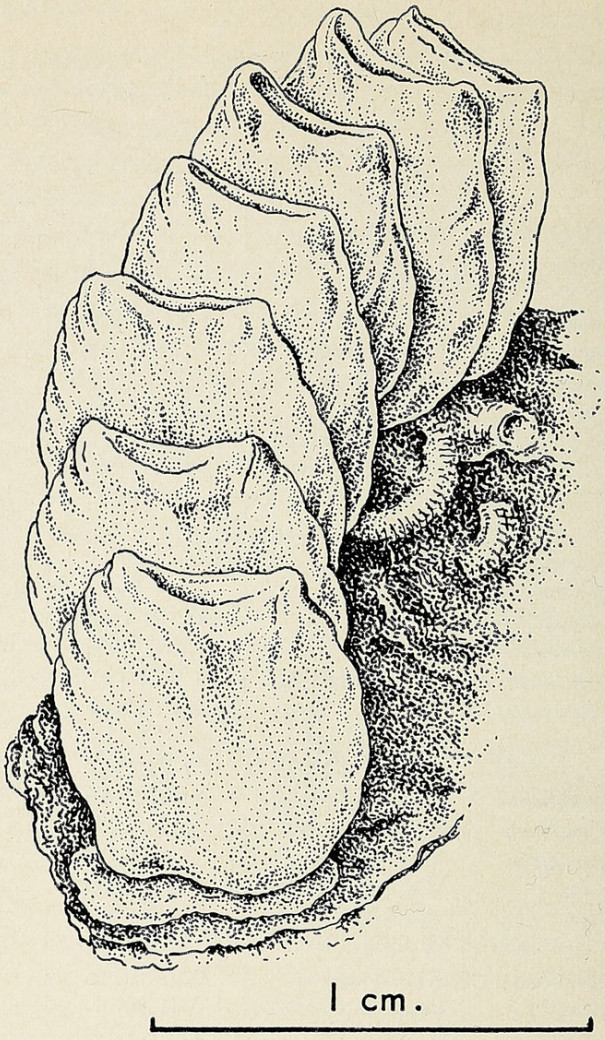


FIG. 2*a*. Egg capsules of *Conus abbreviatus* Reeve. Diamond Head, Oahu, 10 March 1956. Portion of a row of capsules affixed to metal can lid.

Within two days the rest of the veligers appeared to have hatched from the capsules. During the ensuing 10 days no further development was observed and none of the larvae settled to the bottom of the container to assume the benthic mode of life. By the 11th day after hatching, all of the larvae were dead and the observations were terminated. The course of larval development is summarized and compared with that of other species in Table 3.

Conus catus Hwass *in* Bruguière

A specimen of *C. catus* (no. 2180) collected at Lower Paia, Maui, on 5 August 1956, was observed to have affixed a single egg capsule to its shell about 2 hr. after collection. The capsule measured 12 × 10 mm.

On 22 August 1956, a female *C. catus* (no.

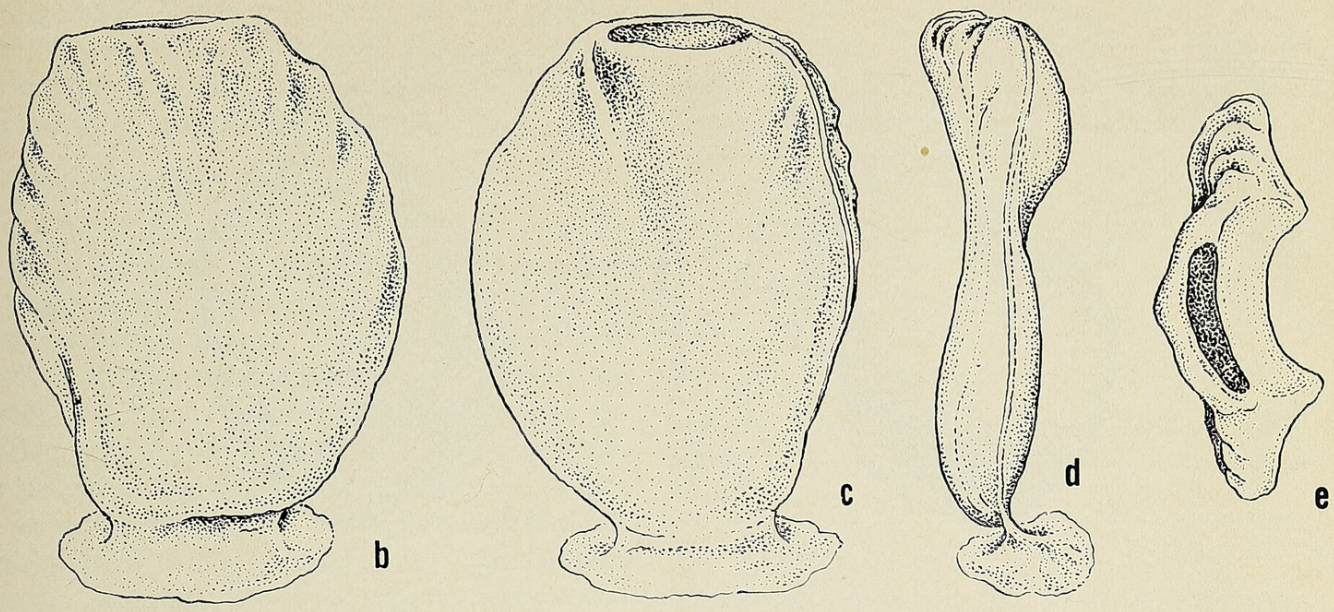


FIG. 2*b–e*. *b,c,d*, Side and edge views of one capsule; *e*, top view of another capsule.

2299, 40 × 26 mm.) was found ovipositing at Koko Head Sandy Beach, Oahu, by M. A. Kohn. Three capsules had been deposited, and spawning probably would have continued had not the adult been disturbed. However, a second cluster of 4 essentially identical capsules, unaccompanied by an adult, was also collected (Table 1). Ostergaard (1950) figured 19 capsules in an egg mass of *C. catus*.

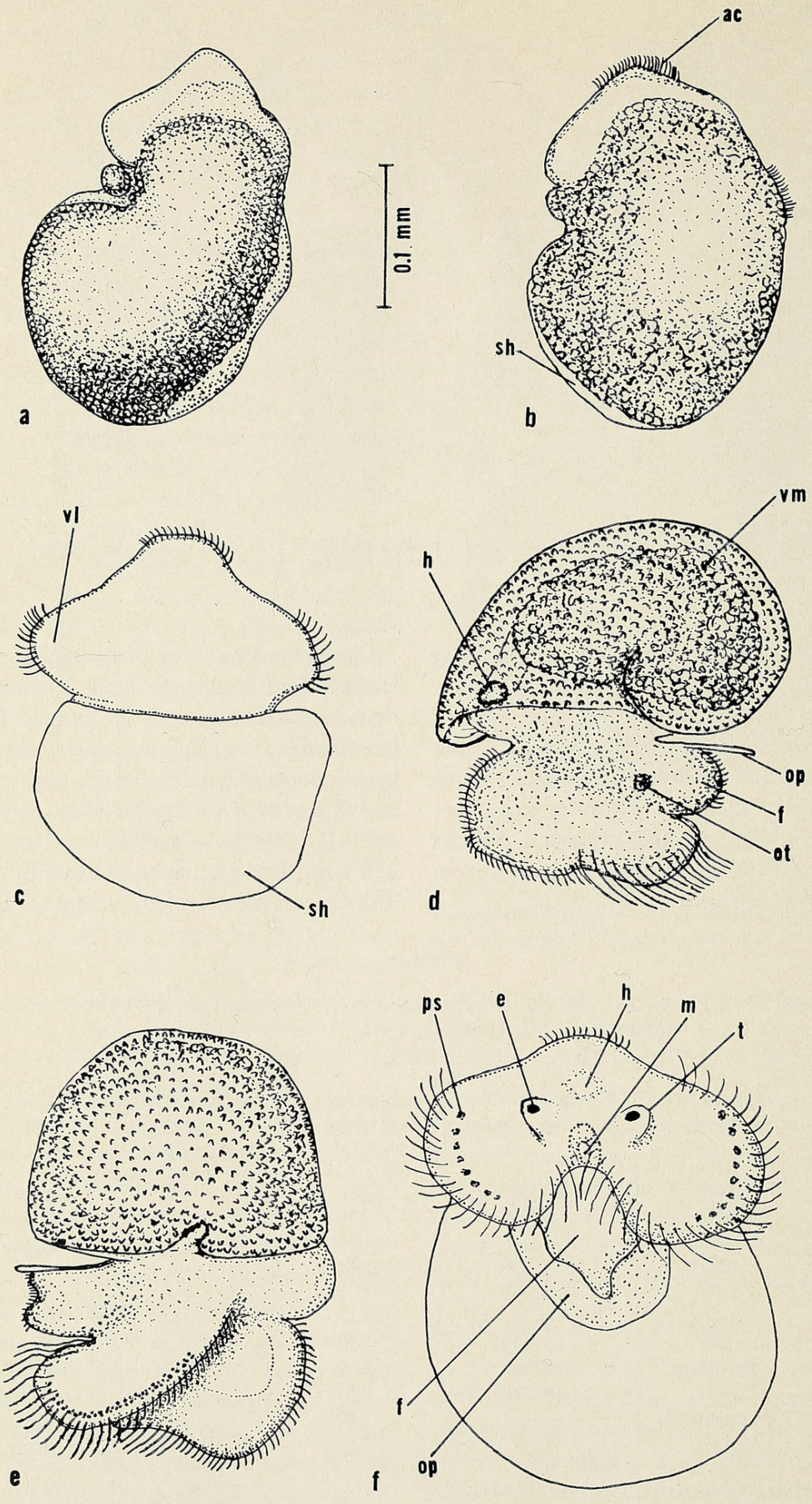
The form of the egg capsules of *Conus catus* is typical, although the stalk is somewhat taller than in other species of the genus (Fig. 4). The lateral edges are slightly convex; the upper edge is quite straight. Capsules in both clusters contained embryos in the 4-cell stage which measured 250–300 μ across. A few uncleaved eggs 235 μ in diameter were present in one capsule. The characteristics of these egg masses are sum-

TABLE 2

NUMBER OF EGGS PRODUCED, EGG DIAMETER, LENGTH OF DEVELOPMENT BEFORE HATCHING, AND STAGE AT HATCHING OF *Conus* IN HAWAII

SPECIES	AVERAGE NO. EGGS/CAPSULE	AVERAGE NO. EGGS/EGG MASS	AVERAGE EGG DIAMETER (μ)	TIME OF DEVELOPMENT IN EGG CAPSULE (days)	STAGE AND SIZE AT HATCHING	
abbreviatus	1,300	44,000	200	14	veliger	270μ
catus	1,650	15,000[1]	220	15–16[1]	veliger	375μ[1]
ebraeus	——	——	——	——	veliger[1]	280μ[1]
imperialis	5,900	(35,400)	225	——	——	——
leopardus	2,950	56,000	——	——	veliger	360μ
lividus (?)	——	——	——	——	veliger	250μ
pennaceus[2]	80	3,500	460	16[1]	veliconcha	1200μ
quercinus	9,700	210,000	215	15–16	veliger	285μ
rattus	2,000[1]	44,000[1]	125[1]	——	(?)veliger	240μ
vexillum[3]	"thousands"[1]	——	140[1]	12[1]	veliger	250μ[1]
vitulinus	——	——	225	14–15	veliger	360μ

[1] Data from Ostergaard (1950).
[2] This species is referred to as *C. omaria* by Ostergaard (1950).
[3] This species is referred to as *C. sumatrensis* by Ostergaard (1950).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marized in Tables 1 and 2. It was not possible to follow the course of larval development, but Ostergaard (1950) has described the development of *C. catus* in some detail.

Conus imperialis Linnaeus

A female *C. imperialis* (no. 1983, 79 × 23 mm.) was observed ovipositing in a depression on the side of a large dead coral head in 0.3 m. of water at Diamond Head, Oahu, on 6 July 1956. Six capsules had been deposited when the rock was turned over and oviposition was interrupted. The capsules are rather long and narrow, measuring about 19 × 13 mm., and do not rise vertically from the stalk and basal plate but are skewed to one side (Fig. 5). Upon return to the laboratory, one of the capsules was pierced and some of its contents withdrawn with a pipette. The eggs were uncleaved and measured 225 μ in diameter. Eggs in the same capsule had not undergone the first cleavage 3.7 hr. later. Twenty-four hr. later, however, eggs in the same capsule had progressed to the 4-cell stage, which measured 250 μ on each side and resembled the 4-cell stage of *C. quercinus* (Fig. 12*c*).

On the 3rd day after oviposition, a second capsule was examined and found to contain embryos in the blastula stage. No further development took place in the cultures and all of the embryos appeared to be dead and were fixed on the 16th day after oviposition. The egg masses and larval development, as far as it could be studied, agree closely in the same species studied in the Seychelles Islands (Kohn, MS). The characteristics of the egg mass from Oahu are summarized in Tables 1 and 2.

Conus leopardus (Röding)

A cluster of 19 very large egg capsules was found adrift in Kaneohe Bay, Oahu, at a depth of 5 m. by A. H. Banner on 25 April 1956. The basal plates of the capsules were confluent, holding the entire mass together. A bright green filamentous alga was associated with the egg

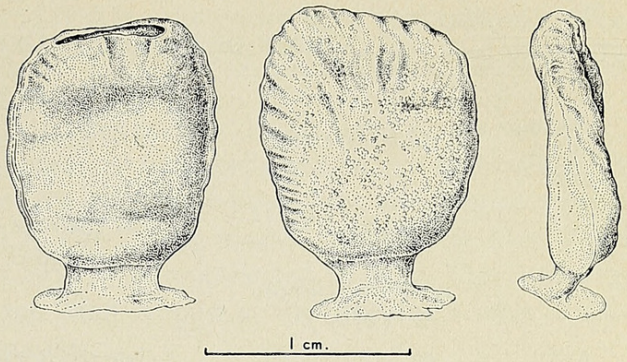

FIG. 4. Views of an egg capsule of *Conus catus* Hwass *in* Bruguière. Koko Head, Oahu, 22 August 1956.

mass when it was collected. However, the original substratum from which the mass presumably became detached is not known. The largest capsule measured 58 × 37 mm., exclusive of stalk and basal plate, and the average size was 54 × 35 mm. This is about twice as large as any other known *Conus* egg capsule. For this reason the egg mass is tentatively assigned to *C. leopardus*, which is by far the largest species in the family in Hawaii, reaching a length in excess of 20 cm. The capsules were collected in an area where *C. leopardus* is known to occur.

The capsules differ in shape from those of other species of *Conus* by having one lateral edge concave (Fig. 6). The capsular wall is roughened by numerous irregular ridges.

It was not possible to examine the contents of the egg capsules until 2 days after collection. At that time typical veliger larvae, measuring 345 μ in maximum shell dimension, were present. Thus although the adults and egg capsules of *C. leopardus* are very large, the veliger larvae, and presumably the eggs, are not significantly larger than those of much smaller species (Table 2). Indeed the veligers are much smaller than those of *C. pennaceus* (Table 3), the adults of which species are typically one-fourth or less the size of *C. leopardus*.

FIG. 3. Developmental stages of *Conus abbreviatus* Reeve. *a*, 3- or 4-day embryo, in modified trochophore stage; *b*, 5- or 6-day embryo, with first trace of shell present; *c*, 7- or 8-day embryo, showing developing velar lobes; *d*, fully-formed veliger, 10 or 11 days, lateral view; *e*, as *d*, but anterior-lateral view; *f*, as *d*, but anterior-ventral view, showing expanded velar lobes and ventral aspect of foot and operculum. *ac*, Apical cilia; *e*, eye; *f*, foot; *h*, heart; *m*, mouth; *op*, operculum; *ot*, otocyst; *ps*, pigment spot; *sh*, shell; *t*, tentacle; *vl*, velar lobe; *vm*, visceral mass.

TABLE 3

COURSE OF EMBRYONIC DEVELOPMENT IN HAWAIIAN *Conus*

DAYS AFTER SPAWNING[1]	*C. abbreviatus*	*C. pennaceus*	*C. quercinus*	*C. vitulinus*
0–1	blastula (200μ)[2]	early cleavage stages (460μ)	uncleaved eggs (200μ)	early cleavage stages (225μ)
2–3	early trochophore (270μ)		early blastula	blastula (225μ)
4–5	well-developed trochophore (240μ)	late trochophore	blastula (200μ)	
6–7	early veliger (255μ)		trochophore (240μ)	trochophore (360μ)
8–9			early veliger (315μ)	veliger (385μ)
10–11	well-developed veliger (270μ)	well-developed veliger (780μ)	well-developed veliger (275μ)	
12–13			well-developed veliger (285μ)	
14–15	hatching (veliger) (300μ)		hatching (veliger) (290μ)	hatching (veliger) (370μ)
16		hatching[3] (veliconcha) (1200μ)		
17–25	no further development			

[1] Probable in *C. abbreviatus*.
[2] Maximum dimensions are indicated in parentheses.
[3] Data from Ostergaard (1950).

Only 2,950 veligers were present in the one capsule which was counted, and they occupied but a small portion of the capsule. As in several other species, yellowish-green pigment spots about 10 μ in diameter were present inside the margins of the velar lobes. A large operculum, a pair of otocysts, each containing an otolith, and black eyes were present. The long (*ca.* 75 μ) velar cilia beat slowly and metachronally. The larval shell was transparent but covered with minute (*ca.* 2 μ) raised dark nodules. The visceral mass appeared white within the shell.

Several hours later on the same day, hatching began and the hatched veligers, which measured 360 μ in maximum shell dimension, swam about slowly in a 4-l. jar of aerated sea water. On the following day, the jar was densely populated with freely swimming veligers, which swam more rapidly than on the previous day. The population was then divided between two 4-l. jars. Three days later, most of the veligers had died. Four of those which remained alive were placed in a large Stender dish (*ca.* 120 mm. in diameter) containing sea water and sand from the reef. Of these, three continued to swim about, but one settled to the bottom, where it actively beat its cilia and possibly engaged in feeding. If disturbed, it swam actively for a few seconds, then returned to the bottom. However, it was not observed to crawl on its foot, nor was there any evidence of resorption of the velar lobes or other manifestation of metamorphosis. On the following day, all four larvae in the dish were dead. Two days later, the 6th day after hatching, a few swimming veligers remained in one jar, but the observations had to be terminated.

Conus lividus Hwass *in* Bruguière (?)

On 7 February 1956, at Maile, Oahu, two clusters of straw-colored egg capsules were found affixed to the underside of a coral rock, under which a large female *C. lividus* (no. 1264, 45 × 26 mm.) was also present. One cluster consisted of 36 egg capsules, all of which were empty, and the other contained 30 capsules, some of which contained dead veliger larvae. Since these capsules were probably deposited

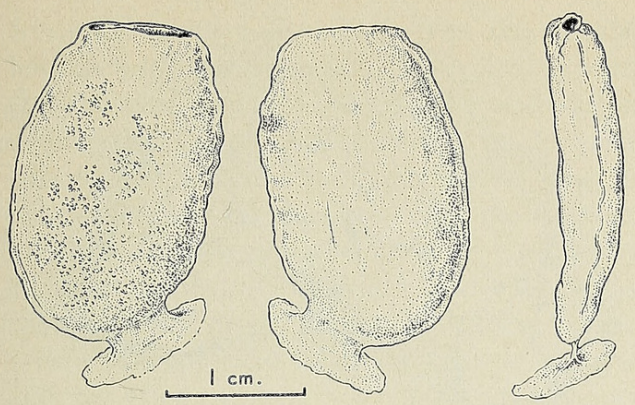

FIG. 5. Views of an egg capsule of *Conus imperialis* Linnaeus. Diamond Head, Oahu, 6 July 1956.

two or more weeks prior to their collection, it is by no means certain that the adult female associated with them was the parent. Indeed, it is not certain that the capsules are actually those of *C. lividus*, and the identification is tentative. It is supported, however, by morphological similarities with capsules known to have been deposited by *C. lividus* in other areas (Kohn, MS).

The capsules are distinguished from those of several other species of *Conus* by being somewhat more discoid in form and bearing crenations along the edges of the otherwise rather smooth capsular wall (Fig. 7). There are also two more or less parallel ridges extending downward from the corners of the exit window, as in *C. abbreviatus*. The capsules in the smaller group, shown in Figure 7, averaged 11 mm. in height and maximum breadth. The capsules in the other group were essentially similar in appearance but were slightly smaller, averaging 9.5 mm. in both dimensions.

The veliger shells, 235–260 μ in maximum dimension, were yellowish brown and bore minute densely-packed, raised, darker brown nodules over the entire surface.

Conus pennaceus Born

Egg masses of *C. pennaceus* have been collected on numerous occasions in Hawaii (Table 1). As noted by Ostergaard (1950) the egg mass of *C. pennaceus*[3] differs from those of other species in that only a few capsules are attached directly to the substratum. Most are affixed to previously deposited capsules, thus forming the "arches and bridges" mentioned by Ostergaard and making the entire mass very compact (Fig. 8). The individual capsules are typical of the genus (Fig. 9).

In the present study, 10 egg masses of *C. pennaceus* were collected on seven occasions, all in the months of June, July, and August (Table 1). The 2 egg masses reported by Ostergaard (1950)[3] were collected in May. The data suggest May–August as the breeding season of this species.

The development of *C. pennaceus* from fertilized egg to hatching has been described and illustrated by Ostergaard (1950). It was possible to follow portions of the course of larval development in 2 of the egg masses listed in Table 1.

On the day after collection, the egg mass from Diamond Head, Oahu, 10 June 1956 (which was found adrift over the reef by P. Helfrich), contained early veliger larvae which appeared to be in the later stages of torsion. A very small shell rudiment, a slowly beating heart, and eyes were present. On the 4th day after collection, the veligers appeared to be between the stages shown by Ostergaard's figures 11d and 11e, or probably about 12–13 days from oviposition. The siphonal canal of the shell had begun to form, and a row of chartreuse pigment spots was present along the margin of the velar lobes.

During the next 7 days, the shells gradually grew to 1.1 × 0.7 mm., and the wall of the exit window became thinner and more transparent, but no capsules hatched. Hatching of a few capsules finally occurred on the 16th day after collection. This probably corresponded to 25–26

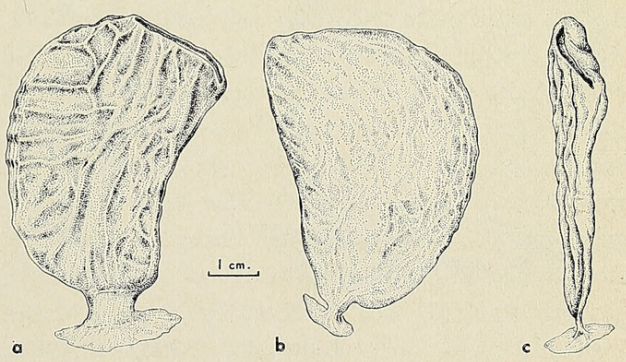

FIG. 6. Egg capsules of *Conus leopardus* (Röding). Kaneohe Bay, Oahu, 25 April 1956. *a*, Side view of one capsule; *b* and *c*, opposite side and edge views of another capsule.

[3] This species is referred to as *C. omaria* Hwass by Ostergaard (1950).

days after oviposition, an abnormally long embryonic period compared with other species and with Ostergaard's observations on *C. pennaceus*. Most of the capsules in the cluster underwent no further change and the observations were terminated.

The egg mass collected at Hauula, Oahu (Table 1) (with an adult female, no. 1811, 35 × 21 mm.) was attached to the underside of a basalt rock in less than 0.5 m. of water. On the day of collection, one capsule was removed from the cluster and found to contain larvae in the advanced veliger or veliconcha stage. The latter term was introduced (Lamy, 1933; Werner, 1939) for fully developed veligers immediately prior to metamorphosis. The larval shells were pale orange pink and measured 1.2–1.3 × 0.7 mm. When released from the capsule, the larvae swam with the velar lobes up, a position apparently determined by the weight of the shell. The larvae closely resembled that illustrated by Ostergaard (1950: fig. 11e). The remaining intact capsules were placed in a vessel of slowly circulating aerated sea water and a substratum of sand from the reef.

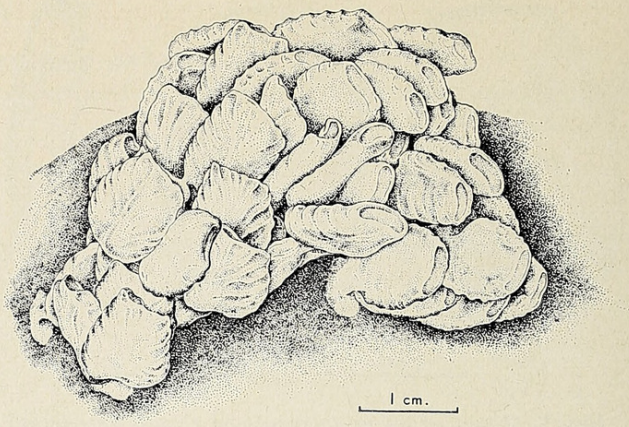

FIG. 8. Egg mass of *Conus pennaceus* Born. Diamond Head, Oahu, 10 June 1956.

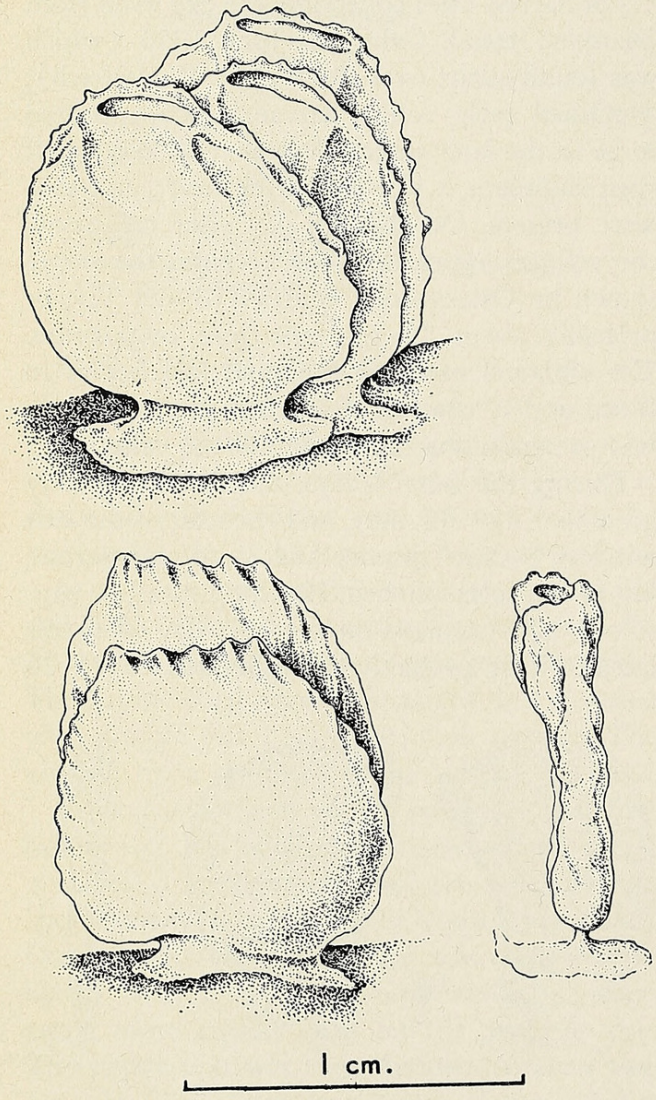

FIG. 7. Views of egg capsules tentatively assigned to *Conus lividus* Hwass *in* Bruguière. Maile, Oahu, 7 February 1956.

On the following day, one larva hatched from an egg capsule and, in contrast with those observed by Ostergaard, was quite able to swim about in the dish. However, its velar lobes and shell aperture always pointed upward, and the shell often rested on the substratum. The foot was not employed in locomotion. On the next day, 10 similar free-swimming veliconchas were observed in the dish. Two days later, although larvae remained in some capsules, many had hatched. A sample of these was observed to be distributed in the container as follows:

Freely swimming	0
Resting on bottom with velar lobes extended	
Velar lobes apparently regressing	3
Settled: crawling on substratum	38
Dead: empty shells	1
Sample size	79

The later stages of larval development in *C. pennaceus* may be summarized as follows: the larvae hatch as veliconchas which may swim

freely for about 1 day. They then rest on the bottom with the velar lobes extended upward and the cilia beating. Ostergaard's observation of propulsion along the substratum by the velar cilia was confirmed. Then the velar lobes begin to be resorbed. This was observed in three larvae, in which the margins of the velum were wrinkled and the length and width of the lobes was about one-half of the earlier dimensions. These veliconchas appeared otherwise normal. On the 2nd day after hatching, the young snail begins to crawl about on its foot (Fig. 10). However, the velar lobes have not been completely resorbed by this time; they are often extended by the crawling snail. When the larva assumes the benthic mode of life, the shell becomes darker orange in color, probably due to thickening, and new shell growth is apparent along the outer lip.

Ten days after the first hatching, the shells of the largest individuals measured 1.38 × 0.80 mm. and consisted of two complete whorls. However, mortality gradually increased in the culture, no individuals advanced beyond the end of the second whorl, and on the 27th day after the first hatching only one individual remained alive and the observations were terminated. Post-larval growth of *C. pennaceus* has been discussed elsewhere (Kohn, 1959*b*).

Conus quercinus Solander

Two clusters of egg capsules of *Conus quercinus* were collected in 1–2 m. of water at Sand (Ahuolaka) Island in Kaneohe Bay, Oahu, on 9 February 1956. The larger cluster contained 40 capsules and was affixed to a large clump of the red alga, *Acanthophora orientalis* J. Agardh.

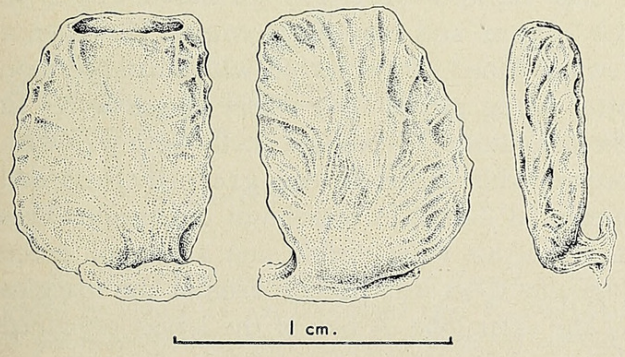

FIG. 9. Views of an egg capsule of *Conus pennaceus* Born. Diamond Head, Oahu, 10 June 1956.

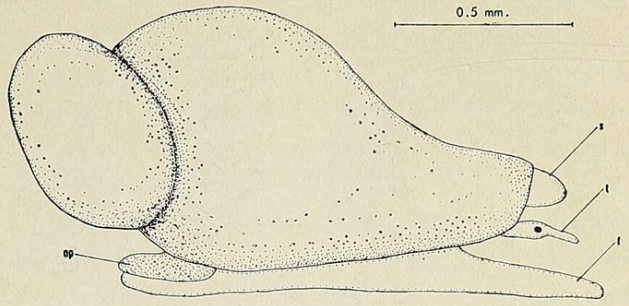

FIG. 10. Settled veliconcha of *Conus pennaceus* Born. *f*, Foot; *op*, operculum; *s*, siphon; *t*, tentacle, bearing the eye.

A pair of adult *Conus quercinus* (no. 1284, ♀, 91 × 56 mm.; no. 1285, ♂) were adjacent to the egg mass, and another pair and three single individuals were present within a radius of 1 m. *C. quercinus* appears to migrate from deeper water and to congregate for spawning in February–April of each year (Kohn, 1959*b*: 81). At this season adults are commonly found in the shallow water around Sand Island, a sand bank which is partially exposed at low tide. At other seasons they are absent from this site (Kohn, 1959*b*: fig. 29). The microhabitat of *C. quercinus* is quite distinct from those of its congeners in Hawaii (Kohn, 1959*b*). It occurs on vast sandy areas generally devoid of coral and rocks. As noted above, the egg capsules in the large mass were anchored to an alga. The other egg mass, which consisted of only three capsules, was affixed to a red sponge.

The congregation of several or many individuals associated with spawning was not observed in any other Hawaiian species of *Conus* but has been observed in other areas and will be discussed more fully elsewhere (Kohn, MS).

Most of the capsules in the large cluster were arranged in rows of up to eight and were affixed to each other by confluence of the basal plates (Fig. 11) as well as to the alga. A few were attached to previously deposited capsules, but this was not as common as in *C. pennaceus* and no bridges were present. The form of the capsules is rather irregular (Fig. 11). One wall bears numerous small ridges; the other has two more distinct ridges proceeding downward from near the corners of the exit window. The capsule is white when deposited but, since the

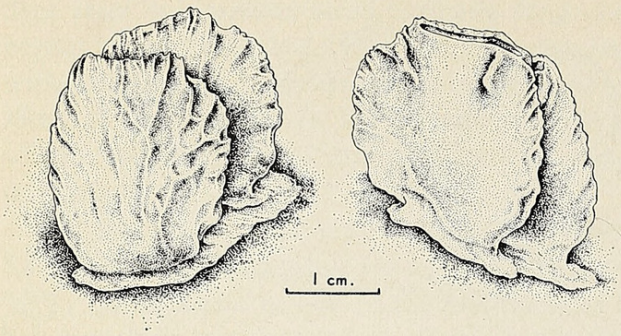

FIG. 11. Portion of a row of egg capsules of *Conus quercinus* Solander. Sand Island, Kaneohe Bay, Oahu, 9 February 1956.

cluster extends upward into the water and is not covered, it soon becomes a substratum for epiflora and epifauna. The characteristics of the egg masses of *C. quercinus* are summarized in Tables 1 and 2.

On the day of collection, one capsule was removed from the large cluster and found to contain pale pink, uncleaved, round-to-ovate eggs embedded in albuminous material and measuring 175–250 μ (Fig. 12*a*). The egg mass had probably been deposited on the same day. On the following day the first cleavage furrow was visible (Fig. 12*b*). On the 3rd day after collection, it was difficult to discern cell outlines, but the embryos, which were now white, appeared to be in the second to fourth divisions (Fig. 12*c, d*) and were motile when released from the capsule into sea water. Another capsule examined on the 5th day after collection showed little further progress. The embryos were quite motile and micromeres were observed in a few. Two days later, the embryos had increased in size to 240 $\times$ 180 μ and were in the modified trochophore stage (Fig. 12*e*).

Two days later, on the 9th day after oviposition, the embryos had grown to a maximum size of 315 $\times$ 195 μ and the shell and velar lobes had begun to form (Fig. 12*f*). Two days later, the fully developed veliger shells had attained a length of 255–295 μ. The velar lobes were well developed, and the heart, kidney (which was bright red), otocysts, eyes, and mouth (which measured 6 $\times$ 23 μ) were visible (Fig. 12*g, h, i*). The small foot rudiment bore a large operculum. The shell was brown and decorated with many rows of brown nodules, which were about 3 μ in diameter, rose 3–4 μ above the surface of the shell, and were about 3 μ apart. The growing lip of the shell was transparent.

On the 13th day after oviposition, the veligers were motile within the capsules and in many they were crowded in the vicinity of the exit window. Veligers removed from one capsule were found to have a row of green pigment spots, about 15 μ in diameter, inside the margins of the velar lobes, which had grown to about 285 μ across. The shells had not increased in size, but the outer lip was no longer transparent, indicating increased thickness. Two days later, on the 15th day after oviposition, some veligers hatched from the capsules and were swimming actively about in the container. By the following day most, and on the next day all, of the capsules had hatched.

Although the foot increased in size during the next few days, no significant over-all growth was apparent, and the velar lobes of some hatched veligers appeared reduced in size (Fig. 12*j*). None of the larvae settled to crawl on the bottom. Mortality in the culture gradually increased and only one or two larvae remained alive on the 8th day after the first hatching, when the observations were terminated.

Conus rattus Hwass *in* Bruguière (?)

A cluster of 31 egg capsules was collected from depressions in the underside of a large coral rock in 1 m. of water on the reef opposite the marine laboratory at Waikiki, Oahu, on 21 March 1956. No adult *Conus* was present in the immediate vicinity, but the capsules closely resemble those of *C. rattus* described by Ostergaard (1950).[4] They are tentatively assigned to that species, which is not uncommon on the same reef.

The capsules (Fig. 13) measured 11–15 $\times$ 10–14 mm. and most were empty. However, a few contained veliger larvae, which hatched soon after being placed in a vessel of sea water in the laboratory. The veliger shells were yellowish brown with darker brown granulations and measured 240 μ in maximum dimension. Eyes and otocysts were visible and a row of green pigment spots was present around the margins of the velar lobe. A few of the larvae remained

[4] This species is referred to as *C. tahitensis rattus* Hwass by Ostergaard (1950).

alive for 13 days after hatching, but they grew only to a length of 250 μ and no further development occurred.

Conus vitulinus Hwass *in* Bruguière

On 7 July 1956, at the reef at Ala Moana, Oahu, an adult *C. vitulinus* (no. 2020, 67 × 38 mm., sex undet.) was collected on sand under a dead coral rock, to the underside of which was attached an irregular cluster of 11 egg capsules. Some of the capsules were attached to others by confluence of the basal plates, but all were affixed to the substratum as well. They measured 23 × 16–17 mm. and their shape was typical of the genus (Fig. 14).

Eight hr. after collection, one capsule was examined and found to contain 1-, 2-, and 4-cell stages, which measured 225 μ in diameter

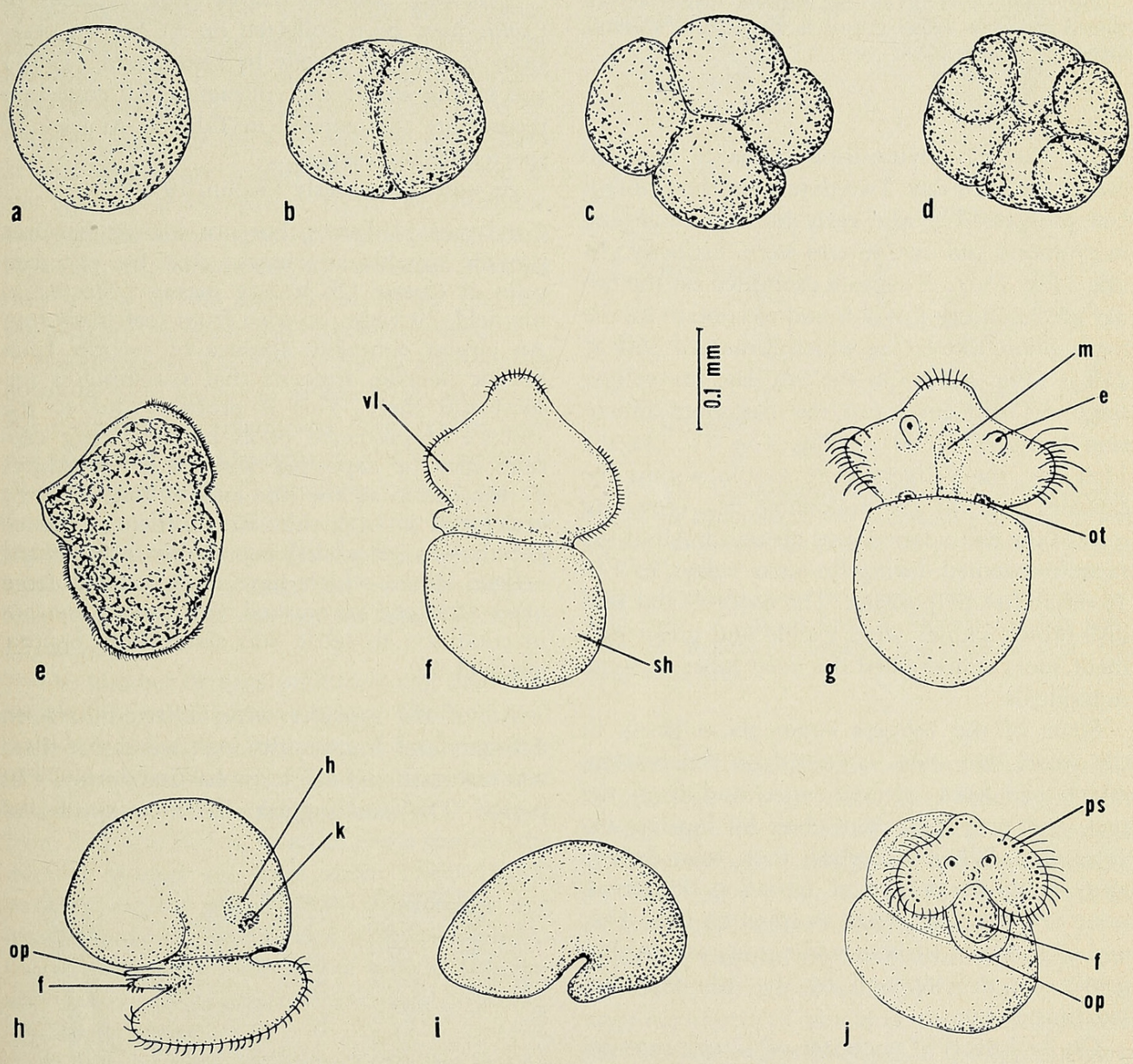

FIG. 12. Developmental stages of *Conus quercinus* Solander, from the same egg mass as the capsules illustrated in Figure 11. *a*, Uncleaved egg; *b*, 2-cell stage; *c*, 4-cell stage; *d*, embryo in third cleavage division; *e*, trochophore-like stage; *f*, early veliger; *g*, developing veliger, anterior-ventral view; *h*, developing veliger, right lateral view; *i*, shell of veliger, left lateral view; *j*, hatched, fully developed veliger. *e*, Eye; *f*, foot; *h*, heart; *k*, kidney; *m*, mouth; *op*, operculum; *ot*, otocyst; *ps*, pigment spots; *sh*, shell; *vl*, velar lobe. Nodules present on shells are not indicated in figures.

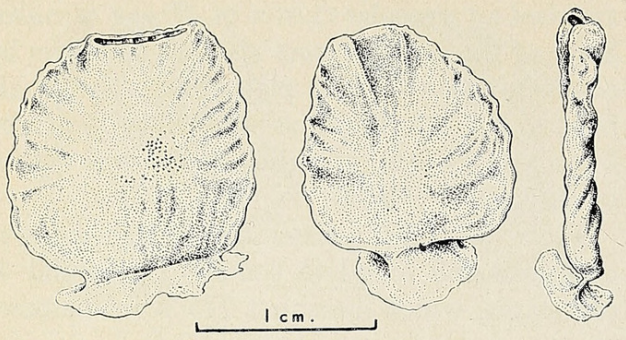

FIG. 13. Views of an egg capsule tentatively assigned to *Conus rattus* Hwass *in* Bruguière. Waikiki, Oahu, 21 March 1956.

(Fig. 15*a*, *b*). Oviposition probably occurred earlier the same day. Two days later, the embryos had progressed to the early blastula stage and macromeres and micromeres were distinctly visible (Fig. 15*c*). A capsule examined on the 6th day after collection was found to contain motile trochophore-like larvae which measured 360 × 210 μ (Fig. 15*d*). On the 9th day, the veliger stage was fully developed, the maximum dimension being 375–400 μ (Fig. 15*e*, *f*). On the 11th day, the veligers were motile within the capsules and on the following day crowding toward the exit window was observed. All of the capsules hatched during the next 3 days, or 14–16 days after oviposition. The otocysts and reddish-brown kidney were visible and green pigment spots almost filled the velar lobes of some individuals.

Some of the veligers swam about freely in the vessel, but most remained on the bottom, which had been covered with sand from the reef, and propelled themselves by beating the velar cilia. When disturbed, they swam briefly away from the source of irritation. However, none of the larvae settled to crawl on their feet, and all had died without undergoing any further growth or development by the 4th day after hatching began.

On 24 July 1957, a cluster of 12 egg capsules was found attached to the underside of a coral rock in a large tide pool at Diamond Head, Oahu. A large adult *C. vitulinus* (no. 7034, 65 × 37 mm., sex undet.) was present on the sand substratum under the rock. Upon return to the laboratory, one of the capsules was examined and found to contain eggs in 1-, 2-, and 4-cell stages; the last measured about 250 μ across. On the second day after collection, a capsule contained embryos which still measured 250 μ in diameter but had progressed to the blastula stage. The observations had to be terminated at this point, but development thus far was essentially similar to that in the egg mass described above.

DISCUSSION

Spawning site and season. Egg capsules of *Conus* have been collected on 31 known occasions in Hawaii, chiefly by Ostergaard (1950) and by the writer and colleagues. All collection records are summarized in Table 1. At least 12 species are represented.

As noted previously (Kohn, 1959*b*):

> Coral reef platforms, but not marine benches, provide suitable attachment sites for egg capsules of *Conus*. Of 36 egg masses collected in the field, 29 were recorded from reef platforms. An almost complete absence of records from marine benches suggests that spawning is unsuccessful there. This is probably due to the absence of protected pools in which egg capsules may be deposited without being subject to desiccation at low tide and/or torn away by heavy surf at high tide. Recruitment of bench populations [of adults] is probably from pelagic veliger larvae which have been carried from other areas and are washed onto marine benches in condition to settle and assume the benthic mode of life.

All of the capsules were collected between February and August, although search for them was not restricted to, or emphasized during, that period. The data suggest that most species of

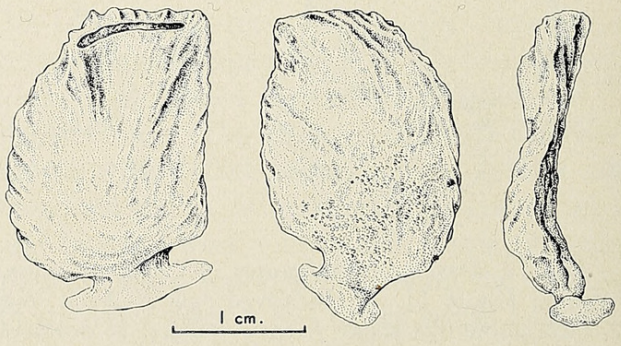

FIG. 14. Views of an egg capsule of *Conus vitulinus* Hwass in Bruguière. Ala Moana, Oahu, 7 July 1956.

Conus spawn during about the same part of the year. The spawning season of most species for which more than one egg mass has been collected is rather extended over the months cited. Capsules containing viable eggs and embryos of *C. rattus* have been collected from February to August, of *C. abbreviatus* from March to July, and of *C. pennaceus* from May to August.

The spawn of most species has been observed only rarely. However, 12 egg masses of *Conus pennaceus* were collected on nine occasions, all in the months of May, June, July, and August, suggesting that these months constitute the breeding season in this species. The preponderance of data for *C. pennaceus* (Table 1) is attributed partly to the fact that the egg masses of this species are readily identifiable, even in the absence of the parent from the collection site. Unlike other species, which attach each capsule to the substratum, *C. pennaceus* attaches only a few to the substratum, while the rest are attached to previously deposited capsules.

Development. The eggs of *Conus* are typically white or pink, spherical or nearly so, and without a surrounding membrane. Polar bodies were not observed, but Ostergaard (1950) reported their occurrence in *C. vexillum*.[5] There are no nurse eggs; all or almost all eggs may develop to hatching in nature, but development was often arrested in a usually small but variable proportion of embryos in egg masses cultured in the laboratory.

The number of eggs produced, egg diameter, length of development before hatching, and stage at hatching are summarized for 11 species of *Conus* from Hawaii in Table 2. Egg diameter was measured in 8 species, of which 7 ranged from 125 μ to 225 μ. In all of these species, the number of eggs was large, about 1,000–10,000 per egg capsule and 15,000–210,000 per egg mass (Table 2). One species, *C. pennaceus*, has much larger eggs (460 μ), of which considerably fewer are deposited (80/egg capsule; 3,500/egg mass).

As can be seen in Table 2, all the species with large numbers of small eggs hatch as free-swimming veligers, while *C. pennaceus* has virtually no pelagic stage, as was discussed in detail above. These data are in agreement with the correlations of large numbers of small eggs with long pelagic life and small numbers of large eggs with nonpelagic development first demonstrated by Thorson (1950, 1952) for mollusks and other benthic marine invertebrates.

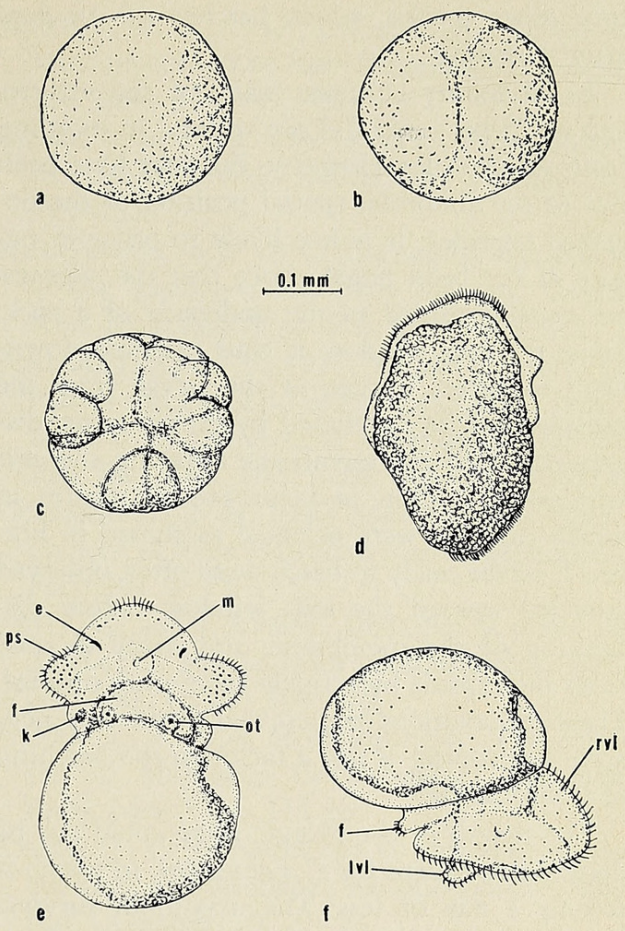

FIG. 15. Developmental stages of *Conus vitulinus* Hwass *in* Bruguière, from the same egg mass as the capsule illustrated in Figure 14. *a*, Uncleaved egg; *b*, 2-cell stage; *c*, early blastula; *d*, trochophore-like stage; *e*, veliger, anterior-ventral view; *f*, veliger, lateral view. *e*, Eye; *f*, foot; *k*, kidney; *lvl*, left velar lobe; *m*, mouth; *ot*, otocyst; *ps*, pigment spot; *rvl*, right velar lobe.

Salient features of development in four species of *Conus* are summarized in Table 3. The eggs are fertilized but have not yet undergone first cleavage when enclosed in the egg capsules. In the species studied, the trochophore stage is entered at 2–6 days, and the veliger stage at 6–10 days, after spawning. Larvae hatch as veligers about 2 weeks after spawning. These observations are in agreement with those of Ostergaard (1950), who also reported on development in

[5] This species is referred to as *C. sumatrensis* Hwass by Ostergaard (1950).

four other species, which hatched 12–16 days after spawning.

In laboratory cultures, many of the veligers (up to 75 per cent) did not succeed in escaping from the capsules. However, this may have been due to the abnormal spatial position of the detached capsules; it is less likely to occur in nature. It has been noted above that the capsules are usually affixed to the underside of a rock. Since the exit window is thus oriented downward in nature, escape of the larvae from the capsule may be facilitated by gravity after disappearance of the membrane covering the exit window. However, in laboratory cultures in which capsules were oriented as shown in Figure 1, larvae ready to hatch were often observed crowded toward the exit window before dissolution of the membrane, and many escaped from the capsule by actively swimming upward. These observations suggest that positive or negative geotropism is not a factor in the hatching of *Conus* larvae.

The length of the pelagic stage could not be determined except for *C. pennaceus*, in which it is only 1 day or less. The maximum survival time of free-swimming veligers in the writer's laboratory was 13 days (*C. rattus*). Partial metamorphosis was observed only in *C. pennaceus*.

The nature of the food of the larval stages is unknown. Protozoa abounded in the cultures. Thorson (1946) concluded that all prosobranch larvae known from the Øresund feed on phytoplankton, and he calculated the theoretical maximum diameter of the food to be 5–45 μ. The mouths of *Conus* veligers measured were of about the same diameter as the esophagus of the smaller larvae measured by Thorson. Thus the larvae of *Conus* probably depend for food on phytoplankton, nannoplankton, and detritus. Examination of squash preparations of *C. pennaceus* a few days after settling revealed the presence of radula teeth. These differ in form from the adult teeth, being shorter in proportion to the thickness, and they are probably not functional. The method of feeding, as well as the food, is thus not known at this stage of the life history. The rather fragmentary information available on post-larval development and growth of *Conus* in Hawaii has been reported elsewhere (Kohn, 1959*b*).

SUMMARY

Egg capsules of 9 of the 33 species of *Conus* found in Hawaii are described and figured. Interspecific variation is usually not sufficient to permit identification of the species to which an egg mass belongs in the absence of the parent.

The complete course of larval development within the egg capsule from spawning (uncleaved egg) to hatching (veliger or veliconcha) is described for 4 species. Early cleavage stages occur 1–3 days after spawning, suppressed trochophore stage at 2–6 days, and veliger stage at 6–10 days. Freely swimming veligers hatched from egg capsules of 3 species 14–15 days after oviposition, in agreement with the developmental time scale of other species of *Conus* previously reported on by Ostergaard (1950).

All species found to have pelagic larval stages produced large numbers (15,000–210,000) of small (125–225 μ) eggs. It was not possible to determine the length of the free-swimming stage in any of these species.

Hatching in one species, *C. pennaceus*, occurs 16–26 days after oviposition at the advanced veliger or veliconcha stage. The larvae swim about for 1 day or less and then assume the benthic habit and begin metamorphosis. This species produces small numbers (3,500) of large (460 μ) eggs. This characteristic is correlated with the absence of a long pelagic larval stage.

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