

## The Biology of *Hastula inconstans* (Hinds, 1844) and a Discussion of Life History Similarities among other *Hastulas* of Similar Proboscis Type<sup>1</sup>

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**ABSTRACT:** Terebrid gastropods of the genus *Hastula* are found in great abundance on fine-sand beaches throughout the tropics. *Hastula inconstans*, a species common to surf beaches in the Hawaiian Islands, is the first *hastula* for which a complete life history is known. *Hastula inconstans* is a primary carnivore, preying exclusively on *Dispio magna*, a tube-dwelling, deposit-feeding spionid polychaete. The gastropod lives just beyond the surf zone and exhibits well-developed adaptations that permit survival in this habitat. The broad, fleshy foot, used in anchoring the snail in the sand and in rapid re-burrowing, is also highly modified as a "sail" which carries *H. inconstans* up and down the beach with the passage of waves. A highly specialized foregut contains long retractile labial and buccal tubes, which, combined with a poison bulb and radular teeth, rapidly sting, immobilize, and ingest prey. The snail lies buried in the sand when not feeding, but emerges when prey are detected by distance chemoreception. Nearby prey are reached by rapidly crawling over the sand surface, and prey at a distance are reached by using the foot to "sail" to their location. In either case, contact with the prey is first made by the propodium of the foot, rapidly followed by proboscis eversion. After contact is made, the prey is stabbed by a radular tooth held by the buccal tube, poison is injected into the wound, and engulfing of the worm begins. This entire sequence occurs between the passage of waves, and the snail usually reburrows to continue feeding before the next wave arrives.

The sexes in *Hastula inconstans* are separate. Mating takes place above the sand while the animals are coupled and rolling freely in the surf, and approximately 40 spherical eggs are later deposited in a capsule covering a small piece of basalt. Larvae metamorphose when they are less than 1 mm in length and reach 3–5 mm in length by late spring. Individuals grow between 0.5 and 0.8 mm per month, reaching a maximum size of 34 mm, which suggests an average life-span of 3–4 years. Other *hastulas* with a proboscis nearly identical in structure to that of *H. inconstans* exhibit similar life history aspects, including habitat choice and prey specificity. It is suggested that feeding types may not only be useful as a diagnostic characteristic, but also in predicting basic life history aspects throughout the family.

GASTROPODS OF THE FAMILY Terebridae are among the most abundant mollusks found in

tropical and subtropical sand environments, ranging from the intertidal to depths of several hundred meters. Despite their abundance and relative ease of collection, little has been published on any species in the family. This report represents the first detailed life history study for any member of the genus *Hastula*, a group of small, active animals found primarily in shallow waters throughout the tropics.

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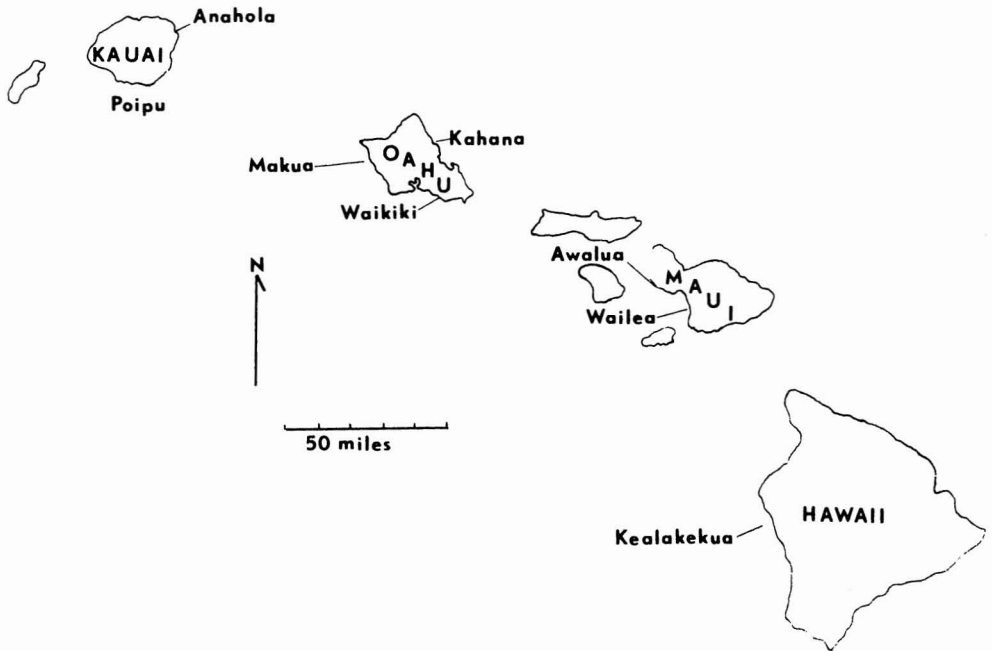


FIGURE 1. Map of the Hawaiian Islands, showing the location of collection sites of *Hastula inconstans*.

*Hastula inconstans* (Hinds, 1844) is Indo-Pacific in distribution and is commonly found throughout the Hawaiian Islands where large populations of the species occur on surf-washed beaches characterized by fine, well-sorted sand, gentle slopes, and rolling breakers. I have never found the species on coarse-sand beaches, nor on other fine-sand areas protected from wave action. The locations in which it is found generally exhibit open ocean conditions of salinity and temperature throughout most of the year.

#### METHODOLOGY

Studies on the ecology and life history of *Hastula inconstans* were conducted between September 1968 and July 1969. Observations on life history in the field and laboratory were primarily concerned with locomotion, food and feeding, reproduction, development, growth, and predation. Animals were observed and collected from eight surf beaches on the islands of Hawaii, Maui, Oahu, and Kauai using standard skin- and

scuba-diving gear. All study sites are indicated in Figure 1, but most studies were done at Kealakekua, Wailea, and Poipu.

#### GENERAL MORPHOLOGY

The shell of *Hastula inconstans* is glossy, reaches a maximum length of approximately 34 mm, and exhibits the flared aperture typical of other hastulas. Shell color within a population is fairly uniform and often similar to the color of the sand beach habitat. Because of the wide range of beach colors in Hawaii, color among populations from different beaches is extremely variable, with individuals shading from light tan through pure black (Figure 2).

The animal has a large, fleshy foot, short eyestalks, and a long siphon which is extended to the sand surface when the snail is buried. One of the most characteristic features of *Hastula inconstans* and the other Hawaiian hastulas is the nature of the foregut and the distinctive behavioral patterns associated with this type of feeding appa-

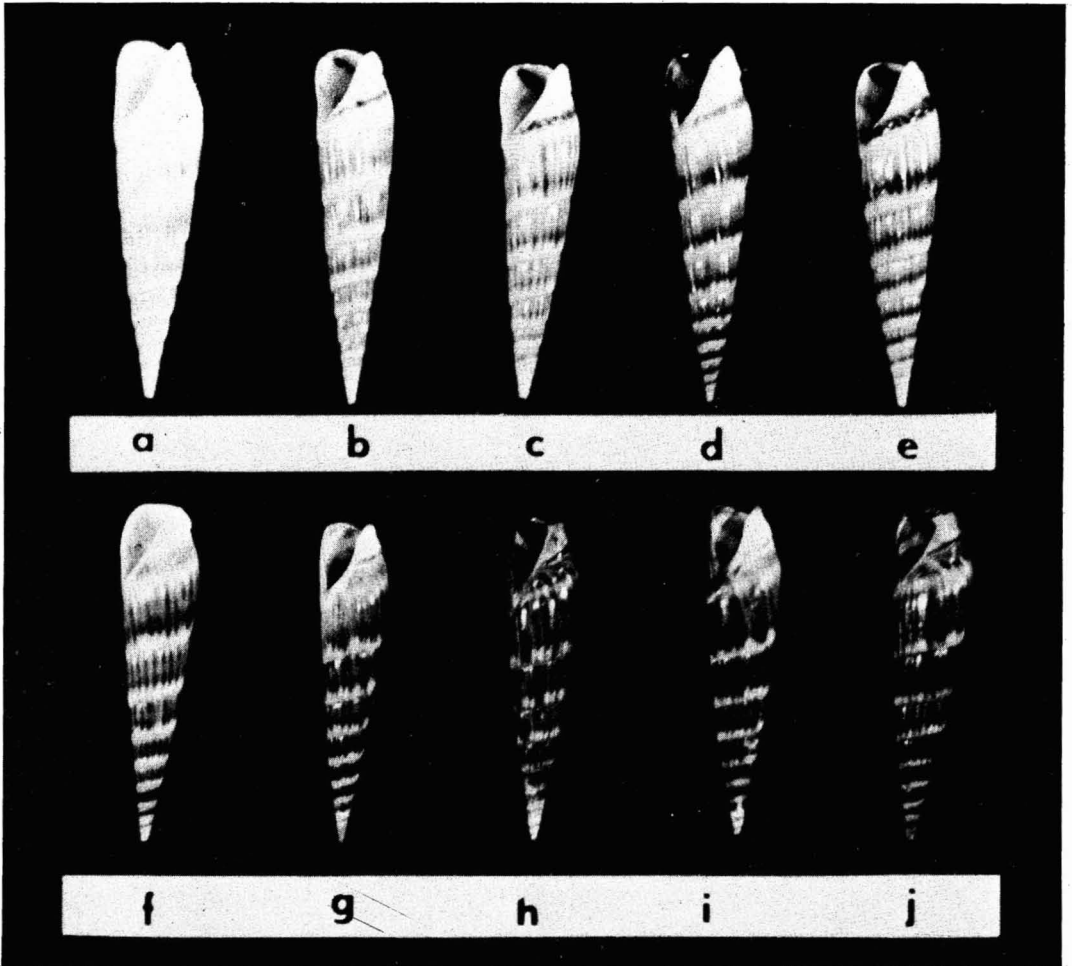


FIGURE 2. Variation in shell color among *Hastula inconstans* populations from different Hawaiian beaches: *a*, Waikiki, Oahu; *b-e*, Poipu, Kauai; *f-h*, Kealakekua, Hawaii; *i-j*, Awalua, Maui.

ratus. Termed a type IIA polyembolic proboscis (Miller 1970), its most distinctive feature is a specialized poison apparatus uniquely suited for rapid prey capture.

#### LOCOMOTION

Both the morphology of the foot and general locomotory behavior of hastulas differ markedly from animals of the genus *Terebra*. The foot of *Hastula inconstans* is very fleshy and has a broad propodium. It is capable of rapid contraction and maintains a

degree of flexibility not evidenced in other terebrids living in less rigorous habitats.

Locomotory behavior was studied in the field and laboratory using techniques described by Miller (1975). There are two basic movements involved in locomotion: a forward gliding of the foot to a position anterior to the shell, followed by cessation of propodial movements and contraction of the body musculature to advance the shell and visceral mass. I call one complete cycle a step. Compared with most other terebrids, locomotion in hastulas is very fast, averaging from 20 to 30 steps per minute. In

addition, hastulas exhibit a locomotory behavior not seen in other genera of terebrids. First described as the "sail effect" by Kornicker (1961), it permits the animal to move rapidly up and down the beach by using its broadly extended foot as a sail to catch the waves.

Use of these locomotory behaviors is dependent upon both the size of the animal and severity of surf conditions. When the waves are small or absent, the animal does not crawl on the sand surface, but rather remains deeply buried, with the long extensible siphon extending above the sand surface. The animal tends to bury itself to a depth roughly equal to the length of its shell.

Calm conditions are rare on the beaches it inhabits, however, and waves of 1 m or more in height generally wash the shore. Under these conditions several millimeters of sand are agitated with the passage of each swell, and the shells of small animals are then uncovered. Following the passage of a wave, *Hastula inconstans* may exhibit one of three behavioral patterns, presumably depending on the presence or absence of prey in the vicinity: In the absence of prey, the snail immediately burrows back into the sand before the passage of the next wave. If prey are detected, the snail may either begin rapid locomotory behavior over the sand in the immediate area, or exhibit the sail effect (described in detail below).

With stronger wave action, 5–10 mm of sand may be overturned during the passage of each wave, and the smaller specimens of *Hastula inconstans* are completely dislodged. Under these severe conditions, reburrowing is not successful, and the small snails glide back and forth just beyond the surf zone with the foot completely extended. Even under this extreme wave action, the larger specimens are rarely completely dislodged.

Since sand trails are rapidly eradicated in the field, it is impossible to determine the distance or general direction an animal crawls each day. Specimens of *Hastula inconstans* have been observed crawling at all hours of the day, but evidence to be presented later indicates that the peak period of feeding, and hence locomotion, takes

place during the night and early morning hours. This is consistent with data for species of *Terebra* (Miller 1975).

#### FOOD AND FEEDING

##### *Introduction and Methods*

Several references exist concerning food and feeding in terebrids of the genus *Hastula*. Hedgpeth (1953) suggests that *H. salleana* may prey on the beach clam *Donax*, although this is not probable. Marcus and Marcus (1960) studied *H. cinerea* on the beaches of São Paulo from Ubatuba to Cananeia. Although they had no success in feeding the animals, setae in the gut suggested that the prey at Ubatuba may be *Nerine agilis*.

Feeding in *Hastula inconstans* was observed in both the field and the laboratory on several occasions throughout the study period and on animals collected from surf beaches on all the islands studied. Data on food and feeding were gathered by two methods. Gut analyses were performed on animals collected by sieving in the surge zone just beyond the surf with a fine-mesh bag. Samples were taken during three periods, 7–10 AM, 2–4 PM, and 6–7 PM, to determine the time of feeding, the number of prey captured each day, and the percentage of the population feeding each day. Night samples were not taken due to the presence of observed inshore shark and barracuda. Food preference studies were also conducted in the field on Kauai, Maui, and Hawaii. Approximately 1 m<sup>2</sup> of sand in the surge zone at each study site was dug up and sieved through the fine-mesh bag. All the polychaetes remaining in the bag were placed in a bucket of seawater containing 50–100 freshly collected *H. inconstans*. The animals were allowed to feed for 5 min and then 20 animals from each study area containing prey in their proboscises were dropped in 70 percent alcohol, which resulted in immediate regurgitation. Prey were then returned to the laboratory for identification.

Details of the anatomy of the feeding apparatus were worked out through dissec-

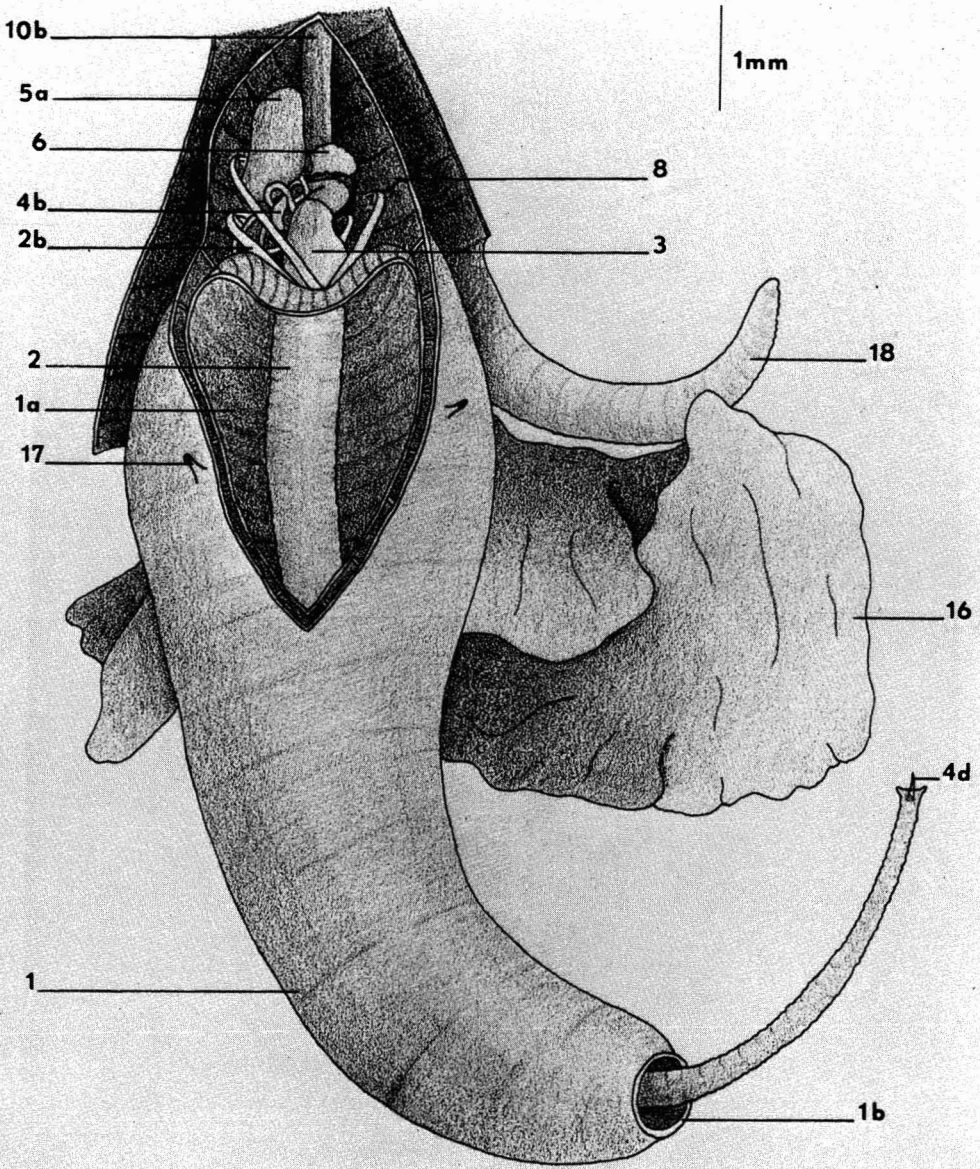


FIGURE 3. Gross morphology of the anterior digestive system of *Hastula inconstans* with the proboscis everted (exposed by cutting through the dorsal mantle and body wall): 1, labial tube; 1a, labial cavity; 1b, sphincter of the labial tube; 2, buccal tube; 2b, longitudinal retractor muscles of the buccal tube; 3, buccal cavity; 4b, radular sac; 4d, radular tooth; 5a, poison bulb; 6, salivary gland; 8, cephalic hemocoel; 10b, postganglionic esophagus; 16, foot; 17, eyestalk; 18, siphon.

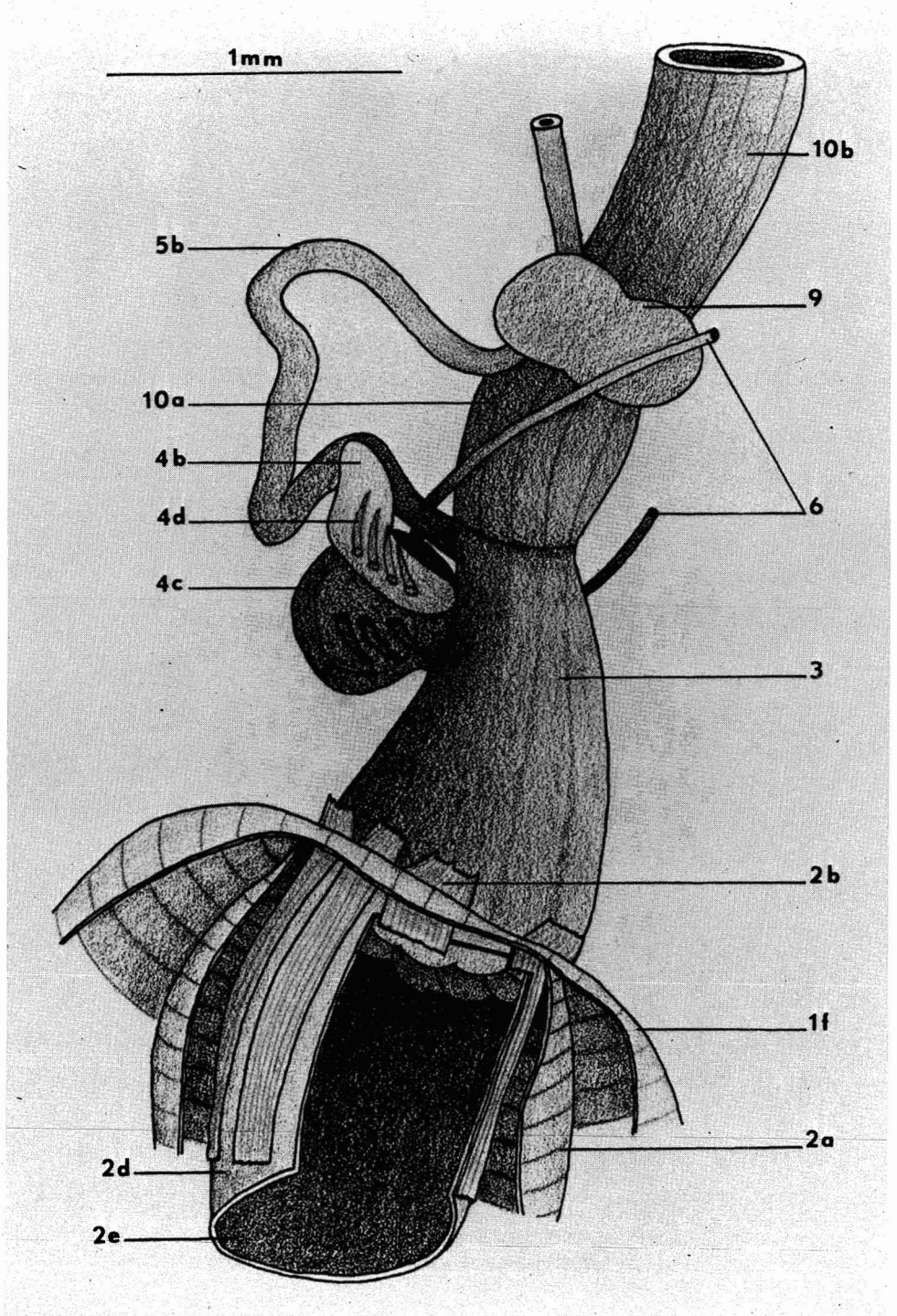


FIGURE 4. Dorsal view of the organs contained within the cephalic hemocoel of *Hastula inconstans*: 1f, inner circular muscles of the labial tube; 2a, outer circular muscles of the buccal tube; 2b, longitudinal retractor muscles of the buccal tube; 2d, inner circular muscles of the buccal tube; 2e, lumen of the buccal tube; 3, buccal cavity; 4b, radular sac; 4c, radular caecum; 4d, radular teeth; 5b, poison gland; 6, ducts of the salivary gland; 9, nerve ring; 10a, preganglionic esophagus; 10b, postganglionic esophagus.

tion of fresh specimens removed from the shell after quick freezing.

### *Gross Morphology of the Alimentary Tract*

Figure 3 illustrates the foregut of *Hastula inconstans* with the proboscis everted. As is the case for all terebrids with the type IIA polyembolic proboscis (Miller 1970), the primary functional components utilized in prey capture in *H. inconstans* are a long eversible labial tube, terminating in an anterior sphincter and containing a long retractile buccal tube that can be extended beyond the labial tube. The cephalic hemocoel contains the longitudinal retractor muscles of the buccal tube and several organs that enter into the muscular buccal cavity (Figure 4). The radular sac and radular caecum open into the buccal sac on the ventral wall of the buccal cavity. A small bipartite salivary gland overlies the preganglionic esophagus and opens through two ducts into the buccal sac on both sides of the radular caecum. The coiled poison gland leads from a large muscular poison bulb located in the right half of the cephalic hemocoel and enters the ventral wall of the buccal cavity posterior to the opening of the radular apparatus. The short, thin-walled preganglionic esophagus passes through the nerve ring and continues as a long postganglionic esophagus, tubular stomach, and slender intestine.

### *Diet and Feeding Behavior*

Analyses of gut contents were made on 66 specimens of *Hastula inconstans* collected from Kealakekua Beach on Hawaii, and prey preference records were obtained for 60 *H. inconstans* from Kauai, Maui, and Hawaii. The results of gut analyses are shown in Table 1. While there are several species of polychaete worms living in the surf beach habitats studied, both gut analysis and feeding preference records indicate that *H. inconstans* in Hawaii feeds exclusively on the spionid polychaete *Dispio magna*. This deposit feeder inhabits fine sand on many of the surf beaches in Hawaii, utilizing

a pair of ciliated palps that stretch over the substratum to gather food particles. It lives buried in the sand to a depth of up to 0.5 m in a burrow lined with a fragile mucoid secretion and is generally found where there is sufficient water agitation to keep the detritus moving. Greatest abundance of the worm occurs in the surge and lower surf zone, and densities of 100–300 animals per square meter are common on fine-sand beaches such as Kealakekua on Hawaii, Wailea on Maui, and Poipu on Kauai.

As in other terebrids (Miller 1975), feeding appears to be initiated by distance chemoreception. Observations in the laboratory indicate that worm extract will elicit emergence from the sand, rapid propodial undulation, and limited swelling of the cephalic hemocoel. Marcus and Marcus (1960) indicate that the anterior of the foot of *Hastula cinerea* is heavily innervated, probably serving as an important sensory organ. This also appears to be true in *H. inconstans*, for under most conditions complete swelling of the cephalic hemocoel will not occur until the propodium of the foot comes into contact with pieces of prey or sections of the prey tube (Figure 5A). When this occurs, relaxation of the retractor muscles, along with contraction of the circular muscles, leads to eversion of the labial tube and extension of the buccal tube through it. It is not known how the radular tooth is moved into position, but Smith (1967) is probably correct when he states that contraction of radular sac muscles carries a tooth into the buccal cavity, and peristalsis then moves the tooth to its normal functional position at the tip of the buccal tube. As the broad foot searches rapidly through the sand, the sphincter of the labial tube remains in close contact with the sand surface, and the radular tooth held by the extended buccal tube can be seen darting in and out. When the anterior end of *Dispio magna* is sensed by the propodium, the labial tube rapidly moves toward the worm and the buccal tube may extend to a considerable distance beyond the sphincter (Figure 5B). As the radular tooth comes into contact with the worm, the poison bulb appears to contract, causing the entire body

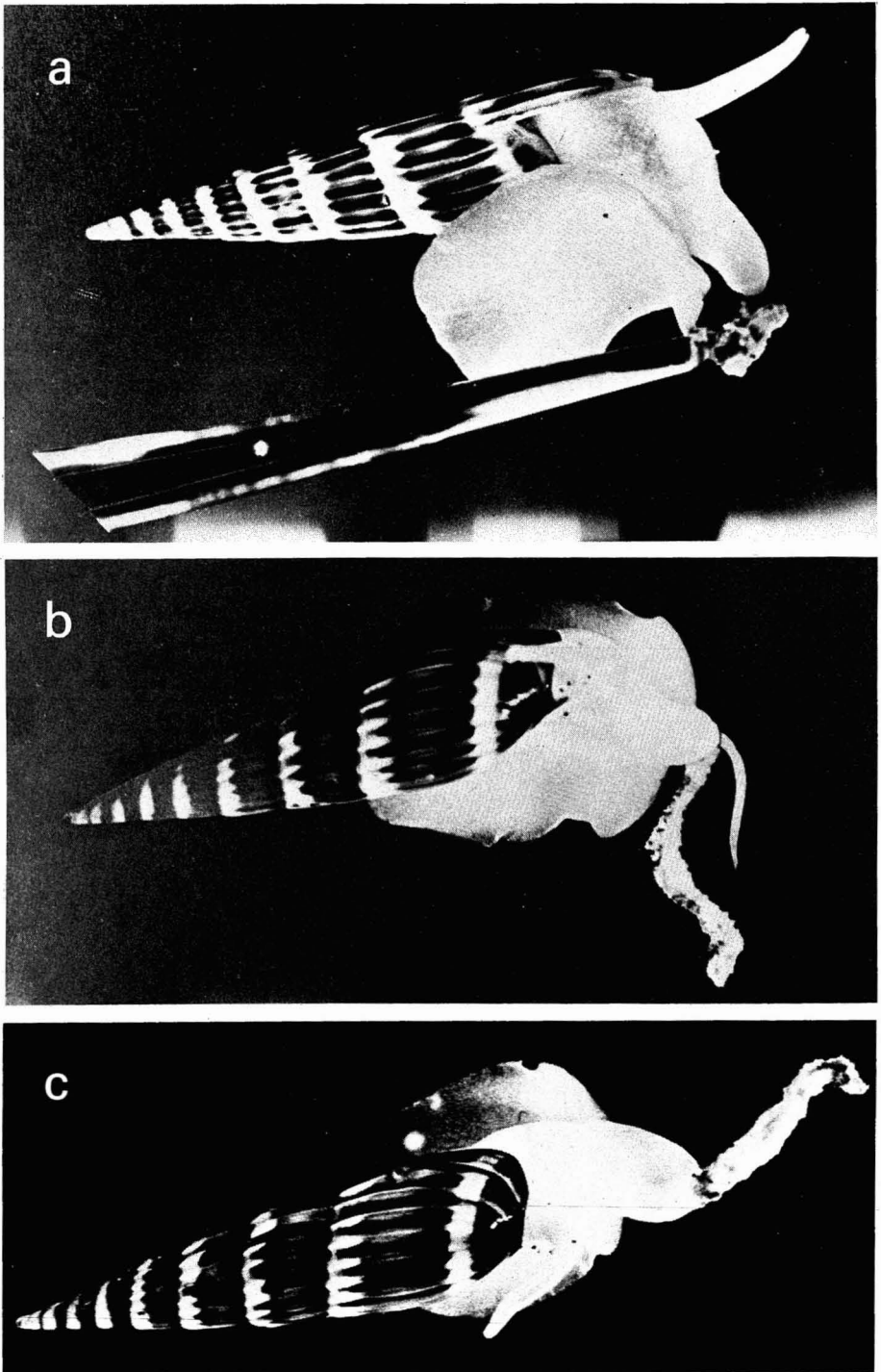


FIGURE 5. The rapid ingestive phase of feeding behavior in *Hastula inconstans*: *A*, feeding behavior is elicited by bringing a *Dispio magna* into contact with the propodium of the foot; *B*, after stimulation of the propodium, the labial tube everts and the long buccal tube bearing the radular tooth searches for the prey; *C*, following impalement, the buccal tube rapidly retracts and the labial tube extends to engulf the prey; *D*, *E*, the labial tube retracts and then extends a second time to further engulf the prey; *F*, when the labial tube inverts for the second time, the labial cavity is full and further ingestion occurs slowly.



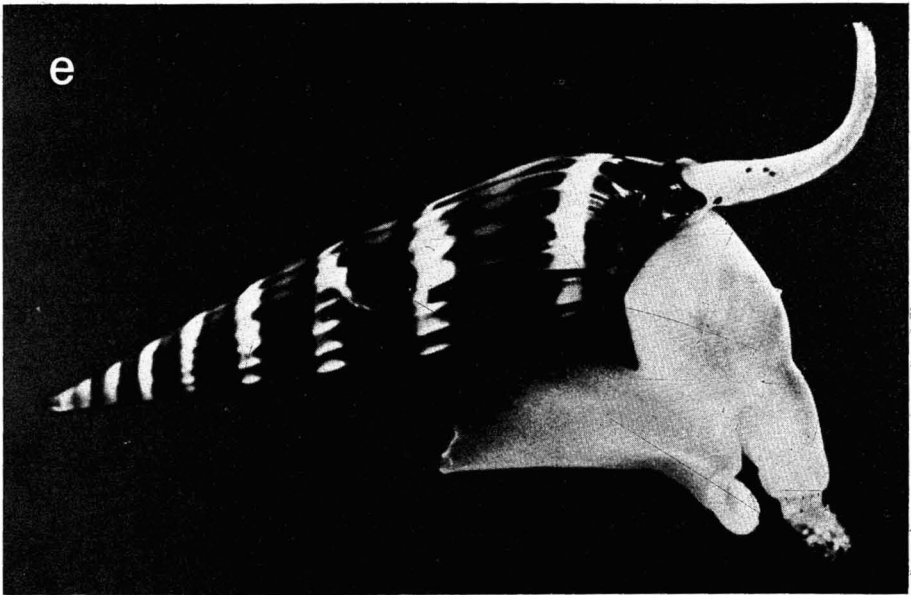
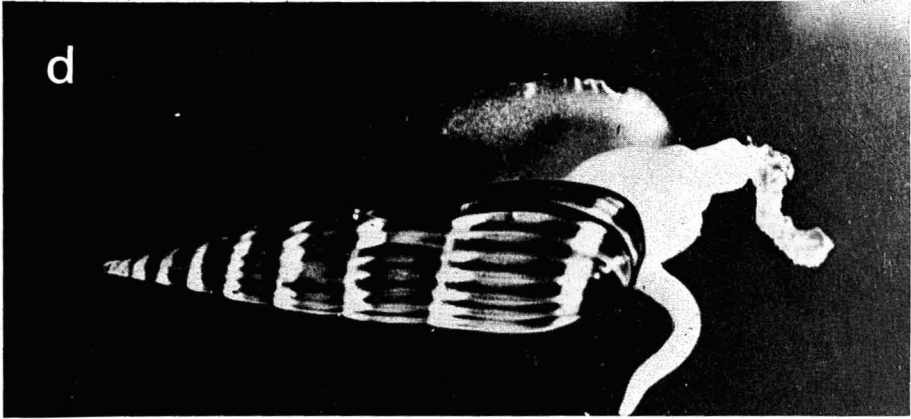


TABLE 1  
ANALYSIS OF PREY CHOICE OF *Hastula inconstans*

DATE	NUMBER OF SPECIMENS EXAMINED	COLLECTION SITE	PREY	NUMBER OF SPECIMENS WITH PREY	POSITION OF PREY IN GUT		MAXIMUM NUMBER OF PREY PER SNAIL
					Fore	Hind	
13 Oct. 1968	18	Kealakekua, Hawaii	<i>Dispio magna</i>	4	1	3	1
18 Feb. 1969	48	Kealakekua, Hawaii	<i>Dispio magna</i>	13	4	9	1
3 May 1969	20*	Wailea, Maui	<i>Dispio magna</i>	20	20	—	—
1 June 1969	20*	Poipu, Kauai	<i>Dispio magna</i>	20	20	—	—
18 June 1969	20*	Kealakekua, Hawaii	<i>Dispio magna</i>	20	20	—	—

\*Results of food preference test.

of the snail to lunge violently. On several occasions a milky substance could be seen flowing from the tip of the buccal tube. The tooth is thus not fired at prey as reported by Jaekel (1952), but rather is used as Smith suggests, merely to make an opening to admit the discharged poison. As soon as the poison has been injected, the labial tube begins to engulf the worm and the buccal tube rapidly contracts to pull the worm in (Figure 5C, D, E).

Prey capture is a rapid process, and in the laboratory a considerable portion of the worm may be completely engulfed in less than 1 min. Once the labial cavity is full, further rapid ingestion cannot occur and the snail begins to crawl (Figure 5F). In the field, the entire process of prey capture takes place between the passage of successive waves, and as soon as the poison has been injected, *Hastula inconstans* begins to burrow into the sand, entering nearly straight down so that only the spire of the shell is exposed before the next wave passes. The snail continues to reburrow until the shell is completely covered and free from wave disturbance. Feeding then continues at a slower rate until the worm is completely ingested.

No definite conclusions can be reached concerning the peak feeding period of *Hastula inconstans*. Animals will feed in the field and laboratory any time they are presented with prey, and they have been observed feeding throughout the early morning hours in the field. However, gut analyses of 48 animals collected from Kealakekua showed a higher percentage of prey in the

upper digestive tract at 10 AM (14 percent) than at 4 PM (5 percent). William Stewart, a graduate student at the University of California, Santa Barbara (1968, personal communication), found that *H. cinerea*, a surf-dwelling species from Florida, usually feeds at night on the spionid worm *Nerine agilis*.

#### *Ingestion and Digestion*

Estimates on the duration of the ingestive and digestive processes were obtained through gut analyses of animals fed in the laboratory and dissected at intervals of 4–40 hr after feeding and through observations on the amount of time elapsed between ingestion and defecation.

Evidence indicates that the entire feeding process in terebrids of the genus *Hastula* is of similar duration to that of species of the genus *Terebra* (Miller 1975). Capture, immobilization, and initial ingestion of the prey are rapid, but once the labial cavity is full, ingestion of the entire worm continues at a considerably reduced rate for 5–10 hr after capture. Digestion begins in the upper esophagus and prey remains are found in the intestine 18–24 hr after ingestion begins. Feces in the form of setae and sand are voided considerably later, usually not appearing in the rectum until 2 days after prey capture.

#### *Use of the "Sail Effect" as a Method of Prey Capture*

*Hastula inconstans* and other surf-dwelling hastulas differ from other terebrids in their

response to water agitation. As has been shown for certain bivalves (Reese 1964), hastulas kept in a container of still water show little or no movement. However, upon agitation of the water, the foot immediately extends and rapid propodial activity begins, a factor that may be of importance in the feeding response.

Initiation of feeding in *Hastula inconstans* appears to be partially dependent on the presence and intensity of beach surge. On the rare occasions when wave action on the beach is reduced or absent entirely, no hastulas are seen crawling, and it is probable that little feeding takes place under such conditions. During periods of moderate surge action, sand agitation is sufficiently strong to expose partially both the prey and the hastulas and the latter begin searching movements with their propodia while they bury back into the sand.

One of the most curious phenomena associated with locomotion and feeding in the hastulas is the so-called "sail effect" first reported by Kornicker (1961) for *Hastula salleana* along the Gulf of Mexico. He claims that the foot of *H. salleana* is used not only to plough through the sand, but also as a sail to enable an animal to move into deeper water when it is about to be stranded above the swash zone of a falling tide. Assuming that *H. salleana* is indeed exposed as the tide recedes, this is a reasonable explanation.

The sail effect is also very obvious in *Hastula inconstans*, a species that lives well below the swash zone where danger from stranding presents no problem. In this species, the sail effect appears to serve as a behavioral adaptation for feeding by enabling an animal to move from one part of the beach to another with great rapidity. I was first made aware of this while taking bottom samples in the surge zone, when large numbers of *H. inconstans* tended to concentrate in the area from which the sample had been removed. By digging successive core samples from the sand in the same area and then observing this disturbed area during the passage of several waves, it soon became apparent that the animals are initially attracted to prey by distance chemoreception and then moved into the area of disturbance by

use of the sail effect, as diagramed in Figure 6. This rapid feeding behavior consists of the following sequence of events. As an incoming wave passes over the bottom where sand has been disturbed, fragments of spionid worms and their tubes are carried shoreward. As the water containing these fragments passes over the buried hastulas, they sense the prey, crawl to the surface, flip on their side as described by Kornicker (1961), and are carried seaward in the backwash. When the disturbed area is reached, the propodium digs in and the animal flips over. Propodial searching movements immediately begin, the labial tube rapidly everts, and when a worm is located, feeding ensues before passage of the next incoming wave.

#### Feeding Rates

Studies on feeding rates were done on animals collected at Kealakekua Beach from October 1968 to June 1969. Of 66 animals dissected for gut analyses, nine contained digested or partially digested remains of *Dispio magna* in the esophagus and stomach and nine contained setae and sand grains in the rectum. Since it takes longer than 24 hr for prey to pass through the digestive tract into the rectum, the first group represents those animals which had fed less than 24 hr before collection time, and the second group represents those that had fed the previous day. This would suggest an approximate feeding rate of 14 percent per day for the entire population, a figure that is comparable to the 17 percent feeding rate found for the entire *Terebra gouldi* population at Ahu O Laka Island (Miller 1975).

Obviously, this rate cannot be constant throughout the year, for there are times during the winter months when wave action would be too intense for successful prey capture. Indeed, specimens are difficult to locate under extreme surf conditions and it is probable that many migrate into deeper, calmer waters, although it has been impossible to make meaningful collections in these areas during winter storms. Since the prey species maintains greatest density in the shallow surge zone, feeding in the *Hastula*

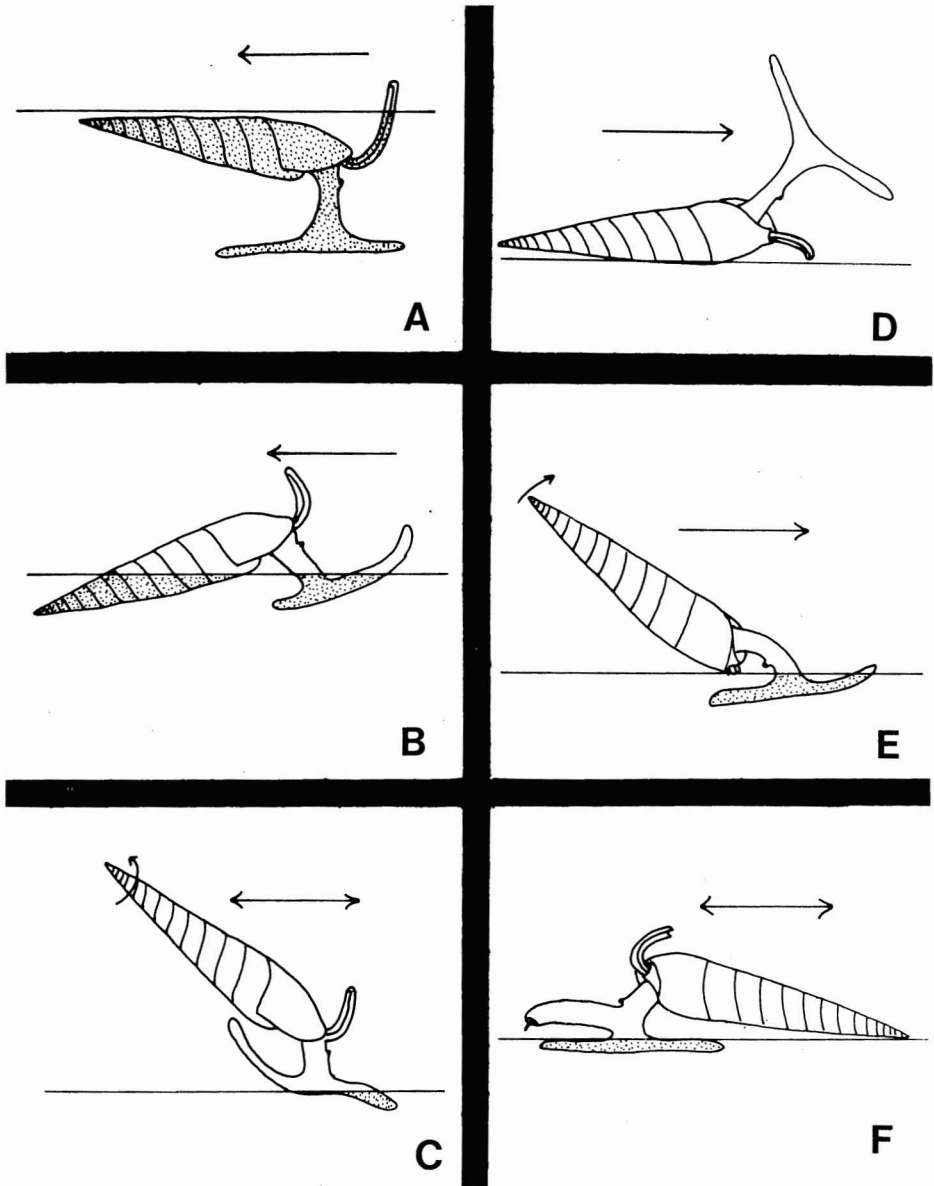


FIGURE 6. Sequence of movements of *Hastula inconstans* exhibiting the sail effect: *A*, *Hastula inconstans* buried in the sand as an incoming wave passes; *B*, the snail rapidly crawls to the sand surface; *C*, the apex of the shell is raised at slack wave and thrown to one side; *D*, using the foot as a sail, the animal is carried seaward by the outgoing wave; *E*, the propodium digs into the sand and the snail rights itself; *F*, searching for prey commences at slack water before the passage of the next incoming wave.

population presumably slows down during times when migration occurs.

As is the case for *Terebra gouldi*, individual feeding rates appear to be low. Because of the relatively long time involved in prey ingestion, it is probable that no more than one prey specimen is eaten per day. Gut analyses failed to show more than one prey specimen in the guts of animals collected in the field, and under no circumstances did any animal feed on more than one prey specimen per day in the laboratory. Based on an approximate feeding rate of 14 percent per day for the Kealakekua population, it would appear that an individual may average one prey per week.

#### REPRODUCTION AND EGG CAPSULES

##### *Mating*

Mating in terebrids of the genus *Hastula*, particularly those species inhabiting surf-swept beaches, differs in several respects from species of *Terebra* living in less rigorous environments. While males of *T. gouldi* and probably most other terebrids living in calmer areas follow a mucous trail laid down by the female (Miller 1975), this is not probable in the case of surf-dwelling hastulas, for the mucous trail would be quickly erased with the passage of each successive wave. *Hastula inconstans* lives in relatively high densities on most beaches, and while there is no evidence to indicate the mechanism of sexual attraction, it is possible that mating results from random contact of sexually ready males and females.

The mating process also differs distinctly from that of *Terebra gouldi*, in which mating occurs while the animals are buried in the sand. In all situations in which mating was observed in the field, the mating pairs were found in the surge zone, coupled together and rolling freely back and forth with each wave. The animals remained tightly clasped together, and unlike the response in *T. gouldi*, did not separate when they were disturbed. Duration of copulation is not known.

Nothing is known on the length of the

mating season or the time of juvenile settling. Individuals were found mating every time the habitat was visited.

##### *Egg Capsules*

Egg capsule deposition differs significantly from the process observed in *Terebra gouldi* (Miller 1975). Since *Hastula inconstans* lives and mates on beaches of moderate wave action and well-sorted, very fine sand, permanently affixed egg capsules are not possible. However, just beyond the actual zone where surf breaks is a region of surge containing beach litter and small bits of basalt rock. This material is on the surface of the finer sand and rolls back and forth with the passage of each wave. *Hastula inconstans* appear to utilize the small rounded bits of basalt, which are generally 1–2 mm in diameter, as bases for egg capsule deposition. It is not known whether the deposition is accomplished with the female exposed to the surface and grasping the small basalt grains or below the surface of the sand where she contacts a piece of buried basalt. However, all the egg capsules recorded in the field were found from surface sieving in the litter zone with the use of the fine-mesh bag previously described.

As shown in Figure 7, the egg capsules are of approximately the same size as the basalt granules and form a caplike covering over them. Each capsule contains approximately 40 spherical eggs, 100  $\mu\text{m}$  in diameter. Development beyond this stage has not been observed. Both the small size of the protoconch and the variability in shell color and sculpture among populations from beaches in the Hawaiian Islands and from other Indo-Pacific areas would indicate that the planktonic stage is either greatly reduced or absent entirely (J. B. Taylor 1968, personal communication). If this is true, some of the eggs in the capsule may serve as nurse cells.

#### GROWTH

Direct observations of growth in toxoglossans have been difficult to obtain, prim-

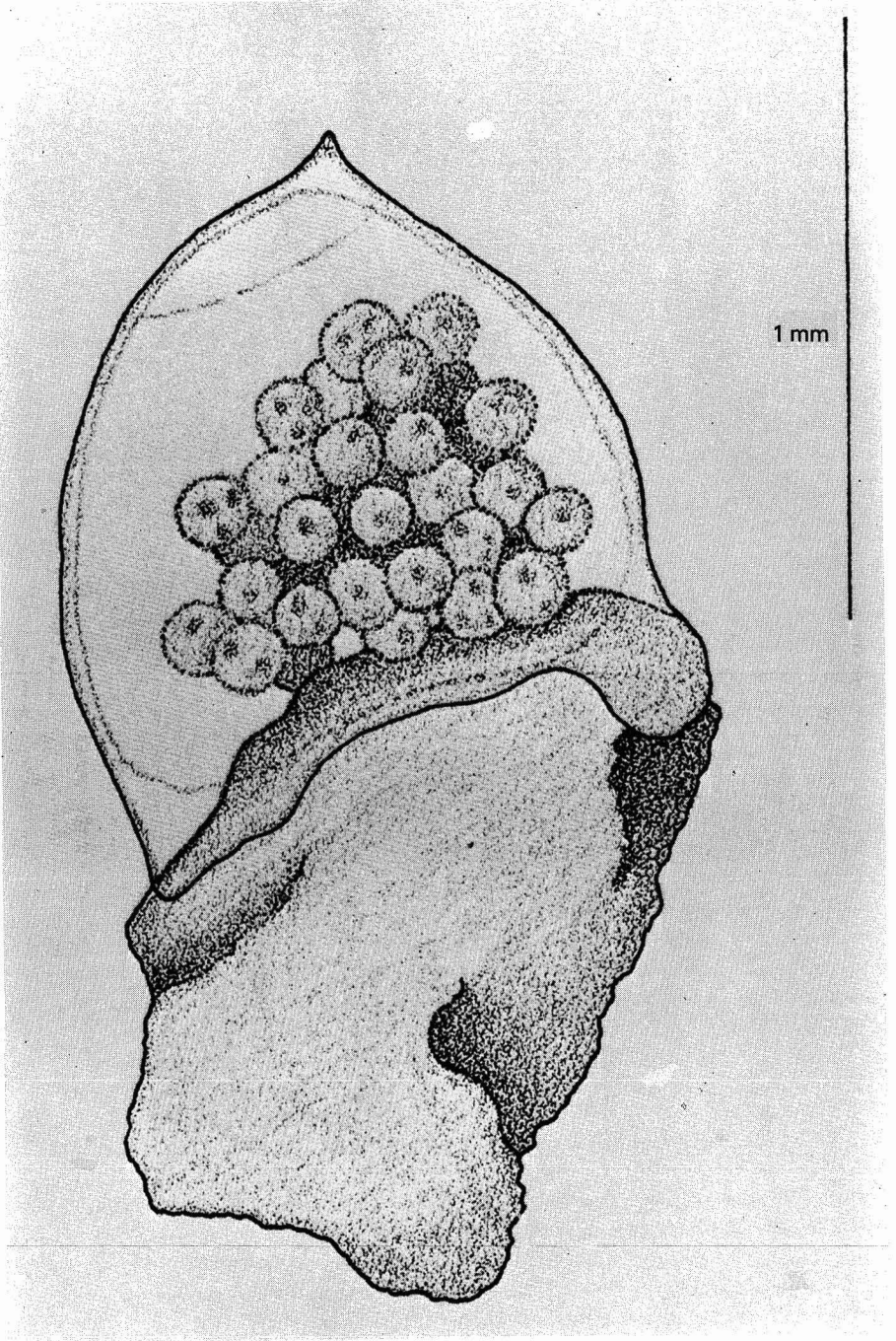


FIGURE 7. Egg capsule of *Hastula inconstans* containing uncleaved ova. The capsule is attached to a small granule of basalt.

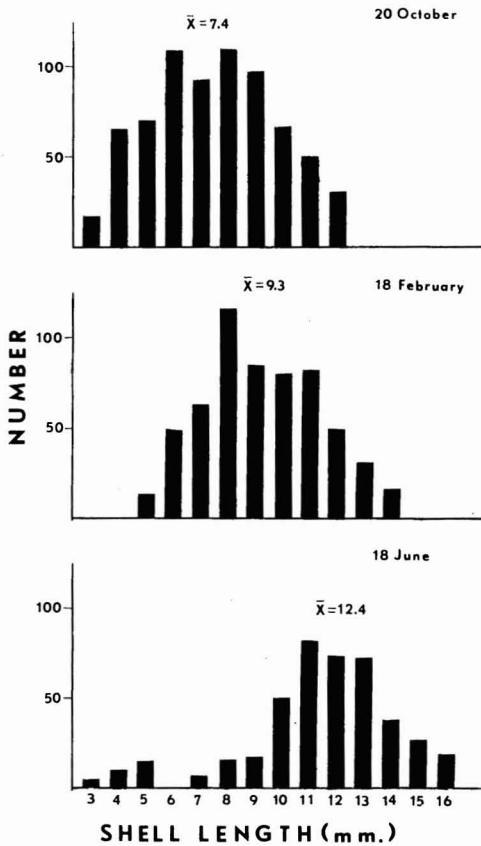


FIGURE 8. Length-frequency distribution of juvenile *Hastula inconstans* from Kealakekua Bay, Hawaii, October 1968–June 1969.

arily because the specialized feeding habits do not permit normal survival in the laboratory and because tagged specimens released in the field can rarely be recovered. No published data on growth exist for the turrids, but Kohn (1959) has made brief observations on the postlarval development of *Conus pennaceus* and Miller (1975) determined growth rates for *Terebra gouldi*.

Because of the unique feeding style and specialized habitat of *Hastula inconstans*, the only conclusive data on growth rates were obtained through periodic collecting and measuring of the first- and second-year classes. To gather large numbers of small specimens effectively under rather turbulent conditions, a 1.0-mm-mesh nylon bag was attached to a metal scoop and pulled through the top centimeter of sand between

passage of successive breakers. The sand was quickly washed from the bag by wave turbulence and sampling was continued until approximately 400 small individuals were gathered. Collections using this technique were conducted at Napoopoo Beach in Kealakekua Bay in October 1968 and February and June 1969. Shell lengths were measured to the nearest millimeter with a vernier caliper and animals were returned to the beach after each measurement. The results are shown in Figure 8.

The individuals collected in October with an average shell length of 7.4 mm probably represent the 1968 year class. By February 1969 the average shell length of this class had increased to 9.3 mm, representing an average growth rate of 0.47 mm per month. Between February and June 1969 the average shell length increased to 12.4 mm, for an average growth rate of 0.80 mm per month. The faster growth rate between February and June may result from reduced surf activity at Kealakekua when the weather changes from southwest winter storms and high surf to summer dry trade conditions characterized by low to moderate surf.

It was not possible to determine the time of juvenile settling, since metamorphosis occurs when the protoconch is less than 1 mm in length (Taylor 1975) and the mesh would not retain individuals this small without also retaining large quantities of sand. However, since individuals collected in October with an average shell length of 7.4 mm appear to represent the 1968 year class, and assuming that the growth rate is approximately 0.8 mm per month throughout the summer, the larvae probably began metamorphosing in late spring. This is reinforced by data from the June collection, which shows the 1969 year class beginning to appear in the 3.0–5.0 mm range.

Adults reach a maximum length of 34 mm, but few individuals longer than 29 mm were found. If the growth rate of between 0.5 and 0.8 mm per month is fairly constant throughout the life-span of the species, and if growth does not significantly plateau, maximum age would be between 3 and 4 years.

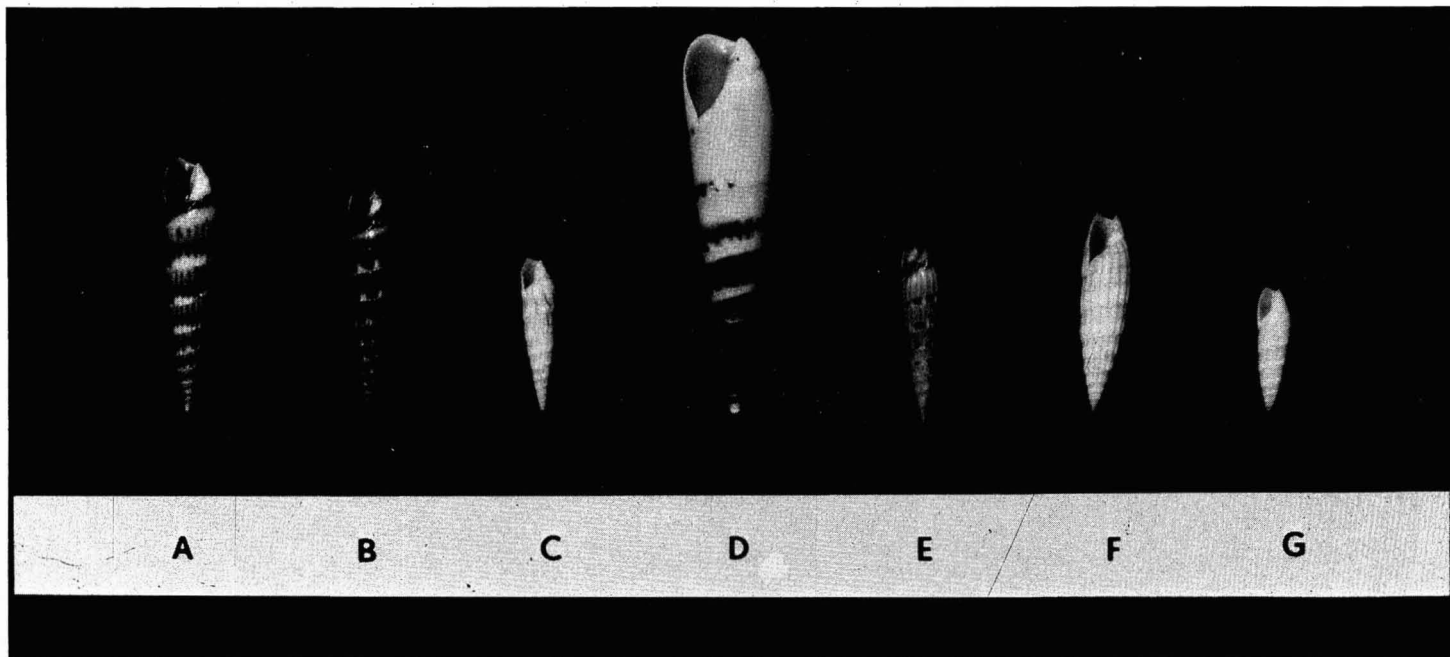


FIGURE 9. Hawaiian species of *Hastula* with the type IIA polyembolic proboscis (0.75 $\times$ ): A, *H. inconstans* (Hinds, 1844); B, *H. strigilata* (Linnaeus, 1758); C, *H. penicillata* (Hinds, 1844); D, *H. hectica* (Linnaeus, 1758); E, *H. lauta* (Pease, 1869); F, *H. solida* (Deshayes, 1857); G, *H. albula* (Menke, 1843).



## PREDATION

The effects of predation on *Hastula inconstans* are difficult to assess. Few empty shells have been found washed on the beach and those that have been found exhibit no obvious evidence of predation. However, some mechanism causes a significant decline in abundance between the first- and second-year classes. Two possibilities exist to explain this observed reduction. During most of the summer and fall tradewinds blow consistently from the northeast and wave action on the leeward surf beach is slight. With a shift in wind direction during the winter months, waves increase in height and the surf often becomes extremely heavy, even in the usually placid bays. At this time hastulas smaller than 1 cm in length are usually unable to remain buried in the sand; they are dislodged and tend to glide back and forth over the surface of the sand with each passing wave. It is possible that as wave intensity increases, large numbers of these small individuals could be carried into the surf zone and eventually cast high on the beaches.

Another possibility is that predation may act on the young during this time. Small animals dislodged from the sand keep their white foot fully extended, presenting a sharp contrast to the generally darker sand. The crustacean *Portunus sanquinolentus* is abundant on the beach, as is a small species of flounder, *Platophys pantherius*. Both of these animals frequent the surge zone and could quite easily prey on the small hastulas when they are exposed. Gut analyses were not done, however, to determine the feeding habits of these species.

## DISCUSSION

In addition to *Hastula inconstans*, I have found four other species of *Hastula* with the type IIA polyembolic proboscis commonly living on surf-washed beaches and three species living in deeper water (Figure 9). They all have a small shining shell with few whorls and a wide aperture. All species are nearly identical in internal morphology, with

a long slender buccal tube and a well-developed radular apparatus.

I have studied in detail only those species living on surf beaches. They all have a broad fleshy foot, crawl and bury rapidly, and show striking similarities in the method of feeding and choice of prey. Gut analyses were performed on three surf species in addition to *Hastula inconstans* and all species were found to feed on spionid polychaetes. Both *H. hectica* (Linnaeus, 1758) and *H. strigilata* (Linnaeus, 1758) feed on *Nerinides* sp., although they live in different zones of the beach. *Hastula penicillata* (Hinds, 1844) feeds on an unidentified spionid.

Spionids apparently are the preferred food of other species of *Hastula* as well. Marcus and Marcus (1960) found the remains of *Nerinides agilis* in the gut contents of *H. cinerea* at Ubatuba, Brazil, and Stewart (1967, personal communication) found the same species of worm in the guts of *H. salleana* from Florida.

It is too early to speculate on the taxonomic relationship of hastulas with the type IIA feeding apparatus. It is probable, however, that species of this feeding type have evolved from one ancestral stock and are specialized to exploit the large numbers of tube-dwelling polychaetes occurring throughout the tropics. The study of more species should make it possible to determine the diagnostic significance of this feeding type in a classification of the family. I suspect that all species with the type IIA proboscis will prove to have similar feeding habits. Similarity in feeding habits and obvious similarities in the morphology of the shell and feeding apparatus may serve to confirm the placement of type IIA series in the genus *Hastula* as proposed by H. and A. Adams in 1858.

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