

SOME ASPECTS OF THE ECOLOGY OF LINGULA
(BRACHIOPODA) IN KANEOHE BAY, HAWAII

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INTRODUCTION

Lingula is one of the most morphologically conservative genera known. This brachiopod has remained essentially unmodified for 350-400 million years (Hyman, 1959; Paine, 1963). It is one of the oldest, if not the oldest, living animal genus with a fossil record; and is well represented in the geologic column from the Ordovician. Deposits containing Lingula are thought to have been formed in a shallow, warm, sea water environment (Weller, 1957; Cloud, 1948). Their fossil remains occur on all continents (except possibly Africa) in most kinds of sedimentary facies, but most frequently in black-shales and related sediments (Moore, Lalicker and Fisher, 1952).

Even though Lingula is of little value as a stratigraphic indicator because of its morphological conservatism, it is considered to be a good indicator of environmental conditions. Yet the ecological work on this genus is incomplete. Prior to this study, field work on the post-larval forms was mainly limited to qualitative observations by Yatsu (1902) and Morse (1902), and a quantitative growth study by Chuang (1961). The closely related Glottidia, the only other living genus in the family Linguladae, was the object of a comprehensive ecological study by Paine (1963), who studied most aspects of the life history of Glottidia pyramidata in Florida.

Living Lingula have been found only in the warm central

Indo-Pacific region. Of the twelve species recognized by Hatai (1936a and b), seven are endemic: four in Japan, two in Northern Australia, and one in the Hawaiian Islands. The remaining five species are distributed mainly about Japan and the Philippines. Although one specimen of Lingula was found at a depth of approximately 90 meters, most members of this genus are found in shallow marine or brackish waters from the intertidal zone to about 20 meters (Craig, 1952; Hatai, 1936b; Yatsu, 1902).

Lingula reevii (Davidson) is relatively common on some of the shallow reef platforms of Kaneohe Bay (Figures 1 and 2) but has not been reported elsewhere in Hawaii. Postlarval forms live burrowed in the soft sediments where they can be readily located by the characteristic shape of their burrow mouths (a knife-like slit encasing three round holes.)

Initiation of this study was stimulated by assertions that it was dying out in Kaneohe Bay either as a result of competition with the recently introduced Japanese littleneck clam (Tapes philippinarum) or from increased pollution in the bay. Since Lingula reevii appears to be found only in Kaneohe Bay, it may be an endangered species. Pollution, dredging and competition could possibly force the extinction of this species.

This investigation, which extended from June 1967 to February 1969, deals with the distribution, limiting factors, interspecific interactions, feeding, growth and other aspects of the life history of Lingula reevii in the southern sector

of Kaneohe Bay. The main objectives were 1) to understand the ecological position of Lingula reevii, especially with respect to limiting factors, interspecific interactions, distributional pattern and growth and 2) to use this ecological information as an aid in the understanding of the ancient environments in which Lingula is found as a fossil.

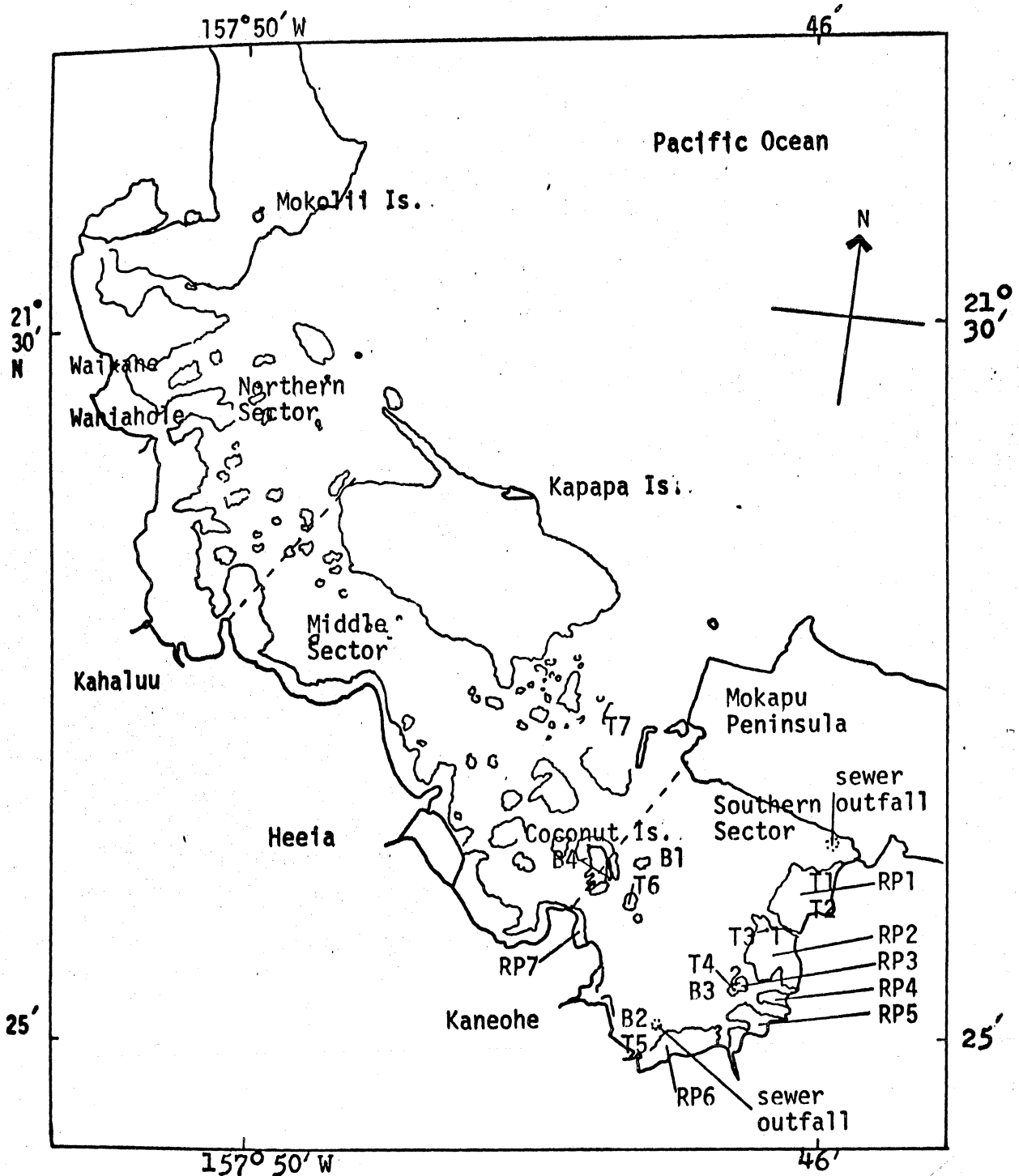


FIGURE 1. MAP OF KANEOHE BAY SHOWING PLACE NAMES, SECTORS, REEF PLATFORMS (RP) AND STATIONS. AFTER TESTER (1951).

DESCRIPTION OF STUDY AREAS

The field study was concentrated on the shallow reef platforms that are on the periphery of the southern sector of Kaneohe Bay because this was the only area where Lingula reevii was found in abundance. These reef platforms (average depth 0.5 m) are partially awash during low tide and covered by about 1 m of water during high tide.

The substratum composing these platforms is varied; seven bottom types were categorized (see Figure 2). Four zones were recognized in a typical reef platform from the reef edge to the shoreline (reeftop, sandflat, mudflat, and the mangrove area). The reeftop is made up of dead coral blocks heavily encrusted with epifaunal invertebrates and algae. The sandflat is inhabited by large numbers of infauna and occasionally by a heavy growth of macro-algae; it is in this zone that L. reevii is most abundant. The mudflat is made up mostly of terrestrially derived sediments and is carpeted by a thin layer of microscopic algae (primarily diatoms); relatively few invertebrate animals live in this zone. In the mangrove area the bottom is composed of very soft muds and the sparse fauna consists mostly of sponges and portunid crabs. Current strengths and wave action vary from moderate at the reeftop to slight near the mangroves.

The southern sector of the bay is partially isolated from the open ocean; yet, the majority of the water has a temperature and salinity character similar to the nearby

oceanic water (Bathen, 1968). The most significant difference between the southern sector and the ocean is the higher productivity, which is at least partially the result of treated sewage, discharged at two locations (see Figure 1).

LIFE HISTORY AND ECOLOGY

General Distribution and Abundance in Kaneohe Bay

A benthic survey of the peripheral reef platforms in the southern sector of Kaneohe Bay was made by Mr. John Higgins and me during the summer of 1967. Transects were run from the shoreline to the reef edges at approximately 100 m intervals. The type of substratum and the relative densities (low, average and high) of Lingula reevii and Tapes philippinarum were recorded and plotted (Figure 2). Notes on the general flora and fauna were also taken.

This reconnaissance showed that L. reevii was distributed over large areas with fairly sharp boundaries. There was no obvious pattern of flora or fauna coincident with the distributional pattern of L. reevii. The brachiopods were absent from areas directly affected by stream runoff and sewer outfalls, the mangrove microenvironment, hard rubbly substratum, and very soft sediments. The high densities of Lingula were near the edges of the reef platforms in firm sediments.

Based on the results of the initial survey, quantitative sampling was performed on reef platforms 1,2,3,4,5, and 7 in the spring of 1968 during minus tides. Rectangular sampling areas 0.5 m wide and from 5 to 150 m long were scratched into the sediments along 15 transects. These rectangular sampling transects are represented in Figure 2 as straight dashed lines. The number of burrows of Lingula were counted every

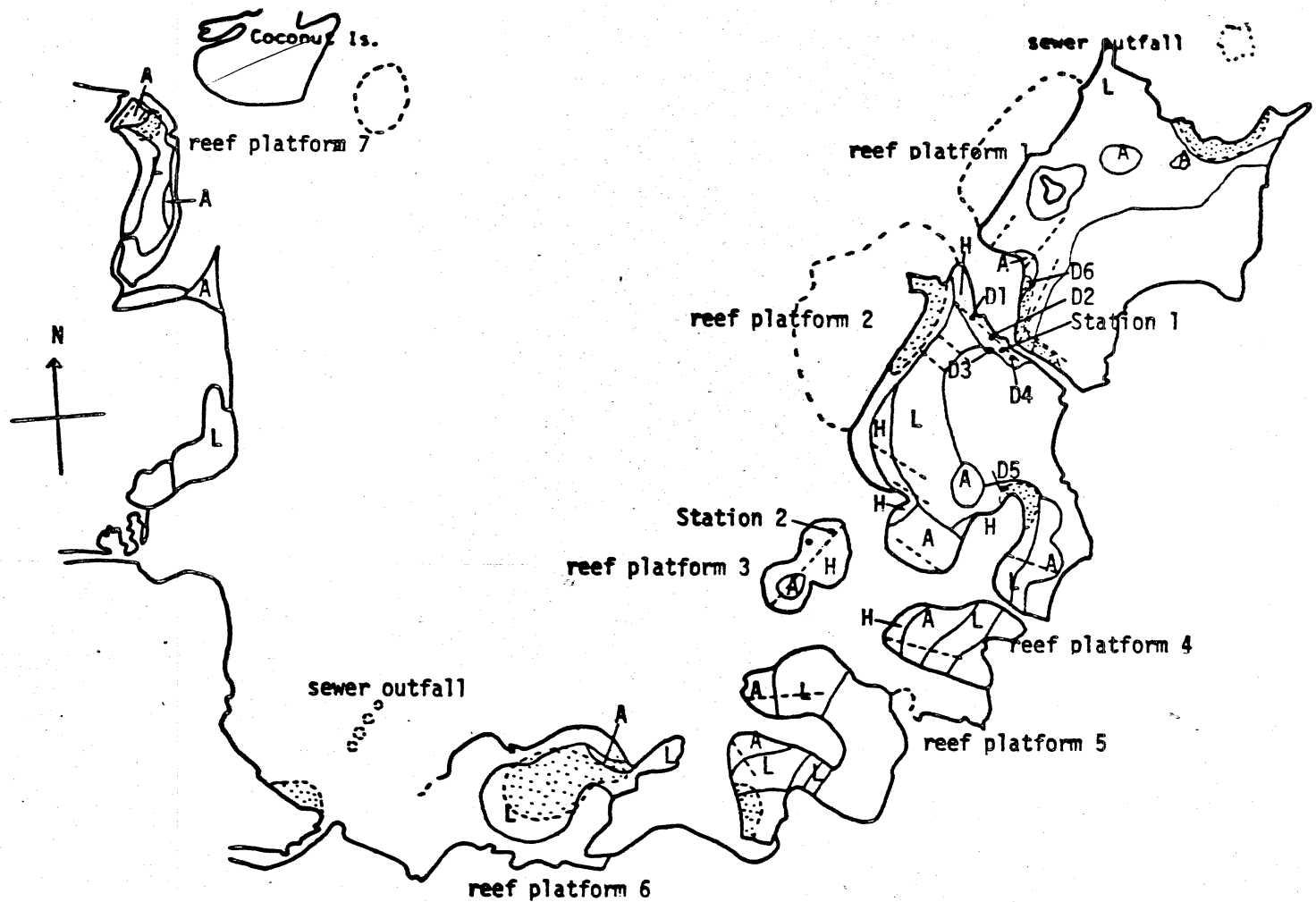


FIGURE 2, OVERLAY. THE APPROXIMATE DENSITIES OF *L. REEVII* IN THE SOUTHERN SECTOR OF KANEOHE BAY; L = 0.2 - 5.0/m²; A = 5.1 - 25.0/m²; AND H = 25.1 - 500/m² (GENERALLY 25.1 - 50/m²). STIPPLED AREAS ARE CLAM BEDS

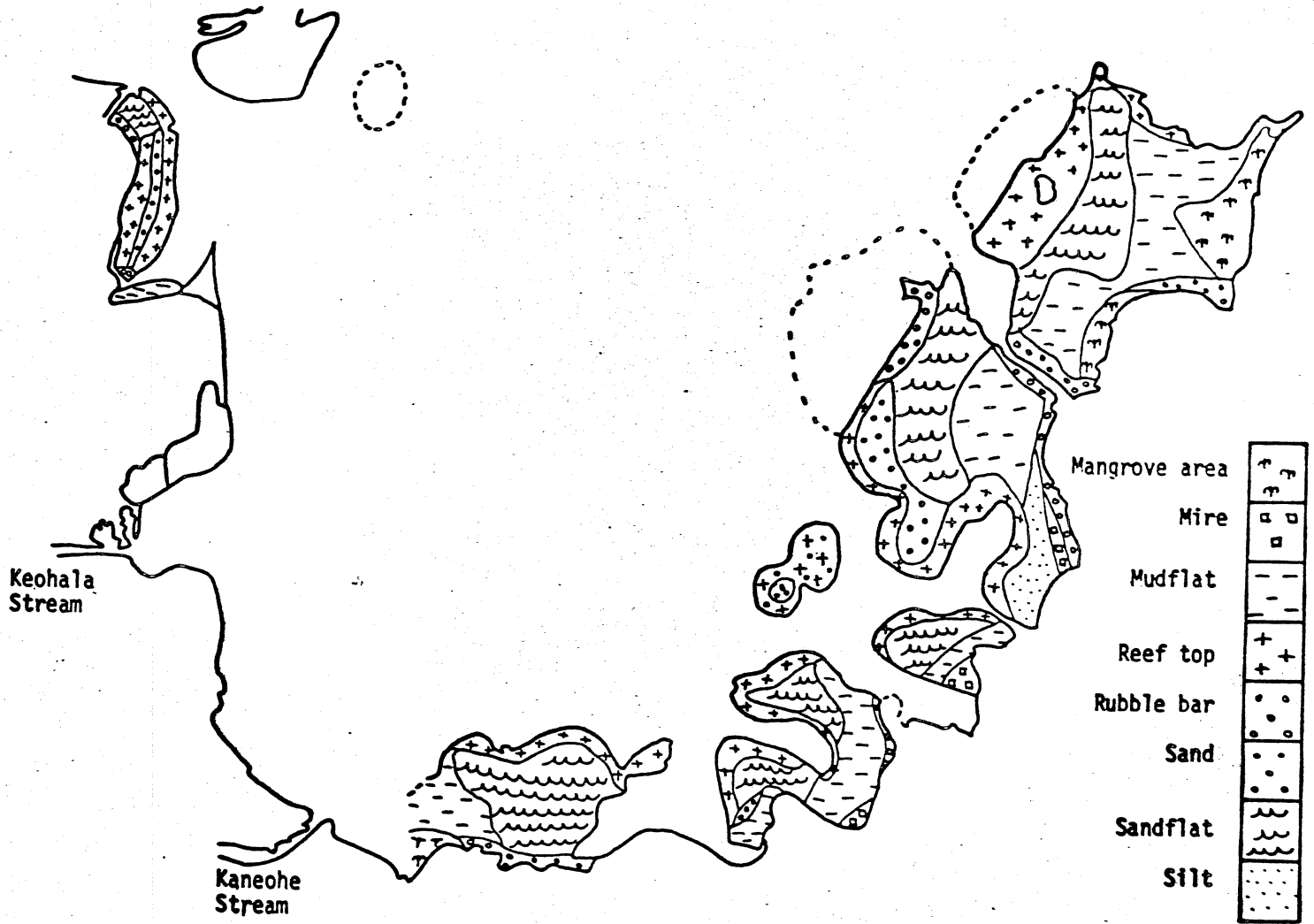


FIGURE 2. THE GENERAL TYPE OF SEDIMENTS. AND THEIR DISTRIBUTION IN SOUTHERN KANEOHE BAY

5 m along the rectangle and recorded. The counts were averaged within the classification categories of the initial survey (low, average, and high density); they are shown in Figure 2 overlay.

Microdistribution and Orientation

It was obvious from the first two surveys that L. reevii was not distributed randomly or uniformly throughout the bay, but rather concentrated near the reef edges. This indicated that environmental conditions such as food, substratum and water activity probably control their large-scale distributional pattern. If the larvae are attracted to settle where Lingula is already present a clumped distribution might be expected on a small scale. If competition occurs it might be expected that this would be reflected in a distribution that tends toward maximum spacing within an aggregation. To investigate these possibilities the nearest-neighbor technique of Clark and Evans (1954) was employed. This analysis gives a numerical index that quantifies the type of spatial distribution.

Two stations were selected for this analysis on the basis of high density and sufficient depth for underwater photography. The distance to nearest neighbor was measured for all L. reevii within a stainless-steel rectangular quadrat (40 x 25 cm). Twenty-five quadrats were placed randomly within a 5 x 5 m area. The position of each brachiopod within each quadrat was marked by placing a

copper staple over the animal parallel with the mouth of the burrow. An underwater compass and an identification plate were included in each quadrat. Photographs of the quadrats were taken underwater at station 2 during high tide. At station 1 the sediments were exposed by a spring tide. The nearest-neighbor measurements were taken from projected transparencies.

The total area covered by each underwater photograph was only slightly greater than the quadrat size, and therefore the nearest neighbor to the animals on the periphery could not be known with certainty. Consequently the nearest neighbor indices were computed on the basis of a 0.05 m^2 area taken from the middle of the larger 0.10 m^2 rectangle. The average distance to nearest neighbor was slightly greater for the entire 0.10 m^2 areas. The area photographed during the minus tide was considerably greater than 0.10 m^2 ; therefore the entire area was used for each quadrat at station 1 to calculate the index.

Regardless of the procedure used or the area surveyed, the averages for the nearest-neighbor calculations do not differ significantly from those expected in a random distribution (see Table I). The nearest-neighbor analysis was run for each individual quadrat, but the data presented in Table 1 are totals for all quadrats within each station. Only two of the 38 quadrats analyzed showed a significant departure from randomness in the direction of clumping. Lingula reevii's distribution does not appear to be influenced

Statistic	Station 2- reef platform 3. Photographs taken underwater of 0.01 m ² rectangular quadrats. Nearest neighbor analysis based on 0.05 m ² areas.	Station 1- reef platform 2. Photographs taken when the area was exposed at low tide. Nearest neighbor analysis based on 0.10 m ² area.
Size of area sampled	25 m ²	25 m ²
Total area sampled	0.70 m ² (**14 samples)	2.4 m ² (**24 samples)
N = number of animals	115	362
$\rho = N-1/\text{cm}^2 = \text{density}$	0.016	0.015
$\bar{r}_A = \text{mean distance to nearest neighbor (cm)}$	4.14 cm	3.92 cm
$\bar{r}_E = \text{expected distance to nearest neighbor from a randomly distributed population of density } \rho \text{ (cm)}$	3.92 cm	3.84 cm
$i = \bar{r}_A / \bar{r}_E = \text{nearest neighbor index All samples}$	1.06	1.02
$t_c = \text{test of significance}$	1.15	0.06

The values of 1.96 and 2.58 respectively the 5% and 1% levels of significance for a two tailed test.

Although 25 quadrats were placed within each station some fell on dead coral heads and the data could not be included.

by the presence or absence of others of the same species. Glottidia pyramidata was found also to have a small scale random distribution when tested with the same nearest-neighbor index by Paine (1963).

The orientation of the burrows of L. reevii was investigated in the field and the laboratory. Since the brachiopod has two lateral feeding siphons and single medial waste orifice, it seemed likely that its most advantageous shell orientation would be perpendicular to prevailing currents. The shell orientation of fossil Lingula then might be indicative of ancient current directions.

Five photographs were taken of the burrows of L. reevii during a minus tide at station 1. The compass direction in degrees of 170 burrows was measured from four of the photographs (each approximately 0.1 m^2) and 102 burrows from a fifth photograph (approximately 0.4 m^2). Since it was not possible to distinguish an animal's dorsal side from its ventral side in the photographs, the angle of orientation was measured through 180° . Orientation angles were grouped into ten-degree sectors and the number in each sector compared to the mean number per sector by the chi-square statistical test. The results, Table II, showed that the orientations did not differ significantly from a random orientation.

In the laboratory, twenty-five brachiopods of various sizes were placed in a long, narrow, sand-filled box (106 x 12 x 24 cm), and allowed to burrow into the substratum. A

TABLE 1, GROUPED BY 10 DEGREE SECTORS

Uncorrected compass direction of the burrows of <u>L. reevii</u> (degrees)	A Total number of burrows in each 10 degree sector for four photos (each approx 0.1 m ²)	B Total number of burrows in each 10 degree sector for a single photo (approx 0.4 m ²)	Total A+B
1-10	12	5	17
11-20	16	8	24
21-30	6	3	9
31-40	7	6	13
41-50	11	1	12
51-60	11	4	15
61-70	9	8	17
71-80	12	7	19
81-90	13	3	16
271-280	8	8	16
281-290	11	11	22
291-300	9	8	17
301-310	5	6	11
311-320	6	6	12
321-330	8	3	11
331-340	9	3	12
341-350	9	7	16
351-360	8	5	13
Total	170	102	272
Mean	9.44	5.66	15.11
Chi-square	14.01	19.38	16.81
P values	0.67	0.31	0.50

current of water flowed through the length of the box. The trajectory of the water appeared quite straight when examined by placing fluorescein dye in the water. The orientation experiment was performed twice. Fifteen and eighteen animals, in the first and second experiment respectively, had established themselves in the sand at the end of three days. Those remaining at the surface were removed. The box was light-tight except while checking orientation. After 14 days the orientation of the animals was measured with a hand compass. As in the field experiment the animals were grouped in ten degree sectors and the mean number per sector was compared with the observed number per sector and tested by chi-square. The probability that orientation was random was 0.25 for the first experiment and 0.30 for the second. It is concluded that they did not orient to the current.

Relation to Sediment Stability

In the laboratory, 19 L. reevii (2.5 - 3.0 cm in length) were covered with sandy sediments 6 and 15 cm deep. The minimum rates of upward movement through the sediment ranged from 5.0 to 60.0 cm/day. The mean rate per animal was 18.2 cm/day. Paine (1963) found that G. pyramidata, under identical conditions, burrowed upward at 5 - 15 cm/day.

To determine upward burrowing rates in the field, sediment-filled chambers (35 x 30 x 30 cm) were placed over dense concentrations of Lingula at field stations 1 and 2.

At each station two chambers were placed over brachiopods. One chamber was filled with 15 cm of sediments and the other with 30 cm. When the brachiopods appeared at the surface they were removed and counted. The mean minimum rates of upward burrowing were 4.5 cm/day in the 15 cm chambers and 7.1 cm/day in the 30 cm chambers (Table III).

A difference in the condition of the brachiopods was associated with the depth of burial and type of sediments in which they lived. At station 2 the brachiopods generally attach to coral rubble about 25 cm below the surface. In order to reach the surface, when buried with the additional sediments, they had to break the lower portion of their pedicles. At station 1 there was at least 30 cm of sand and the brachiopods were not attached to large particles; therefore it was not necessary for them to break their pedicles to reach the surface. Those buried by 30 cm of sediment at both stations were in poor condition when removed; many were without setae, the anterior portion on their shells were chipped and broken, and 5 were dead. Those that burrowed through 15 cm were in good condition, except for one which was dead when collected.

Apparently only small Lingula reevii can re-establish themselves if removed from the substratum. In an aquarium 27 L. reevii ranging from 0.7 to 3.8 cm in shell length were placed on a sandy sediment. Within 5 days, seven animals, all less than 1.7 cm, had established themselves in vertical burrows; while the remainder, 2.0 to 3.8 cm

TABLE III. RESULTS OF ALL EXPERIMENTS ON THE UPWARD BURROWING OF L. REEVII AFTER BURIAL BY SEDIMENTS. L = LABORATORY DATA, F1 = FIELD DATA AT STATION 1, AND F2 = FIELD DATA AT STATION 2

Experiment number	Estimated number of animals buried	Depth of burial (cm)	Minimum rate of burrowing (cm/day)	% of population established at the surface
1,L	6	6	8.9	100.0
2,L	4	15	22.6	75.0
2,L	4	15	15.2	25.0
3,L	9	15	60.0	33.3
3,L	9	15	5.0	66.6
4,F1	23	15	7.5	30.4
4,F1	23	15	5.0	4.3
4,F1	23	15	3.7	39.1
4,F1	23	15	1.0	26.2
5,F1	20	30	15.0	5.0
5,F1	20	30	10.0	10.0
5,F1	20	30	7.5	5.0
5,F1	20	30	5.0	5.0
5,F1	20	30	vandalised	75.0
6,F2	37	15	7.5	43.0
6,F2	37	15	3.7	2.5
6,F2	37	15	2.1	37.9
6,F2	37	15	1.7	5.3
6,F2	37	15	1.1	2.5
6,F2	37	15	*	6.8
7,F2	23	30	15.0	4.3
7,F2	23	30	7.5	52.2
7,F2	23	30	4.3	26.1
7,F2	23	30	*	17.4

* = the animals did not come to the surface

mean rate/day in the laboratory = 18.2 cm/day

mean rate/day in the field = 4.7 cm/day

mean rate/day in the field (30 cm) = 7.1 cm/day

long, did not burrow into the sediments. Morse (1902) and Paine (1963) found that Glottidia pyramidata could re-establish a burrow if removed from the sediments.

Salinity

L. reevii's tolerance to salinity changes was investigated in the laboratory. Ten one-gallon jars were filled with 3,500 ml of water and ten Lingula reevii were added to each jar. The salinities of the water varied from 0 to 35‰. The water was continuously aerated, and it was changed when it became cloudy or had a foul odor. The animals were not fed during the experiment. The time of death was noted for each brachiopod. Table IV lists the results of these experiments. Salinities less than 10‰ immediately caused the animals muscles and internal organs to swell. The tissues, primarily muscle, extruded from the posterior portion between the shells, and the animal soon died. The cause of death at the intermediate salinities (16 to 20‰) was not known, and the exact time of death was uncertain. These uncertainties are indicated in Table IV as question marks. At the intermediate salinities (16 to 20‰) some of the animals were hardier than others. Eighteen parts per thousand seemed to be the minimum salinity necessary for the long term survival. Death due to starvation was probably not a critical factor, because at the higher salinities (greater than 30‰) all the animals survived until the experiment was terminated. Paine (1963) found that

TABLE IV. THE SALINITY TOLERANCES OF L. REEVII IN THE LABORATORY. THE NUMBER CORRESPONDING TO A PARTICULAR TIME AND SALINITY IS THE NUMBER OF BRACHIOPODS STILL ALIVE (OUT OF 10 POSSIBLE) AT THE BEGINNING OF THAT TIME PERIOD

Date	Time	Salinity									
		0‰	5‰	10‰	13‰	16‰	18‰	20‰	24‰	30‰	35‰
6/18/68	0	10	10	10	10	10	10	10	10	10	10
6/19/68	15.5 hrs.	-	-	?	?	10	10	10	10	10	10
6/20/68	36.0 hrs.	10*	10*	?	?	10	10	10	10	10	10
6/20/68	2 days	-	-	?	?	10	10	10	10	10	10
6/21/68	3 days	-	-	-	?	4	6	10	10	10	10
6/22/68	4 days	-	-	-	-	4	6	10	10	10	10
6/25/68	7 days	-	-	-	-	3	5	10	10	10	10
6/27/68	9 days	-	-	-	-	2	4	9	10	10	10
6/28/68	10 days	-	-	-	-	1	3	9	10	10	10
7/ 3/68	15 days	-	-	-	-	?	2	9	10	10	10
7/ 5/68	17 days	-	-	-	-	-	2	8	10	10	10
7/13/68	25 days	-	-	-	-	-	1	8	9	10	10
9/ 6/68	80 days	-	-	-	-	-	1	8	9	10	10

*Experiment repeated with salinities of 0 and 5‰; all animals died within 12 hours.

the critical salinity level for Glottidia pyramidata was between 13 and 18‰.

Feeding

All brachiopods are filter or suspension feeders that apparently ingest a wide variety of food. The most common identifiable organisms in the gut of freshly collected specimens were diatoms of several types, both with and without chloroplasts. Occasionally armored dinoflagellates, spore cases, spermatozoa (not of L. reevii), and crustacean appendages were present. Bacteria were also present. Most of the matter was unidentifiable detritus. Hyman (1959) notes the following in the gut of Lingula sp.: diatoms, dinoflagellates, foraminiferans, radiolarians, mollusc larvae, small crustaceans, sponge spicules, annelid setae, calcareous rods of plutei, vegetable matter, mud and sand. Food selection is probably determined mainly by the size of the food. Paine (1963) found that Glottidia pyramidata (smaller than Lingula) would not accept food particles larger than 125 microns.

Day and night observations in both the field and the laboratory showed that unless disturbed, or under extreme environmental conditions (e.g., salinities below 13‰), L. reevii filter continuously. However, they can survive prolonged starvation. At salinities between 30 and 35‰ twenty animals lived for 80 days without food and all appeared to be healthy. Paine (1963) found that G.

pyramidata survived for 3 months without food.

Predators

Early workers have not reported natural predators of Lingula, but man is known to eat them occasionally (Yatsu, 1902; Banfield, 1918). Paine (1963) noted that G. pyramidata is sometimes eaten by birds. In Kaneohe Bay portunid crabs were seen eating living L. reevii on seven separate occasions: Thalamita arenata (5 times), Calappa calappa (once), and Portunus sanguinolentus (once). T. arenata is commonly found under dead coral heads, but it also burrows in sand. The remains of pelecypods, crabs, and Lingula are almost always found along with Thalamita under the coral heads, where brachiopods are frequently found still alive and partially eaten. Thalamita arenata appears to be the major predator on Lingula reevii in Kaneohe Bay. Calappa calappa is numerous in the sandy areas where Lingula is found and may be an important predator. This crab eats while burrowed and spends most of its time buried in the sand. Therefore its predatory effect is difficult to evaluate. Portunus sanguinolentus was only seen twice in the Lingula beds and is thought to be important as a predator.

Regeneration scars on the valves of living Lingula indicated extensive damage from predators. Forty-seven percent of 782 live animals collected at station 1 had scarred shells. Station 1 is well protected from storm damage so the scars were probably caused by predators. Most of the scarred animals were large, 94% had shells longer

than 2.5 cm and 75% had shells longer than 3.0 cm. The size-frequency distribution of all the brachiopods in this collection shows only 62% of the animals with shells longer than 2.5 and 31% had shells longer than 3.0 cm. Larger animals may be the most frequently scarred because older animals are subject to attack over a longer period, or they may be more able to survive attacks.

Collections of the shells of dead Lingula reevii also indicate extensive predation. Of the 182 shells collected in and around station 1, only one was undamaged, and many were badly mutilated. Most shells were not in good enough condition to measure length, therefore widths were measured and converted to length by the equation: length (cm) = width x 2.29 (cm) + 0.015 (cm). This equation was the result of a least squares linear regression on the shell dimensions of 406 living L. reevii at station 1. As in the instance of the injured live animals the majority of the damaged shells were large, 96% were longer than 2.5 cm and 77% longer than 3.00 cm. These mutilated shells are not necessarily indicators of predation; some could result from scavengers.

In the deep waters (greater than 10 meters) of the southern sector of Kaneohe Bay, the brachiopod was not found. Sixty bottom samples with a Van Veen grab and three dives using SCUBA revealed no evidence of L. reevii. The sediment was extremely soft, and it was difficult to distinguish between the water column and the bottom while

diving. It seemed unlikely that Lingula could live in such soft sediments since it could not firmly attach and they could be easily dug out by predators.

To evaluate predation in this deep environment sand-filled boxes were placed at stations B1, B2, and B3. Each box contained 20 L. reevii deeply burrowed; 10 of the brachiopods were unprotected and 10 protected by $\frac{1}{2}$ inch wire mesh. After two weeks all those that had been protected were alive, had food in their stomachs, and well formed fecal pellets in their intestines. Within one day all the unprotected brachiopods at station B3 were gone, 8 were missing at B2 and 4 at B1. These results (Table V) suggest that predation is severe in the deeper waters of Kaneohe Bay and would limit the distribution of Lingula whether or not the soft substratum is suitable. Similar experiments were performed at stations 1, 2, and B4 in shallow water, but there was little evidence of extensive predation (Table V).

In the laboratory, the crabs Thalamita arenata (carapace width 10.0 - 12.0 cm) and Calappa calappa (carapace width 6.3 - 6.7 cm) were observed to prey upon L. reevii. The crabs were well fed adults that had been collected on reef 2. The brachiopods used in these experiments ranged from 2.5 to 3.0 cm in shell length. Predation rates (number of L. reevii eaten/crab day) in this artificial situation ranged from 0.29 to 2.14 (mean 1.04) when the brachiopods were buried in sediments and as high as 6.87 (range 4.00 to 6.87; mean 5.20) when the brachiopods were without the protective sediments.

TABLE V. RESULTS OF SURVIVAL-PREDATION EXPERIMENTS IN THE FIELD. TWENTY ANIMALS PER CONTAINER, 10 PROTECTED (P) AND 10 UNPROTECTED (Unp). STATIONS B1, B2, AND B3 WERE IN APPROX. 12 m OF WATER, AND STATIONS 1, 2, AND B4 WERE ON SHALLOW REEF PLATFORMS IN ABOUT 0.5 m

Exposure time in days	Station B1 (deep)		Station B2 (deep)		Station 1 (shallow)		Station 2 (shallow)	
	P	Unp	P	Unp	P	Unp	P	Unp
0	10	10	10	10	10	10	10	10
2	10	6	10	9	10	?	10	10
5	10	5	10	9	10	8	10	10
8	10	4	10	8	10	7	10	10
12	10	4	10	0	10	6	10	10

	Station B2 (deep)		Station B3 (deep)	
	P	Unp	P	Unp
0	10	10	10	10
1	10	2	10	0
5	10	0	10	0
15	10	0	9	0

	Station B4 (shallow)		Station B4 (replicate sample) (shallow)	
	U	Unp	U	Unp
0	10	10	10	10
3	10	10	10	10
7	10	10	10	10
12	10	10	10	10
14	10	8	10	10

? = unable to get an accurate count

In this latter situation the estimated rates are not ecologically significant because the crabs often killed but did not eat the brachiopods. In some of these predator-prey experiments in which sediments were not used, the clam Tapes philippinarum (2.5 to 3.0 cm in diameter) was introduced. The larger crabs preyed upon both animals with nearly equal efficiency, while smaller crabs had a definite preference for the brachiopods.

I observed the capture and subsequent consumption of L. reevii by the box crab, Calappa calappa, in an aquarium. The crab walked about the surface of the sediment until its anterior appendages touched the burrow of the brachiopod. It then burrowed backward at about a 45 degree angle into the sandy sediment until its head was directly over the brachiopod. It then grasped the shell of L. reevii below the surface of the sand with one of its chelipeds and with the other clipped pieces off the shell until the visceral mass of the brachiopod was well exposed. The crab then ate the soft body parts with its feeding appendages. This entire capture and feeding process took 25 minutes. The clipping of the brachiopod shell by C. calappa suggests that this is one important source of the regeneration scars on live brachiopods, and for the mutilated condition of dead shells.

Commensals

Numerous types of commensal organisms were found on the

shells of L. reevii in Kaneohe Bay. The following macro-organisms were noted from approximately 5,000 shells: algae ten times, 14 anemones (Aptasia sp.), many bryozoan colonies, 2 polychaete worms, numerous limpets, 6 barnacles, and 1 amphipod.

Only the limpets occurred often enough to consider further. The cup and saucer limpet (Crucibulum spinosum) was present 182 times in a sample of 1,117 from reef platform 3, and rarely on the brachiopods from the other reefs. The limpets ranged from 2 to 15 mm in diameter. Apparently the attachment sites are relatively permanent; the outline of the limpet shell could be seen when it was removed from the brachiopod's shell. In five instances, egg masses were found attached to the shell of Lingula when the limpet was removed.

Interaction with Clams

The abundance of Lingula reevii may be affected by humans in areas where the clam Tapes philippinarum is numerous. On 24 November 1967, prior to clam season, visual counts of L. reevii were made in six 25 m² areas (stations D1, D2, D3, D4, D5, and D6; see Figure 2) where both the clam and the brachiopod were present. The same areas were resurveyed on 6 February 1968. Two of these areas (D5 and D6) were heavily clammed during the season (1 December 1967 to 31 January 1968); the other four areas were not disturbed. Useful observations were not possible during the clam season because the water was extremely muddy from clamming.

During the pre-season observations the waters were

cloudy and the weather poor, so counts and estimates were minimal. Observational conditions were excellent for the post-season series. The post-season densities were higher in the unclammed control areas (Table VI), and the densities in the clammed areas were lower even though sampling conditions were better. This indicates that substantial mortality was caused by the clam diggers, by mutilating the brachiopod, during digging or by leaving them at the surface to be eaten by crabs. During the clam season specimens of L. reevii were shown to a number of clam diggers and most said that they had seen one or more while digging clams.

The question of competition between L. reevii and the clam Tapes philippinarum can be resolved by examining the environmental conditions in which the population of these two species exist in Kaneohe Bay. They have similar food habits and salinity tolerances; they both live primarily on shallow reef platforms, and the major predators for both groups are portunid crabs (Higgins, 1969). They differ in the types of distribution; the clams occur in relatively small high density patches, while the brachiopods occur over large areas (Figure 2). The densest populations of clams occur in sediments composed of considerable amounts of large particles (coral rubble, shells and pebbles) that are near the surface; the brachiopods live primarily in sediments composed of sand-sized particles. The depth to which the animals burrow, a few centimeters (less than 7 cm, Higgins,

TABLE VI. THE DENSITY OF LINGULA REEVII BEFORE AND AFTER CLAM SEASON. AREAS D1, D2, D3, and D4 WERE NOT CLAMMED AND AREAS D5 AND D6 WERE CLAMMED

Station number	Mean density prior to clam season (number/m ²)	Mean density after clam season (number/m ²)
D1	120.4	126.8
D2	49.6	90.0
D3	29.2	101.2
D4	10.0	64.8
D5	95.2	78.0
D6	11.6	4.0

1969) for T. philippinarum and 25 - 30 cm for L. reevii, suggests that predators largely determine their pattern of distribution. In areas of rubble substratum Lingula would have difficulty establishing a burrow, whereas a Tapes would find protection in the large particles from predatory burrowing crabs. In the sandy-type sediments the clams could easily be dug out by crabs. The brachiopods can withdraw deeply into this type of sediment, and it would take considerable time and energy for a crab to capture it. The habitats of these two animals overlap only slightly, but their respective niches appear to be separated by the interaction of predation, substratum type and burrowing depth.

Sex Ratio, Reproduction and Larvae

The sex of an individual L. reevii is easily determined by dissection; males have white, fine-grained gonads, and females have coarse gonads with a tan to yellow color.

All animals greater than 1.90 cm in shell length, that were sexed, had well developed gonads and were sexually mature. The estimated age of Lingula at 1.90 cm is about 1.7 years (see Figure 6).

The sex ratio for Lingula reevii in Kaneohe Bay is 1:1. Of the 509 postlarval animals from station 3 which were sexed, 256 were female and 253, male. This same sex ratio is found in other brachiopods, Glottidia pyramidata (Paine, 1963), Terebratulina septentrionalis (Cloud, 1948) and

Terebratella transversa (Percival, 1944).

I found no secondary sex characteristics of L. reevii that could be used to distinguish between the sexes. The sexes are most likely the same size. Of 265 females and 263 males collected on reef platform 3, the mean shell lengths were 3.30 and 3.32 cm respectively. This difference in mean size was not statistically significant ($p < 0.001$) when tested by the t test.

Lingula reproduce by releasing gametes into the surrounding water; the eggs and sperm unite to form free swimming, non-feeding larvae that remain in the plankton from 2 to 4 weeks (Paine, 1963). Fecundity is variable, but Chuang (1959) found that some females released up to 3,000 eggs per day at Singapore Island. He found that all females greater than 2.20 cm in shell length released viable eggs and that breeding took place throughout the year. Yatsu (1902), in Japan, found that the breeding was seasonal, with peaks in the spring and late fall. Lingula follows the normal pattern of reproduction with year around spawning in low latitudes and seasonal spawning in the higher latitudes (Dunbar, 1960). There is also evidence that the spawning of L. unguis in the tropics is correlated with the lunar cycle (Chuang, 1959).

Data on the occurrence of larvae of L. reevii in the plankton of the southern sector of Kaneohe Bay were obtained from Mr. William T. Peterson (personal communication). He found the larvae present in 33 of 81 plankton samples taken

from December, 1966 to December, 1967. There were no samples taken in March and September. The larvae were found in all months sampled except for January and April. The highest concentrations (greater than or equal to $1.0/m^3$) were found in December, 1966, May and November, 1967, and lower values (less than or equal to $0.5/m^3$) were found in the remaining months. From Peterson's data it is deduced that L. reevii spawns the year around in Kaneohe Bay.

Growth and Age Structure

Growth of postlarval Lingula reevii was investigated by: in situ notching of shells, recovery of notched animals transplanted to various environmental conditions in the bay, and following individual growth in the laboratory.

The best growth data were obtained by notching the shells of the brachiopod in situ at station 1. A 5 x 5 m plot was staked off on 9 September 1967 and v-shaped notch, 2 mm deep was removed from the anterior margin of the shells and mantle of 182 brachiopods with a modified pig ear-notcher. The procedure was performed during high tide using SCUBA. The animals were not removed from the sediment, but grasped with one hand, the sand scraped away to expose the anterior end and then the notch taken from the animal. The burrows were covered with sand. Two hundred and seventy four days later (4 June 1968) all brachiopods in the plot (1,079) were removed, of these 69 had distinguishable notches. The size of the shells, at the time of notching, of the animals

that survived until removal, ranged from 0.71 to 3.58 cm. The growth of each animal for this period was the distance from the top of the notch scar to the top of the new shell material. A plot of the change in length as a function of the initial length is plotted in Figure 3, a least-square linear regression was run on the data. The resulting equation was: $\text{change in length}/274 \text{ days} = -0.445 \times \text{initial length} + 1.603$. A high negative correlation coefficient ($r = -0.88$) was obtained.

L. reevii collected from station 1 were transplanted to various environmental situations in the bay at stations T1 to T7 (see Figure 1). Station T1 is across from the Marine Corp Air Station sewer outfall, T2 is among the mangroves, T3 is near where the brachiopods were collected, T4 is in a dense population of Lingula, T5 is near Kaneohe Stream and the Kaneohe sewer outfall, T6 is in relatively deep water (approximately 4 meters) with a sand substratum, and T7 in waters of oceanic character. There were low population densities of L. reevii already present at stations T1 and T6 and none at T2, T5, and T7. Approximately 75 brachiopods were placed in 1 m² areas at each station. Each individual was notched as described in the previous experiment, then buried in the sediment. The brachiopods at station T2, T4, T5, T6, and T7 were transplanted on 22 January 1968 and the survivors removed 150 days later on 21 June 1968; those at stations T1 and T3 were put out 24 March 1968 and removed 130 days later on 1 August 1968. The number of animals was

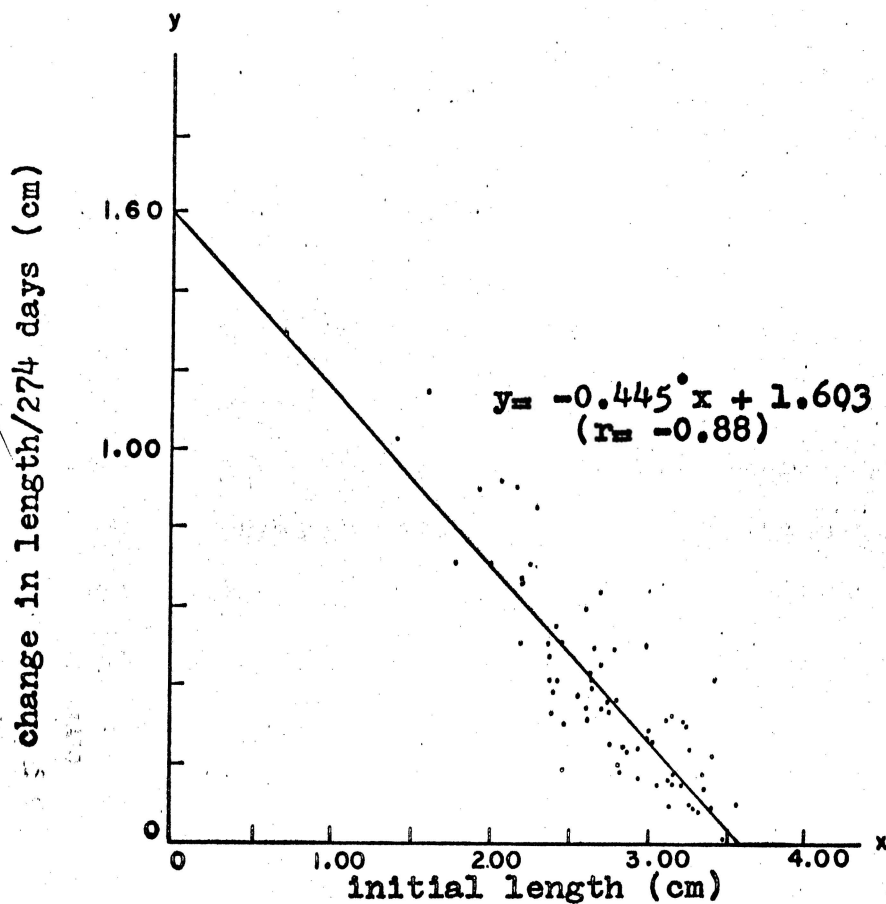


FIGURE 3. GROWTH OF THE SHELLS OF 69 L. REEVII.
DATA FROM IN SITU NOTCHING AT STATION 1

reduced greatly (probably due to crab predation and low salinities) during the growth periods. The number recovered per number transplanted for each station was: T1 - 6/80, T2 - 0/75, T3 - 7/80, T4 - 19/75, and T7 - 14/80. With the exception of 4 brachiopods recovered at T4 the animals that survived were relatively large (greater than 1.63 cm in length at the time of notching) and consequently the growth data obtained is of limited value. Figures 4 and 5 graphically illustrate the results of these experiments. Although inconclusive, the results suggest that the growth rates in the plankton-rich bay are much greater than in the relatively clear oceanic waters found at station T7.

Chuang (1961) using the notch-recovery method, found similar growth for Lingula unguis in Singapore. Its maximum shell length (5.2 cm) is larger than Lingula reevii's (4.2 cm); and L. unguis grew slightly faster. Both species showed decreasing growth rates with increasing shell length. Lingula unguis fastest growth was in areas where sediments were high in organic materials and the water high in nutrients.

Twenty-eight small L. unguis (1.00 to 2.27 cm in shell length) were measured and placed in sand in an aquarium equipped with running water piped from the bay. Their positions were marked by a grid. The experiment began 13 February 1968, and every 33 or 66 days thereafter the animals were removed, remeasured and replaced. Total growth time was 198 days. The smallest animal died between the third and fourth growth period. The shell length of another animal

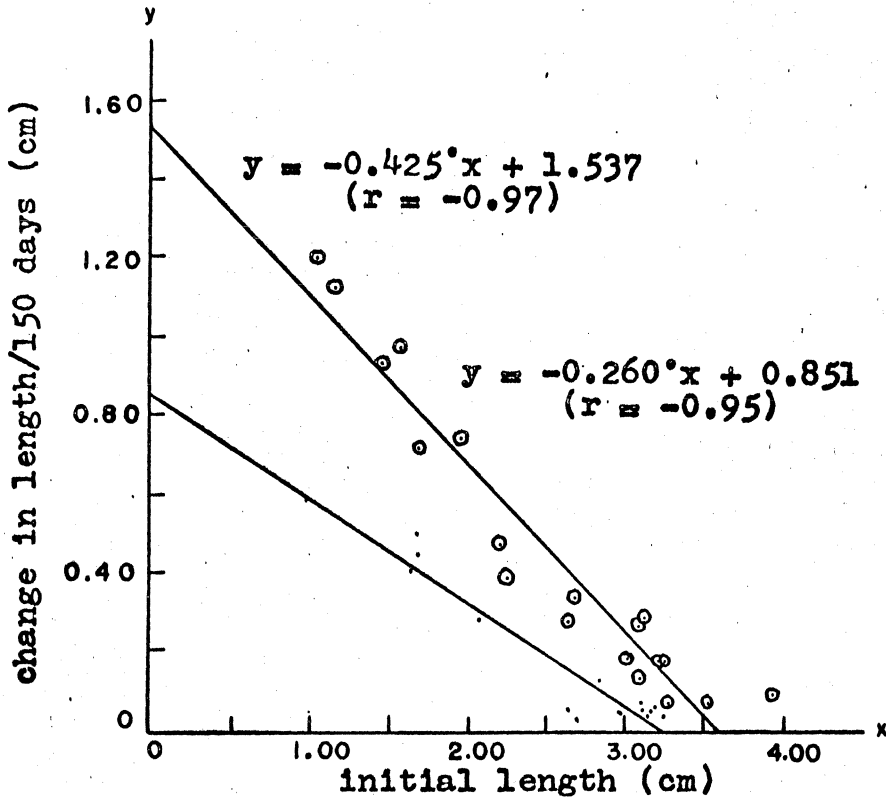


FIGURE 4. GROWTH OF TRANSPLANTED L. REEVII AT STATIONS T4 (○) AND T7 (•).

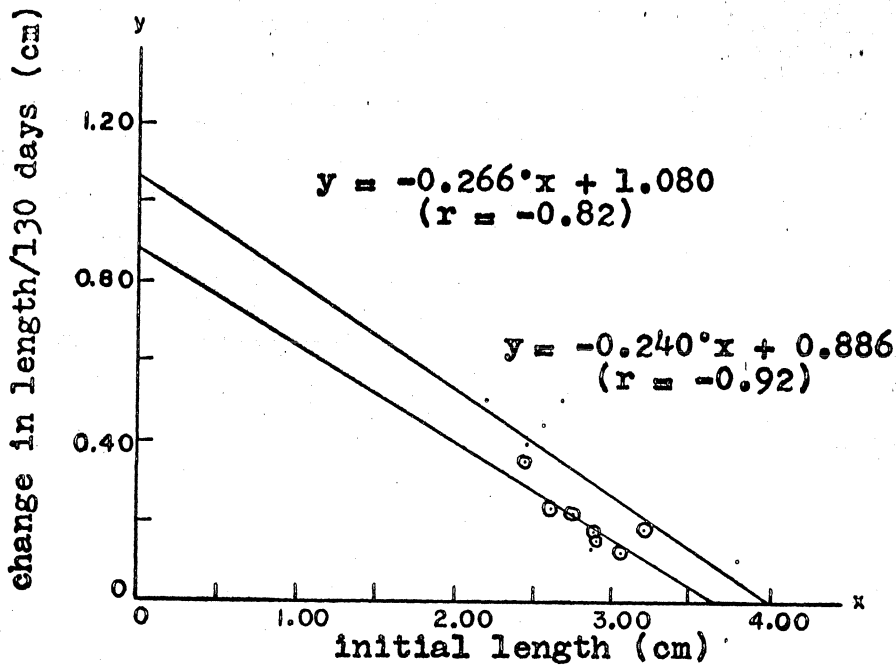


FIGURE 5. GROWTH OF TRANSPLANTED L. REEVII AT STATIONS T1 (•) AND T3 (○).

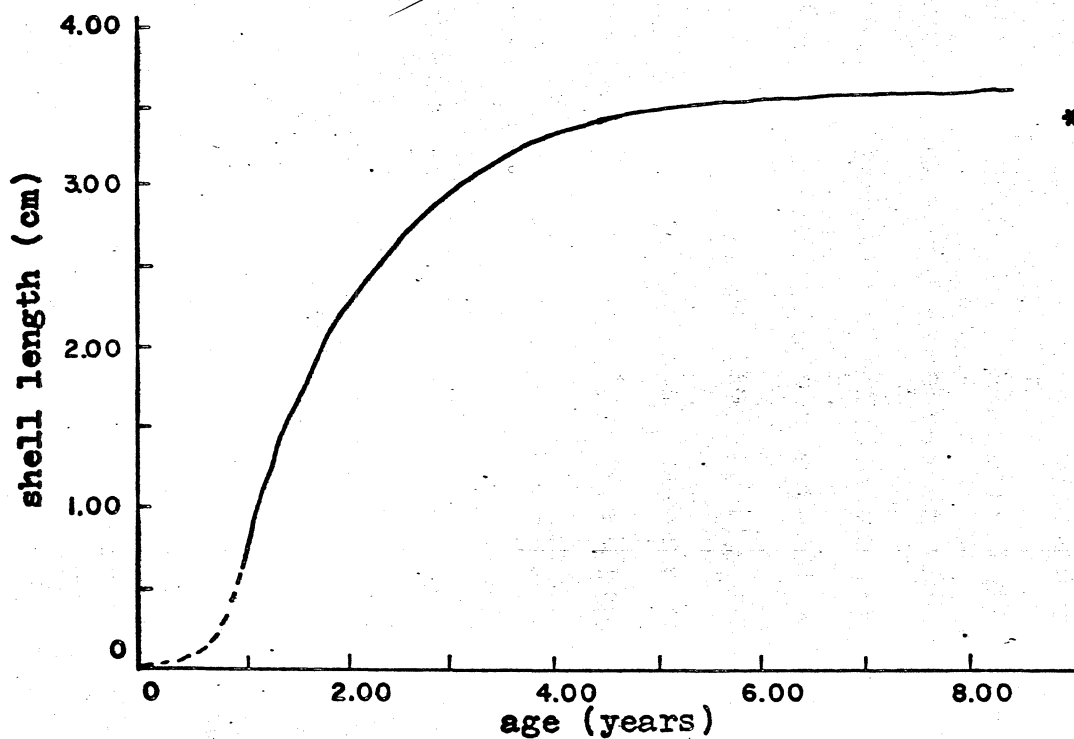
was unavailable for the first growth period.

The data were irregular and confusing. The growth rates varied considerably between the periods; the first and last periods had the lowest rates, and the highest rates were in the middle periods (Table VII). The low growth rates during the first period might be explained as the result of the disturbance caused by being moved from the field to the laboratory situation. It is likely that the quality and quantity of food in the water supply varied and had a significant effect on growth. Because of the large variabilities in growth this experimental situation is of little value in determining a meaningful growth rate of L. reevii. Each animal between 1.00 and 1.46 cm in shell length grew about 0.5 cm for the entire growth period of 198 days (Table VII). This seems to be in opposition to the field data, where growth decreased linearly with increasing size (Figures 3, 4 and 5).

Little is known about the age structure and longevity of the genus Lingula. Estimates of longevity ranges from 1 year (Francois, 1891) to 12 years (Chuang, 1961). I have been able to construct an age-length curve based on the growth data obtained from the in situ notching of L. reevii at station 1 (Figure 6). The observed linear decrease in growth with increasing size could be represented by the von Bertalanffy growth curve if ages and corresponding sizes were known. But at present there is no method of directly aging these brachiopods. Therefore my growth curve was

GROWTH OF 20 *L. REEVEI* IN AN AQUARIUM. GROWTH MEASURED EVERY
 33 DAYS, EXCEPT FOR THE LAST PERIOD WHICH WAS 66 DAYS.
 TOTAL GROWTH PERIOD WAS 198 DAYS.

Animal number	First growth period length (cm)	2nd growth period 33 days (cm)	(cm)	3rd growth period 66 days (cm)	(cm)	4th growth period 99 days (cm)	(cm)	5th growth period 132 days (cm)	(cm)	6th growth period 198 days (cm)	(cm)	Total length increase 198 days (cm)
1	1.00	1.00	0.00	1.10	0.10	1.36	0.26	died	-	-	-	-
2	1.00	1.06	0.06	1.20	0.14	1.39	0.19	1.48	0.09	1.54	0.06	0.54
3	1.03	1.08	0.05	1.24	0.16	1.39	0.15	1.48	0.09	1.56	0.08	0.53
4	1.08	1.09	0.01	1.25	0.16	1.42	0.17	1.52	0.10	1.58	0.06	0.50
5	1.09	1.11	0.02	1.25	0.14	1.43	0.18	1.54	0.11	1.58	0.04	0.49
6	1.09	1.13	0.04	1.28	0.15	1.49	0.19	1.57	0.08	1.63	0.06	0.54
7	1.09	1.18	0.09	1.28	0.10	1.49	0.21	1.57	0.08	1.64	0.07	0.55
8	1.14	1.18	0.04	1.30	0.12	1.50	0.20	1.58	0.08	1.65	0.07	0.51
9	1.15	1.20	0.05	1.33	0.13	1.50	0.17	1.59	0.09	1.65	0.06	0.50
10	1.17	1.24	0.07	1.33	0.09	1.52	0.19	1.62	0.10	1.65	0.03	0.48
11	1.19	1.25	0.06	1.36	0.11	1.54	0.21	1.67	0.13	1.67	0.00	0.48
12	1.20	1.26	0.06	1.37	0.11	1.54	0.17	1.63	0.09	1.70	0.07	0.50
13	1.20	1.29	0.09	1.47	0.18	1.55	0.08	1.63	0.08	1.70	0.07	0.50
14	1.20	1.29	0.09	1.47	0.18	1.55	0.08	1.72	0.17	1.72	0.00	0.52
15	1.24	1.31	0.07	1.49	0.18	1.65	0.16	1.72	0.07	1.76	0.04	0.52
16	1.28	1.32	0.04	1.49	0.17	1.66	0.17	1.73	0.07	1.78	0.05	0.50
17	1.30	1.35	0.05	1.49	0.14	1.67	0.18	1.80	0.13	1.85	0.05	0.55
18	?	1.37	-	1.51	0.14	1.69	0.18	1.80	0.11	1.87	0.07	-
19	1.37	1.41	0.04	1.56	0.15	1.69	0.13	1.82	0.13	1.87	0.05	0.50
20	1.40	1.50	0.10	1.58	0.08	1.75	0.17	1.84	0.09	1.89	0.05	0.49
21	1.42	1.50	0.08	1.63	0.13	1.78	0.15	1.87	0.09	1.90	0.03	0.47
22	1.46	1.54	0.08	1.64	0.10	1.79	0.15	1.87	0.08	1.92	0.05	0.46
23	1.58	1.59	0.01	1.65	0.06	1.80	0.15	1.89	0.09	1.95	0.06	0.37
24	1.58	1.64	0.06	1.79	0.15	1.92	0.13	1.97	0.05	1.98	0.01	0.40
25	1.81	1.88	0.07	1.94	0.06	2.06	0.12	2.09	0.03	2.09	0.00	0.28
26	1.85	1.90	0.05	1.98	0.08	2.08	0.10	2.12	0.04	2.17	0.05	0.32
27	1.96	2.00	0.04	2.08	0.08	2.23	0.15	2.29	0.06	2.26	-0.03	0.30
28	2.27	2.36	0.09	2.37	0.01	2.47	0.10	2.49	0.02	2.56	0.07	0.29
mean	1.339	1.394	0.559	1.515	0.121	1.675	0.160	1.774	0.087	1.819	0.045	0.465
std. dev.	0.320	0.320	0.027	0.294	0.042	0.270	0.041	0.249	0.032	0.239	0.027	0.083
variance	0.102	0.102	0.001	0.087	0.002	0.073	0.002	0.062	0.001	0.057	0.001	0.007



age (years)	length (cm)	change in length for 274 days
0.00	0.00	?
*1.00	0.71	1.29
1.75	2.00	0.71
2.50	2.71	0.40
3.25	3.11	0.22
4.00	3.33	0.12
4.75	3.45	0.07
5.50	3.52	0.04
6.25	3.56	0.02
7.00	3.58	0.01
7.75	3.59	0.01
8.50	3.60	0.00

*estimate based on Yatsu's data (1902).

FIGURE 6. AGE-LENGTH CURVE OF L. REEVII BASED ON GROWTH DATA OBTAINED AT STATION 1. DOTTED LINE IS HYPOTHETICAL. THE SOLID LINE COULD BE SHIFTED EITHER RIGHT OR LEFT DEPENDING ON A BETTER ESTIMATE OF AGE AT SIZE (0.71 cm).

constructed using the growth data and inferring age from it. The method used was as follows: the change in length during the growth period (274 days) of the smallest animal (0.71 cm) was calculated from the linear regression equation (change in length/274 days = $-0.445 \times \text{initial length} + 1.603$ cm). The calculated change in length (1.29 cm) was added to the original length (0.71 cm), and this new length (2.00 cm) then represents the estimated size of the original animal after 274 days. This same procedure was used on the new length to calculate its size at the end of the next growth period and so on until the change in length approached zero. It was difficult to determine the amount of time from fertilization to the length of the smallest animals in my growth study (0.71 cm). An estimate of one year is used based on the data of Yatsu (1902), who found that in Japan Lingula anatina spawned once a year and the smallest found the next year were 0.5 cm in shell length.

Fossilization

Paleontologists rely heavily on Lingula as an indicator of the near shore environment (Allen, 1936; Schuchert, 1911). Recent literature and data from this study suggests that caution is in order. Storm waves displace great numbers of Lingula sp. to beaches. Fenton (1966) reports piles of Lingula 12 to 30 inches high along miles of beaches after storms in the Philippines.

Fossils of Lingula may have been displaced from their

life habitat by currents. I found that when L. reevii died in an aquarium its body emerged from the burrow and rested on the surface of the sediment, the pedicle decomposed, and the body floated to the surface. It floated for at least four days before the muscles decomposed enough to allow the shells to separate, release the decomposition gases, and sink. Morse (1902) also notes that L. lepidula floated in an aquarium after death. In Kaneohe Bay this process would probably not go to completion since scavengers (crabs) would consume the bodies before floatation. I have not seen L. reevii resting on the surface of the sediments or floating in Kaneohe Bay.

The shells of L. reevii decompose rapidly, presumably as a result of both biological and chemical degradation. I placed 10 freshly killed animals, protected from large organisms by a cage, on the bottom for 90 days. When removed, only fragments of the shells remained and these were so fragile that they could not be picked up without crumbling. I did not find any shell remains of L. reevii deeper than about five cm in the sediments on the reef platforms. These sediments below approximately five cm are black, have the odor of hydrogen sulphide, and are assumed to be anoxic. Whether these conditions accelerate the degradation of the shells is not known.

There seems to be no relationship between Lingula's fossil assemblages and the kinds of organisms found with it in Kaneohe Bay. Fossil assemblages range from full marine

to terrestrial organisms. In the bay the most common members living with L. reevii are soft bodied (macro-algae, polychaetous worms, holothurioids, sea anemones, and sedentary tunicates) and are unlikely to leave fossil remains. The sediments in which L. reevii lives are dominated by fossils of coral and bivalve mollusks.

DISCUSSION

Factors Affecting Lingula in Kaneohe Bay

The distribution and abundance of Lingula in Kaneohe Bay appears to be determined largely by predators, type of substratum and food supply. The temperature extremes in Kaneohe Bay, 19 and 28°C (Bathen, 1968), are probably not great enough to affect the distribution of Lingula. Twelve degrees centigrade was the lowest temperature at which Glottidia pyramidata showed normal activity (Paine, 1963). Salinity does not appear to limit the distribution of Lingula except where very low values occur. Low salinities bring swift death to Lingula; this probably accounts for the absence of brachiopods near the mouths of streams.

Predators interacting with substratum largely determine L. reevii's localized distribution in Kaneohe Bay. Portunid crabs are very abundant in the soft sediments of the mud-flats and mangrove areas. It is reasonable to assume that brachiopods settling in these areas would soon be dug out and eaten by the crabs. Predators were proven to be a major potential reason for the absence of Lingula in the deep basin of southern Kaneohe Bay.

The macro-distribution of Lingula in the bay seems to be a function of the availability of food, as the growth rate is affected by the quantity of food. Brachiopods are only abundant in the southern sector of Kaneohe Bay. The waters in the other sectors are clearer and presumably have a

smaller standing crop of food than the southern sector of the bay. It is suggested that an inadequate food supply may be partially responsible for the rare occurrence of Lingula in the other parts of Kaneohe Bay. Since Lingula appears to be endemic to Kaneohe Bay and abundant only in the southern sector, it is possible that the productivity of this sector has been about the same in the past as now.

Brachiopods rarely occur in clam beds because the two animals seem to have different substratum optima. Clam diggers undoubtedly affect the densities of brachiopods that do live in and around clam beds. Many brachiopods are severely injured or left exposed by diggers. Only small brachiopods are capable of re-entering the sediment, and this takes about one day. A day on the surface renders the animal extremely susceptible to predation.

Although the welfare of Lingula is largely determined by the external environment in Kaneohe Bay, the brachiopods have little influence on that ecosystem. Hedgpeth (1957, p. 40) defines the niche as "the role or function of the species in the community or ecosystem." The role of Lingula appears to be quite limited. In Kaneohe Bay it occupies only a small amount of the available space. Other filter and suspension feeders live with Lingula and this implies that competition for food is not severe. They are not the exclusive prey and probably not even the preferred prey of their main predators, the portunid crabs. For example, Thalamita arenata is abundant not only in brachiopod beds

but also in clam beds, mudflats and in the mangrove areas. If Lingula became extinct in the bay, I doubt that any appreciable secondary change would take place in the ecosystem.

Ecological Considerations

Lingula is highly specialized for the near shore environment. Since morphological changes within the genus have been small, it is assumed that these specializations occurred before their known fossil history early in geologic time. If it can be assumed that Lingula has been ecologically as well as morphologically conservative, a few generalizations can be made about its present and past environments.

Today, the genus is found only in warm and shallow waters of the tropical, sub-tropical and temperate zones. Fossil evidence also indicates a warm, shallow water environment. The salinity in this type of environment can vary widely. I found that L. reevii survived well at salinities from 20 to 35‰. Possibly they can also live in even lower salinities, if the water is gradually diluted. Therefore, it is concluded that fossil Lingula could have lived in salinities ranging from at least 20 to 35‰. Also it could have lived under hypersaline conditions; Paine (1963) found that Glottidia pyramidata could tolerate salinities between 18 and 42‰.

The sediments in which Lingula is found in Kaneohe Bay

are varied, (see Figure 2) as are the fossil sediments in which Lingula is found. Since Lingula is capable of upward burrowing and smaller individuals can re-establish if washed out, it can survive in areas of unstable sediments and under conditions of rapid sedimentation or submarine erosion. However, firm sediments that extend to at least 25 - 30 cm appear to be necessary to support dense populations of Lingula. If it lives in sediments that are too loose, it is more susceptible to predation. If Lingula is now essentially restricted to firm sediments by predators, it is probable that this was not the case in the past. Crabs, the only confirmed predators, did not appear until the Jurassic Period (Moore, Lalicker and Fisher, 1952).

The ability of Lingula to survive long periods of starvation and their apparent ability to eat many food types allows them to live in environments with a varying food resource. On the other hand, growth is dependant on the food supply; I believe that Lingula lives best in waters that are reasonably productive.

Since the sexes are separate it is obvious that Lingula must live close enough together to allow for fertilization of the eggs. This appears to be the only intraspecific interaction shown by this genus. A random microdistributional pattern indicated that neither positive nor negative relationships were occurring within dense aggregations of post larval forms. The distribution of Lingula appears to be largely controlled by the external environment.

A relatively long life, estimated to be at least 5 years, with almost continuous spawning from about age 2 insures that even in an environment that might produce 3 or 4 consecutive years of low larval survival, a population of this Lingula could sustain itself. In addition, brachiopods are highly fecund.

Considering the factors required to sustain a stable population of Lingula, a positive estuary appears to be the ideal environment. Such an environment is characterized by have wide fluctuations in salinity and temperature, high productivity, unstable and heterogeneous sediments, and sediments high in organic materials that yield black shales (Emery, Stevenson and Hedgpeth, 1957). Moreover, in estuaries genetic stocks can be maintained at low evolutionary rates (Emery, Stevenson and Hedgpeth, 1957).

Lingula is a common fossil, but apparently fossilization of L. reevii is not occurring in Kaneohe Bay. The shells rapidly decomposed and none were found below 5 cm in the sediments. Yet, fossil lingulids show excellent preservation of both internal anatomy and shell structure (Paine, 1963). I suggest that catastrophic environmental changes may cause the fossilization of Lingula. An abnormal influx of fresh water, killing most marine organisms, coupled with rapid sedimentation, is an example of such an event. This would also partly explain why fossils of other marine, brackish water and terrestrial animals are often found together with Lingula.

SUMMARY

The ecology of the brachiopod Lingula reevii was investigated in Kaneohe Bay, Oahu, Hawaii. The results of the study are as follows.

1. The species was found to be abundant only on the shallow reef platforms of the southern sector of the bay. Although found over large areas of the reef platforms, their greatest densities were found in sandy sediments near the reef edges. The distribution and abundance appear to be related mainly to substratum, predators, food supply and clam diggers.

2. It had a random microdistributional pattern, in areas of high density, that suggests intraspecific independence.

3. It did not have a preferred shell orientation.

4. It proved to be well adapted to sediment instability.

5. It can survive in waters having salinities between 20 and 35‰.

6. It can endure prolonged starvation.

7. Portunid crabs are important predators of L. reevii. Their predatory effect may be severe. Predation can account for the absence of the brachiopod in the deeper parts of the bay.

8. Although L. reevii and the clam Tapes philippinarum co-occur, their niches appear to be separate and competition is not considered to be significant.

9. L. reevii has a 1:1 sex ratio and appears to spawn most of the year.

10. Shell growth was estimated by a notch-recovery method. Shell length decreased linearly with increasing size. Growth depended on the food supply of the waters.

11. A synthetic age-length curve was constructed on the basis of growth data. Longevity is estimated to be 5 to 8 years.

12. L. reevii is not considered to be an important member of the Kaneohe Bay ecosystem.

13. Positive estuaries are thought to be the typical environment of Lingula

14. Fossilization of Lingula probably is not occurring in Kaneohe Bay. It is suggested that abnormal environmental events are responsible for fossil Lingula.

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