SECTION B

ECOLOGY

I. INTRODUCTION

The ecological studies that have been made of *Donax* have been mostly concentrated on two special features of the life of the clam. The first is its remarkable ability to develop and maintain populations on wave-swept sandy beaches, an environment which is one of the most difficult of marine habitats. *Donax* is so successful in this habitat that it is one of the most abundant animals living on these beaches and, except for the mole crabs (Hippidea), has possibly the widest distribution throughout the world of any sand-beach dwelling animal. Enormous populations of *Donax* have been reported by Coe (1955) who estimated densities of over 20,000 clams per square metre of beach for *D. gouldi* in Southern California, and by Loesch (1957) who estimated 32,000 clams per linear yard of beach for *D. variabilis* and *D. tumidus* on the Texas coast. So world-wide is the presence of *Donax* on sandy beaches that Gauld and Buchanan (1956) have suggested that a *Donax* zone should be recognised as a widespread feature of sandy beaches throughout the world.

The second aspect of the ecology of *Donax* which has often been described is its ability to migrate synchronously with the tides and thus to maintain itself in the same zone relative to the line of the breaking surf at high and low tides.

The attention that has been paid to these two aspects of Donax has been so specific that other features of its ecology have been almost completely ignored. As a result, while there is much published literature purporting to be on the ecology of the clam, we actually know very little of the less obvious but equally important ecological features. Except for the work of Loesch (1957), there has been no attempt at a comprehensive study of the ecology of Donax, although unfortunately, Loesch's work suffered from two major setbacks. First, he was only able to study the clams for eight interrupted months over a period of two and a half years, and second, his work was confined almost entirely to one beach in Texas. Because of this, there are important omissions in what would otherwise have been a most thorough study.

The work recorded by me in this section was carried out chiefly on D. denticulatus although wherever and whenever possible, similar studies were made on D. striatus. Observations and experiments were performed from October 1962 to December 1964 inclusive, a period of twenty-seven months, of which twenty-four months were spent in Jamaica where the major work was done and the remaining three months in the Eastern Caribbean (September 1963 and April-May 1964). In Jamaica, field operations were based from the Marine Laboratory of the University of the West Indies at Port Royal. From here, three sandy beaches on which Donax lived were easily accessible by boat, and whenever necessary, clams could be brought back to the laboratory and kept alive in sand in tanks with running sea water. Occasionally, other beaches around the island on which Donax occurred were observed and sampled, but in these cases, it was not possible to keep the clams alive for further observation. Fixing was normally done in 4% Formalin in sea water.

Basic field equipment consisted of the following:-

(1) Two sieve boxes of the following dimensions: 45 cm. long, by 30 cm. wide, by 20 cm. deep. One box had a coarse sieve of mesh size 3 mm^2. and the other a fine sieve of mesh size 1.5 mm^2.

(2) A shovel with a 25 cm. wide blade, and a garden hand trowel.

(3) A 10 metre cord line marked off at 5 cm. intervals, and a metre rule.

(4) A spirit level.

(5) Polyethylene buckets and basins.

The use of this equipment varied with the particular study and will be described in the relevant sections.

II. HABITAT

1. Description of sandy beaches

Sandy beaches in tropical waters have not been studied extensively and such work as has been done is so specific that general descriptions of the habitat are almost non-existent. Shepard (1948) developed an elaborate terminology for the physical characteristics of beaches in general, but as many of the features he described do not exist in the West Indies, his terminology cannot be wholly applied. He defined three main areas, the offshore, the foreshore, and the backshore which, however, have found almost world-wide application. Hedgpeth (1953) adopted this general nomenclature in a description of beaches on the coast of the Gulf of Mexico. Dahl (1953) applied to sandy shores, the same criteria that had been previously applied to rocky shores. His zones were (1) the sublittoral fringe; (2) the midlittoral zone; (3) the subterrestrial fringe. With these zones he coupled a description of the characteristic fauna, and thus provided a biotic as well as a physical description of the beaches he studied. Gauld and Buchanan (1956) examined the sandy beaches of the Gold Coast mainly in terms of the biotic environment and found that Dahl's idea of zonation could not be applied universally as they considered that at least two more zones needed to be added.

As a result of the absence of a proper description of sandy beaches such as exist in the West Indies, and the divergence of opinion regarding the general zonation of beaches throughout the world, I have found it necessary to adopt my own terminology in respect of the beaches I have studied on which Donax occurs. In principle, however, the zones that I have demarcated may be loosely correlated with those of Shepard, Dahl, and Gauld and Buchanan. These zones are illustrated in Figure 9, and are:-

A. The Surf Zone: As the ocean waves break a few metres out from the beach, they roll on to it as turbulent surf and produce a well defined zone. Characteristic features are (a) the sand-roiled water, (b) the coarse shell-textured sand, and (c) the strong under currents. This zone, because of its high degree of disturbance, is very unsuitable for supporting animals.

B. The Wash Zone: When the surf reaches the beach, it makes its final splash and runs up the slope as a smooth and even film of water to cover that part of the beach designated as the wash zone. Between the surf and the wash zones is a small but steep scarp which clearly demarcates their boundaries. The wash zone may be subdivided into two sub-zones:

(1) The saturated zone: With each splash of the surf, there is a rapid uprush of water followed by a less rapid backwash. Before any one backwash can recede right down the beach, however, it is encountered by a second

uprush which runs up and covers the upper reaches of the beach again. As a result of this sequence, the lower reaches of the wash zone are always covered with a continuous slick of water and provide an environment in which the sand is always saturated.

(2) The unsaturated zone: Above the saturated zone is that part of the beach which drains out between each successive wash. In the upper parts, it may be wetted only after a very large wave has broken, and thus becomes saturated only once in every ten minutes or so. This area of periodic wetting and drying is designated the unsaturated zone.

The upper limit of the wash zone is defined by that level of beach which is occasionally wetted at high tide by the largest waves and thus represents the high tide mark. Here may be washed up windrows of shells, sea weed, and debris.

C. <u>The Spray Zone</u>: Above the wash zone is a part of the beach which is never covered with sea water but which is usually dampened by spray and seepage. This is the spray zone and in it may be found growing a few halophytic plants.

D. <u>The Coast</u>: The landward limit of the beach proper is demarcated by a steep scarp at the upper edge of the spray zone. Above this, complete terrestrial conditions exist and thus represents the true coast line.

In profile, each of the four zones is characteristically sloped. The surf zone has a gentler slope than the wash zone and between the two is the previously

Figure 9

Profile of typical sandy beach in the West Indies showing surf, wash (saturated and unsaturated) and spray zones, and coast. (see also Figure 10B).

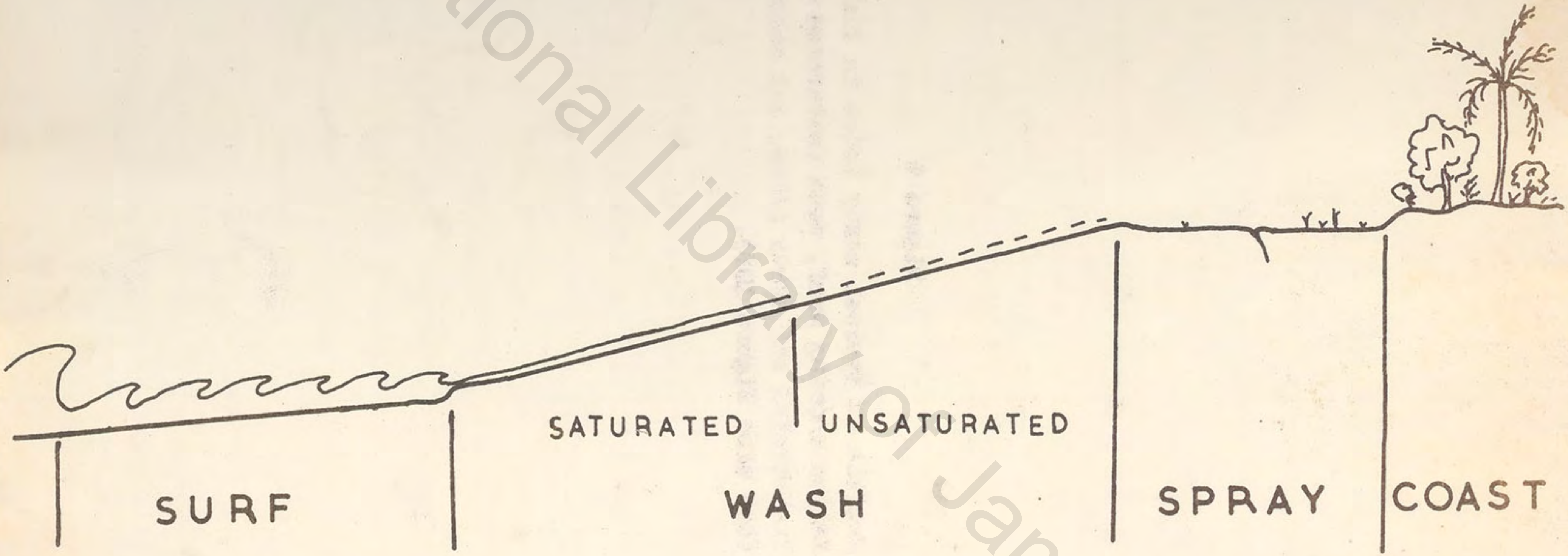


Figure 9

mentioned scarp. The wash zone is the steepest part of the beach and is well marked off from the spray zone which is flat.

A comparison of this zonation and nomenclature with those of Shepard and Dahl is given in Table I.

TABLE 1:- Three proposed systems of zonation and nomenclature of sandy beaches

Shepard	Offshore	Foreshore	Backshore	Coast
Dahl	Sublittoral fringe	Midlittoral	Subterrestrial fringe	-
Wade	Surf	Wash 1)Saturated 2)unsaturated	Spray	Coast

2. The beach fauna.

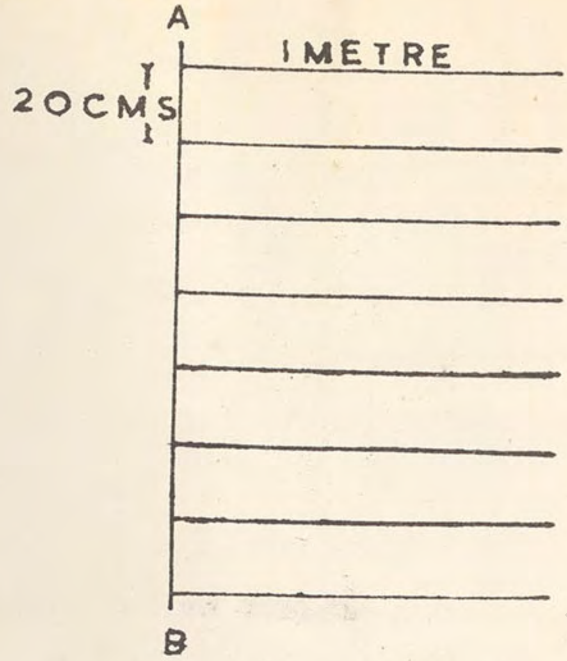
To study the distribution of the beach fauna, an interrupted line-transect method of sampling was used. First, a line was laid down across the beach from the top of the spray zone to well into the surf zone. At 20 cm. intervals along this line, one metre transects were laid down at right angles to it (Figure 10). With a hand trowel, sand the width of the trowel below the transect was scooped up 10 cm. deep and passed through the coarse and fine sieves successively. All the animals retained in the sieves were collected and counted. By doing this, the macrofauna on the beach could be analysed according to their levels of

Figure 10

A: Diagram of interrupted line-transect method of sampling beach fauna.

B: Line-transect sampling of beach fauna at Green Bay, Jamaica. Note main line from top of wash zone into surf zone, one-metre transect line at right angles to the first, and sieve boxes. Note also the zonation of the beach - surf, wash (saturated and unsaturated) and spray zones, and the coast in the background.

A



B

Figure 10

distribution. Figure 11 represents the results (Appendix IV) of such a study carried out at two stations at Green Bay, Jamaica. The fauna was distributed as follows:-

(1) Spray zone: A few unidentified oligochaetes, pulmonates, and insect larvae were found near the coast. These are considered to be representatives of the terrestrial fauna. A talitrid amphipod, _Talorchestia marcuzzi_ (Ruffo), and an isopod, _Excirolana braziliensis_ (Richardson) were common. The talitrids are surface dwellers living in the midst of debris and are confined almost entirely to the spray zone. The isopod was found in the spray and wash zones, but was most abundant in the upper limits of the latter.

(2) Wash zone: Other than the isopod, _E. braziliensis_, the inhabitants of this zone are the mole crab, _Emerita portoricensis_ (Schmidt), the clam, _Donax denticulatus_, and the spionid worm, _Scolelepis squamata_ (Müller). The mole crabs were most abundant just within the unsaturated zone while the worms were more concentrated at the level of the surf and saturated zones. _D. denticulatus_ was found in the saturated and unsaturated zones.

(3) Surf zone: The gastropod, _Terebra cinerea_ (Born), was found in sparse numbers in the surf zone.

In later observations and on beaches other than at Green Bay, the following animals were found on a few occasions and in sparse numbers:-

Spray zone:	Brachyura	-	_Ocypode albicans_ (Bosc)
Wash zone :	Anomura	-	_Hippa cubensis_ (Saussure)
" "	Anomura	-	_Albunea oxyopthalma_ (Leach)

Wash zone : Bivalvia - *Heterodonax bimaculatus* (Linné)

Surf zone : Echinoidea - *Mellita quinquiesperforata* (Leske)

In Table 2, the pattern of zonation found on the local beaches is compared with those described by Dahl (1953), Gauld and Buchanan (1956), and Rodriguez (1959).

TABLE 2:- The patterns of zonation of the beach fauna in four tropical areas

	Dahl	Gauld & Buchanan	Rodriguez	Wade
BACKSHORE	"Talitrid" Ocypode	Ocypode Excirolina Nerine	Ocypode	Ocypode Talorchestia
	-	-	"Talitrid"	-
FORESHORE	Cirolina	-	-	Excirolina
	Emerita	-	-	Emerita Hippa Albunea
		Donax	Emerita Donax Tivela	Donax Heterodonax
		Hippa		Scolelepis
OFFSHORE			Mellita	Mellita Terebra

Although these patterns vary in detail, they are basically similar, and reveal that in the foreshore or wash zone, *Donax*, a mole crab, and an amphipod are usually the predominant fauna. On the beaches in the West Indies, *Donax* is usually the most abundant of the three (Appendix IV) and comprises the largest biomass. As a result, it may be

Figure 11

The pattern of zonation of the beach fauna at Green Bay, Jamaica, illustrated as relative numbers per level of beach.

Ta. - Talorchestia marcuzzi

Ex. - Excirolina braziliensis

Em. - Emerita portoricensis

Do. - Donax denticulatus

Sc. - Scolelepis squamata

Te. - Teribra cinerea

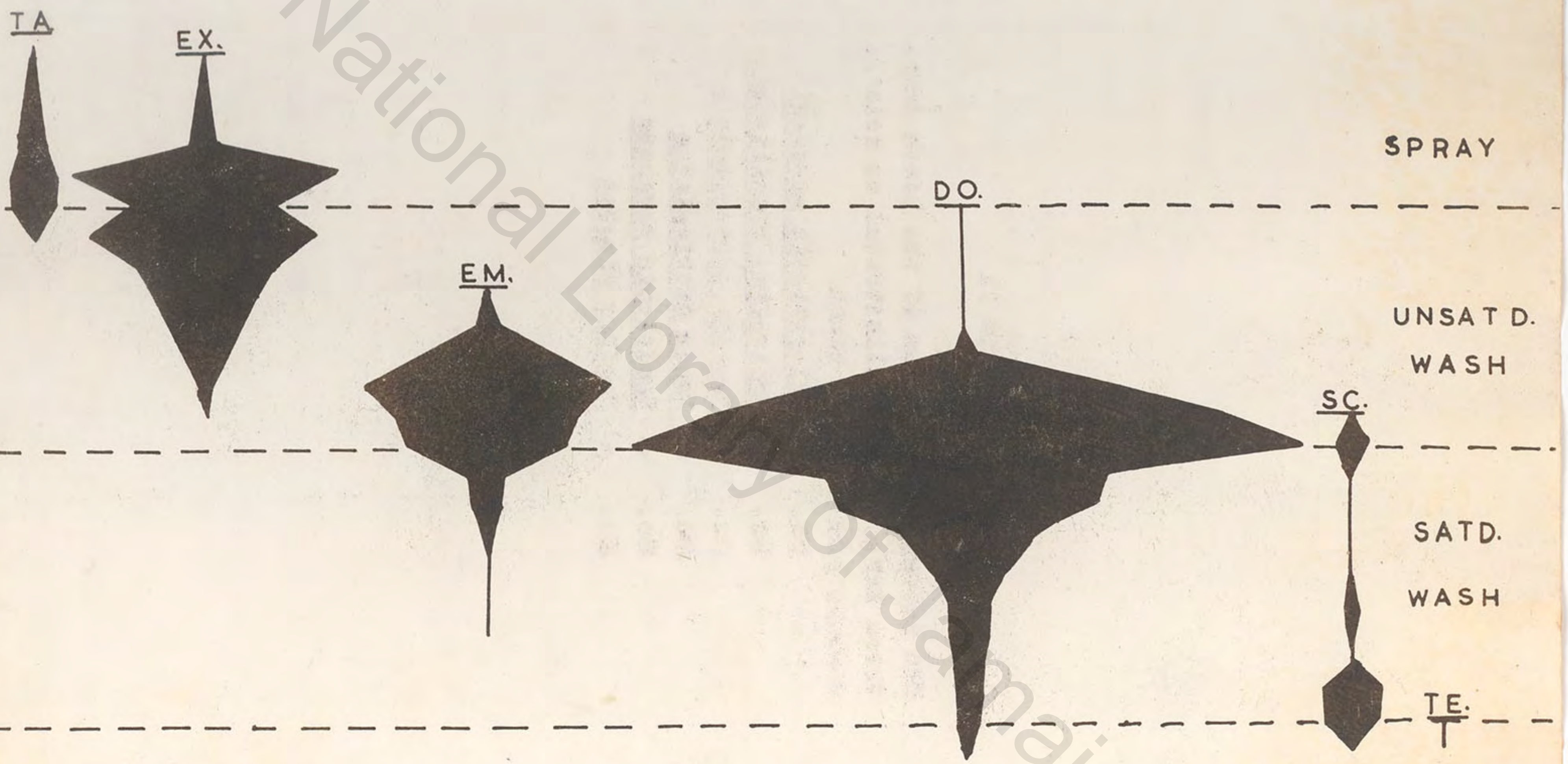


Figure 11

concluded, that as in other parts of the world, Donax is one of the most successful inhabitants of the foreshore.

3. Zonation of Donax populations

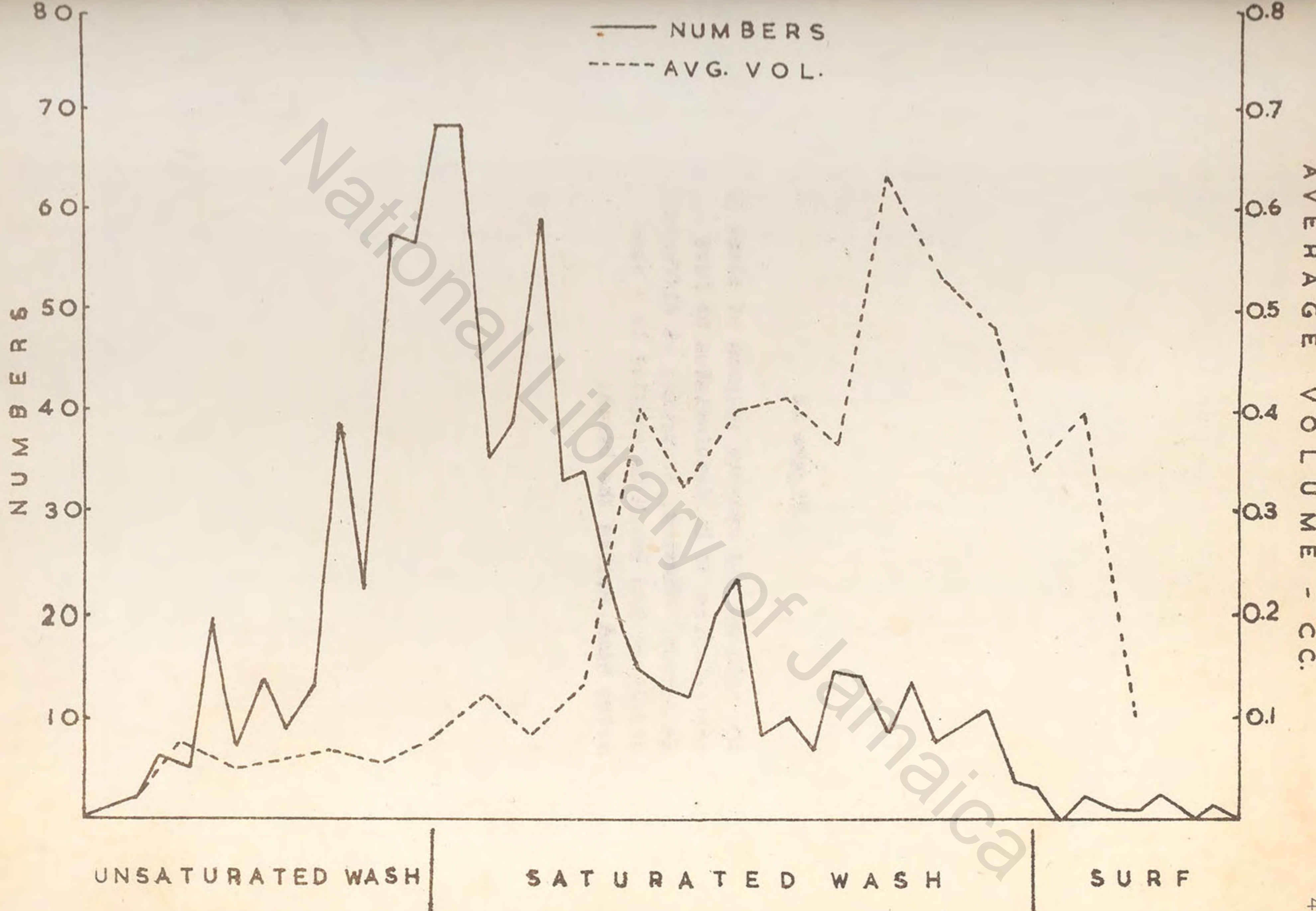
Reports on the vertical distribution of Donax populations have revealed that the patterns of zonation among species vary considerably. Mori (1938) found that at high tide D. semigranosis had its maximum density at high water mark, but that at low tide, the maximum density varied between high and low water mark depending on the slope of the beach. Buchanan (1954) reported D.acutangulus (Deshayes) as being common on the seaward side of the line of the breaking surf, and D. rugosus (Deshayes) as being found in the shallow water of the surf zone. Coe (1955) observed that young D. gouldi are first found in a broad band near the middle of the intertidal zone, but that they are later scattered widely by the action of the surf, principally to lower levels and sometimes into water beyond the low tide limit. Pearse, Humm, and Wharton (1942) indicated that the population of D.variabilis at Fort Macon was most dense near the low tide mark, whereas at Bird and Sheep's Head Shoals, the greatest density was near the high tide mark. Loesch (1957) noted that in Texas, D.variabilis and D.tumidus were always found at the water's edge in spring, but that with the approach of summer, D.tumidus could only be found in water one to three feet deep. Edgren (1959) found that on Clearwater Beach in Florida, D.variabilis appeared to occupy a relatively stable zone on the beach close to the high tide mark. Transects across this zone suggested a skewed distribution that roughly approximated a normal curve with the tail extending toward the water.

Turner and Belding (1957) made a series of observations on D.variabilis in North Carolina to determine whether or not this species was sorted according to size on the beach, but found that no such sorting took place.

Measurements have been made in this study on beaches at Green Bay and Port Henderson in Jamaica to determine the vertical distribution of D. denticulatus both in terms of the levels of abundance and the degree of sorting according to size. The method used was essentially the same as that described for a study of the beach fauna except that transects were taken at closer intervals. For each transect sample, the clams collected were counted, measured for length, and the total volume estimated by water displacement. Several samples were taken at different phases of the tide throughout the year on the two beaches and observations and less precise measurements were also made on other beaches in Jamaica and throughout the West Indies. The results obtained in each case were essentially the same and showed that D.denticulatus had a very definite pattern of zonation. This pattern is illustrated in Figures 12 and 13 which are graphical representations of the results (Appendix V,A) of one sample taken at high tide at Port Henderson in October 1962. Four features of zonation emerge from these results. These are:-

Figure 12

The numbers and average volumes of clams of a population of D. denticulatus at Port Henderson, Jamaica, occurring at different levels on the beach as sampled in a one-metre band across the beach.



NUMBERS
AVG. VOL.
NUMBERS
80
70
60
50
40
30
20
10
AVERAGE VOLUME - CC.
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
UNSATURATED WASH
SATURATED WASH
SURF

Figure 12

Figure 13

The total volume of clams of a population of *D. denticulatus* at Port Henderson, Jamaica occurring at different levels on the beach as sampled in a one-metre band across the beach.

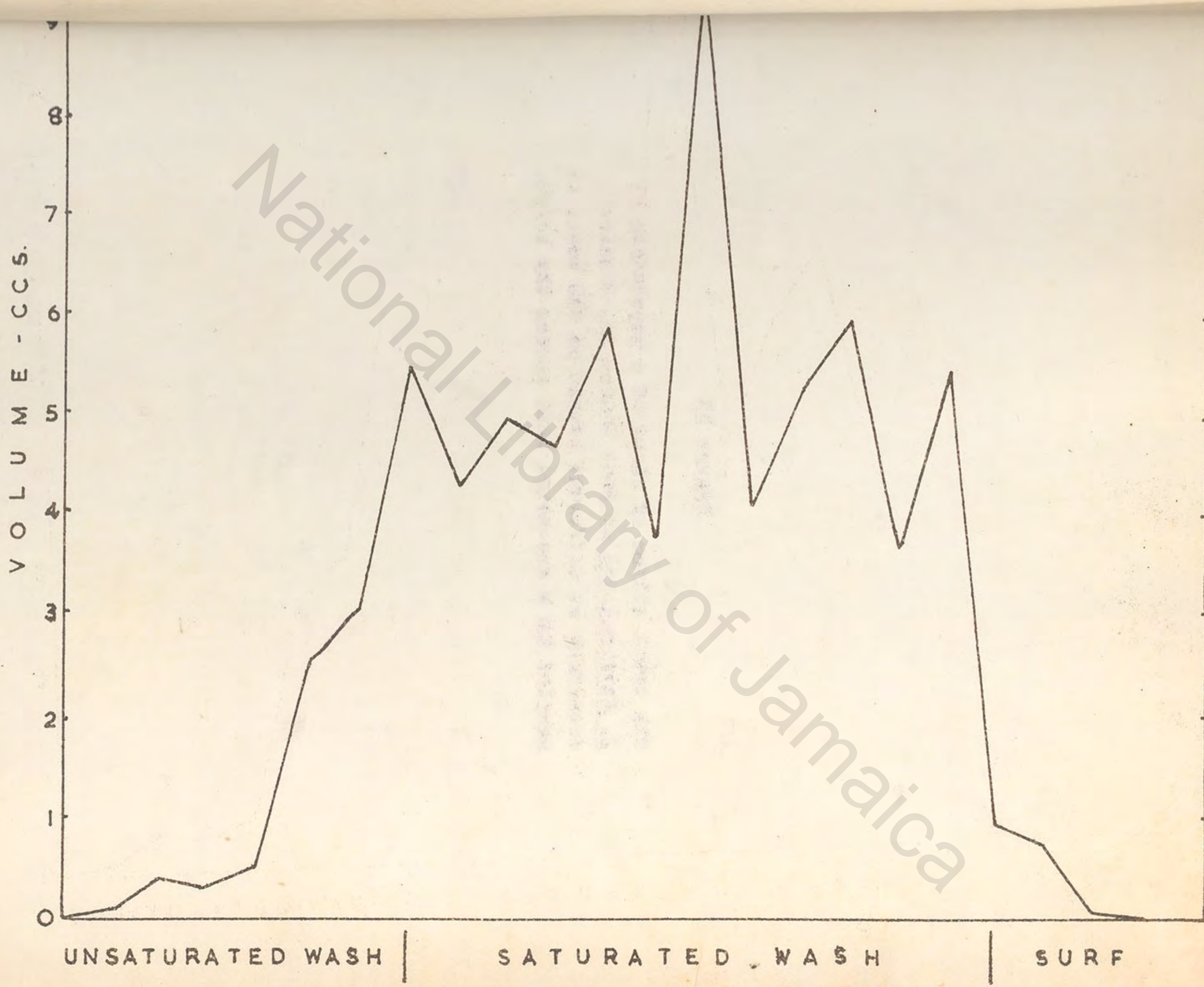

VOLUME - CCS.
8
7
6
5
4
3
2
1
0
UNSATURATED WASH
SATURATED WASH
SURF

Figure 13

(1) Almost the entire population is confined to the wash zone. Only a few clams are found in the surf zone, and none in the spray zone.

(2) The distribution in the wash zone is uneven. The majority of the clams are found on the edge of the saturated and unsaturated zones while, in the remainder of the saturated zone, the clams are fairly evenly distributed with perhaps a slight taper seawards.

(3) There is a pronounced sorting according to size. The adult clams are confined almost entirely to the saturated zone while only the small clams are found in the unsaturated zone.

(4) As a result of the uneven distribution of numbers and sizes in the wash zone, more than 90% of the biovolume is evenly distributed throughout the saturated zone. Less than 10% of the biovolume is thus confined to the unsaturated zone.

These results indicate that the saturated zone is that part of the beach which is most favourable for supporting a population of <u>D. denticulatus.</u> The reason for this is best understood on consideration of the habits of the clam and some of the features of the habitat.

Normally, <u>D.denticulatus</u> lives buried in the sand with its large foot extended to act as an anchor, and its two siphons also extended and lying flush with the surface of the sand (Figure 14A). Occasionally, however, they are flushed out of the sand by the advancing surf, but then they quickly bury themselves again. To maintain a footing, it is essential that the sand be of the right texture, neither too coarse and loose

Figure 14

A: The appearance of D. denticulatus when buried in the substratum.

B- F: Five stages in the burrowing of D. denticulatus.

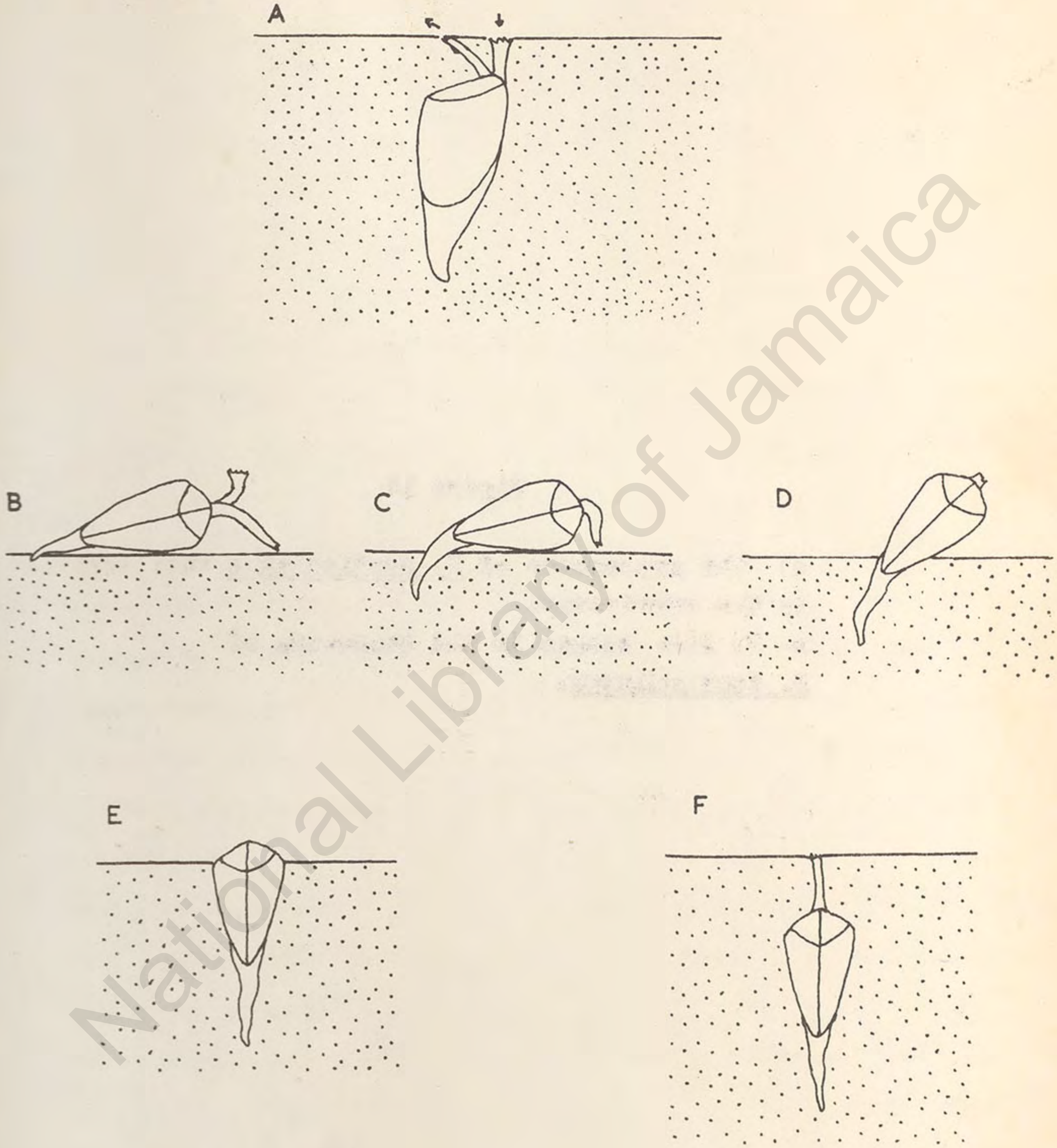


Figure 14

or too fine and tight. In the surf zone, the turbulence is so great that all the fine sand particles are washed out leaving only very coarse particles such as shell fragments. Here the substratum is so loose and the current so strong that the clams cannot remain buried in it for any length of time. This can be seen quite vividly when clams are transferred by hand to this zone. In the saturated zone, there is a continuous slick of water on the surface and the interstitial spaces between the sand grains are saturated with water. Turbulence is not as great as in the surf zone and the sand grains maintain a greater stability. These features therefore provide an environment in which the substratum is of such a texture that the clams can burrow quickly and maintain a footing, and yet at the same time have an external medium of water providing oxygen and food. In the unsaturated zone, drainage of the water between each wash and sometimes periodic drying between large waves cause the environment to be dry and tight and therefore unsuitable for burrowing and feeding.

As the surf beats on the shore, flushing from the sand and subsequent burrowing of the clams vary with their ability first to anchor firmly and then to burrow quickly. It has been found that the larger the clams, the stronger is their grip on the substratum and the greater is their burrowing ability. Because of this, the small clams tend to be flushed out more and washed further up on the beach than the large clams and, as a result, sorting by size takes place.

D. striatus

Attempts at a study of the vertical distribution of D. striatus have produced inconclusive results. In Jamaica, this species was found only in the saturated zone along with D. denticulatus, but the small sizes of the populations made it impossible to determine any sorting. In Trinidad, I found D. striatus stranded in the unsaturated zone in April and May 1964, but J.S. Kenny (personal communication) reports having collected clams from the same locality in September and October 1964 in more than one foot of water. R.K. Trench (personal communication) also reports this species as occurring in the surf zone in British Honduras.

III. TIDAL MIGRATIONS

1. Introduction

In Jamaica and throughout most of the West Indies, the maximum tidal range is about 30 cm. although in Trinidad it is greater and may reach up to 100 cm. Although these tidal ranges are not large, they do nevertheless have an effect on the nature of the beaches so that on a rising tide the upper limits of the surf and wash zones advance shorewards, and on the ebbtide, they recede seawards. Thus on a beach sloped 1:10, a vertical tidal range of 30 cm. results in a shift of about three metres in the horizontal limits of these zones.

Measurements of the zonation of D. denticulatus at high and low tides (Appendix VA & B) revealed that the clams were able to maintain their position in the saturated zone despite the change in levels of the beach. To accomplish this, synchronous migration with the tides must have taken place. Observations and experiments were thus performed to determine the means whereby this was done.

The tidal migrations of Donax have been studied since 1938. Mori (1938 & 1950) observed the movements of D.semigranosis on a beach along the coast of Japan and described the way in which migrations took place. Hedgpeth (1953), Turner and Belding (1957), and Loesch (1957) later reported that migrations were accomplished in much the same way in some of the American species. According to them, the clams accomplish their flood tide migration by jumping out of the sand in advance of the uprush of the surf, thereby placing themselves in a position to be transported landward. While riding the surf up the beach, the foot is extended so that as the velocity of the wash subsides, it can be inserted in the sand and the clam dug in before the backwash retreats. In this way an entire population may "hitch a ride" up the beach. On the ebbtide, the clams remain below the surface of the sand until the surf begins to retreat down the beach. They then jump out into the backwash where they are carried seaward.

This mechanism of migration necessitates that the clams change their pattern of behaviour simultaneously with the change of the tide. On the flood tide it was reported that jumping in advance of the surf was in fact a response to the accoustic shock generated in the sand by the breaking waves and that this jumping could be induced by artificially initiated shocks. On the ebbtide, however, the clams no longer responded to the acoustic shock but only to the flow of water over them by a backwash. Mori suggested that this change of behaviour was due to an intrinsic rhythm within the clams which was synchronous with the tidal cycle, but Turner and Belding regarded this as an unlikely phenomenon. They, in turn, put forward three hypotheses by which change of behaviour might be accomplished. First, they suggested that the clams may be capable of sensing some variation between the conditions prevailing during the opposite phases of the tide and that this perception triggers the appropriate behaviour. Secondly, it is possible that Donax may be equipped with a timing mechanism that acts as a controlling stimulus. Thus, for example, the acoustic stimulus would affect only those clams that had been situated in saturated sand for a certain length of time on the rising tide, and on the ebbtide the stimulus of the wash would affect only those that had been long enough in the unsaturated sand. Finally, a trigger-and-memory hypothesis was proposed. According to this, it is possible that conditions that occur at each extreme of the tidal cycle trigger the clam to commence the appropriate behaviour pattern for the particular phase and that this pattern persists until reversed by the opposite stimulus.

Neither the hypotheses of Turner and Belding nor that of Mori was experimentally tested by the workers, and so they remain unproven. They will be analysed further on in this account, however, in the light of my findings on D. denticulatus.

Before describing migrations in D. denticulatus, the observations of three other workers should be mentioned. Pearse, Humm, and Wharton (1942) reported that D. variabilis moved up and down the beach with the rise and fall of the tide, but did not explain how this was accomplished. Jacobson (1955) studied D. fossor and concluded that this species was merely flushed from the sand by the surf and washed up and down with the rising and ebbing tide. He could find no evidence of either a response to an acoustic shock on the flood tide or to the flow of water on the ebbtide. Edgren (1959 & personal communication, 1963) reported that at Clearwater Beach in Florida, D. variabilis remained quiescent in the sand just below the high tide mark, and that there was no evidence to suggest a tidal migration for this species on the beach.

2. The mechanism of migration

The tidal migrations of D. denticulatus were observed regularly on two beaches at Green Bay and Port Henderson in Jamaica. These beaches differed in their slopes and the texture of their sand grains and provided useful variations in conditions. At Green Bay the beach sometimes had a slope of 1:15 whereas at Port Henderson, the slope was never gentler than 1:8. The sand at Green Bay was of a finer texture than at Port Henderson. Observations at spring tide proved to be the most profitable.

On a rising tide, clams in the lower part of the saturated zone are flushed from the sand by the advancing turbulent surf and appear on the surface as a wash passes over them. They are then transported up the beach in the uprush, and as the backwash recedes, they are washed down again eventually coming to rest in the saturated zone where they quickly dig in. On the backwash, however, the clams extend their siphons and foot to act as a braking mechanism so that they are not carried down as far as their original level. Thus on a wave sequence, although the clams are transported in both directions, they are able to advance landward so that flood tide migration actually takes place gradually and in several steps. In the uprush, the clams are transported with their posterior end shoreward and their longitudinal axis at right angles to the sea, whereas in the backwash, their posterior end is seaward.

On an ebbing tide, the upper limits of the saturated zone begin to dry out and the clams detect this. Their reaction is to withdraw their siphons and foot thus losing their grip on the substratum. Sometimes they may even rise nearer to the surface of the sand and lie half exposed so that as an uprush passes over them, they may be easily washed out of the sand and carried seaward in the backwash. Usually the backwash deposits them far enough into the saturated zone where they may dig in, but if not, they remain partly or fully exposed until another backwash accomplishes this. Later on in the ebb tide as the sand dries out further, the whole sequence takes place again so that migration seaward is gradual.

Each phase of this migration mechanism has been treated experimentally.

On a rising tide it has been claimed that Donax responds to an acoustic shock generated by the breaking waves by jumping out of the sand in advance of the uprush. This has been investigated at Port Henderson and Green Bay with varying results. At Port Henderson where the sand is coarser and the beach slope steeper, no jumping in advance of the surf was seen no matter how big the breaking waves were or at what phase of the tide observations were made. Moreover, it was impossible to induce jumping as Turner and Belding did by splashing a bucket of water on the sand or by stamping. At Green Bay, jumping in advance of the uprush was seen on a few occasions only and at every instance, the beach was very heavily waterlogged as a result of unusually high tides. With clams from both these beaches, however, it was possible to observe jumping in response to an acoustic stimulus by placing them in a bucket with sand completely covered with water and applying a strong and sharp force to the side of the bucket. This could be done with positive results at all phases of the tide providing that the sand had enough interstitial water. These results showed that although D. denticulatus does exhibit a definite response of jumping to an acoustic stimulus, this is influenced primarily by the amount of interstitial water in the sand and not by the tidal phase. The role of the interstitial water is almost certainly to provide a continuous medium through which the shock can be transmitted, and this condition is much more likely to occur on gentle beaches with fine sand than on steeper beaches with coarse sand. It is interesting to note in this respect that the beach on which Turner and Belding observed jumping had a slope of about 1:40, while the beach on which Jacobson worked and saw no jumping had a slope of about 1:5. The fact that jumping was occasionally seen at Green Bay but never at Port Henderson supports this conclusion.

In the uprush and backwash, the orientation of the clams at right angles to the sea is influenced by the shape of the shell. Jacobson has suggested that the foot and siphons may act as steering organs, but this is not necessarily so. To investigate this, dead but intact clams were placed on the beach and allowed to be transported freely in the wash. Without the extension of siphons and foot it was found that in every case the dead clams became orientated at right angles to the sea, showing that shape alone must have been the influencing factor.

Dead intact clams were also used to determine the importance of the siphons and foot as braking organs. In repeated instances, live and dead clams of the same sizes were placed side by side in the saturated zone and allowed to be washed up and down. In every case, both were washed up to the same level by the uprush, but in the backwash, the dead clams were always washed down further, usually right into the surf zone. The siphons and foot could be clearly seen acting as brakes in the live clams, and at the beginning of every backwash assumed characteristic positions. With the clam lying on one of its valves the foot is extended to its full length and partly curved downwards probing the substratum (Figure 14B). The exhalant siphon hangs downwards and the inhalant held upwards drawing in water. As the clam is washed into the saturated zone, the foot which has been probing the sand from the beginning of the backwash now obtains a purchase in it and begins to dig vigorously. The siphons which by this time both bend downwards into the sand (Figure 14C) are then withdrawn (Figure 14D and E), and by three or four convulsive jerks, the clam completely buries itself in the sand. Braking by the siphons and foot is in three ways. First, the increased area they present to the flowing water acts as a braking device. Second, the exhalant current of the ventrally placed siphon creates a jet force in a direction opposite to that of the wash. Third, the probing action of the foot creates increased friction between the clam and the substratum thus slowing it down.

Besides braking, there is another mechanism which ensures that when D. denticulatus is washed out of the sand it only buries again in the saturated zone. The frequency of wave splash normally varies from six to eight seconds. When a clam is washed out, it takes about three seconds to be carried up and down the beach before coming to rest in the saturated zone. It then takes another two seconds of digging before it is completely buried again. This means that after being uncovered, there is a lapse of approximately five seconds before the clam regains its original position, and thus by the time the next wash passes over it, it is completely buried. If by chance a clam comes to rest in the unsaturated zone, burrowing becomes a difficult and slow process because of the relatively dry and tight sand, and may take as much as ten seconds. Usually the clam never manages to cover itself completely, as by the time the next wash reaches it, it is only half buried and therefore easily washed out on to the surface again. Thus by a combination of wave interval time, firmness of the substratum, and digging speed, the clams are kept confined to the saturated zone.

On an ebbtide, D. denticulatus may exhibit two distinct patterns of behaviour. That which is most common, however, and responsible for seaward migration has been shown to be influenced primarily by the amount of water in the sand and not by the tidal phase. To demonstrate this, clams were taken from the beach at all phases of the tide and placed in containers with saturated sand which was then allowed to drain freely. In every instance after a few minutes as the water drained out the sand, some of the clams retracted their siphons and foot while others raised themselves to a level where they became half exposed before withdrawing. The result in both cases, however, was to lessen their grip on the substratum, a situation which on the beach would enable them to be washed out of the sand more easily. Mori, and Turner and Belding claim that on the ebbtide Donax migrates seawards by only responding to the flow of water over them in a seaward direction. Thus a clam remains below the surface as an uprush passes over it, but then as the backwash begins to retreat down the beach, it jumps out of the sand and allows itself to be washed down. This behaviour has been examined in D. denticulatus with three conclusions. First, in a normal tidal sequence, it is not usually apparent. As a result, it appeared to me after several tidal cycles that this behavioural pattern did not occur at all in D. denticulatus. With further observations, however, and a change in conditions on the beach, it was observed. Second, for a clam to respond in this way, it is necessary for it to be left in the unsaturated zone for at least ten minutes. The first time clams were observed exhibiting this behaviour was occasioned by the formation of a berm on the beach resulting in several clams being stranded above the saturated zone at low tide. It was noticed that whenever a very large wave produced a wash which reached the clams, they would jump out of the sand as the water passed over them and lie exposed on the surface. If the backwash was sufficiently strong the clams were transported seaward, but if not, they attempted to burrow again. Subsequent experiment showed that this jumping was independent of the tidal phase and could be made to take place whenever the clams were left in drying sand for at least ten minutes. Moreover, jumping did not depend on the direction of the flow of water over them. Thus if clams were made to be stranded by artificial means, jumping could be evoked by flowing water over them from any direction. The third conclusion on this behavioural pattern is that it does not normally contribute to seaward migration in D. denticulatus since it requires the clams to be in drying sand for a longer time than normally occurs on the beach. It may however, play an important part in helping clams which are left stranded at low tide to right themselves again.

3. Stranding

Although tidal migrations normally occur in Donax, instances have been recorded of a part or whole of a population being left stranded above the water level at low tide. This phenomenon has been observed in D. denticulatus and

D. striatus. Stranded clams usually lie half exposed on the beach with a little circlet of sand about them.

D. denticulatus

Stranding in D. denticulatus usually results after one or other of two occurrences:

(1) A very rough high tide followed by a very calm low tide: During the flood tide, the clams are washed so high up on the beach that when the tide begins to recede, the smaller waves are unable to reach them and wash them down again. Usually, however, with the return of a more normal sequence of tides, the clams regain their proper zonation. Occasionally, as a result of storm conditions, the clams may be deposited so high up on the beach that they never regain their position in the saturated zone, and in such cases they die.

(2) A change in profile of the beach with the formation of a berm: At some times of the year, large amounts of sand are deposited on the beach resulting in the formation of a berm which, occasionally, may have a slight slope landward. At high tide, clams may be deposited on this berm and remain stranded there when the tide recedes since the opposite slope of the berm makes it impossible for backwashes to retreat seaward. Clams stranded on a berm usually never regain their proper zonation.

D. striatus

In Jamaica, the conditions which produced stranding in D. denticulatus had similar effects on D. striatus.

In Trinidad, however, stranding in D. striatus seemed to occur under normal conditions and, in fact, over a period of one month, tidal migrations were not observed at all. Transects across the beach at high and low tides showed that at high tide, the populations of D. denticulatus and D. striatus were mixed, whereas at low tide, D. striatus remained above the water level while D. denticulatus migrated seaward. (Appendix VI, Figure 15).

4. Conclusions

From the foregoing account it is possible to draw some conclusions on the tidal migrations of D. denticulatus in particular, and of the genus as a whole. These conclusions are here outlined:-

(1) Tidal migrations in D. denticulatus do not occur all at once at specific phases of the tide, but are gradual processes in which the clams maintain a dynamic equilibrium with the environment by constantly being washed up and down the beach, but only being able to bury themselves in the saturated zone. This mechanism is significantly different from that described for D. semigranosis by Mori (1938 & 1950) and for D. variabilis by Turner and Belding (1957) in which migration landward or seaward takes place in big steps as a result of transportation in one direction only.

(2) The mechanism of migration in D. denticulatus does not necessitate that the clams change their pattern of behaviour synchronously with the tidal phases. Instead,

Figure 15

Graphs showing the mixing and separation of populations of D. denticulatus and D. striatus at high and low tides at Mayaro, Trinidad.

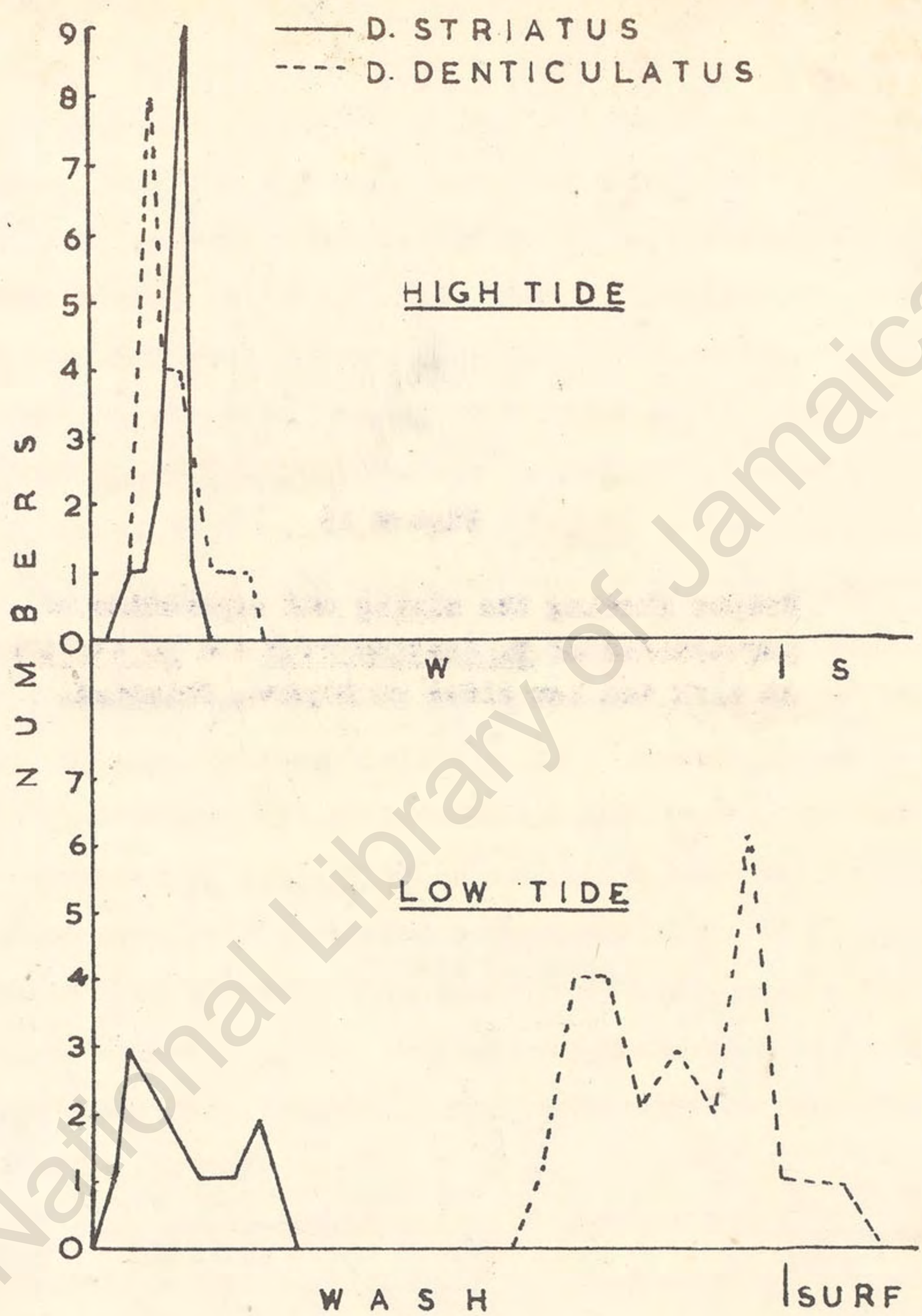

D. STRIATUS
D. DENTICULATUS
HIGH TIDE
LOW TIDE
NUMBERS
9
8
7
6
5
4
3
2
1
0
W
S
WASH
SURF

Figure 15

the operative factors controlling migrations are the changing conditions of the environment as the tide moves in and out. It is suggested from observations and experiments on this species, that the apparent change of behaviour reported by Mori, and Turner and Belding is merely incidental to normal migration and, in fact, is non-tidal in character varying from one beach to another. Thus at Wrightsville, Turner and Belding observed jumping as a response to an acoustic shock in D. variabilis, whereas at Rockaway Beach, Jacobson could see no such response in D. fossor, a species which is now regarded as a cold water variety of D. variabilis. Similarly at Green Bay, D. denticulatus sometimes showed this response, whereas at Port Henderson, jumping on the beach was never evoked either by the breaking waves or by artificial means. It is noteworthy that Turner and Belding only observed D. variabilis on one beach and over a period of three days only (personal communication). It is possible that had they observed this species on more beaches and over a longer period of time, they would have seen other patterns of behaviour and, perhaps like Edgren, observe stranding as a frequent occurrence.

(3) Since migrations as described for D. denticulatus and suggested for other species do not necessitate tidal changes in behaviour, we need not expect to find intrinsic timing mechanisms or tidal synchrony in the clams. Moreover, if they did exist and were responsible for migrations, we would expect them to be more widespread throughout the genus and certainly without variation in a single species. The

reports of those who have observed migrations in Donax reveal, however, that species do behave differently, and that even within a single species, there is much variation in behaviour from one beach to the next. As a result of this evidence, the hypotheses of Turner and Belding, and that of Mori, therefore, appear to be without sound foundation.

(4) The mobile siphons and foot of Donax are important organs in effecting tidal migrations, and without them maintaining a zonation on the sandy beach would be impossible. These organs perform at least three main functions in this respect. First, they help the animals to grip the substratum and thus to maintain an anchorage in the sand. Second, the large muscular foot makes rapid digging possible enabling the animals to regain their position in the sand when washed out. And third, when carried up and down the beach in a wash, braking by the siphons and foot prevents the clams from being deposited in the unsaturated zone or washed out into the surf zone.

(5) The fact that occupancy of wave-swept beaches by Donax would be impossible without the skilful use of the long mobile siphons and the large muscular foot has been overlooked by previous workers. Yonge (1949a) described these organs in the Tellinacea as adaptations for a deposit-feeding habit, although it is clear that in Donax they have assumed new functions, and in so doing, have made it possible for members of the genus to live in a habitat which is unsuitable for most other bivalves.

IV. DISTRIBUTION

1. Introduction

The distribution of D. denticulatus and D. striatus in the West Indies is fairly well known (Warmke and Abbott, 1961, and Abbott, personal communication) although there has been no previous attempt to determine the controlling environmental factors. This problem was therefore undertaken in studying the general ecology of the two species.

Collections were made throughout the West Indies to cover as wide an area as possible (Section A, chapter III). At each beach on which Donax was found, samples of the sand from the saturated zone were taken from the top 3 cm. for analyses. Some of the physical characteristics of the beaches were measured on the spot and any other significant features noted. On many beaches, there were old Donax shells but no living animals, and although such beaches were examined, the data obtained were not used for analyses. As a result, the data reported and discussed in this chapter have been gathered from a study of twenty-two beaches on which I found live Donax. Their locations are listed below:-

D. denticulatus

Jamaica: Port Henderson, St. Catherine; Green Bay, St. Catherine; Small Point, St. Catherine; Farquhar's Beach, Clarendon; Gut River, Manchester; Alligator Pond, Manchester;

Black River, St. Elizabeth; Hope Wharf, Westmoreland; Negril, Westmoreland and Hanover; Lucea, Hanover; Montego Bay, St. James; Puerto Seco, St. Ann; Port Maria, St. Mary; Port Antonio, Portland (Figure 16)

Nevis: Gallows Bay; Pinneys.

Antigua: Jolly Beach.

St. Vincent: Calliaquo.

The Grenadines: Hamilton A, Bequia; Hamilton B, Bequia.

Trinidad: Cocal Beach; Mayaro.

D. striatus

Jamaica: Port Henderson, St. Catherine; Green Bay, St. Catherine; Hope Wharf, Westmoreland; Lucea, Hanover.

Trinidad: Cocal Beach; Mayaro.

At Port Henderson and Green Bay in Jamaica, the occurrence of D. striatus is spasmodic and lasts for only a few months after breeding seasons. Population samples have shown that none of the clams reach a breeding condition and therefore suggest that this species has not been successfully established on these two beaches.

2. Environmental factors

In considering the environmental factors which determine the distribution of Donax in the West Indies, the observation of Holme (1954) should be borne in mind:

"The distribution of any organism is controlled by a complex of factors, each of which may act at a different point in the life history of the individual . . . . Any one factor interacts both with the organism and with its

Figure 16

A distribution map of D. denticulatus in Jamaica.

1 - Port Henderson
2 - Green Bay
3 - Small Point
4 - Farquhar's Beach
5 - Gut River
6 - Alligator Pond
7 - Black River
8 - Hope Wharf
9 - Negril
10 - Lucea
11 - Montego Bay
12 - Puerto Seco
13 - Port Maria
14 - Port Antonio

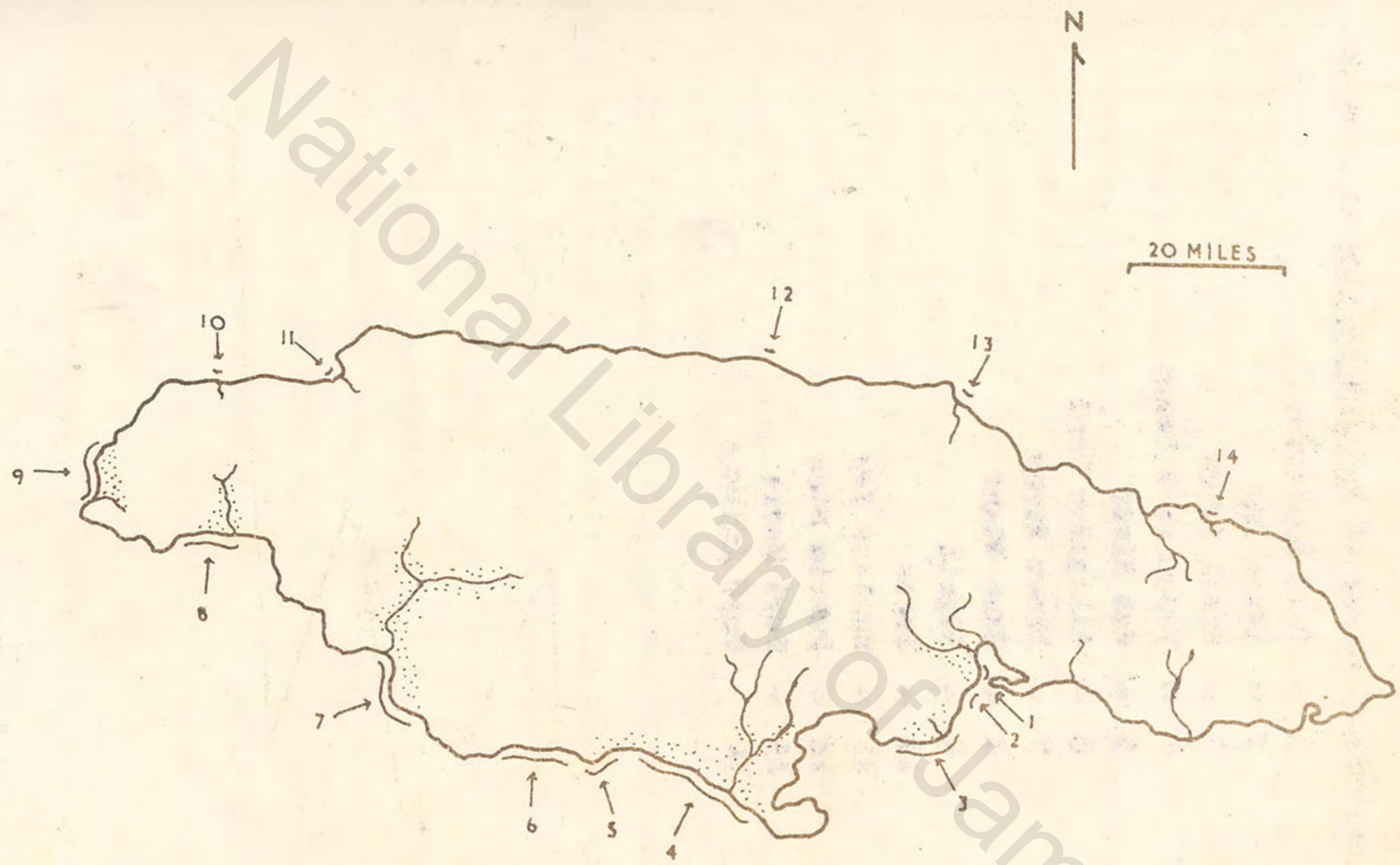


Figure 16

environment, and it is often difficult to distinguish whether the action of a factor is direct or indirect".

From field observations, the influence of the following environmental factors appeared to be significant and were therefore analysed critically. They are discussed, however, in no particular order of importance.

A. Nature of the sand: Beaches in the West Indies are generally formed from volcanic and/or carbonate sands. Carbonate sands may be derived either directly from calcareous deposits of marine animals and plants or may be the result of weathering of limestone rocks deposited and uplifted thousands of years before. On the small coral islands common in the West Indies, the sands are formed as direct deposits whereas on the larger islands, the carbonate sands are often formed from limestone weathering.

The sands in which *Donax* was found were analysed in the Geology Department of the University of the West Indies to determine their geological nature. The results, given in Table 3, show that of the twenty-two sands analysed, fourteen were predominantly volcanic, six predominantly carbonate, and two equally mixed, and suggest a definite preference of the clams for volcanic sands. These are composed mostly of quartz, epidote, and magnetite, and are derived from rocks in the vicinity. Some show signs of river rounding, but nearly all are of the angularity normally associated with beach conditions.

TABLE 3:- The geological nature of the beach sands in which <u>Donax</u> occurs in the West Indies

Locality	% Volcanic	% Carbonate	Angularity
Port Henderson	95	5	angular
Green Bay	30	70	angular
Small Point	25	75	angular
Farquhar's Beach	95	5	angular
Gut River	95	5	angular
Alligator Pond	90	10	subangular
Black River	75	25	angular
Hope Wharf	10	90	angular
Negril	0	100	angular
Lucea	90	10	subangular
Montego Bay	70	30	subangular
Puerto Seco	5	95	angular
Port Maria	80	20	subangular
Port Antonio	90	10	subangular
Gallows Bay	80	20	angular
Pinneys	50	50	subangular
Jolly Beach	5	95	subangular
Calliaquo	95	5	angular
Hamilton A	50	50	angular
Hamilton B	95	5	angular
Cocal Beach	95	5	angular
Mayaro	75	25	angular

B. <u>Size and sorting of the sand grains</u>: Sand samples taken from the beaches were air dried and subject to grade analysis by mechanically shaking 100 gm. portions through a successive series of sieves of the following pore sizes:- 0.5 mm., 0.21 mm., 0.105 mm., 0.053 mm. The amounts separated in each grade after 15 minutes shaking were then weighed and the results used in plotting cumulative curves for each sample (Appendix VII). From these, the Median Diameter and the Coefficient of Sorting[1] for each sand sample were calculated (Pettijohn, 1949). The results are given in Table 4.

From a study of the habits of D. denticulatus, it has been found that the clams cannot maintain a footing in coarse sand which packs together loosely nor in very fine sand which is firm and tight. Between these two extremes, however, is an optimum size-range of sand in which populations are supported. From grade analyses, this range has been found to be between 0.150 mm. M.D. and 0.375 mm. M.D. (Table 4) although as Figure 17A reveals, the populations do not show a normal distribution pattern within this range. This is so because packing of sand grains is influenced not only by their sizes but also by their degree of sorting. Thus, when the Coefficient of Sorting of the sands is combined with their Median Diameters, it is possible to arrive at a more critical measurement for the sands which are most suitable for supporting populations. This measurement, the Size-Sorting Index, obtained by multiplying together Median Diameter and Coefficient of Sorting, ranges from between 0.182 to 0.541 for the sand samples, and when plotted against

---

[1]Median Diameter is determined by the point of crossing of the cumulative curve and the 50% line. Coefficient of Sorting is determined as:

$$S_o = \sqrt{\frac{Q_3}{Q_1}}$$

where Q3 is greater than QI. Q3 and QI are the size values associated with the intersection of the 25% and 75% values with the cumulative curve (Appendix VIIB, Figure 54).

Figure 17

Histograms showing the distribution of populations of D. denticulatus in respect of (A) Median Diameter, and (B) Size-sorting Index of the beach sands.

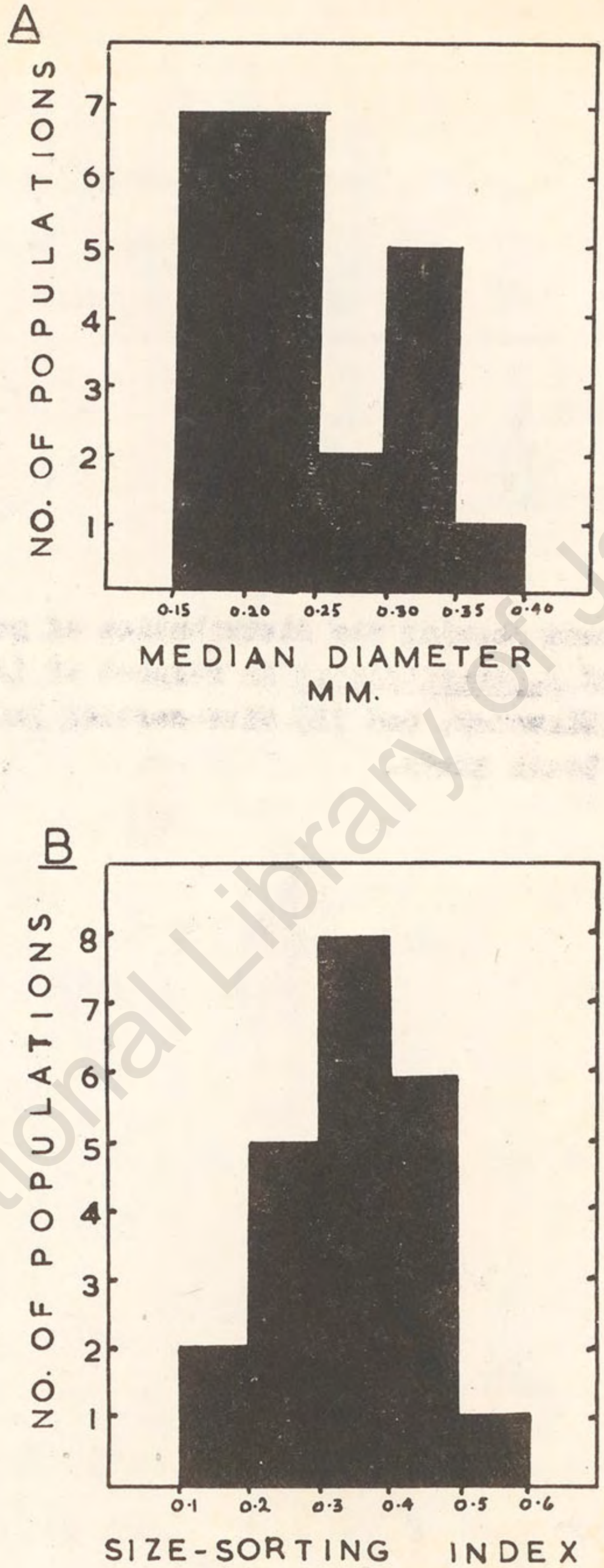

A
NO. OF POPULATIONS
7
6
5
4
3
2
1
0.15
0.20
0.25
0.30
0.35
0.40
MEDIAN DIAMETER
MM.
B
NO. OF POPULATIONS
8
7
6
5
4
3
2
1
0.1
0.2
0.3
0.4
0.5
0.6
SIZE-SORTING INDEX

Figure 17

the number of populations occurring in each grade, shows a normal distribution pattern (Figure 17B). The greatest number of populations of D. denticulatus occur in sands having a size-Sorting Index of between 0.3 and 0.4.

TABLE 4:- The Median Diameter, Coefficient of Sorting, and Size-Sorting Index of the beach sands in which Donax occurs in the West Indies

Locality	M.D.	So.	S-S.I.
Port Henderson	0.320mm.	1.342	0.429
Green Bay	.175	1.225	.214
Small Point	.340	1.594	.541
Farquhar's Beach	.170	1.277	.217
Gut River	.325	1.463	.475
Alligator Pond	.180	1.442	.259
Black River	.200	1.505	.301
Hope Wharf	.310	1.546	.479
Negril	.205	1.536	.314
Lucea	.205	1.543	.316
Montego Bay	.325	1.360	.442
Puerto Seco	.205	1.768	.362
Port Maria	.245	1.507	.369
Port Antonio	.155	1.330	.206
Gallows Bay	.265	1.503	.398
Pinneys	.200	1.526	.305
Jolly Beach	.240	1.520	.364
Calliaqua	.285	1.667	.475
Hamilton A	.375	1.265	.474
Hamilton B	.155	1.183	.183
Cocal Beach	.150	1.217	.182
Mayaro	0.165	1.217	0.200

Beaches with Donax generally have a depth of sand in the saturated zone of at least 20 cm. so that even when there is maximum sand disturbance in rough seas, there is sufficient sand on the beach to ensure a fairly suitable substratum. Sometimes the underlying sand is of a much coarser texture than on the surface, but this seems to have little or no effect on the clams as it never usually forms their immediate environment. Loose rocks and stones are not present on the beaches on which Donax lives.

C. Slope of the beach: The slope of each beach was estimated by laying a horizontal line across the wash zone and measuring at a known distance its height above the surface of the sand. The slope was calculated by dividing the horizontal by the vertical measurements. The results are given in Table 5.

The slope of a beach partly depends on the texture of the sand grains (King, 1951). As a result, the beaches sampled with the exception of two in Trinidad all had slopes of about the same gradient and were between 1:6 and 1:10. The coarser sands tended to produce the steeper beaches.

D. Wave exposure: There is no way of making accurate measurements of the degree of wave exposure of a beach. Rough estimates may be made, however, from the frequency of wave splash and in this way the beach classified as having good or poor wave exposure. The beaches on which Donax is found in the West Indies are all exposed to the open sea and have a frequency of wave splash of once every six to eight seconds. This represents good wave exposure. The waves coming in from the sea beat against the beach directly and thus provide continuous surf and wash conditions. As a result, no Donax populations are ever found in sheltered bays or on beaches behind offshore bars.

TABLE 5:- The slopes of the beaches on which <u>Donax</u> lives in the West Indies

Locality	Slope
Port Henderson	1:7
Green Bay	1:10
Small Point	1:7
Farquhar's Beach	1:8
Gut River	1:6.5
Alligator Pond	1:9
Black River	1:6
Hope Wharf	1:7
Negril	1:7
Lucea	1:7
Montego Bay	1:7
Puerto Seco	1:7.5
Port Maria	1:7
Port Antonio	1:7
Gallows Bay	1:10
Pinneys	1:8
Jolly Beach	1:10
Calliaquo	1:8.5
Hamilton A	1:10
Hamilton B	1:9
Cocal Beach	1:22
Mayaro	1:19

The degree of wave exposure of a beach partly determines its slope and both are related to the depth of disturbance of the sand by the waves. King (1951) has shown that the disturbance varies directly with slope and exposure, and since <u>Donax</u> populations are only found on steep beaches with good exposure, it may be concluded that the clams require an environment in which there is a fair amount of sand disturbance. The reason for this appears to be threefold:-

(1) Continuous churning of the sand ensures that the environment remains well aerated and clean.

(2) Organic detritus can be kept in suspension in the sea water. Loesch (1957) has shown that growth ceases when D. variabilis is removed to an environment in which there is no wave action.

(3) Tidal migrations can only take place where the wash is strong enough to flush the animals from the sand.

E. Organic content of sand: The organic content of sand samples was determined by using Walkley and Black's Rapid Titration Method with the necessary corrections made for the previously determined chloride content (Piper, 1942). This method is known to give a mean recovery of about 75% organic carbon, and so the results cannot be considered as absolute. Values obtained by this method are reported as "Organic carbon, Walkley and Black values". An estimated "true" percentage of organic carbon is obtained by multiplying Walkley and Black's values by a factor of 1.33. A factor of 1.8 (Trask, 1939) is used to convert the values from organic carbon into those for organic matter.

The results obtained for the organic content analyses are given in Table 6 and reveal that the sands in which D. denticulatus lives are all low in organic content with a maximum estimated "true" percentage of organic matter of 0.531 and a minimum of 0.020. The average estimated "true" percentage of organic matter for the twenty-two

TABLE 6:- Organic content of the sands in which Donax occurs in the West Indies

Locality	Organic Carbon (Walkley & Black)	Estimated true Organic Carbon	Estimated true Organic Matter
Port Henderson	0.045%	0.060%	0.108%
Green Bay	.133	.176	.317
Small Point	.144	.191	.344
Farquhar's Beach	.018	.024	.043
Gut River	.008	.011	.020
Alligator Pond	.018	.024	.043
Black River	.005	.065	.117
Hope Wharf	.218	.290	.522
Negril	.222	.295	.531
Lucea	.059	.078	.140
Montego Bay	.088	.117	.211
Puerto Seco	.169	.225	.405
Port Maria	.059	.078	.140
Port Antonio	.059	.078	.140
Gallows Bay	.016	.021	.038
Pinneys	.179	.238	.428
Jolly Beach	.065	.086	.155
Calliaquo	.011	.015	.027
Hamilton A	.020	.027	.049
Hamilton B	.029	.038	.068
Cocal Beach	.138	.183	.329
Mayaro	0.060	0.080	0.144
Average values	0.080	0.109	0.196

sands is only 0.196. Generally the carbonate sands have more organic matter than the volcanic sands (compare Tables 3 & 6) but this does not seem to be ecologically significant.

On none of the beaches on which Donax lives is there a black layer below the surface of the sand indicating reducing conditions. Where dead seaweed or other decaying organic matter gets buried in and incorporated in the sand, Donax is absent.

3. Discussion

The distribution map of D. denticulatus in Jamaica (Figure 16) reveals two important features. The first is that the clams are more common on the south coast than on the north coast and offshore cays. Secondly, populations are frequently found near to the mouth of a river or swamp. These features can be explained on consideration of the environmental factors outlined above.

On the north shore and offshore cays of Jamaica, and in Barbados, much of St. Lucia, Antigua, and Tobago, the beaches have been formed in association with coral reefs and the sand is composed of coarse calcareous deposits, mostly of dead alga and coral. Such sands may have a Median Diameter of as much as 0.5 mm. and a Size-Sorting Index of 0.7. They pack very loosely together and provide a substratum which is so unstable that it can support only a few animals. On the south coast of Jamaica as also in Nevis, St. Vincent, The Grenadines, and Trinidad, the beaches are formed from alluvial deposits and the sand is of a finer texture. They form a more stable substratum than the algal sands, and produce beach conditions which the clams prefer. Hence, because of the interacting influences of the nature of the sand grains, their size and sorting, and the slope of the beach, populations of D. denticulatus tend to be more concentrated in areas where there is no coral formation.

Although the sands in which D. denticulatus lives must be low in organic content, the clams nevertheless require much organic matter for food. This is provided most readily in the vicinity of rivers and swamps where there is a constant outflow of nutrients into the sea. Only on such beaches which are exposed to the open sea and have good exposure, however, is there a rapid turnover of these nutrients as well as organically clean sand, and it is on these that Donax occurs. Hence, the organic content of the sand and the degree of wave exposure seem to be the factors which influence the occurrence of populations near rivers and swamps.

Throughout the West Indies, D. striatus has been found established on only four beaches and as a result, it is difficult to draw conclusions from the sparse data obtained. A few observations can be made, however. The most important is that of the four localities in which this species occurs, by far the larger populations are found in Trinidad where the beaches have gentle slopes of 1:19 and 1:22. On these the depth of the water table below the beach sand is never more than about 5 cm. and provides a condition where even at low tide, there is a fair amount of interstitial water in the sand. Remembering that on these beaches, D. striatus does not migrate with the tides, it would seem that such conditions favour a population which has to remain stranded above the water mark at low tide. In Jamaica, however, where there are steeper beaches and where D. striatus migrates up and down the beach, the same is not true. As a result, there is more overlap in habitat with D. denticulatus resulting in greater inter-species competition. It is not unnatural, therefore, that in such circumstances D. striatus, which appears to be the more recent and less established of the two species in the West Indies, suffers at the expense of D. denticulatus and only just manages to survive. Thus whereas on the steep beaches, D. striatus is less common than D. denticulatus, on the gentle beaches such as in Trinidad, it has been able to establish itself as the more abundant species.

V. POPULATIONS

1. Introduction

On all the beaches on which Donax was found, representative samples were taken to determine the salient features of the populations. Two methods of sampling were attempted at first as follows:-

(1) A one-quarter metre quadrat was laid down in the wash zone and the top 10 cm. of sand within this was scooped up with a hand trowel and sieved. All the animals retained were counted and the density of population calculated for one square metre of beach by multiplying by sixteen. At one station at Port Henderson, this was done on successive occasions to determine its reliability and was found to be unsatisfactory for two reasons. First, because of the uneven distribution of the clams across the beach, quadrats from different levels produced varying amounts of clams thus making it impossible to arrive at consistent density determinations. Second, since the animals were sorted by size on the beach, a quadrat from any one level produced results with a definite bias for clams of a certain size. Because of these defects, this sampling method was discarded. (It should be noted here that both Coe (1955) and Loesch (1957) used this method in their work).

(2) Using a shovel with a one-quarter metre wide

blade, a cut of sand of the same width and 10 cm. deep was scooped up from the upper limit of the wash zone to well into the surf zone and sieved. The clams retained were counted and the population density estimated for one linear metre of beach by multiplying by four. This method ensured that all cuts produced samples which were representative of the entire population and was therefore preferred to the first. In execution, however, it was more difficult since cuts had to be taken right across the beach, and in high seas, this meant scooping up sand which was constantly being disturbed by the waves. As a result, samples taken under such conditions usually resulted in a reduction of the number of clams retained. Nevertheless, the margin of error was small enough for the method to be adopted for general use.

The pore size of the fine sieve (1.5 mm^2.) determined that no spat smaller than this were retained.

2. Population features

On analysis of twenty-two populations of D. denticulatus, three important features were revealed. These are:

A. Density: The density of populations varies significantly at different localities and from one time of the year to the next (Table 7). The greatest density of population recorded on four occasions over a period of two years was at Farquhar's Beach in April 1963 where there were 4,120 clams per metre of beach, while on two beaches, Puerto Seco and Calliaqua, the densities were as low as ten clams per metre. The greatest fluctuation over this period was at Farquhar's Beach where from April 1963 to September 1964, the population density fell from 4,120 clams per metre to 360 per metre.

TABLE 7:- The densities of populations of *D. denticulatus* as clams per linear metre of beach on beaches in the West Indies.

Locality	April '63	Sept. '63	April '64	Sept. '64
Port Henderson	2370	1390	1040	1010
Green Bay	1810	440	2120	750
Small Point	260	..	..	100
Farquhar's Beach	4120	..	..	360
Gut River	160	..	..	740
Alligator Pond	390	..	..	120
Black River	..	..	..	1750
Hope Wharf	1800	..	..	3910
Negril	1270	..	..	1010
Lucea	80	..	..	0
Montego Bay	720	..	..	20
Puerto Seco	10	..	..	10
Port Maria	750	..	..	300
Port Antonio	40	..	..	0
Gallows Bay	..	520	..	..
Pinneys	..	650	..	..
Jolly Beach	..	820	..	..
Calliaquo	..	10	..	..
Hamilton A	..	120	..	..
Hamilton B	..	1450	..	..
Cocal Beach	..	..	80	..
Mayaro	..	..	570	..

B. Size of the clams: There are significant differences in the sizes to which the clams of different localities grow. On some beaches, adult individuals are as large as 23 mm. in length, whereas on others they may be dwarfed and seldom attain 15 mm. For the Jamaican populations in September 1964, length frequency graphs were plotted after measuring every clam in each sample (Appendix VIII). Figure 18 shows such graphs for four populations at Small Point, Black River, Gut River, and Negril. At the time of sampling, spawning had just commenced and the adult clams could therefore be considered as having achieved their maximum sizes[1]. As a result, the modal peaks of the most advanced size-class of clams in any population in September 1964 were indicative of the sizes to which the clams grow. At Small Point, the adult peak was at 20 mm. and the largest clams 23 mm. in length, whereas at Negril, the adult peak was at 9 mm. and the largest clams only 12 mm. in length. Results of the size analyses for populations of D. denticulatus in Jamaica are given in Table 8, and Figure 19 shows photographs of adult clams from four localities.

C. Coloration: Although there is a great variety in colour and pattern of the shells of D. denticulatus, some populations often show a distinct tendency towards one particular colour or pattern. At Negril and Puerto Seco in Jamaica, for example, the shells are nearly all completely white while at L'anse aux Epines in Grenada, and Mayaro in Trinidad, the shells though light coloured are nearly all radially streaked with shades of cream, purple, or brown. Shells from Black River and Small Point mostly have a deep shade of purple while those from Port Maria are light

[1]Most clams die after spawning, but even those that survive show little or no subsequent increase in size (Section C, chapter III)

Figure 18

Length-frequency graphs for samples of four populations of *D. denticulatus* in Jamaica in September 1964.

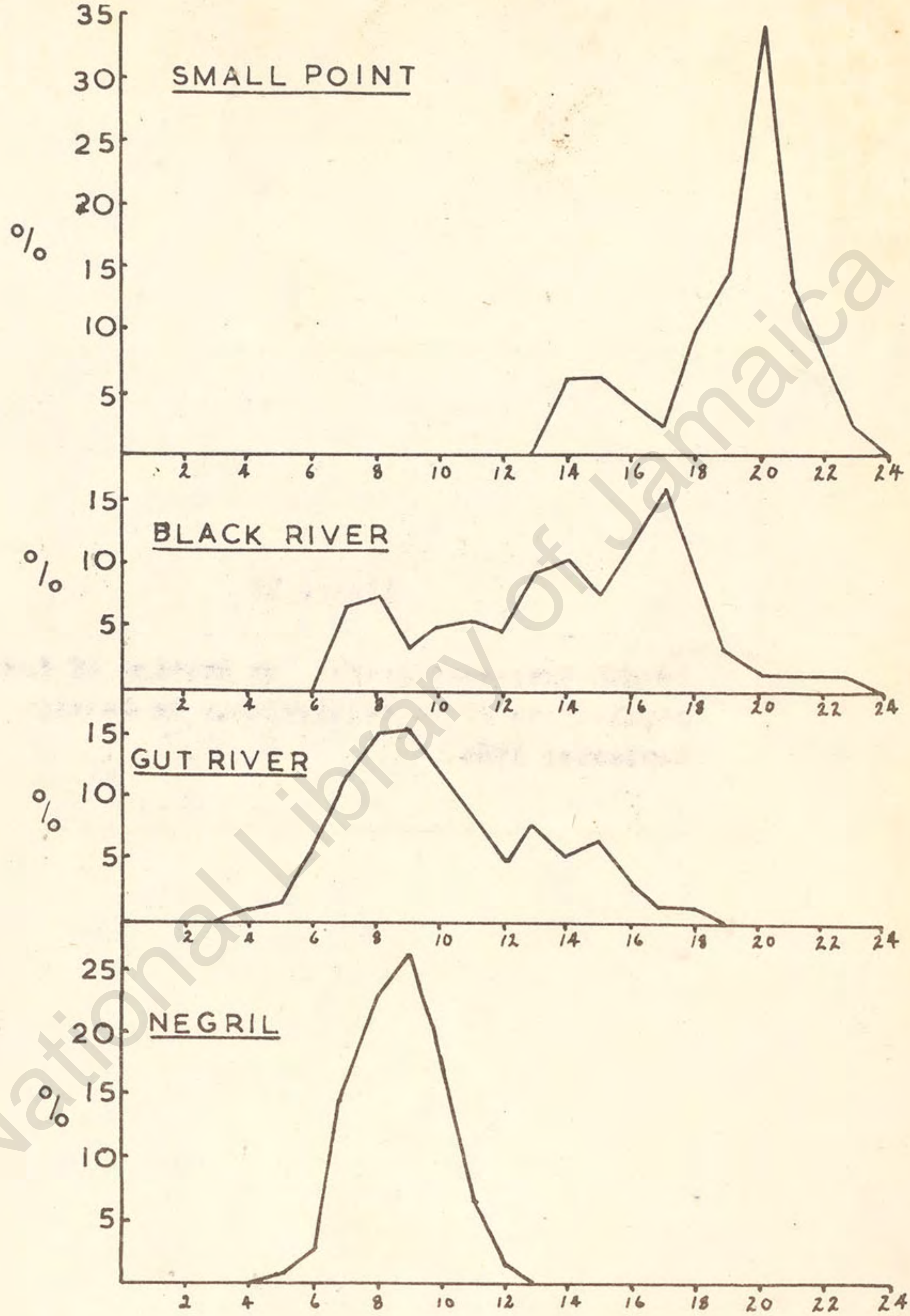


Figure 18

Figure 19

Adult clams of <u>D. denticulatus</u> from four different localities showing variation in sizes.

Figure 19

TABLE 8:- The adult modal peaks and maximum sizes of clams in populations of D. denticulatus in Jamaica in September, 1964.

Population	Adult modal peak	Maximum size
Port Henderson	18 mm.	23 mm
Green Bay	14	20
Small Point	20	23
Farquhar's Beach	21	23
Gut River	15	18
Alligator Pond	12.5	16
Black River	17	23
Hope Wharf	20	23
Negril	9	12
Lucea	..	..
Montego Bay	..	18
Puerto Seco	..	12
Port Maria	12.5	16
Port Antonio	..	..

purple and green. Figure 20 shows photographs of samples of these different colour tendencies.

In view of the prominence that has been given to colour variation in Donax as a taxonomic feature by some systematists, it should be mentioned here that in personal communication, R.T. Abbott affirms that there are no sub-species of D. denticulatus in the West Indian islands.

In order to determine the reasons for the population features exhibited by Donax in the West Indies, a comprehensive study was made of the life history of the clams and of the environmental factors which regulate the populations. The results of this study with an analysis of the data comprise Section C of this thesis.

Figure 20

Samples of clams of D. denticulatus from four different localities showing tendencies towards certain colours and patterns.

Top left	-	Negril
Top right	-	L'anse aux Epines
Bottom left	-	Port Maria
Bottom right	-	Black River

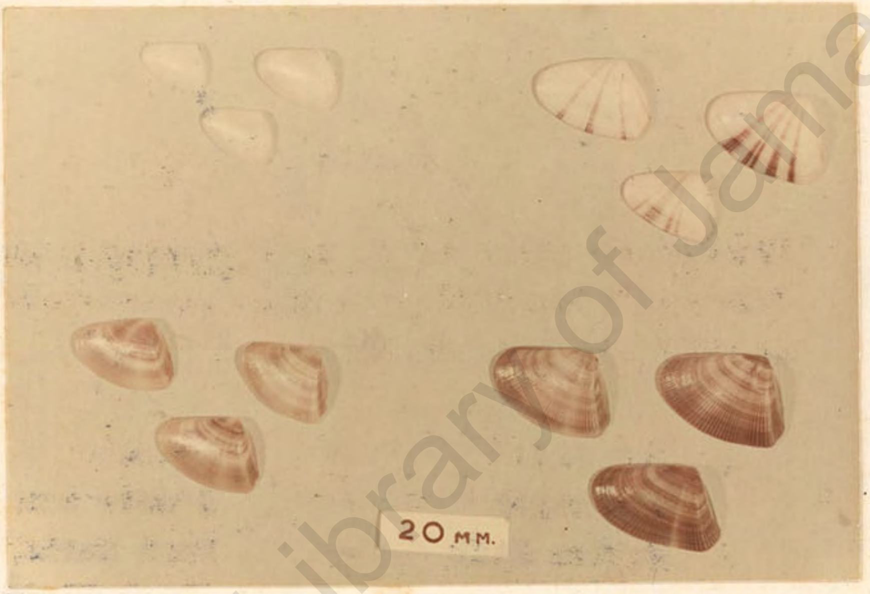


Figure 20

VI. PREDATORS, PARASITES, COMMENSALS

1. Predators

Several invertebrates, birds, and fishes are known to feed on species of *Donax*. Loesch (1957) lists twelve different predators. Observations throughout the West Indies have shown that the following animals are regular predators on *D. denticulatus* and *D. striatus*:

A. *Crabs*: Three species of crabs are known to eat *Donax* in the West Indies.

(1) *Arenaeus cribrarius* (Lamarck). During the day the spotted crab lives in more than one foot of water but moves up on to the wash zone of the beach at night and feeds actively on *Donax*. Night observations on the beach and in the day with captured crabs have revealed certain features of this predatory habit. First, the crab locates a clam to be eaten by digging into and forwards in the sand with its two pairs of front legs. If there is a clam buried underneath the crab, this action scoops it out of the sand and deposits it just in front of the crab. It is then seized immediately by one or both of the claws and manipulated to a position in front of the mouth. With its maxillipeds the crab orientates the clam so that it is held firmly at right angles to the mouth with its anterior end inwards. Pressure from one of the claws is then exerted on the clam

until the shell is cracked, after which the shell is carefully removed and rejected by the maxillipeds and the meat ingested. The whole process takes about one minute. Adult male crabs are able to crack the shells of the largest clams in this way, but immature and female crabs are only able to overcome the smaller ones. Sometimes, however, a clam too large to be cracked is opened by inserting a claw between the two valves and snipping the anterior adductor muscle, but this seems to happen merely by chance after trial and error.

To determine the number of clams eaten by adult crabs, a tank was set up containing one hundred clams in sand and an adult crab, and the numbers eaten over each twenty-four-hour period were checked. After one week, the adult crab was replaced by another and the experiment repeated. In one week, an average of eighty-four clams was eaten by one crab with as many as twenty-four being consumed in one night on one occasion. The cracked shells of these twenty-four clams are shown in Figure 21.

(2) *Callinectes exasperatus* (Gerstaecker). This crab handles and cracks the shells of *Donax* in much the same way as *Arenaeus* does although it locates the clam in a different way. With one claw inserted in the sand, the crab walks sideways until the claw comes upon a clam which it then grips and brings to the surface. Walking ceases and the crab settles down to open and ingest it. Occasionally, the crab may pounce upon a clam which has been washed out of the sand, but this is not often.

Callinectes has stronger claws than *Arenaeus* and

Figure 21

The cracked shells of twenty-four clams of *D. denticulatus* which were eaten by an adult crab, *Arenaeus cribrarius*, in one night.

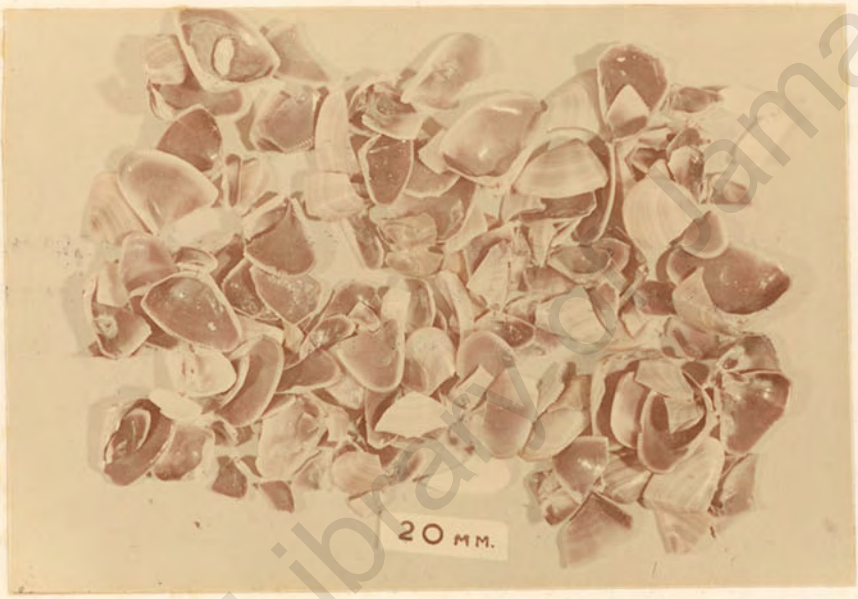


Figure 21

immature crabs are able to crack larger shells. Their appetite for Donax, however, seems to be about the same.

(3) Ocypode albicans (Bosc). The ghost crab was not observed eating Donax at any time. On beaches, however, shells were frequently found in the vicinity of burrows, and in the laboratory clams offered to the crab were eaten during the night. Loesch reports from personal communication with Burkenroad that ". . . ghost crabs were seen to roll Donax around in their claws until they succeeded in opening the clams".

B. Boring gastropods: Drilled shells of Donax were frequently found (Figure 22) although no borers were actually seen drilling. On most beaches, the only borer present is Terebra cinerea (Born) and it is believed that this gastropod is responsible for the drilled shells. Mostly young clams are drilled.

C. Birds: The sanderling, Crocethia alba (Pallas) was observed eating Donax on many beaches. This bird, though present throughout the year, is more common in the winter months. Loesch (1957) describes the way in which the sanderling eats Donax:

"The bird probed with its beak in the sand with its head completely under water. A Donax about 12 to 14 millimeters long was brought up. The bird rolled the clam around in its beak so that it was lengthwise and then swallowed it".

No other bird is known to prey on Donax in the West Indies.

Figure 22

Shells of <u>D. denticulatus</u> believed to have been drilled by the gastropod, <u>Terebra cinerea</u>.

Figure 22

D. Mammals: The pig is a frequent predator on Donax on local beaches. Walking at the water's edge, it digs its snout in the sand and scoops up hundreds of clams as it goes along. Periodically, it stops to crunch and swallow the clams it has scooped up, and then moves on again. Its appetite is immense, and it seems that one pig in an hour may devour more than what all other predators consume in months.

2. Parasites

The parasitology of several species of Donax have been extensively studied in the past (Pelseneer, 1896; Giard, 1897a & b.;Chatton & Lwoff, 1923) and recent work is directed primarily towards the description of new parasites. Cable (1956) reported a new cercarial larva from D. denticulatus and Hopkins (1958), in the most recent paper on the parasites of Donax, named and described the trematodes of D. variabilis.

In the samples of D. denticulatus from Port Henderson and Green Bay, Jamaica, a few adult clams were found to be infected in the visceral mass with a trematode larva subsequently identified as Cercaria caribbea XLII (Cable). This is a bucephalid cercaria similar to one described by Hopkins for D. variabilis.

Cable commented on the life history of C. caribbea XLIII as follows:

". . . it may be assumed that this species encysts in a fish that is eaten by a larger fish serving as a definitive host. Thus the adult of this cercariae probably is among the bucephalids that (are) often found in the intestines of fishes".

In all the clams in which C. caribbea XLII were found, parasitic castration had taken place and the gonadial region had assumed a pale yellow colour. Otherwise, however, the clams appeared normal.

Unidentified flagellates and other protozoa were frequently seen in the visceral mass of D. denticulatus.

3. Commensals

A hydroid, Clytia bakeri, and an alga, Enteromorpha flexuosa (Wulfen) grow on the posterior end of the shell of many species of Donax (Loesch, 1957). In the West Indies, a hydroid was found on the shells of D. denticulatus and D. striatus, but only in Trinidad. This hydroid has not yet been identified because of the absence of gonozooids on the polyps collected.

Although algae do not normally grow on the shells of D. denticulatus and D. striatus in the West Indies, green blotches were once observed on the posterior slope of some shells of D. denticulatus at Negril in Jamaica. Microscopic examination indicated the presence of a small filamentous alga, but the material was so poor that identification was not possible.

Loesch (1957) found that Donax having growths of either hydroids or algae were less frequently infested by cercarial or precercarial parasites. This has not been observed in D. denticulatus and D. striatus.

VII. SUMMARY

The ecological features of *D. denticulatus* and *D. striatus* are summarised here to illustrate the way in which these clams inhabit the wave-swept sandy beaches of the West Indies.

The habitat in which the clams live is hostile for two reasons. Firstly, because of the pounding action of the surf on the relatively loose sand grains, the substratum is more unstable than most others and the animals live in danger of being either flushed out of the sand or buried alive. Secondly tidal changes necessitate that the clams must be able to migrate synchronously with the tides or else be subject to frequent stranding and dessication.

D. denticulatus and *D. striatus* occupy the saturated region of the wash zone on the beach, but *D. striatus* may also be found at times in the surf zone. The pattern of zonation of the *Donax* populations is influenced by several factors of which the most important seem to be the turbulence of the substratum and its wetness. Occasionally with unfavourable environmental conditions, the clams may lose their normal pattern of zonation for a few days in which case heavy mortality may result.

Tidal migration occurs with each shift of the tide. In D. denticulatus and D. striatus this is accomplished by the clams being transported up and down the beach in the wash but only and always burying themselves in the saturated wash zone. In doing this, the large muscular foot and the mobile siphons play an active role and these organs are therefore essential for the maintenance of the most favourable position on the beach. Originally in the Tellinacea these organs become adapted for a deposit-feeding habit, but in Donax it is clear that they have assumed new functions which enable the clams to live on the beach.

D. denticulatus occurs in dense populations throughout the West Indies while D. striatus is found in large numbers only in the larger islands. The factors which influence the distribution of D. striatus are uncertain, but those which affect D. denticulatus are such as to determine that populations occur only on clean alluvial beaches which are exposed to the open sea. Beaches of this sort are common throughout the West Indies and as a result D. denticulatus is found in most of the islands. Evidence suggests that D. denticulatus is the older and more established of the two species in the West Indies.

The populations of D. denticulatus at different localities vary greatly in density, size of clams, and colour of shells, and there are wide fluctuations in population densities from one year to the next. Nevertheless, this clam is usually the most abundant animal on the sandy beaches and comprises the largest biomass. Few animals challenge D. denticulatus in its occupancy of the saturated wash zone and the clams appear to suffer little from competition from the other beach-dwellers. As a result of their exposure, however, the clams are prey to several predators from other habitats.