SECTION C

LIFE HISTORY

I. INTRODUCTION

1. Scope of Study

Preliminary observations of *Donax* populations in the West Indies showed that populations vary greatly in density, size of clams, and colour of shells, and that there were wide fluctuations in population densities from one year to the next. To understand the reasons for this, it was necessary to work out the basic life history of the clams and to investigate the environmental factors which may operate on the populations.

Previous work on the life history of *Donax* has been carried out mostly in the higher latitudes. Coe (1955) reported *D. gouldi* as normally biennial in Southern California with periods of spawning, maximum growth, and mortality corresponding to definite climatic seasons. Loesch (1957) found that *D. variabilis* lived only for one year in Texas although like *D. gouldi*, there was a period of relative inactivity and lack of growth during the winter. In the West Indies, there is no need for overwintering as the sea temperature fluctuates little throughout the year and many of the other climatic factors which affect *Donax* populations in higher latitudes are unlikely to have the same effect in the West Indies. As a result therefore, it was expected at the outset of this study that the life history of Donax in the West Indies would show several major differences from that of the temperate and subtropical species.

2. Materials and methods

The populations of D. denticulatus at Port Henderson and Green Bay in Jamaica were observed and sampled regularly from March 1963 to December 1964 inclusive, a period of twenty-two months. These beaches, the locations of which are shown in Figure 23, were chosen for three reasons. First, they were easily accessible by road or sea at all times of the year. Second, their populations had marked differences in density and size of clams (Tables 7 & 8). And third, although they were in near proximity to one another, they had noticeable environmental differences. Three stations were set up at Port Henderson and two at Green Bay, each station being spaced approximately fifty metres apart, and at monthly intervals the population at each was sampled as described in Section B, Chapter V. Length - frequency graphs were made for all the stations, and the data compiled to make monthly composite length-frequency graphs for each beach. The twenty-two graphs so compiled for Port Henderson and for Green Bay are shown in Figures 24 and 25 and the data presented in Appendices IX & X. Using these data, the reproductive cycles, growth rates and survival curves for the populations were determined by methods which are described later.

Plankton hauls for a study of the larval forms were made in the waters off the two beaches using 97 and 140 mesh-per-inch nets.

Temperature and salinity measurements were made from October 1963 to December 1964 with a combined thermometer and hydrometer unit of the G.M. Manufacturing Company, New York.

Rainfall and wind-speed records for Palisadoes Airport from January 1963 to December 1964 were supplied by the Meteorological Service of the Government of Jamaica.

Information on the currents of Kingston Harbour was obtained from the Government of Jamaica Report on the Harbour of Kingston (1960) and is quoted by permission of the Ministry of Development and Welfare, Jamaica.

Morphological investigations and laboratory experiments were performed at the Marine Laboratory of the University of the West Indies.

Figure 23

Map of Kingston Harbour showing the locations of Port Henderson (PH) and Green Bay (GB), and the tidal currents on the flood (---->) and ebb (——>) tides in the vicinity (data on currents obtained from the Government of Jamaica Report on the Harbour of Kingston, 1960).

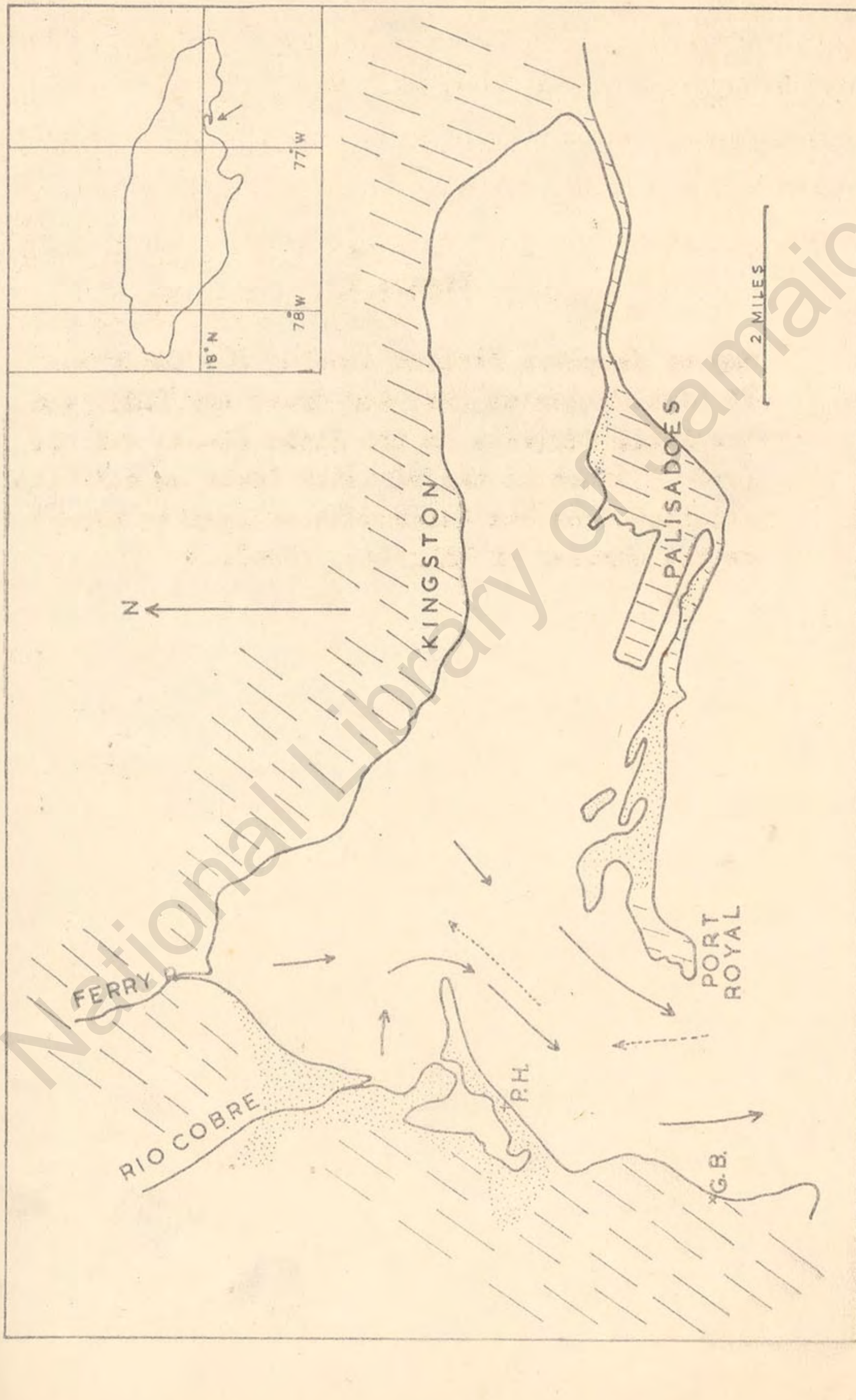

18°N
78°W
77°W
N
KINGSTON
PALISADOES
2 MILES
PORT ROYAL
FERRY R.
RIO COBRE
P.H.
G.B.

Figure 23

Figure 24

Composite length-frequency graphs for population samples of D. denticulatus at Port Henderson, Jamaica, from March 1963 to December 1964. The density of the population as clams per linear metre of beach in each month is shown. Data are given in Appendix IX.

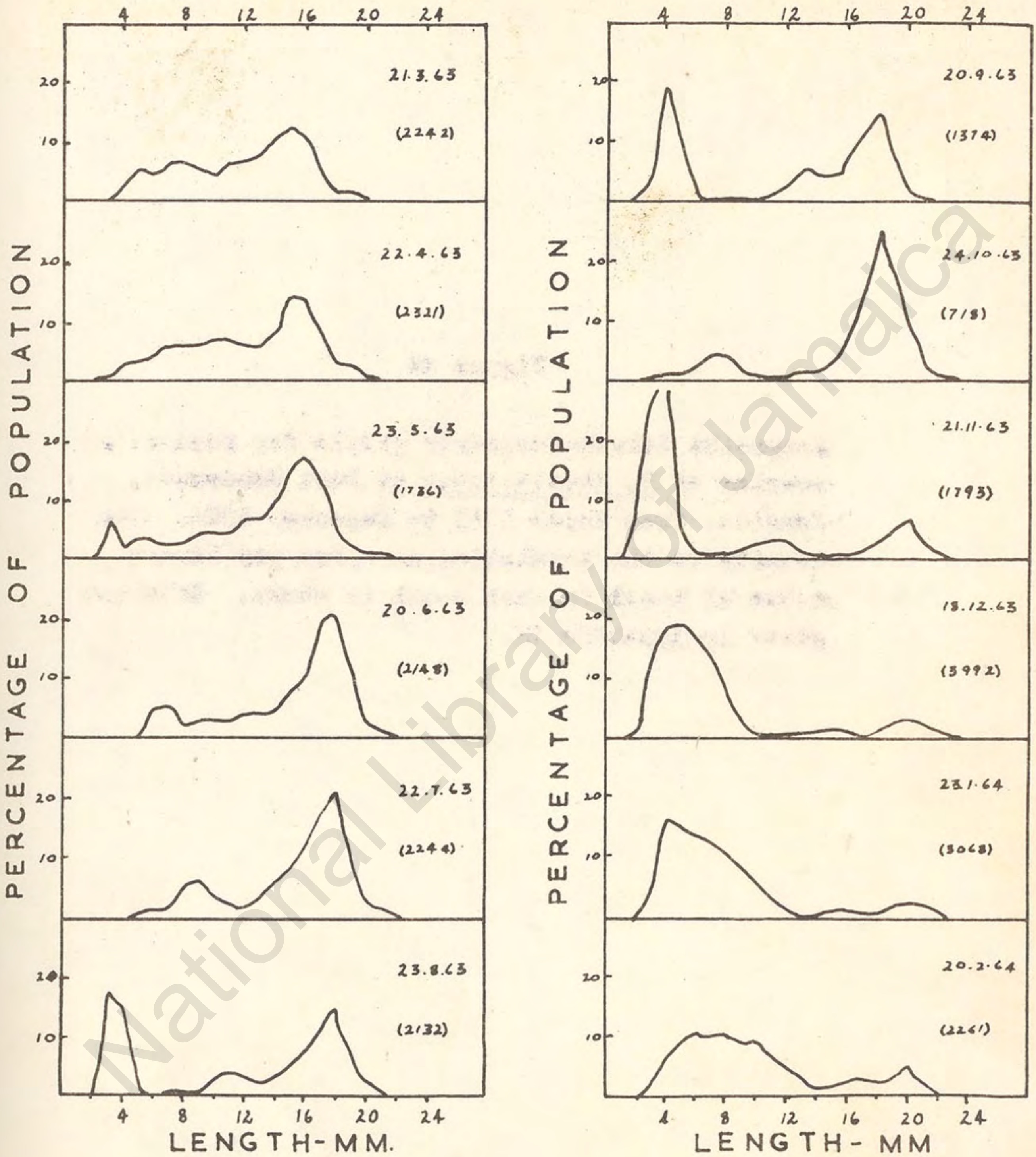
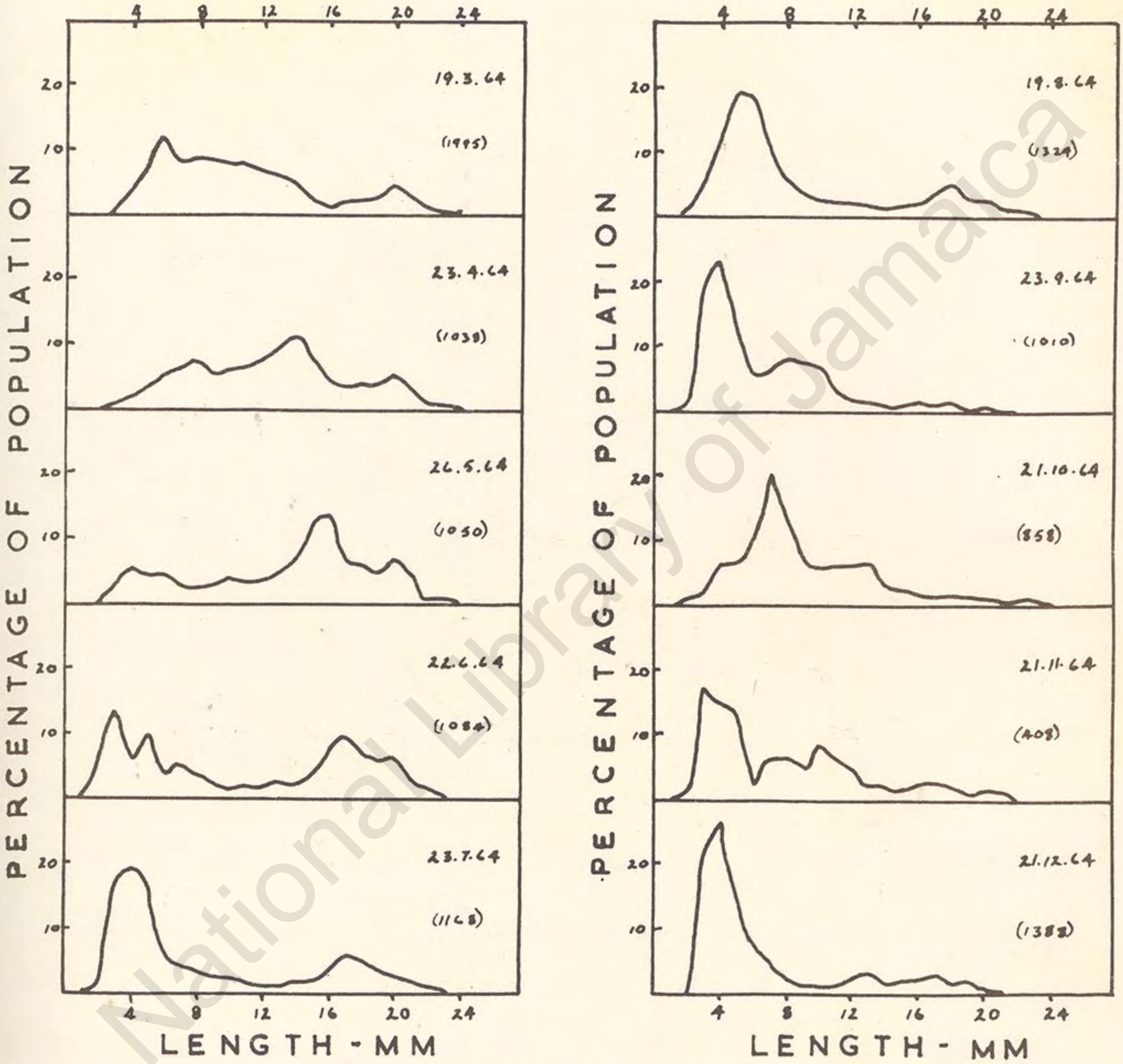

4 8 12 16 20 24
21.3.63
(2242)
22.4.63
(2321)
23.5.63
(1736)
20.6.63
(2148)
22.7.63
(2244)
23.8.63
(2132)
20
10
PERCENTAGE OF POPULATION
LENGTH-MM.
20.9.63
(1374)
24.10.63
(718)
21.11.63
(1793)
18.12.63
(3992)
23.1.64
(3068)
20.2.64
(2261)
LENGTH-MM

Figure 24



4 8 12 16 20 24
19.3.64
(1995)
23.4.64
(1038)
26.5.64
(1050)
22.6.64
(1084)
23.7.64
(1168)
PERCENTAGE OF POPULATION
LENGTH - MM
19.8.64
(1324)
23.9.64
(1010)
21.10.64
(858)
21.11.64
(408)
21.12.64
(1388)
PERCENTAGE OF POPULATION
LENGTH - MM

Figure 24

Figure 25

Composite length-frequency graphs for population samples of D. denticulatus at Green Bay, Jamaica, from March 1963 to December 1964. The density of the population as clams per linear metre of beach in each month is shown. Data are given in Appendix X.

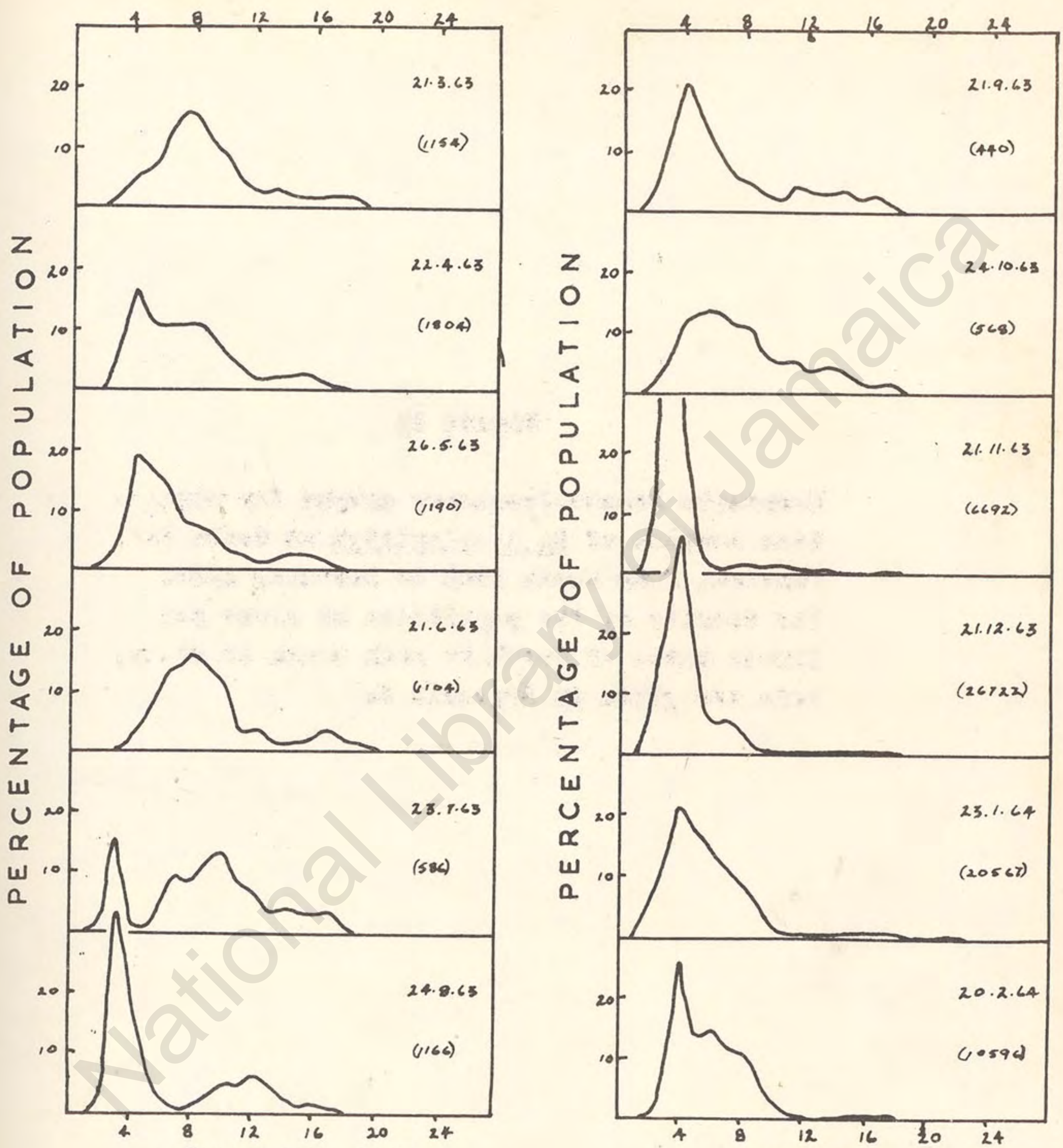
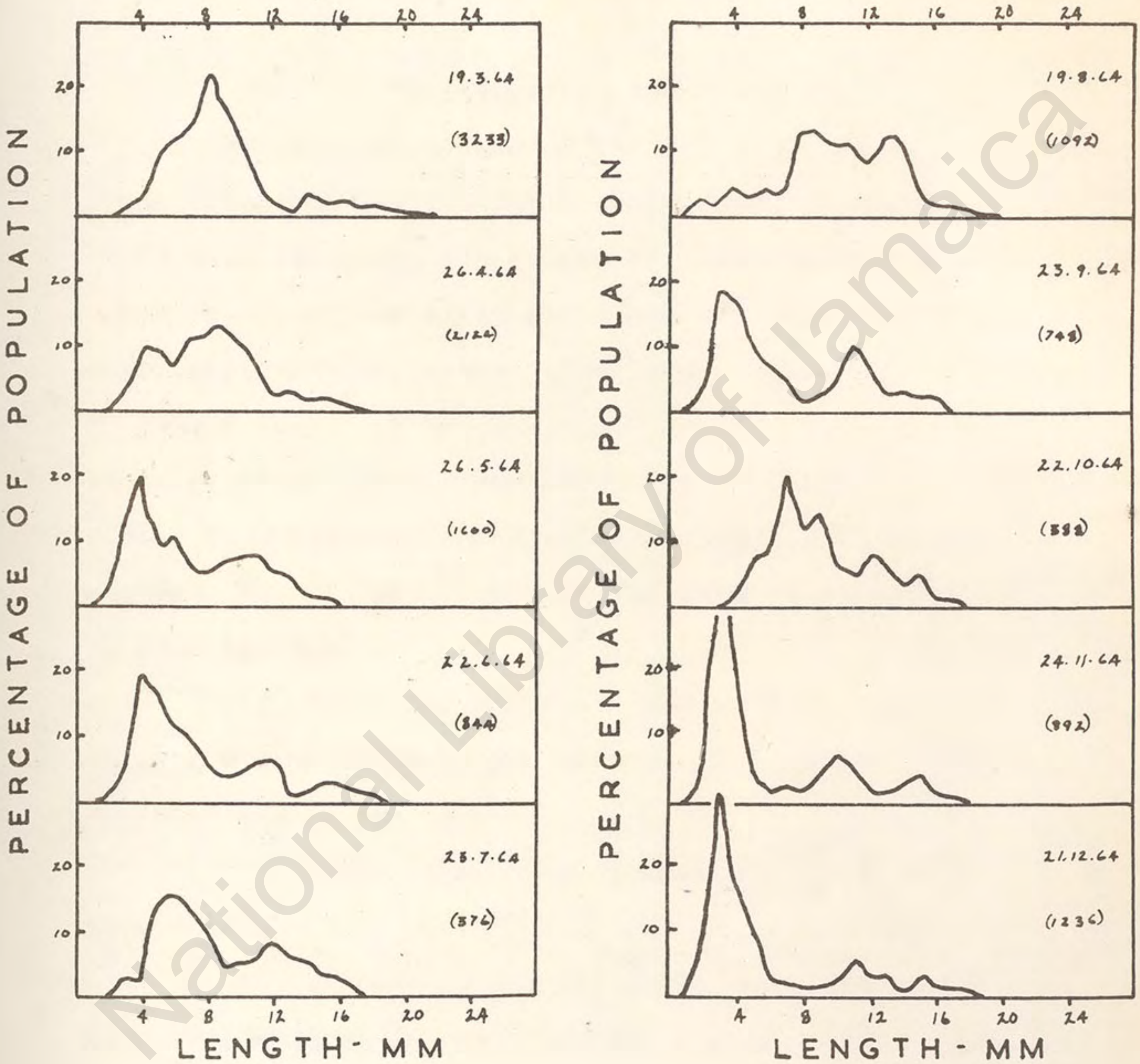

PERCENTAGE OF POPULATION
LENGTH- MM
21.3.63
(1154)
22.4.63
(1804)
26.5.63
(1190)
21.6.63
(1104)
23.7.63
(586)
24.8.63
(1166)
21.9.63
(440)
24.10.63
(568)
21.11.63
(6692)
21.12.63
(26722)
23.1.64
(20567)
20.2.64
(10596)

Figure 25



PERCENTAGE OF POPULATION
LENGTH - MM
4
8
12
16
20
24
10
20
19.3.64
(3233)
26.4.64
(2124)
26.5.64
(1600)
22.6.64
(844)
28.7.64
(376)
19.8.64
(1092)
23.9.64
(748)
22.10.64
(388)
24.11.64
(892)
21.12.64
(1236)

Figure 25

II. REPRODUCTION

1. Sexuality and spawning

In order to determine the sex of clams of <u>D. denticulatus</u> and the state of gonadial development throughout the year, the gonads of clams collected each month from Port Henderson and Green Bay were examined microscopically as smears. Generally, clams below 10 mm. in length showed no indication of sex and those in the range of 10 to 12 mm. were sometimes impossible to determine. From examination of animals larger than 12 mm., however, the following conclusions were drawn concerning <u>D. denticulatus</u>.

(1) The clams are dioecious. At no time was there any indication of the presence of gametes of the opposite sex in the gonads.

(2) There is an equal number of the sexes in populations.

(3) The gonads are ripest between August and January during which time they are creamy and full and liberate gametes freely when ruptured. Between February and July the gonads of the adult clams left in the population become pink and relatively empty and, although they usually contain some residual gametes, appear to be in a spent condition. In these months, the growing clams of

the younger year class have creamy gonads but they are not full and are immature.

Attempts to discover what factors trigger spawning and how it takes place were unsuccessful. At no time in the field was spawning observed and experiments to induce it in the laboratory met with negative results. Five different types of stimuli were used as follows:

(1) Temperature: Two methods were tried. In the first, ripe clams were transferred directly from sea water at room temperature (29°C) to water at 10, 20, 30, 35, 40, 45, and 50 degrees Centigrade. In the second, the temperature of the sea water was raised gradually from room temperature to 50°C over a period of an hour.

(2) Salinity: Ripe clams were left overnight in sea water of salinities 10, 15, 25, and 30 parts per thousand and returned the following day to normal sea water (35 parts per thousand).

(3) Exposure: Clams were left exposed on damp sand for one, two, and three days after which they were returned to sea water.

(4) Mechanical shock: A beaker containing clams was shaken vigorously for one hour.

(5) The introduction of gametes: Varying amounts of a suspension containing gametes of the opposite sex were introduced into the sea water with the clams.

In natural populations, spawning occurs at the age of about one year, and although a few adults may survive for a second year, the majority die shortly after (see Section C. Chapter IV).

2. Larval life

Very little is known of the larval life of Donax and there have been only two references to it in the literature. Rees (1950) described what he believed to be the veliconcha of D. vittatus although he had some doubts about it. Coe (1955) inferred that D. gouldi must have a larval life of two to three weeks or more and that the free-swimming larvae may be carried many miles from the parent population before settling. It does not seem, however, that he identified and described the larva. In the present study, observations and experiments were performed to determine the appearance and habits of the larval forms of D. denticulatus in the plankton, although some aspects were not clearly elucidated.

A. Veliger larva: In order to discover the form and dimensions of this larval form, it was necessary to perform an artificial fertilisation of the eggs and to rear the larvae in the laboratory. Fertilisation was done by first teasing out ripe gonads in filtered sea water and making up separate suspensions of the gametes. A few drops of sperm suspension were added to about 5 cc. of egg suspension and the mixture left for about half an hour during which time the fertilised eggs settled to the bottom of the glass dish. Excess sperm was then removed with an open-mouthed pipette and several changes of fresh filtered sea water made (Costello et al, 1957, page 105, for detailed description). Within one hour of fertilisation, first cleavage took place and after five hours, gastrulation occurred. The trocophore stage was reached in about ten hours and by twenty-four hours it had grown its velum and bivalve shell and become a typical straight-hinged veliger larva.

The larvae were reared at room temperature and fed with microplankton present in coarse-filtered sea water. (Changes of water were made twice daily). Although these conditions seemed to satisfy the larvae none survived beyond the tenth day. After death, shells were mounted on a slide and microprojected to trace and measure their outlines as shown in Figure 26A.

Once the characters of the veliger of D. denticulatus had been determined, plankton hauls were made with a 140 mpi. net to see if similar forms could be identified in the plankton. Examination of several straight-hinged shells revealed that although there was strong indication that some of them were that of Donax, there was no clear diagnostic feature on which to base a positive identification, and because of this, further attempts were abandoned.

B. Veliconcha larva: It is likely that death of the veliger larva in laboratory cultures after the tenth day was due to special requirements for metamorphosis to the veliconcha stage. Since this could not be provided successfully, another approach to obtaining veliconchas was adopted. Rees (1950) has outlined a key in which veliconchas may be identified to their superfamily by features based on the shape of the shell and the structure of the hinge. By a process of elimination, all the bivalve larvae found in

Figure 26

Three stages in the development of the planktonic larva of D. denticulatus.

A - Veliger

B - Early veliconcha

C - Late veliconcha (D, dissoconch)

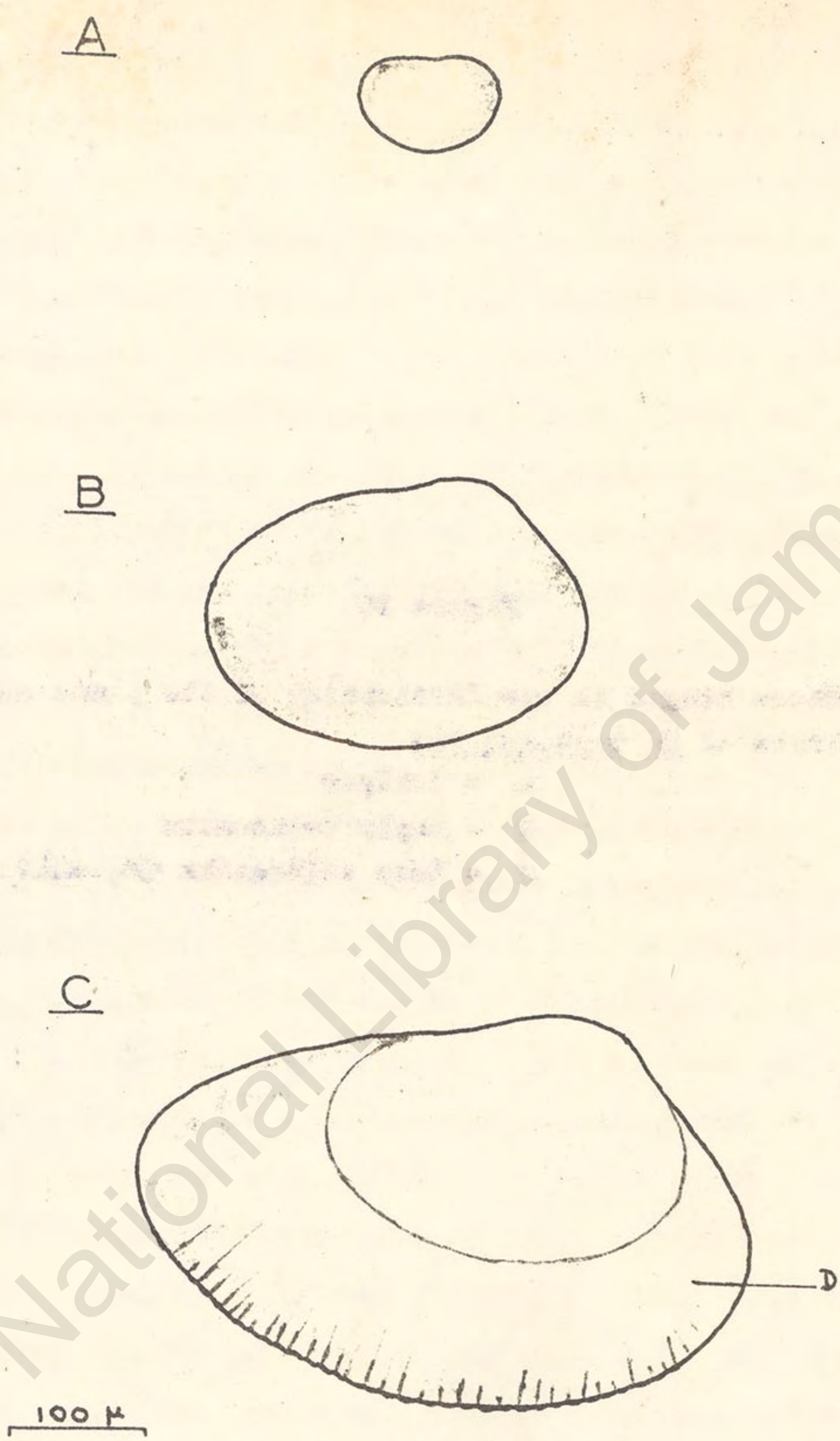


Figure 26

monthly plankton samples over two years were screened according to this key and it was found that in this period, there were six different representatives of the Tellinacea. The shape, dimension, and hinge structure of each were determined so that larvae belonging to any of them could be easily identified. Of these it was found that four occurred spasmodically in sparse numbers while the other two were common especially during the settling periods of Donax. During one such period (November to December, 1964), the plankton was sampled weekly and members of the two larval types of the Tellinacea found were removed and cultured in the laboratory. They were kept at room temperature (29°C) and fed twice daily on microplankton present in the sea water from which they were taken. The main purpose of this was to see if they would metamorphose into the adult forms and thus show which, if any of them, was the veliconcha of Donax. A daily check was made of both groups of larvae.

In the first group, the larvae were active and free-swimming for about four days, after which they lost their velum and settled down inactively on the bottom of the glass dish. They remained this way for about another week while metamorphosis took place after which they began to extend their long siphons and foot. A few days later, they all died. Examination of the new shell after death as well as the appearance of the siphons indicated that this adult form was not that of Donax.

In the second group, the larvae began by swimming actively for as much as ten days after which, on the loss of their velum, they ceased swimming and started probing around on the substratum with their larval foot. After another two days, they became completely inactive and remained like this while metamorphosis took place. During this time, new shell growth was rapid and the mantle papillae could be seen protruding below the shell. In no case, however, was metamorphosis completed before the larvae died although attempts were made to vary the conditions by adding beach sand to the culture dishes.

Despite the fact that internal metamorphosis was never completed in these larvae, it was possible to examine the new adult shell or dissoconch and thus to make a positive identification. Three features revealed that this veliconcha larva was in fact that of Donax:

(1) there were radial grooves on the newly formed shell;

(2) the ventral margin was crenulated;

(3) the shell had a purplish tinge.

Of the Tellinacea present in this area, only Donax possesses these three features, and since only D.denticulatus occurred nearby at the time, it was concluded that the larva taken from the plankton and reared was of this species.

A guide to the identification of the veliconcha larva is drawn up in Table 9, and representative stages in its development to the adult form are shown in Figure 26 B & C. The hinge structure is detailed in Figure 27.

Rees' (1950) description of what he believed to be the veliconcha of D. vittatus fits well enough with that of

Figure 27

Details of the hinge structure of the veliconcha larva of <u>D. denticulatus</u>.

U - umbo
PT - provincular tooth
L - ligament
ST - special tooth (right valve)
LST - large special tooth (left valve)
SST - small special tooth (left valve)

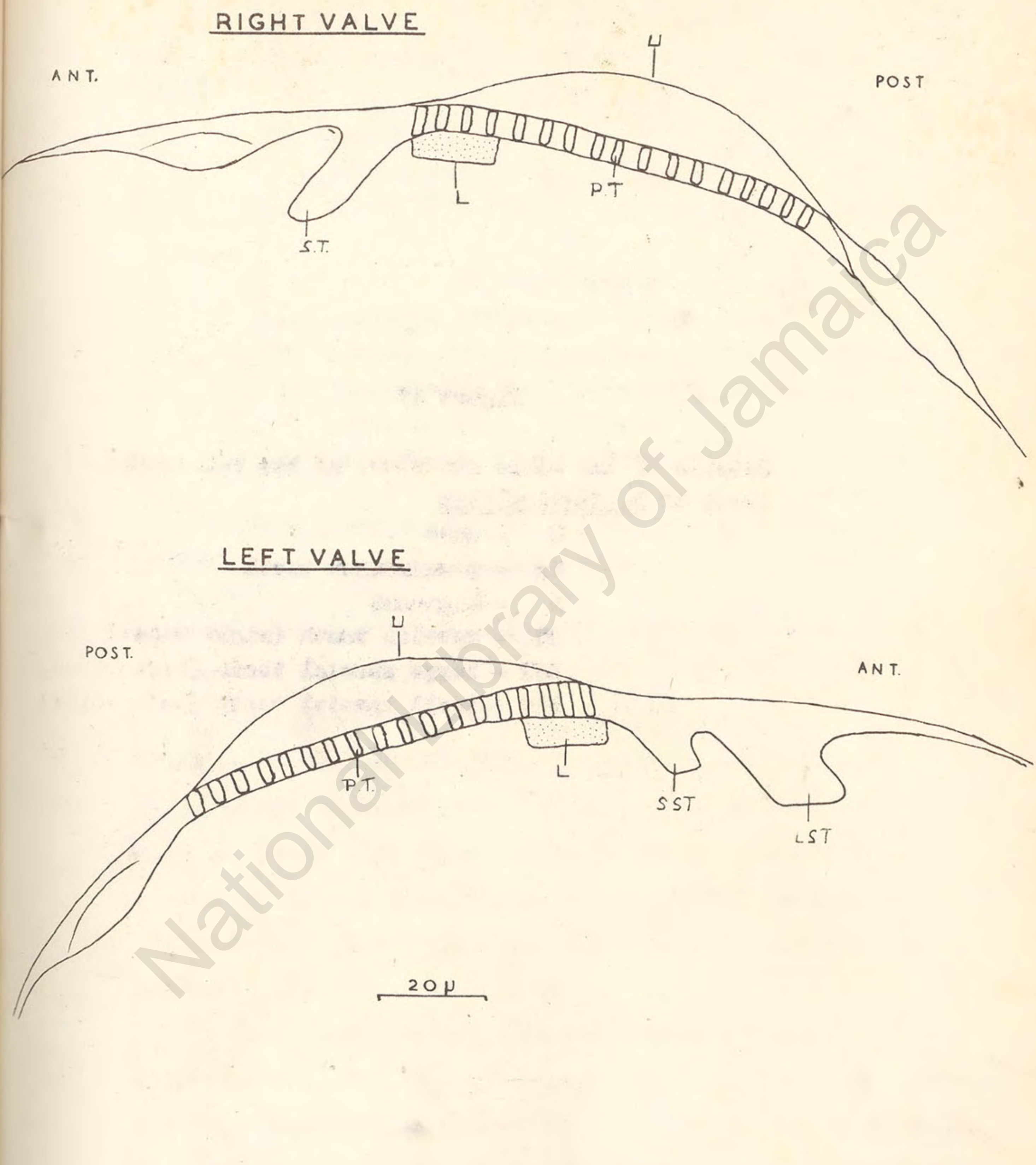

RIGHT VALVE
ANT.
U
POST
L
P.T
S.T.
LEFT VALVE
U
POST.
ANT.
L
P.T.
SST
LST
20µ

Figure 27

TABLE 9:- A guide to the identification of the veliconcha larva of D. denticulatus

SHAPE

(1) Broad side anterior.
(2) Umbo flat.
(3) Shell 245μ long x 190μ deep to 330μ long x 260μ deep.

HINGE STRUCTURE

(1) Ligament anterior 14μ - 17μ long.
(2) Sixteen to eighteen rectangular provincular teeth.
(3) Right valve with one special tooth, anterior, approximately 20μ long.
(4) Left valve with two special teeth, anterior.
Large tooth approximately 23μ long.
Small tooth approximately 10μ long.

D. denticulatus to make it appear that his identification was correct at least for the genus.

The veliconcha of D. denticulatus was found in the plankton throughout the year, but was especially abundant in November, December, and January. Under certain conditions, there were fewer larvae in the plankton and, as a result, the effects of three environmental factors were investigated. These were reduced salinity, currents, and wave action.

The normal salinity in the waters off Port Henderson and Green Bay is about 35 to 36 parts per thousand, but twice yearly it is likely to fall appreciably as a result of heavy rainfall which causes the Rio Cobre and the Ferry River (Figure 23) to flood. In June and October 1963, flooding of this sort resulted in a great deal of fresh water being emptied into Kingston Harbour, and on these occasions, the salinity fell to well below twenty parts per thousand (Table 10). In June and October 1964, heavy rains again caused a marked reduction in salinity by about five parts per thousand. During these periods, which coincided with the rainy seasons in Jamaica, it was noticeable that there were very few larvae in the plankton although there was reason to believe that, at least in October, Donax was still spawning actively. It seemed as a result that, although gametes were being shed into the water, fertilisation was either not taking place or the larvae were being killed.

Associated with reduced salinity at these times of the year was a high degree of fouling of the sea water by dead animals and plants, and it is believed that this had a secondary harmful effect on the larvae. Usually a return to normal salinity preceded the clearing of the water, and this fouling may therefore have had a more prolonged effect on the larvae than the reduced salinity itself.

Coe (1953) has drawn attention to the fact that tidal and ocean currents play an important role in transporting marine invertebrate larvae away from the parent population to settle elsewhere. This phenomenon has been investigated for D. denticulatus in the West Indies.

The predominant currents in the vicinity of Port Henderson and Green Bay as described in the Government of

TABLE 10:- The salinity of the waters off Port Henderson and Green Bay in 1963 and 1964

Date	Port Henderson	Green Bay
4. 6.63	17.0 pts/thous.	-
9.10.63	9.0	7.0 pts/thous.
18.10.63	32.0	30.5
21.11.63	33.5	32.5
18.12.63	34.5	33.0
23. 1.64	36.0	35.4
20. 2.64	36.0	35.7
19. 3.64	36.0	36.1
23. 4.64	36.0	36.6
26. 5.64	36.7	36.5
4. 6.64	33.0	32.2
23. 7.64	36.2	37.0
19. 8.64	36.5	36.5
23. 9.64	36.0	36.7
6.10.64	31.3	31.5
21.11.64	35.5	35.7
21.12.64	35.5	35.3

Jamaica Report on The Harbour of Kingston (1960) are shown in Figure 23. In monthly plankton samples over two years, it was found that whereas there were normally more veliger larvae off Port Henderson than off Green Bay, the veliconchas were more abundant near the latter, suggesting that there was a definite transport of larvae from within the harbour out to the open sea. Further indication of this was obtained from the fact that settlement at Green Bay was usually in excess of that at Port Henderson although the population at the latter always contained more breeding adults. During April and May 1964, the significance of this transport of *Donax* larvae by currents was clearly demonstrated on the east coast of Trinidad.

In one locality where there was no evidence of a previous population, spat were settling at the rate of more than 1,000 per metre of beach per month, while at another locality about ten miles away where there was a large spawning population, spat were not settling as might be expected. It seemed from this that due to the prevailing currents at the time, larvae were being transported many miles away from the established population to set up the new population.

With a planktonic life of at least two weeks - one week veliger and one week veliconcha - it is obvious that *Donax* must have great potentialities for dispersal during the larval stages.

The complete effect of wave action on the larvae of *D. denticulatus* is not known, but observations have been made which suggest that in its absence, metamorphosis and settling is affected. In the laboratory cultures, it was found that larvae left for a few days in still water tended to accumulate excess mucus and become fouled with debris whereas, with periodic agitation of the water, this was prevented. Moreover, swimming was always more active in the latter condition. In plankton sampling, equivalent observations were made as on very calm days, the larvae were concentrated near the bottom and were not as clean as otherwise. Larvae recovered from such samples usually never did as well in the laboratory as those taken on days when the waves were high.

3. Breeding cycles

The breeding periods of Donax may be determined from a knowledge of the state of the gonads, the presence of larvae in the plankton, and the periodic settling of spat. Of these, the last mentioned has now to be described before a consideration is made of the overall breeding cycles of the clams.

The composite length-frequency graphs in Figures 24 and 25 show that in some months of the year, a large number of spat enter the populations whereas at other times there is almost no settlement. Generally when spat settle in the course of a month, they are represented in the population as individuals having a length of 2, 3, or 4 mm. Thus for example in the August 1963 population at Port Henderson, the numbers which entered the population on one metre of beach was determined by counting the clams less than 5 mm. in length, and when this was done for all the monthly samples[1], data representing the rate of settlement per month were obtained (Table 11 and Figure 28).

From these data, it is seen that at least a few spat of D. denticulatus settled on the beaches every month over a period of nearly two years and that during this time, there was one very well defined peak of settlement on both beaches

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[1]Except ~~in November~~ and December, 1963, and January and February, 1964, when estimations were made by counting fractions of the entire sample.

Figure 28

The monthly rate of settlement of spat of *D. denticulatus* per linear metre of beach at (A) Port Henderson, and (B) Green Bay (Jamaica) from March 1963 to December 1964.

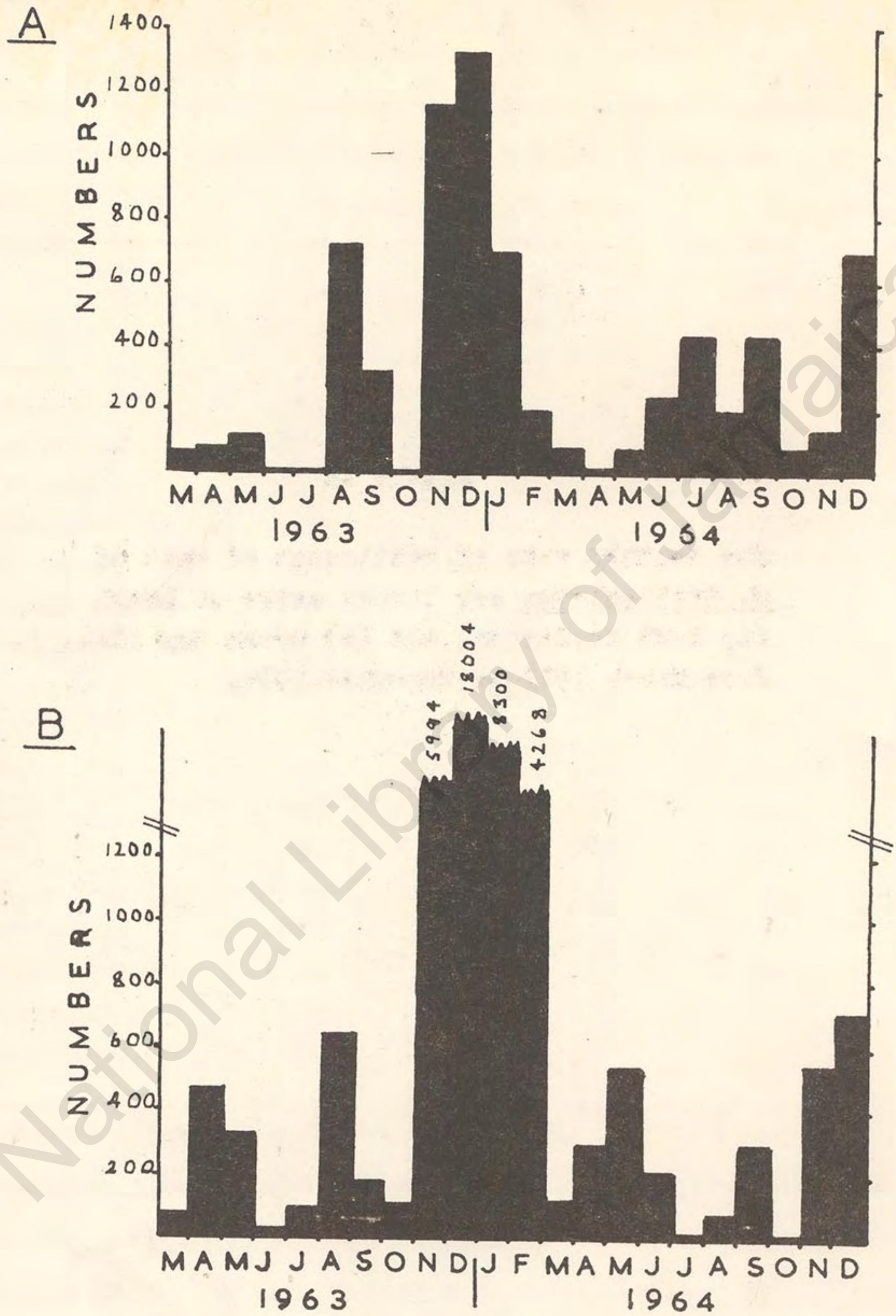

A
NUMBERS
1400
1200
1000
800
600
400
200
M A M J J A S O N D J F M A M J J A S O N D
1963
1964
B
NUMBERS
1200
1000
800
600
400
200
5994
18004
8300
4268
M A M J J A S O N D J F M A M J J A S O N D
1963
1964

Figure 28

TABLE 11:- The number of spat of D. denticulatus which settled on one metre of beach at Port Henderson and Green Bay from March 1963 to December 1964.

Month	Port Henderson	Green Bay	Average settling
March 1963	74	88	81
April	79	474	276
May	120	336	228
June	8	36	22
July	7	104	55
August	721	654	687
September	318	184	251
October	7	114	60
November	1156	5994	3575
December	1329	18004	9666
January 1964	694	8300	4497
February	202	4268	2235
March	78	120	99
April	24	304	164
May	83	548	315
June	237	208	222
July	442	20	231
August	204	84	144
September	433	300	366
October	81	8	44
November	138	548	343
December	700	724	712

from November 1963 to February 1964. In November and December 1964 settlement was again high and gave indication of the beginning of another peak settlement, although cessation of sampling prevented a clear demonstration of this[1].

[1] Subsequent observations made during an undergraduate Marine Biology Field Course in January, 1965 confirmed that settlement continued at a high rate into this month.

At Port Henderson, other large settlements were in August 1963 and July to September 1964, and at Green Bay, peaks were in April and August 1963, and May 1964.

Because of the evidence that spawning at Port Henderson often results in settlement at Green Bay, it is necessary to combine the rate of settlement at both beaches in order to illustrate the general settling pattern of the populations. On doing this (Figure 29), it is seen that the greatest settlement occurred in and around the month of December while the lowest settlements were in and around March, June and July, and October. These results may be correlated with observations on the condition of the gonads throughout the year and the presence of larvae in the plankton.

At around August each year, the gonads of the growing clams become fully matured and large-scale spawning commences. As a result, there is a rapid increase in the rate of settlement although in September and/or October with the onset of the rainy season, this is interrupted due to fouling and a drop in the salinity of the sea water. For one or two months, therefore, there is very little settlement, but by the time the sea water returns to normalcy in November or December, spawning is still occurring and there is heavy settlement again. By around February, most of the adult clams have died after having spawned and those that do survive are in a spent condition. There is therefore a great reduction in settlement from this time onwards until with the maturation of the clams of the new year class in August, large-scale spawning commences again.

Figure 29

The combined average monthly rate of settlement of spat of D. denticulatus per linear metre of beach for Port Henderson and Green Bay (Jamaica) from March 1963 to December 1964. A suggested normal distribution curve is superimposed on the histogram (see text).

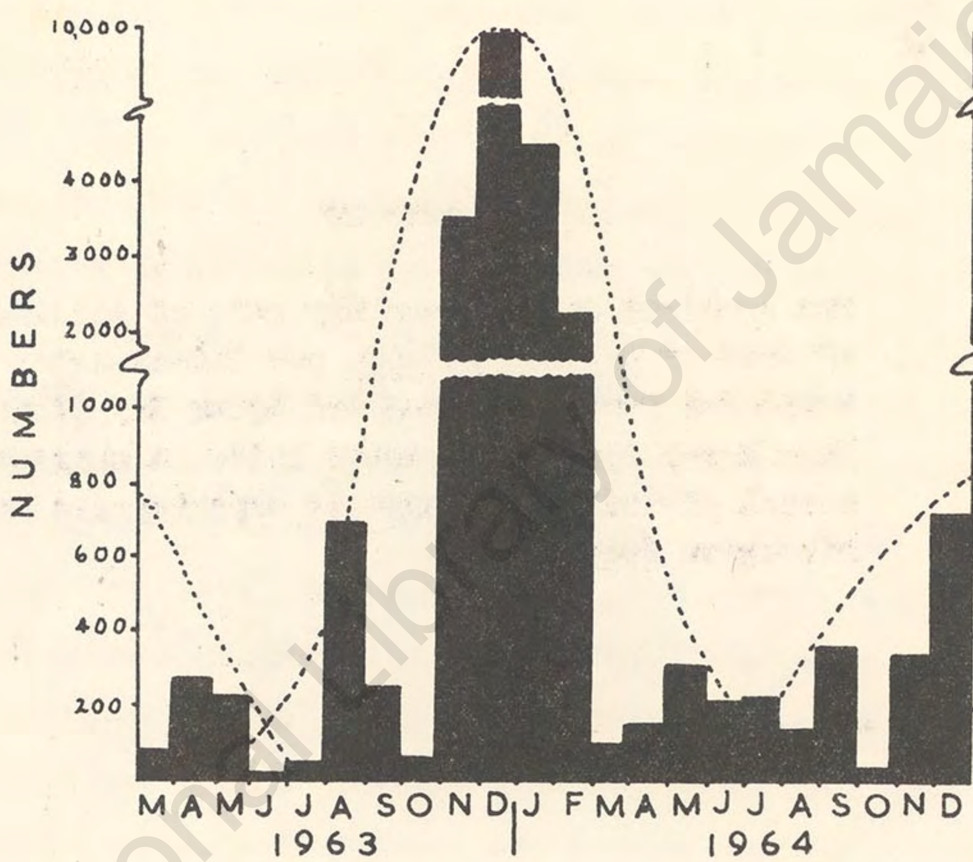

10,000
4000
3000
2000
1000
800
600
400
200
NUMBERS
M A M J J A S O N D J F M A M J J A S O N D
1963
1964

Figure 29

In March 1963, as also in March and April 1964, settlement was surprisingly low. In these months of low settlement, however, the beaches were debris-strewn as a result of high seas, and it is likely that although larvae may have arrived at the beaches, they may have been prevented from settling due to the unfavourable conditions. Furthermore and for the same reason, even if they did settle, mortality of the spat would have been higher than normal.

Since the peak settlement of November to February coincides with the ripening of the gonads and the greatest abundance of larvae in the plankton, it may be concluded that breeding activity is highest at this time of the year. Similarly because of the spent condition of the gonads, the lack of larvae in the plankton, and the low rate of settlement, it may be assumed that breeding activity is lowest in June and July. For these reasons it may be feasible to superimpose a suggested normal distribution curve on the histogram of Figure 29 to represent the annual breeding cycle of the clams. If this is done, it is seen that except for the periods around March and October when environmental conditions are unfavourable for settling, the curve fits well enough to indicate that this is in fact, the annual breeding pattern.

D. striatus

The only evidence of the breeding activity of D. striatus was obtained from the fact that a few spat of this species (less than ten per metre of beach) settled at

Port Henderson and Green Bay in November 1963 and again at Port Henderson in August, October, and December 1964. These periods are the same as those of peak settlement for D. denticulatus and may mean that the reproductive activity is similar in both species.

4. Discussion

The breeding cycles of only a few species of Donax have been mentioned in the literature. Nayar (1955) found that in India, D. cuneatus begins to spawn in January just after there is a sudden drop in salinity, and reaches its peak in April after a period marked by a steady increase in temperature. Coe (1955) reported that in Southern California, D. gouldi has an extended breeding season from April to November corresponding to the warm months of the year. Loesch (1957) observed that spat of D. variabilis were most numerous in September, but gave no indication of the periods of spawning.

Because of the lack of much knowledge about the breeding periods of other species of Donax, it is not possible to draw conclusions on the breeding habits of the genus as a whole. However, it is possible to compare the activity of Donax in the West Indies with that of other marine invertebrates in the area and to investigate the environmental conditions which favour breeding at the particular time. Goodbody (in press) has described the reproductive activity of Emerita portoricensis (Schmidt) at Green Bay, Jamaica, and notes that while there is activity throughout the year, there may be two peaks centred around February and June. In the same paper, Goodbody also reports that the mysid, Mysidium columbiae (Zimmer) breeds continuously throughout the year with uniform activity in the mangrove area of Kingston Harbour. In similar studies on three species of ascidians in the environment of Kingston Harbour, Goodbody (1961a) found that while breeding was continuous, definite peaks of settlement occurred at certain times of the year:

"In Diplosoma macdonaldi the peaks are ill defined but in both Ascidia nigra and Symplegma viride there is a noticeable peak of settlement from September to the end of December."

From these works and from the present findings on Donax, it is seen that in the vicinity of Kingston Harbour, at least six species of marine invertebrates breed continuously, and that four of these have a peak of activity somewhere between September and February. Goodbody (1961a) has shown that there is no obvious correlation between this peak of activity and the fluctuations in temperature and tides, and from this present study, there is nothing to indicate that salinity is related. Goodbody (1962) has suggested, however, that there may be some relationship between breeding periods and the presence of a particular fraction or species in the phytoplankton at a certain season of the year; but until data on the local phytoplankton is available, this cannot be substantiated.

Figure 30

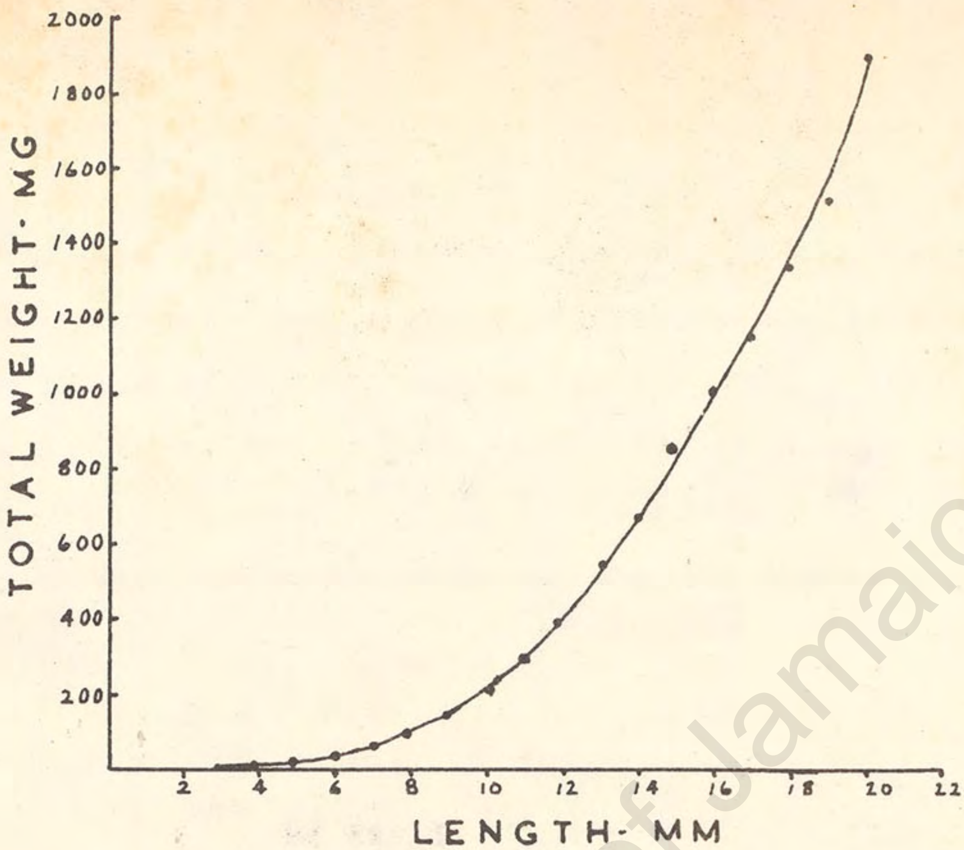
Graphs showing the relationship of growth parameters in <u>D. denticulatus</u>.

III. GROWTH

1. Measurement of growth

The growth rates of four species of Donax have been studied and in each it has been represented as a monthly increase in shell length (Nayar, 1955; Coe, 1955; Loesch, 1957). Nayar has, however, produced data to show that in D. cuneatus there is a simple relationship between this measurement and those for increase in depth, thickness, and total weight. Similar data have been obtained for D. denticulatus and are presented in Figures 3 and 30, Appendices I and XI and show that as in D. cuneatus, these parameters have a simple relationship to one another. For this reason, growth in D. denticulatus may be reliably represented as increase in shell length.

In order to measure the growth rates of D. denticulatus at Port Henderson and Green Bay, modal peaks of individual size-classes in the monthly composite length-frequency graphs (Figures 24 and 25) were followed from month to month and the increase in growth determined from the observed shift of the modal peaks along the length scale. Generally as the clams grew older the peaks became less distinct although, in most cases, they could be detected even after growth had ceased. Four groups of clams were observed throughout their life span at Port Henderson whereas at


TOTAL WEIGHT - MG
2000
1800
1600
1400
1200
1000
800
600
400
200
2
4
6
8
10
12
14
16
18
20
22
LENGTH - MM

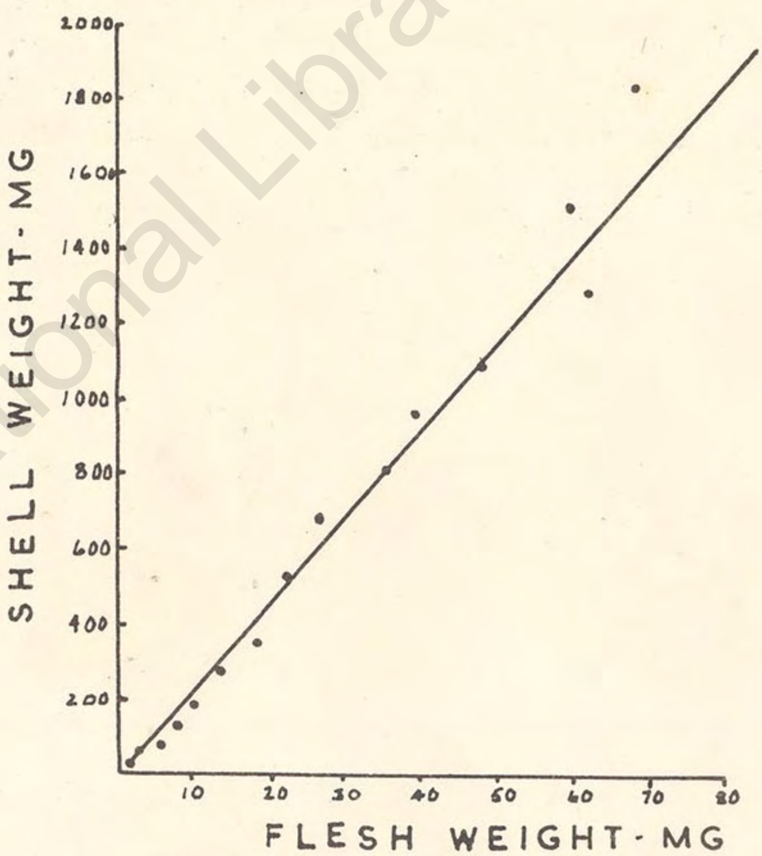

SHELL WEIGHT - MG
2000
1800
1600
1400
1200
1000
800
600
400
200
10
20
30
40
50
60
70
80
FLESH WEIGHT - MG

Figure 30

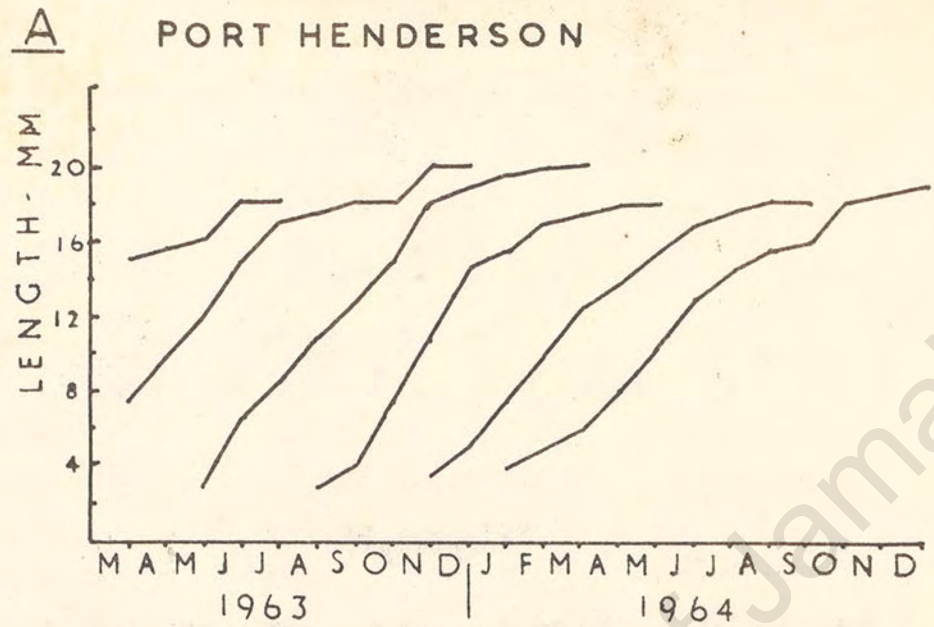
Green Bay where the peaks were less distinct and tended to merge into one another, only three groups could be followed. Data obtained by this method and representing the lengths of the groups of clams in successive months are given in Tables 12 and 13 and illustrated in Figure 31.

TABLE 12:- The monthly modal shift of size-classes of clams of <u>D. denticulatus</u> at Port Henderson from March 1963 to December 1964.

Month	Modal shift					
March 1963	15.0mm	7.5mm				
April	15.5	10.0				
May	16.0	12.0	3.0mm			
June	18.0	15.0	6.5			
July	18.0	17.0	8.5			
August		17.5	11.0	3.0mm		
September		18.0	13.0	4.0		
October		18.0	15.0	7.5		
November		20.0	18.0	11.0	3.0mm	
December		20.0	19.0	14.5	5.0	
January 1964			19.5	15.5	7.0	4.0mm
February			20.0	17.0	10.0	-
March			20.0	17.5	12.5	6.0
April				18.0	14.0	8.0
May				18.0	15.5	10.5
June					17.0	13.0
July					17.5	14.5
August					18.0	15.5
September					18.0	16.0
October						18.0
November						-
December						19.0

Figure 31

The monthly shift in modal peaks of size-classes of clams of D. denticulatus at Port Henderson and Green Bay (Jamaica) from March 1963 to December 1964.


A
PORT HENDERSON
LENGTH - MM
20
16
12
8
4
M A M J J A S O N D J F M A M J J A S O N D
1963
1964

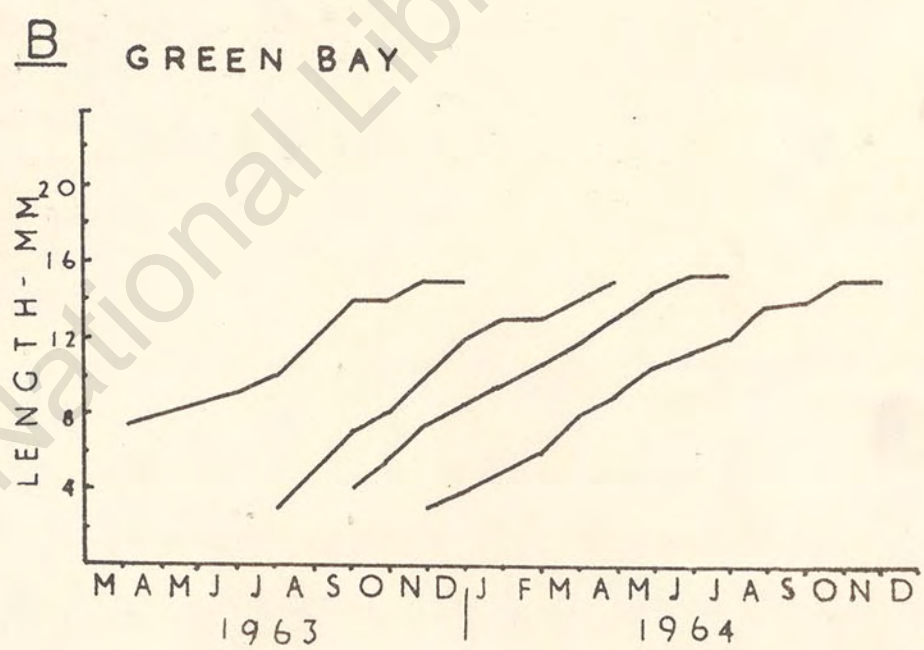

B
GREEN BAY
LENGTH - MM
20
16
12
8
4
M A M J J A S O N D J F M A M J J A S O N D
1963
1964

Figure 31

TABLE 13:- The monthly modal shift of size-classes of clams of D. denticulatus at Green Bay from March 1963 to December 1964.

Month	Modal shift			
March 1963	7.5mm			
April	8.0			
May	8.5			
June	9.0			
July	10.0	3.0mm		
August	12.0	5.0		
September	14.0	7.0	4.0mm	
October	14.0	8.0	5.5	
November	15.0	10.0	7.5	3.0mm
December	15.0	12.0	8.5	4.0
January 1964		13.0	9.5	5.0
February		13.0	10.5	6.0
March		14.0	11.5	8.0
April		15.0	13.0	9.0
May			14.5	10.5
June			15.5	11.5
July			15.5	12.0
August				13.5
September				14.0
October				15.0
November				15.0
December				15.0

2. Growth rates

In analysing the growth measurements of D. denticulatus, particular emphasis was placed on the variations in the growth of the clams as a result of age, habitat, and seasons.

A. Age: The age of clams in any size-class was determined from the month in which the modal peak of the newly settled spat began to advance along the length scale. Spat having a length of less than 5 mm. were considered as having entered the population in the course of the month and were therefore regarded as being not more than one month old. By averaging for each locality the lengths of each size-class of clams in progressive months of their life span (Tables 12 and 13), data representing the average monthly sizes of the clams were obtained (Table 14).

TABLE 14:- The average lengths of size-classes of clams of D. denticulatus at Port Henderson and Green Bay in progressive months of their life span.

Age	Port Henderson	Green Bay
1 month	3.2mm.	3.3mm.
2	5.2	4.8
3	7.2	6.5
4	10.0	7.5
5	12.6	9.8
6	14.4	10.5
7	16.2	11.6
8	17.2	12.5
9	17.7	13.5
10	18.2	14.6
11	19.0	14.7
12	19.0	15.0

From these data, growth curves were plotted (Figure 32A) which show a pattern in which growth is constant for the first seven months of life after which it slows down gradually and finally ceases about the eleventh month. This means that for clams which settle during the peak period of settlement in and around December, growth is at its

Figure 32

A: Average growth curves for clams of <u>D. denticulatus</u> at Port Henderson and Green Bay (Jamaica).

B: Growth curves of clams of <u>D. denticulatus</u> which entered the populations at Port Henderson and Green Bay (Jamaica) in November 1963.

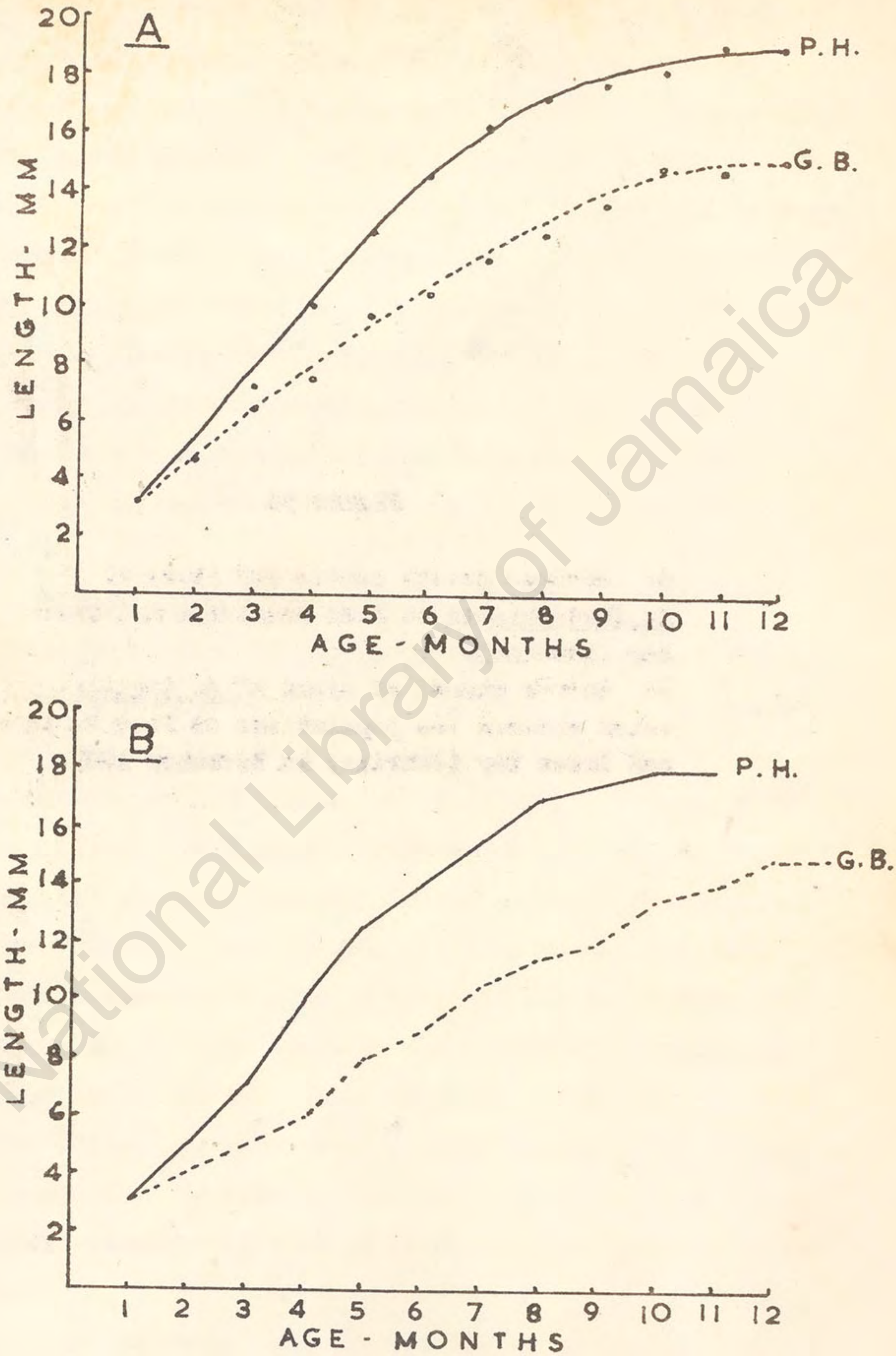

A
LENGTH- MM
20
18
16
14
12
10
8
6
4
2
1 2 3 4 5 6 7 8 9 10 11 12
AGE - MONTHS
P. H.
G. B.
B
LENGTH- MM
20
18
16
14
12
10
8
6
4
2
1 2 3 4 5 6 7 8 9 10 11 12
AGE - MONTHS
P. H.
G. B.

Figure 32

maximum while the gonads are developing, but then as they become ripe and spawning commences, it slows down and eventually ceases. Occasionally a few adults survive after spawning and growth may continue, but this is among so few animals that it cannot be reliably measured by the length-frequency method. The maximum growth rate recorded for D. denticulatus is between 2.5 to 3.0 mm. per month and is about the same as for D. cuneatus in India. In Texas D. variabilis has a maximum rate of 1.75 mm. per month and D. tumida a maximum rate of less than 1 mm. per month. D. gouldi in Southern California also grows less than 1 mm. per month.

B. Habitat: From Figure 32A, it can be seen that the average growth rate of D. denticulatus at Port Henderson is greater than at Green Bay. Specifically, this is well illustrated by the growth curves of the groups of clams which entered the populations on both beaches in November 1963 (Figure 32B). As a result of these differences in growth rates, the sizes of the adult clams on the two beaches are correspondingly different, and whereas a spawning individual at Port Henderson is usually about 18 mm. in length, that at Green Bay is only about 15 mm. Similarly, the maximum size of the clams at each locality is influenced by their growth rates, and whereas individuals as large as 23 mm. in length were frequently found at Port Henderson, the largest animals occurring at Green Bay were only 20 mm. in length.

In an analysis of populations occurring in Jamaica

(Section B, Chapter V) it was found that the sizes of the adult clams varied appreciably from one beach to the next (Table 8 and Figure 18). This variation may now be inferred to be the result of differences in growth rates of the clams at the different localities.

C. Seasons: Pronounced variations in the growth of clams over the period of study occurred on three occasions and involved at each time a rapid increase in the growth rate of the near-adult individuals (Figure 31A and B). These occasions were in May to June 1963, October to November 1963, and September to October 1964, and corresponded to the periods of lowest salinity and maximum rainfall in the area (Tables 10 and 18). At these times also, growth rings and colour bands appeared on the shells of the clams (Figure 33A and B).

3. Growth rings

Growth rings in bivalve molluscs are formed as a result of variation in growth rate. Wilbur and Owen (1964) have reported from the work of other authors that at least four environmental conditions may bring this about. These are low temperature, high temperature, physical disturbances, and violent wave action. Nayar (1955) suggested that growth rings in D. cuneatus were probably formed when the environmental conditions are unfavourable for growth as a result of high winds and rough seas. In the case of D. denticulatus, however, none of these factors appear to be responsible for ring formation.

Figure 33

Growth variations in D. denticulatus in Jamaica

A: growth rings in mature clams

B: colour bands in young clams

A

B

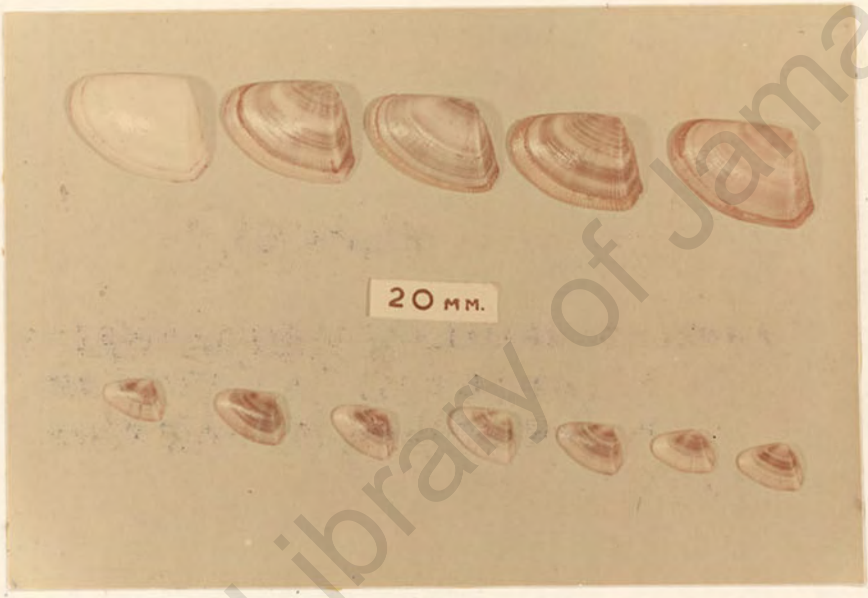


Figure 33

During the months of May, June, September, October, and November when growth rings are formed in <u>Donax</u> in Jamaica, the significant changes in the environmental conditions are a drop in salinity of the sea water and an increase in its turbidity. From a study of growth rates, it has been found that accompanying the formation of rings there is a rapid increase in growth, and not a decrease as is usually reported for other genera. Moreover, this increase occurs primarily in the near-adult clams which have almost ceased growing and suggests that at such times, there is a stimulus for increased growth as a result of improved conditions. If this were the result of reduced salinity, it would be expected to have the same effect on clams of all ages; but as these conditions are limited to the older clams, this cannot be the case. Increased turbidity may, however, be associated with a rise in the food content of the water, and if the amount of available food is at any time a limiting factor on the growth of the larger animals this increase would be preferential to them. Data in support of this are given in a later section in which the environmental factors affecting growth are considered.

Although actively growing clams do not normally produce growth rings, they do nevertheless have concentric colour bands which correspond to the periods of ring formation in the larger animals (Figure 33B). These bands are most often formed by a different shade of the same colour of the shell, although in some, a new colour may be laid down. Usually after some months the band reverts to the original colour of the shell.

In Section B, Chapter V it was mentioned that the shells of clams at different beaches vary significantly and frequently show a tendency towards one particular colour (Figure 20). If colour bands are formed as a result of the same environmental conditions which bring about the formation of growth rings, that is as suggested, a change in the food content of the water, then it is feasible to propose that the variations in shell colour from one beach to the next may similarly be caused by differences in the amount and/or nature of the food. For this reason, we would expect to find differences in the food content of the water at Negril where the shells are nearly all white from that at Black River where most of the shells have a strong shade of purple. This is partly supported by data obtained in an analysis of the environmental conditions which affect growth and will be considered next.

4. Environmental conditions

Variations in temperature, solar radiation, salinity, and food supply are known to have a considerable effect on the growth of some marine bivalves (Fox & Coe, 1943; Coe, 1947; Coe, 1948). In the West Indies, sea temperature fluctuates only about 5°C (Lewis, 1960 and Table 15) and solar radiation is the same throughout the year. Salinity of the water is maintained at a relatively constant level for most months except in the vicinity of rivers where it may fall appreciably during the rainy seasons. Variation in food content has not been previously determined.

TABLE 15:- The monthly surface sea temperatures at Port Henderson and Green Bay during 1964.

Month	Port Henderson	Green Bay
January	28.3°C	28.3°C
February	28.8	29.0
March	29.8	29.5
April	29.0	30.0
May	31.2	32.0
June	31.9	29.5
July	28.0	28.5
August	31.5	31.5
September	30.8	30.6
October	32.5	30.3
November	28.0	27.0
December	27.8	28.0

In Part 2 of this Chapter, it was mentioned that the main seasonal variation in growth of D. denticulatus is a rapid increase in the growth of the near-adult clams with the formation of growth rings during the rainy seasons. Furthermore, it was proposed that these variations are brought about by an improvement in growth conditions due to an increase in the food content of the sea water and not by the adverse factors associated with reduced salinity. In order to assess the validity of this hypothesis, an experiment was performed during 1964 to measure the monthly fluctuations in food content of the water at Port Henderson and Green Bay and to determine its influence on the growth rates of the clams.

Fox, Isaacs, and Corcoran (1952), and Fox (1957) explained the importance of the suspended organic detritus in the sea water (leptopel) as the major component of the food of suspension feeders[1] and described a method for its recovery and measurement. This method has been employed with necessary modifications (Appendix XII) at Port Henderson and Green Bay and has provided relative measurements of the differences and fluctuations in the food content of the water.

The results (Table 16) reveal first that during 1964, there was usually more organic leptopel at Port Henderson than at Green Bay, and second that during the period of ring formation and increased growth rate, the food content of the water at both beaches was at its highest. At Port Henderson the average organic leptopel content for the year was 7.3 mg. per litre while at Green Bay it was 4.44 mg. per litre. The ratio of these quantities, approximately 7:4, is about the same as the ratio of the average maximum growth rates of the clams at both beaches - 2.5 mm. per month to 1.5 mm per month (Figure 32) - and indicates a definite relationship between the two. This was further investigated by measuring the organic leptopel content of the water at the beaches in Jamaica on which Donax occurs and correlating the results with the known maximum sizes of the clams at

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[1]Yonge (1949a) described the Tellinacea as a deposit-feeding group of bivalves. In Section D of this thesis, however, it is shown that Donax is a suspension feeder.

TABLE 16:- Results of quantitative studies of the leptopelic organic matter present in the sea at Port Henderson and Green Bay during 1964.

Month	Port Henderson	Green Bay
January	5.85 mg/litre	4.16 mg/litre
February	10.72	7.03
March	7.58	4.79
April	2.83	2.83
May	5.74	2.56
June	8.04	3.34
July	7.39	4.16
August	4.49	4.34
September	12.17	4.15
October	13.66	10.06
November	7.97	3.67
December	2.20	2.20
AVERAGE	7.39 mg/litre	4.44 mg/litre

these localities.[1] The data obtained are shown in Table 17 and Figure 34, and reveal that with the exception of Port Henderson where the water was unusually turbid at the time of sampling, the two sets of measurements show a positive linear regression on one another[2]. These results along with those from the monthly samples at Port Henderson and Green Bay demonstrate that the rate of growth in D. denticulatus is directly correlated with the food content of the sea water and increases proportionately with it.

[1]Since the maximum sizes of the clams are determined by their growth rates, this measure can be substituted as an index of growth rates.

[2]Regression values: b= 0.424 a= -3.98 P= 1%

Figure 34

Regression line showing the correlation between the maximum length of clams of *D. denticulatus* and the organic leptopel content of the sea water at ten localities in Jamaica. Data for Port Henderson have been omitted (see text).

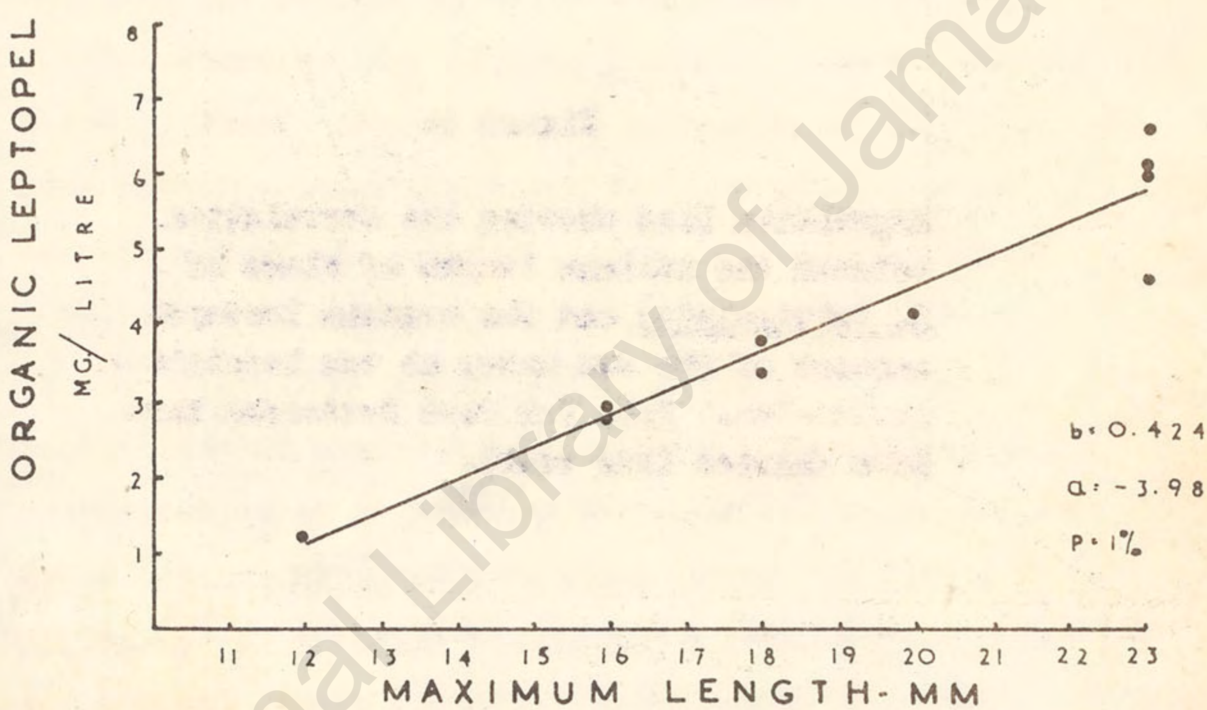

ORGANIC LEPTOPEL
MG/ LITRE
8
7
6
5
4
3
2
1
11
12
13
14
15
16
17
18
19
20
21
22
23
MAXIMUM LENGTH- MM
b = 0.424
a = -3.98
P = 1%

Figure 34

Because of this, it follows that any environmental factor which may affect the amount of suspended organic detritus in the water will also have an influence on the growth of the clams, and three such factors are known. These are:

A. Proximity to river: From the distribution map of *D. denticulatus* in Jamaica (Figure 16) it is seen that most of the populations occur near the mouth of a river or swamp and that the beaches on which the largest clams are found (Port Henderson, Small Point, Farquhar's Beach, Black River, and Hope Wharf) are in closest proximity to the large rivers. From previous considerations, it has been seen that this is as a result of the greater food supply in such localities although there may be two reasons why there is more food in the vicinity of rivers. In the first place when a river empties itself into the sea, the detritus settles out of suspension as it is transported along the coast so that the water becomes progressively less turbid and poorer in leptopel. As a result the nearer a beach is to the river, the greater is the amount of suspended organic matter that it receives directly from it. At Port Henderson and Green Bay this was very noticeable as, whenever the Rio Cobre and the Ferry River flooded, the food content at Port Henderson increased a great deal more than at Green Bay. Secondly, a region of high organic matter supports more extensive and diversified organisms resulting in a greater turnover of organic carbon in the area. As the food chains become more intensified, the production of detritus increases so that with time, more and more suspended organic matter is

TABLE 17:- The organic leptopelic content of the water in September 1964 at beaches in Jamaica on which Donax occurs and the maximum sizes of the clams at these localities.

Locality	Organic Leptopelic content	Maximum sizes of clams
Negril	1.23 mg/litre	12mm
Puerto Seco	-	12
Alligator Pond	2.84	16
Port Maria	2.88	16
Montego Bay	3.31	18
Gut River	3.73	18
Green Bay	4.15	20
Small Point	4.62	23
Hope Wharf	6.05	23
Farquhar's Beach	6.13	23
Black River	6.62	23
Port Henderson	12.17	23

N.B. No measurements were taken at Puerto Seco, Lucea, and Port Antonio. At Puerto Seco, harbour dredging in the vicinity at the time of sampling resulted in abnormal fouling of the water while at the other two beaches, the populations could not be detected.

added to the sea.

B. Rainfall: It has already been stated that the growth rates of clams at Port Henderson and Green Bay increase significantly during the rainy seasons because of the increase in food content of the water. Figure 35, compiled from Tables 16 and 18, show how closely rainfall and organic leptopel content are related.

With the exception of January, February, and March, the pattern in both sets of histograms is the same,

Figure 35

A: Rainfall at Palisadoes Airport for 1964.
B: The organic leptopel content of the sea water at Port Henderson, Jamaica, in 1964.

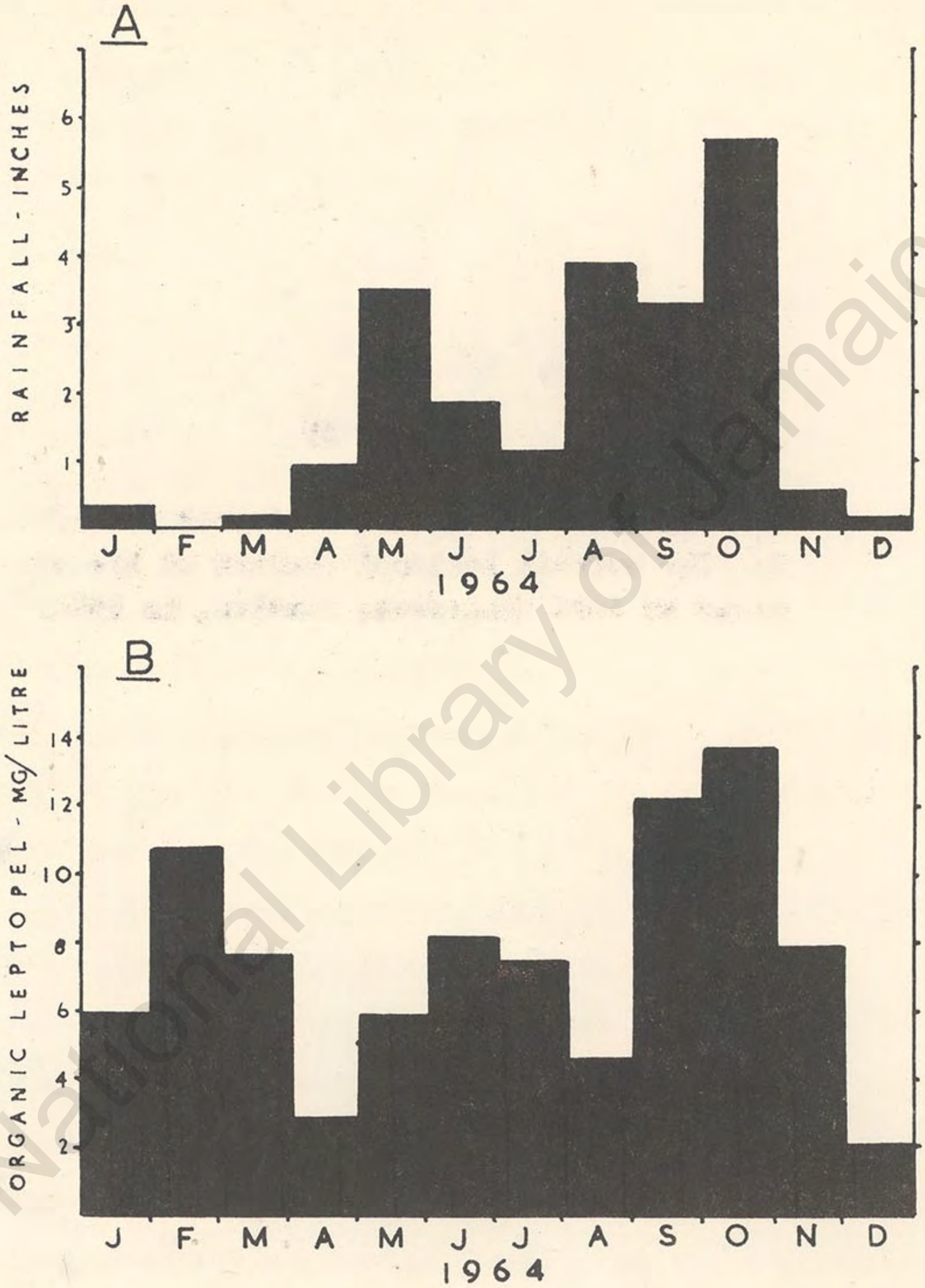

A
RAINFALL - INCHES
1
2
3
4
5
6
J F M A M J J A S O N D
1964
B
ORGANIC LEPTOPEL - MG/LITRE
2
4
6
8
10
12
14
J F M A M J J A S O N D
1964

Figure 35

TABLE 18:- Rainfall figures for Palisadoes Airport for 1963 and 1964.

Month	Rainfall 1963	Rainfall 1964
January	0.21 inches	0.34 inches
February	1.69	Trace
March	1.24	0.20
April	1.08	0.94
May	10.03	3.48
June	5.12	1.85
July	1.72	1.12
August	0.78	3.87
September	1.54	3.30
October	19.92	5.69
November	4.07	0.57
December	2.98	0.21

that is with distinct peaks in May - June, and October, and is due to the greater amount of detritus brought down to the sea when the rivers flood after rains.

C. Wave Action: Much of the organic detritus that *Donax* fees on originates from decaying organic matter deposited on the sea bottom. During the period of the year when the wind is high and the seas are rough, this detritus is stirred up into suspension and contributes appreciably to the food content of the sea. Monthly wind-speed records for Palisadoes for 1964 are given in Table 19 and show the correlation between the high organic leptopel content of the water in February and March and the increase in wind-speed at this time.

TABLE 19:- Average monthly wind-speed records for Palisadoes Airport for 1964

Month	Wind-speed
January	15.3 knots
February	18.0
March	20.1
April	18.6
May	18.0
June	19.6
July	21.0
August	19.2
September	17.5
October	15.4
November	15.8
December	12.0

IV MORTALITY

1. Mortality factors

The chief causes of mortality in *Donax* that have been reported are high winds (Orton, 1929), predators (Coe, 1955 and Loesch, 1957), and parasites (Coe, 1953 & 1955). The influences of four factors which may be responsible for death in *D. denticulatus* have been investigated and are described below.

A. *Reduced salinity and fouling of the water*: Previous reference has been made to the appreciable drop in salinity of the sea water in the vicinity of Kingston Harbour during the months of May, June, October, and November each year. Goodbody (1961b) has reported mass mortalities in a mangrove community of Kingston Harbour following heavy rains in these months, and Goreau (1964) has described the effects of the severe reduction in salinity in October 1963 on the coral reef community of eastern Jamaica.

Throughout the period of study on the *Donax* populations at Port Henderson and Green Bay, high mortality was recorded on three occasions corresponding to periods of heavy rainfall. These were in May-June 1963, October 1963, and October 1964. In May and October 1963 there was very heavy rainfall over a period of 48 hours resulting in severe flooding of the Rio Cobre and the Ferry River and a sudden drop in salinity of the harbour water[1]. Following the October 1963 rains, the salinity fell to less than ten parts per thousand, and a period of more than two months was required for a recovery to normal (35 - 36 parts per thousand) (Table 20). In October 1964, the drop in salinity was less severe and the recovery period was about two weeks.

TABLE 20:- The salinity of the sea water at Port Henderson and Green Bay after flood rains on October 5th and 6th, 1963.

Date	Port Henderson	Green Bay
9 October	9.0 pts/thous.	7.0 pts/thous.
11	17.5	15.0
18	32.0	30.5
24	30.0	15.0
31	34.0	28.5
14 November	33.5	31.5
21	33.5	32.5
5 December	33.5	33.5
18	34.5	33.0

Following the periods of reduced salinities, highest mortality in the Donax populations occurred among the smaller clams. At Port Henderson in October 1963, for example, there was more than 75% mortality of the spat as compared with less than 15% of the adults. In order to discover to what degree the reduction in salinity was responsible for this high mortality and why it was that the smaller clams were more affected than the others, salinity tolerance experiments were performed

[1]Over May 30, and 31, 6.28 inches of rain fell at Palisadoes Airport, and over October 5, and 6, the rainfall figure for the same station was 13.74 inches.

in the laboratory with clams of three size-groups - spat (4-7 mm.), juveniles (11-14 mm.), and adults (18-23 mm). In these experiments, ten clams of each size-group were subjected to water of reduced salinities and the number of days taken for 100% mortality among each group was recorded. The results are shown in Table 21.

TABLE 21:- Results of salinity tolerance experiments with three size-groups of clams of D. denticulatus.

	100% Mortality		
Salinity	Spat	Juveniles	Adults
35 pts/thous.	>40 days	>40 days	> 40 days
25	>40	>40	> 40
15	21	21	21
10	10	8	11
5	2	2	2

Two important facts are revealed by these results. First, it is seen that the clams of all sizes are reasonably tolerant to sea water as dilute as 15 parts per thousand, and secondly, that the smaller clams are not more affected by the reduced salinities than are the larger ones. Since, however, on the three occasions of heavy rainfall, the salinity of the water only fell below 15 parts per thousand in October 1963, and the smaller clams were always more affected than the others in the field populations, reduced salinity alone cannot be considered to have been responsible for the death that occured.

Accompanying the three periods of low salinity in Kingston Harbour in 1963 and 1964 was a high mortality of bottom and sessile communities resulting in fouling of the water. Goodbody (1961b) has reported in detail the mass mortality and fouling that occurred on three previous occasions in 1956 and 1958, and Goreau (1964) has described the fouling that resulted from the October 1963 rains.

In the experiments with diluted sea water, the water was kept clean and well aerated so as to eliminate the effect of fouling and deoxygenation following the death of any clam. When, however, the water was permitted to become contaminated, it was found that death of the clams was hastened and that the spat showed less resistance than the others. Thus, whereas clams of all sizes survived for as much as twenty-one days in clean 15 parts per thousand sea water, in contaminated water of the same salinity, the spat died after three days and the adults after ten. Because of this, it would appear that under natural conditions, fouling of the water resulting from the decay of other organisms may be more responsible for death in the Donax populations than the reduced salinity itself.

Since many populations of D. denticulatus occur near the mouths of rivers and heavy rainstorms in May and October are a feature of the local climate, high mortality of the clams once or twice a year can be regarded as a common occurrence of Donax populations in Jamaica. Furthermore, since one of the rainy periods occurs during peak reproductive activity of the clams, the danger of populations being exterminated at this time is very great, and although this was not known to take place on any beach during the two years of study, it may be considered as a potential threat to populations.

B. Dessication: When clams are stranded above the water level at low tide, it may take them several days to recover their proper zonation on the beach. During the period of stranding, many clams may die and in certain months of the year, this may result in increased mortality in the populations. An experiment was therefore performed to determine the dessication tolerance of the clams.

Twenty clams of each size-group - spat, juveniles, and adults - were placed in containers with saturated sand which was then allowed to drain freely and become air-dried at room temperature (29°C). At regular intervals after draining of the sand, the clams were checked to assess their condition, and the dead ones removed when necessary[1]. The periods of mortality were recorded and the results tabulated

TABLE 22:- Dessication tolerance of spat, juveniles, and adults of D. denticulatus.

		Percentage Survival		
Time	Sand T°	Spat	Juveniles	Adults
0 hrs.	29.2°C	100	100	100
16	27.8	100	100	100
24	28.4	100	100	100
40	28.0	100	100	100
48	28.1	100	100	100
64	27.6	100	100	100
72	27.5	75	100	95
88	28.3	40	60	60
96	28.3	20	15	25
112	28.4	0	0	0

[1] Dead clams were detected by their gaped shells.

to represent the percentage survival with time (Table 22).

The data show that when clams are left in drying sand for more than three days, heavy mortality results, and that after four or five days, there is almost no survival. Furthermore, these data reveal that no size group is any more tolerant than the others although it should be remembered that in the field populations, the spat are more vulnerable to stranding than are the larger animals (see Section B, Chapter II).

The environmental conditions which cause stranding and subsequent dessication have been outlined in Section B, Chapter III.

C. Predators: The importance of any one predator as a mortality factor varies considerably with locality and time. Thus, whereas pigs have a greater capacity for *Donax* than any other predator, they are confined to fewer localities, and although crabs (*Arenaeus*, *Callinectes*, *Ocypode*) and birds (*Crocethia*) prey on *Donax* on most beaches, they may have periods of abundance at different times of the year. Boring gastrópods are not widespread and do not appear to feed on very many clams on any beach.

With the exception of the pig, all the predators prey more upon the smaller clams than upon the larger ones, and for this reason, may have an important regulatory effect on the size of populations.

D. Parasites: Parasitic infection of *D. denticulatus* at Port Henderson and Green Bay by the cercarial larva, *Cercaria caribbea XLII* (Cable) remained at a negligible percentage during the period of study. Furthermore, only adult clams were ever found to be infected. For these reasons, there was nothing to indicate that this parasite was a major cause of death at any time in the populations.

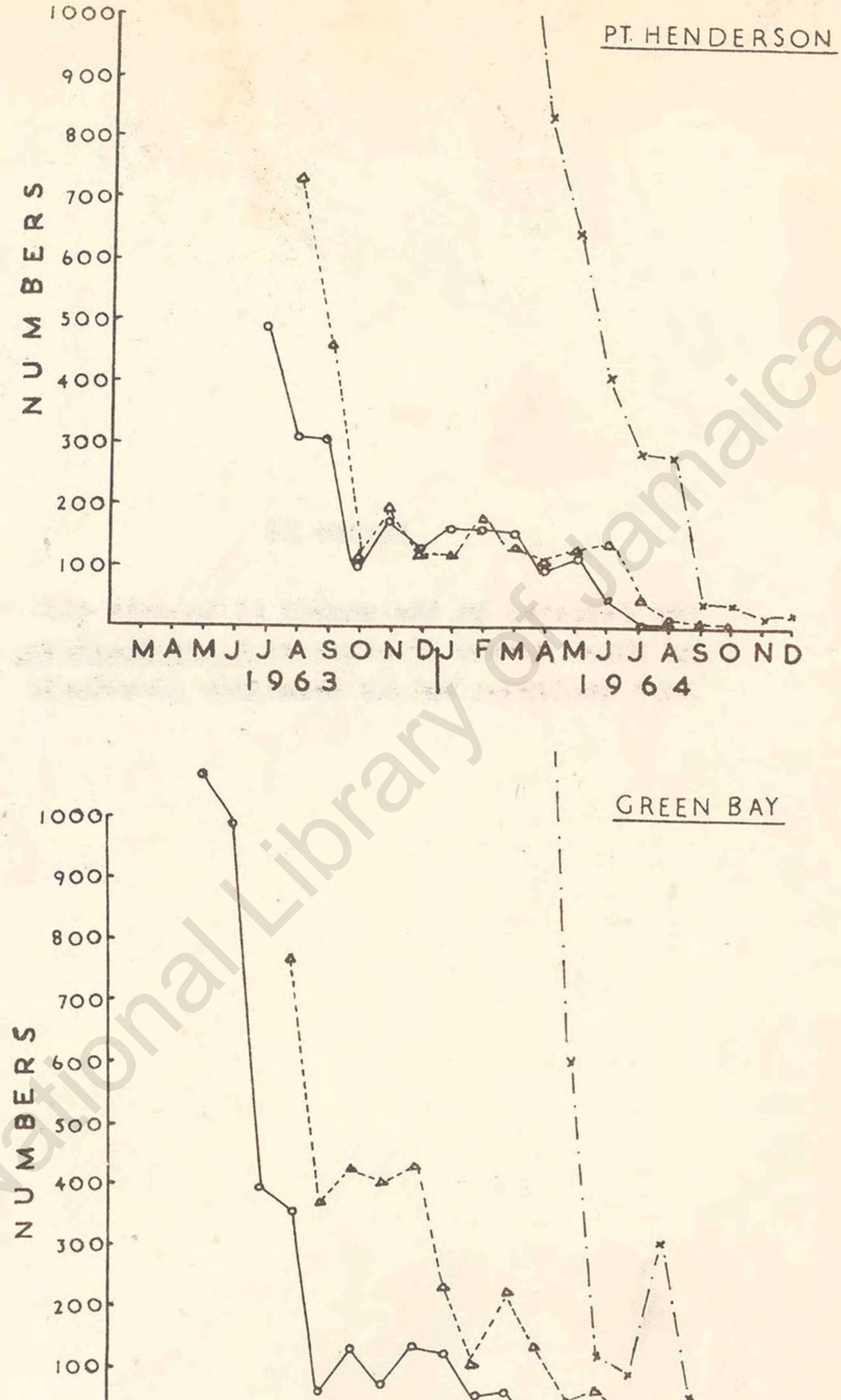
2. Rate of mortality

Indication of the mortality rate of D. denticulatus at Port Henderson and Green Bay was obtained from the monthly composite length-frequency data obtained for the two localities. The number of animals in any one size group of clams was recorded on successive months by counting all the individuals falling within its upper and lower modal troughs. Thus, at Port Henderson in July 1963, for example (Figure 24), one distinct group was represented by the animals between 2 and 12 mm. in length, and in the following month, by those between 6 and 13 mm. The mortality of each group was determined from the month in which it comprised most clams, and generally this tended to be in the second month of spatfall. Tables 23 and 24 show the data obtained for three groups each at the two beaches and in Figure 36, the decrease in the sizes of the groups with time is illustrated graphically. In Tables 23 and 24 also, the decreasing numbers of animals in each group are represented as survivors of cohorts of one thousand of the original populations and in Figure 37, these are illustrated as the number of survivors with age.

These data and figures reveal that generally on both beaches, there is more than 70% mortality in groups of clams within the first four months of life followed by the

Figure 36

The decrease in the number of animals with time in three groups of clams of D. denticulatus at Port Henderson and at Green Bay (Jamaica).



PT. HENDERSON
NUMBERS
1000
900
800
700
600
500
400
300
200
100
M A M J J A S O N D J F M A M J J A S O N D
1963
1964
GREEN BAY
NUMBERS
1000
900
800
700
600
500
400
300
200
100
M A M J J A S O N D J F M A M J J A S O N D
1963
1964

Figure 36

Figure 37

Projected survival curves in three groups of clams of <u>D. denticulatus</u> at Port Henderson and at Green Bay (Jamaica).

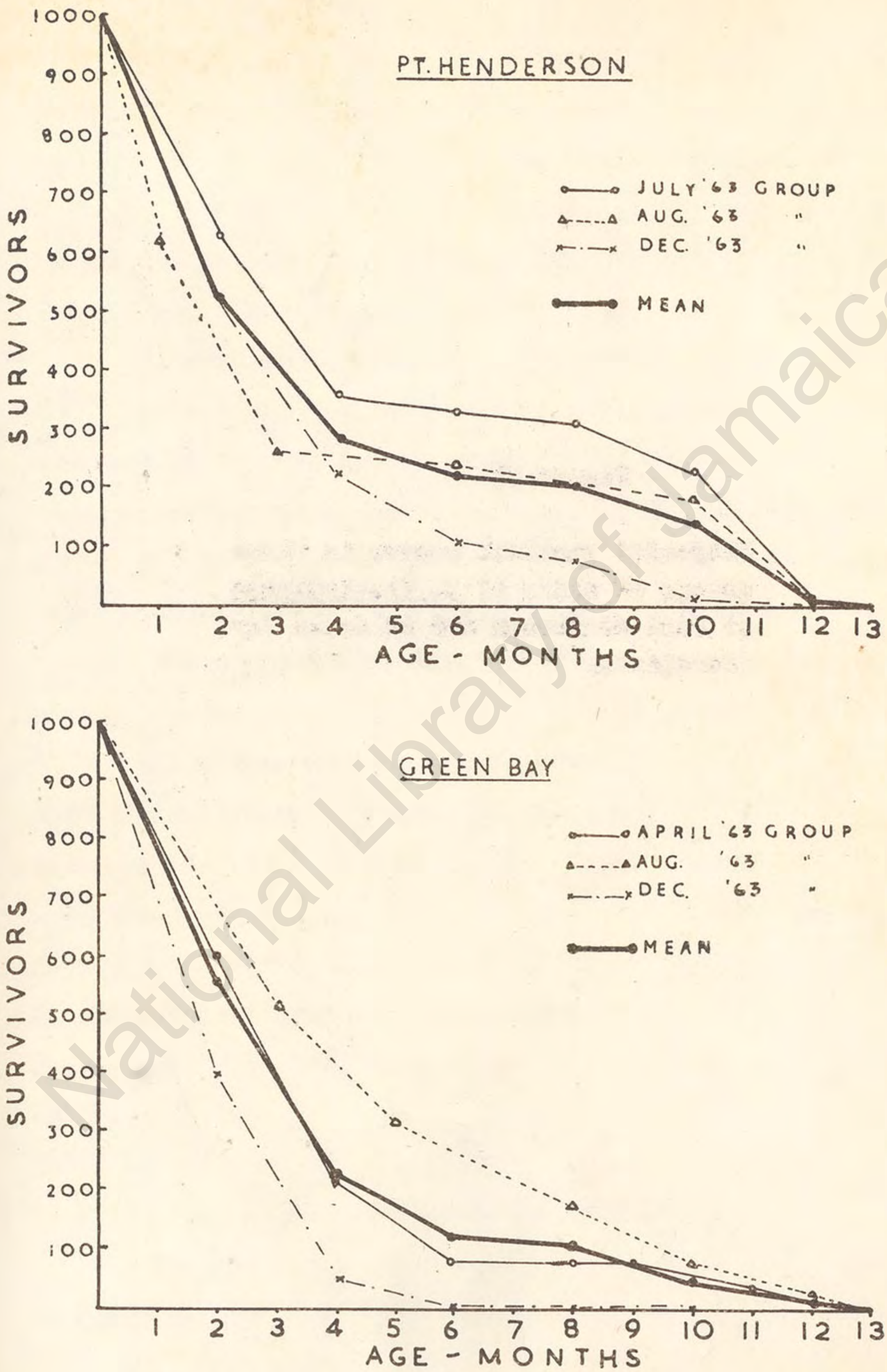

PT. HENDERSON
JULY '63 GROUP
AUG. '63 "
DEC. '63 "
MEAN
SURVIVORS
1000
900
800
700
600
500
400
300
200
100
1 2 3 4 5 6 7 8 9 10 11 12 13
AGE - MONTHS
GREEN BAY
APRIL '63 GROUP
AUG. '63 "
DEC. '63 "
MEAN
SURVIVORS
1000
900
800
700
600
500
400
300
200
100
1 2 3 4 5 6 7 8 9 10 11 12 13
AGE - MONTHS

Figure 37

second four months in which the numbers steady off considerably with only about 10 to 15% mortality. After this mortality again increases so that by the twelfth month, only about 1% of the original number is left. At Port Henderson, mortality during the first ten months is less than at Green Bay, although following spawning after this time, there is a rapid and almost complete mortality of the adults.

The higher mortality rate at Green Bay is possibly due to more deaths being caused by stranding and dessication as a result of the smaller sizes of the clams. This is in turn, however, controlled by the low amount of food and the slower growth rates, two factors which may in themselves be directly responsible for death.

The maximum life span of clams at the two beaches has been estimated by the presence of growth rings in adults to be about eighteen months. Thus, after June 1964, no clams with rings formed in October of the previous year could be found on the beaches. Coe (1955) reported that in Southern California, D. gouldi sometimes lived for as much as three years, while Nayar (1955) observed that most clams of D. cuneatus perished after the second year. In Texas, D. variabilis and D. tumida live for only one year (Loesch, 1957).

3. Population fluctuations

The monthly fluctuations in population densities of D. denticulatus at Port Henderson and Green Bay in 1963 and 1964 are given in Appendices IX and X and are illustrated in

TABLE 23:- The number of animals per metre of beach in three size groups of clams of <u>D. denticulatus</u> at Port Henderson between March 1963 and December 1964.

	July '63 group			August '63 group			December '63 group		
Month	Spread	Nos	$^{o}/_{oo}$	Spread	Nos	$^{o}/_{oo}$	Spread	Nos	$^{o}/_{oo}$
M '63									
A									
M	1-4 mm	120							
J	1-8	286							
J	1-12	486	1000						
A	6-13	309	636	1-5 mm	727	1000			
S	7-15	307	632	1-6	451	618			
O	10-16	93	191	1-9	110	151			
N	15-19	176	362	7-14	194	266	1-6 mm	1252	
D	17-19	131	270	11-16	118	162	1-10	3557	1000
J '64	18-20	161	331	13-17	116	159	1-12	2751	773
F	19-20	158	325	14-18	176	241	1-13	1881	528
M	19-20	152	313	16-18	128	175	1-15	1654	465
A	20-21	94	193	17-19	102	140	1-16	831	233
M	20-21	114	235	18-19	111	152	7-17	646	181
J	21-22	47	97	19-20	135	185	10-18	408	115
J	22-24	7	14	20-21	45	62	11-19	289	81
A	22-23	6	12	21	8	10	13-20	280	79
S				21-22	2	3	15-20	44	12
O				22-23	3	4	17-21	42	12
N							17-22	22	6
D							19-21	28	8

Figure 38. At Port Henderson, the lowest numbers of animals were recorded in October 1963 and November 1964, and at Green Bay, the lowest numbers were in September and October 1963, and July and October 1964. The greatest densities at both beaches were recorded in December 1963.

TABLE 24:- The number of animals per metre of beach in three size groups of clams of D. denticulatus at Green Bay between March 1963 and December 1964.

	April '63 group			August '63 group			December '63 group		
Month	mm Spread	Nos	°/oo	mm Spread	Nos	°/oo	mm Spread	Nos	°/oo
M '63									
A	1-12mm	1618	1000						
M	1-12	1074	664						
J	1-13	986	609						
J	5-13	394	243	1-4mm	104				
A	7-15	352	217	1-6	768	1000			
S	10-15	62	38	1-9	364	473			
O	10-16	132	81	1-9	428	556			
N	12-16	74	46	6-11	396	515	1-5mm	6204	
D	14-17	138	85	10-13	426	554	1-9	26098	1000
J '64	15-18	126	78	11-14	231	300	1-10	20189	773
F	16-18	60	37	12-15	104	135	1-11	10432	399
M	17-19	68	42	13-16	222	288	1-12	2933	112
A	18-21	16	10	14-17	132	172	7-13	1316	50
M				14-17	48	62	8-13	608	23
J				15-18	60	78	10-14	124	5
J				15-18	28	36	11-14	92	3
A				17-20	20	26	13-16	312	12
S				18-20	4	5	14-17	56	2
O				18	4	5	15-17	24	1
N				18	4	5	16-17	16	1
D				18	4	5	16-17	16	1

Following the period of peak settlement in December, the numbers decrease rapidly until about March or April when they steady off for a few months before falling again sharply in September, October, or November. The rapid decrease in numbers after December is due to the high mortality among the young clams, while that in October is as a result of the unfavourable environmental conditions which cause death among young clams and the death of adults after spawning.

Figure 38

The fluctuation in density of populations of <u>D. denticulatus</u> at Port Henderson and Green Bay (Jamaica) between March 1963 and December 1964.

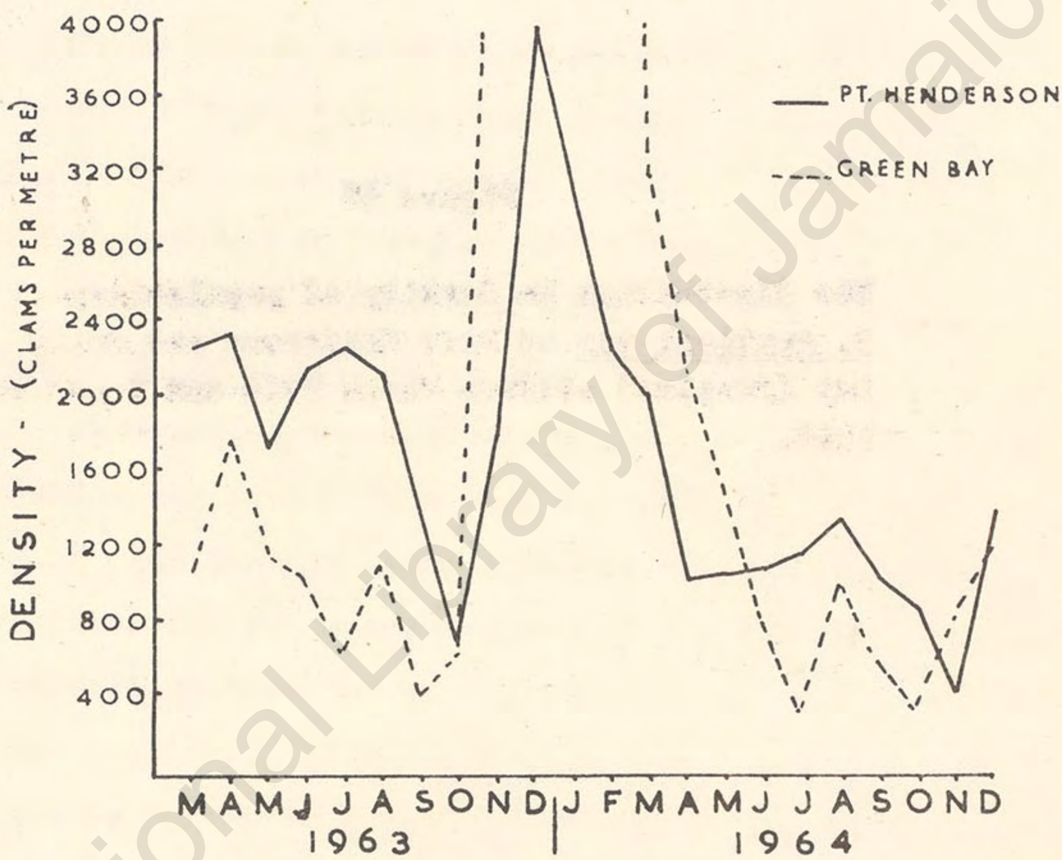

4000
3600
3200
2800
2400
2000
1600
1200
800
400
DENSITY - (CLAMS PER METRE)
PT. HENDERSON
GREEN BAY
M A M J J A S O N D J F M A M J J A S O N D
1963
1964

Figure 38

V. SUMMARY

Based on the life history studies at Port Henderson and Green Bay over a period of nearly two years along with the periodic observations and samples of other populations throughout Jamaica and the West Indies, it is possible to draw some conclusions on the life history of D. denticulatus in particular and of the genus as a whole.

It has been found that like most other marine bivalves, D. denticulatus is dioecious with fertilisation of the eggs taking place externally. Breeding is continuous throughout the year with a high in December and a low in June and July; but what triggers spawning and how it takes place are not known. There are two larval stages, the straight-hinged veliger larva which may live for as much as ten days, and the near-adult veliconcha stage which may also live for as long as a week or more. These larvae are most common in the plankton from November to February corresponding to the period of peak reproductive activity, although at least a few may be recovered from the sea at any time of the year. Marked reduction in salinity accompanied by fouling of the sea water often causes high mortality among the larvae. Tidal and ocean currents and the degree of wave action may influence metamorphosis and settling of the larvae. Occasionally, larvae may be transported several miles away from the parent population to settle elsewhere and establish a new population.

Growth of the clams is rapid for the first seven months of life after which there is a gradual slowing down of the process until it ceases after about ten or eleven months. The main factor which affects growth appears to be the amount of available food so that depending on the size and age of the clams and their localations, it may be the most important limiting factor. The maximum growth rates, measured as increase in shell length, is between 2.5 to 3.0 mm. per month, and the maximum sizes to which clams may grow is approximately 23 mm. in length. Growth rings are only formed in the near-adult clams, although younger individuals often form distinct colour bands at periods corresponding to those of ring formation in the older ones. The appearance of the shells, although highly variable in colour and pattern, appears to be at least partly determined by the amount and/or nature of the nutrients in the sea.

Highest mortality occurs during the first four months of life during which at least 70% of the spat which settle on the beach die. Less than 15% of an original population ever survive after spawning. The maximum life span has been estimated as eighteen months. Highest mortality is in May-June and September, October, and November when unfavourable environmental conditions exist. Death by bacterial contamination and dessication is high among the spat. Predation and parasitisation do not appear to be significant mortality factors. Populations fluctuate appreciably during the year with peak densities around December, and lowest densities around June-July, and October-November.

The environmental conditions which affect the populations most are dependent on the proximity of rivers and the amount of rain which falls in their catchment areas. These conditions may either be unfavourable therefore resulting in increased mortality or may be favourable and bring about an improvement in growth. During the rainy seasons when the rivers flood, the salinity of the sea water falls appreciably and widespread fouling of the water follows. This may cause a high mortality of the larvae and spat and therefore greatly affect the sizes of populations. At these times also, the food content of the sea increases rapidly so that there is a marked increase in the growth rates of the near-adult clams with the subsequent formation of growth rings. This change is greatest on beaches which are nearest to rivers and where the food content is highest, and therefore results in the clams at these localities being larger than at others. Thus for these reasons, proximity to a river may have both beneficial and harmful effects on populations.

Tidal and ocean currents and the degree of wave action are important factors in the dispersal, metamorphosis, and settling of larvae. However, these vary so much with time and locality and are therefore so unpredictable that they may be regarded as having only a chance effect on populations.

Fluctuations in temperature, solar radiation, and tidal ranges are small in the West Indies and seem to have little or no effect on the populations of D. denticulatus. In other parts of the world, however, some of these climatic factors and others influence Donax populations appreciably. Thus maximum growth and reproductive activity in D. gouldi, D. variabilis, and D. tumidus take place in the warm summer months while during the winter there is very little activity (Coe, 1955; Loesch, 1957). In Britain, heavy mortality is caused in D. vittatus by the high spring tides at certain times of the year (Orton, 1929), while in India, the greatest mortality follows regularly on the annual monsoon winds (Nayar, 1955).

Seasonal heavy rainfall has not been reported elsewhere to affect Donax populations, and in fact, very few marine animals are known to be influenced by this factor. Goodbody (1961b) has described the result of tropical rainstorms on sessile marine communities in Jamaica; but even in these cases, rainfall does not have the same regular and prolonged effect on the populations as with Donax. This occurrence in D. denticulatus may therefore be one of the few examples in which the life of a marine invertebrate is so directly and continuously affected by a factor which originates inland and which may be properly described as terrestrial[1].

The status of Donax populations on beaches in the West Indies as in other parts of the world must be regarded as precarious. As a result of high fecundity, and favoured by suitable currents and an unlimited food supply, very

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[1]Webb and Hill (1958) described the effect of reduced salinities caused by rainfall on the lancelet Branchiostoma nigeriense (Webb) in Lagos Harbour and Lagos Lagoon.

large populations of D. denticulatus may be established and thrive on beaches near to rivers; and yet at the same time, because of the possibility of frequent periods of reduced salinity, fouling of the sea water, and unfavourable currents, these populations stand in danger at least once a year of being rapidly exterminated.