SECTION E

GENERAL DISCUSSION

I. THE BIOLOGICAL SUCCESS OF DONAX IN THE WEST INDIES

In this discussion an attempt is made to assess with what degree of success Donax inhabits the wave-swept sandy beaches of the West Indies. Since, however, there is only scattered data on one of the two species in the West Indies, D. striatus, this discussion must be confined to the other species, D. denticulatus, on which a more thorough study has been made.

The success of Donax must be considered along two main lines; first, the ability of the clams to maintain themselves in their relatively unstable habitat; and second, their ability to keep populations going from one year to the next.

The exposed sandy beaches on which Donax lives is a difficult habitat for several reasons chiefly because of the instability of the substratum and the changing nature of the beach with each tidal shift. The first danger, that of being either buried alive or flushed from the sand, necessitates that an animal living on the beach must be able to obtain a good anchorage in the substratum, and then to quickly bury itself again if washed out of the sand. Both of these D. denticulatus is able to do and it is therefore capable of maintaining a fixed pattern of zonation on the beaches in the West Indies. The second danger, that of being stranded in drying sand above the water level at low tide, is overcome by a synchronous migration of the clams with each tidal shift and this involves on their part a remarkable ability to appreciate their immediate environment and to bury themselves only where the substratum is suitable.

Mortality resulting from washing out of the substratum or stranding is normally low, although occasionally, with severe environmental conditions, it may be greatly increased. Such conditions may be brought about by high seas and unusual tidal sequences, but as these do not occur often, the clams suffer little from them. Nevertheless, they remain as potential dangers.

The types of beaches on which Donax may live are present on most of the West Indian islands and, as a result, Donax is distributed widely throughout the islands. Only on those in which all the sands are of calcareous origin is Donax absent. In many localities, especially in Jamaica, Antigua, and Trinidad, populations of Donax reach great densities, and more than 4000 clams per linear metre of beach have been recorded. The Donax populations are usually in excess both in density and biomass of those of the associated beach fauna, and it may therefore be feasible to regard Donax as a dominant species in its habitat.

Despite the fact that large populations of Donax frequently develop in many localities in the West Indies, populations may fluctuate greatly from year to year. The most important factors responsible for this seem to be environmental and affect both the rate of natality and mortality. Those which affect natality are reduced salinity, fouling of the water, tidal and ocean currents, and lack of wave action, while those which affect mortality are reduced salinity, fouling of the water, and high seas. Of these, there are three in Jamaica (reduced salinity, fouling of the water, and high seas) which are likely to occur twice a year especially during the rainy seasons (May and October), and in 1963, for example, these had adverse effects on populations. Because of the possibility of failure of spat to settle or of sudden mass mortality resulting from the above conditions, the establishment and maintenance of populations from one breeding cycle to the next becomes more difficult, and in some localities, it appears that some populations have been exterminated as a result. Nevertheless, the evidence suggests that in most places even where these conditions have been most severe, populations have managed to survive and/or recover in a short time, and they have therefore been able to perpetuate themselves.

Many of the factors which affect Donax populations in other places do not have the same influence in the West Indies. Fluctuations in temperature and solar radiation, for example, are not important factors, and parasitic infection and predation are not known to deplete populations significantly. As a result, there appear to be fewer factors in the West Indies which have a continuous regulatory effect on Donax populations than in other places where similar studies have been made.

The climatic factors which determine the geographical range of D. denticulatus are unknown and so is the history of the species in the West Indies. Consequently it is not possible to assess its evolutionary success in these parts or to say what the trend may be in regards to its distribution and numbers. From the above considerations, however, it may be concluded that at the present time in the West Indies, D. denticulatus achieves a high degree of success both in securing itself in its difficult habitat and in maintaining populations.

II. EVOLUTION WITHIN THE GENUS *DONAX*

The possible course of evolution within the Tellinacea was discussed by Yonge (1949a) who noted that the Donacidae had evolved within the group as one of the less specialised families of deposit feeders. Yonge was unable to consider, however, the course of evolution within the Donacidae since his and previous studies had been concerned with only one member of the family, *D. vittatus*. Since then subsequent studies of different species of *Donax* have thrown light on some of the ecological trends within the genus, and this knowledge considered along with the present findings on *D. denticulatus* and *D. striatus* may now be discussed in order to elucidate the possible course of evolution within the genus.

It is clear, as has been pointed out by Yonge and further substantiated in this study, that *Donax* represents a line of evolution within the Tellinacea away from the deposit-feeding habit towards that of a suspension feeder. This has been concurrent with (a) a change in the morphology of the animals, and (b) the occupancy of new habitats. Because these two are very closely related, this discussion of the evolutionary trend within the genus must include a consideration of both.

Although members of the Tellinacea are now found in all types of bottom material at varying depths, the earliest types almost certainly lived in soft muddy substrata in the sublittoral zone from and out of which Donax appears to have evolved and moved into firmer substrata in the litteral zone. This shift into the littoral zone necessitated morphological adaptations for coping with the rigours of a tidal environment, and correlated with the reduction in the organic content of the substrata was the need for a suspension-feeding habit.

Ecological studies have shown that the greatest dangers Donax faces in the intertidal zone are those of being either flushed from the sand or buried alive, and being stranded above the water level at low tide. To prevent any of these from happening, rapid burrowing and a high degree of mobility are required, and these Donax has achieved with great success. Yonge (1949a) has shown that of the burrowing bivalves only the Tellinacea can move actively in both horizontal and vertical directions, and this is done with the help of a foot of maximum size and activity. In its rate of burrowing Donax is more rapid than other members of the Tellinacea and possibly all other bivalves, and this is undoubtedly due, as has been pointed out by Yonge, to the presence in the clam of a more rotund and anteriorly pointed foot as well as an additional elevator pedis muscle. The wedge-shaped type of shell also favours rapid burrowing and the posterior end with its truncated margins ensures that the clams do not have to bury very deeply before they are completely covered by the substratum. The mobility of the siphons is reduced in Donax, but is retained sufficiently for the clams to move them about as braking devices on the beach.

The morphological adaptations for suspension-feeding in Donax have occurred mostly in the siphons, ctenidia and labial palps, and stomach. The siphons have assumed a new role of passively but selectively taking in water with food particles and have developed sensitive straining tentacles with associated musculature and nervous supply. The labial palps have increased in size and efficiency and the ratio of gill size to palp size has been reduced. The stomach has become better suited for dealing with small particles by the development of an additional pouch and sorting area, and its orientation has changed; it has also lost its triturating function and the postero-dorsal caecum has become reduced in size and importance.

Donax occupies habitats in both the sublittoral and littoral zones although most members of the genus are confined to the latter[1]. D. vittatus "extends into the sublittoral zone down to depths of about ten fathoms" (Yonge, 1949a), and is therefore unlike most other species which live only in the intertidal habitats. Among these, however, are species which occur at different levels including some found only in the shallow water of the surf zone (D. rugosus, D. acutangulus) and others confined entirely to the wash zone (D. semigranosis, D. variabilis); then there are also

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[1]See Section B, Chapter II for a review of the zonation of Donax populations.

a few which occur at different depths throughout the year (D. gouldi, D. tumidus). It would appear that species which extend into deep water represent the earliest types in the genus and that those which are confined to the wash zone the most recent; those which occur only in shallow water would therefore be of earlier origin than those which move up into the wash zone only at certain times of the year. If the above is valid, then it is to be expected that species which occur in deep water will be more similar to the deposit-feeding Tellinacea than those which live in the wash zone, and this is borne out by the features described for D. vittatus, D. denticulatus and D. striatus.

D. vittatus, like the deposit feeders, projects its siphons beyond the surface of the sand while feeding whereas D. denticulatus and D. striatus keep theirs flush with the surface. Furthermore, there is indiscriminate intake of material in the first while the latter two, unlike any deposit feeder, selectively strain and reject particles above a certain size. The stomach also in D. vittatus is more representative of those found in the deposit feeders, while that in D. denticulatus and D. striatus possesses many features similar to the stomach in suspension feeders.

A noticeable point is that in one important respect, that is the size and functioning of the postero-dorsal caecum, D. striatus is more like the deposit feeders than D. denticulatus, and suggests that this species is of earlier origin than D. denticulatus. This is supported by the fact that whereas D. denticulatus is confined entirely to the wash zone, D. striatus interchanges between the surf and wash zones.

In conclusion it may be noted again that Donax occupies a niche on exposed beaches in which few other bivalves can survive. The ability of Donax to do this is due mainly to certain morphological structures which originally became adapted in the Tellinacea for deposit-feeding but which have evolved along new lines in the genus for performing new and different functions. These adaptations have helped to improve the mobility of the clams and change their mode of feeding, and they have therefore been fundamental factors in ensuring the survival and success of the genus in its difficult habitat.

SUMMARY

SUMMARY

1. Beach clams of the genus Donax are small active bivalve molluscs which live in the intertidal zone of sandy beaches throughout the world.

2. Previous work on Donax has been concentrated on a few interesting aspects of the life of the clam and there has been no comprehensive study of any one species.

3. D. denticulatus (Linné) and D. striatus (Linné) are the representatives of the genus in the West Indies and are available for study throughout the year.

4. D. denticulatus and D. striatus can be readily identified by features based on the markings, shape, and colour of the shells.

5. D. denticulatus occurs only in the wash zone of the beach. The other main occupants of this zone in Jamaica are the isopod, Excirolina braziliensis (Richardson), the mole crab, Emerita portoricensis (Schmidt), and the spionid worm, Scolelepis squamata (Müller).

6. D. denticulatus is sorted according to size in the wash zone and the adult clams are confined almost entirely to the saturated region. As a result, more than 90% of the volume of populations is distributed throughout the saturated zone.

7. The turbulence of the substratum and its degree

of wetness are the main factors which influence the pattern of zonation in *D. denticulatus*

8. *D. striatus* is not always confined to the wash zone but has been observed in the surf zone in Trinidad and British Honduras. The reasons for these differences are not known.

9. Both *D. denticulatus* and *D. striatus* migrate synchronously with the tides. This is accomplished by the clams being transported up and down the beach in the wash but only and always burying themselves again in the saturated zone. No intrinsic mechanisms are necessary in this process.

10. The large muscular foot and the mobile siphons are important organs in maintaining the clams in their right position on the beach.

11. Stranding of the clams above the water level at low tide sometimes occurs especially after high seas and the formation of a berm on the beach.

12. *D. denticulatus* occurs throughout the West Indies while *D. striatus* is found in large numbers only in the larger islands.

13. The factors which determine the distribution of *D. denticulatus* are the nature of the beach sand, the size and sorting of the sand grains, the slope of the beach, the degree of wave exposure, and the organic content of the sand.

14. Most populations of *D. denticulatus* occur on alluvial beaches near the mouths of rivers and swamps.

15. The factors which determine the distribution of D. striatus are uncertain, but the larger populations are found in Trinidad where the beaches have very gentle slopes.

16. It appears that D. denticulatus is the older and more established of the two species in the West Indies.

17. Populations of D. denticulatus from 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. The largest population of grown clams recorded had a density of more than 4,000 clams per metre of beach.

18. Donax has several predators. In the West Indies three species of crabs, Arenaeus cribrarius (Lamarck), Callinectes exasperatus (Gerstaecker), and Ocypode albicans (Bosc), - a boring gastropod, Terebra cinerea (Born), - a bird, Crocethia alba (Pallas), - and pigs are known to prey on Donax.

19. A trematode larva, Cercaria caribbea XLII (Cable) parasitises D. denticulatus and causes parasitic castration.

20. An unidentified hydroid grows on the shells of D. denticulatus and D. striatus in Trinidad and an unidentified filamentous alga has been found on one occasion on the shell of D. denticulatus in Jamaica.

21. D. denticulatus is dioecious and there is an equal proportion of the sexes in populations. The gonads are ripest in Jamaica between August and January.

22. D. denticulatus has two planktonic larval forms

each of which lives for at least a week.

23. Reduced salinity and fouling of the water, tidal and ocean currents, and low wave action are known to have considerable effects on the larvae of *D. denticulatus*.

24. Settlement of spat of *D. denticulatus* in Jamaica is highest in December and lowest in March, June and July, and October. Low settlements in March and October are as a result of unfavourable environmental conditions, and in June and July as a result of low breeding activity.

25. *D. denticulatus* breeds continuously throughout the year in Jamaica with maximum activity in and around December and minimum activity in June and July.

26. There is evidence to suggest that in Jamaica *D. striatus* has a similar breeding activity as *D. denticulatus*.

27. The environmental conditions which favour the pattern of breeding activity in *D. denticulatus* are not known.

28. The growth of clams of *D. denticulatus* is constant for the first seven months of life while the gonads are developing, but then as they become ripe and spawning commences it slows down and eventually ceases. The maximum growth rate measured as increase in shell length is about 3.0 mm. per month.

29. The growth rate of clams of *D. denticulatus* at different localities differ appreciably and as a result the maximum sizes to which the clams grow vary.

30. Marked increases in the growth of clams of *D. denticulatus* in Jamaica occur during the rainy seasons. Growth rings and concentric colour bands are formed at such

times.

31. Growth rings and colour bands in D. denticulatus are formed as a direct result of the sudden increase in food content of the sea.

32. The growth rate in D. denticulatus is directly correlated with the amount of food in the sea and food supply is the main limiting factor on growth.

33. Proximity to a river, rainfall, and the degree of wave action, determine the amount of food available to clams and therefore influence their growth.

34. The chief causes of death in D. denticulatus are reduced salinity and fouling of the water, dessication, and predation. Parasitisation does not appear to be an important mortality factor.

35. In the first four months of life of a population of D. denticulatus, at least 70% of the clams die, but mortality is not high again until the adults spawn in about the eleventh month.

36. Only about 1% of a population of D. denticulatus survives after the first year and the maximum life span has been estimated as approximately eighteen months.

37. Populations of D. denticulatus in Jamaica have their highest densities in December and lowest densities in October. High density in December is as a result of recent settlement and low density in October is as a result of death of the adults after spawning and death of spat due to unfavourable environmental conditions.

38. D. denticulatus and D. striatus feed by

drawing in food-laden water through the inhalant siphon.

39. Adult clams of D. denticulatus are capable of filtering more than 300 cc. of water per hour although this rate is reduced when there is very much material in suspension.

40. The orifice of the inhalant siphon is lined by forty-eight sensitive tentacles which selectively prevent particles above about 250 μ in diameter from entering the mantle cavity.

41. The structure and nervous supply of the inhalant siphon are adapted for the selective rejection of particles. In the distal region of the siphon are layers of circular muscle which constrict the aperture when particles are caught on the tentacles, and in the tentacles themselves are sub-epithelial nerve cells which apparently serve as mechano-receptor units for detecting the presence of the particles on the tentacles.

42. The organs of the mantle cavity are adapted for dealing with much finely particulate material and there is much rejection of particles on the labial palps.

43. The stomach is more suited for dealing with particles less than 200 μ in diameter. It has two large food pouches and does not perform a triturating function. The postero-dorsal caecum is reduced in size and function.

44. The major part of the diet of the clams is comprised of organic detritus and phytoplankton, but other organic material in suspension may also be taken in and digested.

45. The general conclusion of nutrition in D. denticulatus and D. striatus is that these clams are better adapted for feeding on material in suspension than on bottom deposits.

46. It is concluded that at least one of the two species of Donax in the West Indies, D. denticulatus, has attained a high degree of success.

47. The possible course of evolution within the genus Donax is discussed and the view expressed that the trend has been away from a deposit-feeding habit in the sublittoral zone towards a suspension-feeding habit in the littoral zone.

APPENDIX

APPENDIX I

Average length, depth, and thickness measurements for clams of D. denticulatus of 1 mm. size intervals.

Length	Depth	Thickness
3.9 mm.	2.8 mm.	1.8 mm.
4.5	3.2	2.0
5.5	3.9	2.5
6.5	4.5	2.8
7.4	5.5	3.5
8.5	6.3	3.8
9.4	6.5	4.2
10.4	7.7	5.0
11.5	8.2	5.5
12.5	8.8	6.0
13.4	10.0	6.7
14.5	10.8	6.8
15.4	11.3	7.3
16.5	12.1	8.0
17.5	12.0	8.0
18.7	13.7	9.2
19.5	14.1	8.5
20.6	15.0	9.5
21.5	15.5	9.8
22.7	16.5	10.4
23.1	16.9	10.6

Regression Values

Length: depth	b=+0.732	Length: thickness	b=+0.462
	a= 0.09		a=+0.043
	P= 0.001%		P= 0.001%

APPENDIX II.

Average length, depth, and thickness measurements for clams of D. striatus of 1 mm. size intervals.

Length	Depth	Thickness
3.7 mm	2.8 mm	1.6 mm
4.5	2.9	1.7
5.7	4.4	2.2
6.5	4.6	2.4
7.4	5.2	2.8
8.4	5.9	3.2
9.5	7.0	3.8
10.6	7.8	4.5
11.4	8.3	4.6
12.0	8.5	4.7
-	-	-
14.6	10.9	5.6
15.7	11.4	6.7
16.5	11.5	7.0
17.5	12.4	7.5
18.4	13.1	7.0
19.9	14.7	9.0
20.5	14.4	9.0

Regression values

Length: depth b=+0.697	Length: thickness b=+0.442
a=+0.25	a=+0.373
P= 0.001%	P= 0.001%

APPENDIX III

Average length and depth measurements for clams of *D. striatus* of 1 mm. size intervals from two different localities.

Locality A. Length	Locality A. Depth	Locality B. Length	Locality B. Depth
21.3 mm.	16.3 mm.	21.6 mm.	14.8 mm.
22.2	16.6	22.4	14.9
23.8	17.4	23.5	14.5
24.6	17.6	24.5	15.3
25.3	17.7	25.5	15.9
26.4	18.8	26.4	15.8
27.4	18.6	27.4	15.9
28.3	19.4	28.2	17.4
29.5	19.0	29.4	17.0

Regression values

Locality A	Locality B
Length: depth b=+0.382	Length: depth b=+0.349
a=+8.248	a=+6.782
P= 0.1%	P= 0.1%

APPENDIX IV.

Numbers of animals taken in an interrupted line transect sample of the beach fauna at Green Bay in Jamaica in January, 1964. Transects weree taken at 20 cm. intervals.

Transect	Talorchestia	Excirolinaa	Emerita	Donax	Scolelepis	Terebra
1	1	1				
2	3	4				
3	12	46				
4	23	46				
5	48	262				
6	41	140	5	3		
7	2	224	-	1		
8		145	-	-		
9		107	-	2		
10		72	9	1	1	
11		42	132	7	-	
12		5	245	275	7	
13			183	515	-	
14			162	669	31	
15			38	288	7	
16			24	260	7	
17			6	131	1	
18			1	68	4	
19			1	38	10	
20			1	39	12	
21				25	3	
22				24	63	
23				10	52	1
24				2	-	1

APPENDIX V.

A.

Results of a line transect sample of a population of D. denticulatus at high tide at Port Henderson, Jamaica, in October 1962. Transects were taken at 5 cm. intervals.

Transect	Nos.	Total Vol.	Average Vol.	Max. Length	Min. Length
1	1	-	-	8.0 mm.	8.0 mm.
2	2	0.04 ccs.	0.020 ccs.	7.5	4.0
3	6	-	-	10.5	4.0
4	5	0.38	0.076	9.0	5.0
5	20	-	-	11.0	4.0
6	7	0.35	0.050	9.0	4.0
7	14	-	-	11.5	3.0
8	9	0.55	0.061	11.5	4.5
9	13	-	-	18.5	4.0
10	39	2.60	0.066	10.5	4.0
11	22	-	-	13.0	4.5
12	57	3.00	0.053	12.5	4.0
13	56	-	-	19.0	4.5
14	68	5.60	0.082	22.0	4.0
15	68	-	-	19.0	4.0
16	35	4.30	0.123	19.5	4.0
17	38	-	-	21.0	4.0
18	59	5.00	0.085	22.0	4.0
19	33	-	-	20.0	4.0
20	34	4.70	0.140	21.0	4.0
21	22	-	-	22.0	5.0
22	15	6.00	0.400	19.5	6.5
23	13	-	-	20.5	7.0
24	12	3.80	0.317	21.0	6.0
25	20	-	-	21.5	6.5
26	24	9.50	0.400	22.5	6.0
27	8	-	-	22.0	8.0

APPENDIX V (Contd.)

Transect	Nos.	Total Vol.	Average Vol.	Max. Length	Min. Length
28	10	4.10 ccs.	0.410 cc.	21.5 mm.	6.0 mm.
29	7	-	-	21.0	4.0
30	15	5.30	0.360	20.0	5.0
31	14	-	-	20.5	6.0
32	9	6.00	0.660	20.5	9.0
33	14	-	-	22.0	5.5
34	7	3.70	0.530	20.5	5.0
35	8	-	-	17.5	6.0
36	11	5.50	0.500	22.0	6.0
37	4	-	-	20.5	6.0
38	3	1.00	0.330	20.5	9.5
39	0	-	-	-	-
40	2	0.80	0.400	21.0	11.0
41	1	-	-	11.0	11.0
42	1	0.10	0.100	10.5	10.5
43	2	-	-	9.5	7.5
44	0	-	-	-	-
45	1	-	-	9.5	9.5
46	0	-	-	-	-

APPENDIX V

B

Results of a line-transect sample of a population of D. denticulatus at low tide at Port Henderson, Jamaica, October 1962. Transects were taken at 10 cm. intervals.

Transect	Nos.	Total Vol.	Avg. Vol.	Max. height	Min.height
1	19	0.15 cc	0.008 cc	6.0 mm	3.0 mm
2	44	0.22	0.005	6.0	2.5
3	49	0.30	0.006	6.0	2.5
4	62	0.78	0.012	9.0	3.0
5	59	0.80	0.013	9.5	2.5
6	41	1.10	0.027	10.0	2.5
7	16	0.65	0.040	10.5	3.0
8	34	2.30	0.070	16.5	4.0
9	26	1.40	0.055	11.0	3.0
10	23	2.00	0.090	13.0	3.0
11	21	5.10	0.243	21.0	4.0
12	29	4.00	0.140	20.0	3.5
13	28	5.00	0.198	18.0	3.0
14	11	2.50	0.227	21.0	5.5
15	31	7.30	0.235	21.0	4.0
16	10	1.80	0.180	20.0	4.0
17	16	3.20	0.200	19.0	4.5
18	15	2.00	0.133	20.0	4.0
19	5	1.20	0.240	18.5	6.0
20	6	1.30	0.216	19.0	4.5
21	4	1.00	0.250	17.0	5.0
22	7	1.50	0.214	13.0	7.0
23	4	1.00	0.250	11.5	7.5
24	5	1.00	0.200	11.5	10.0
25	6	1.30	0.216	17.5	5.5
26	6	0.50	0.083	12.5	5.0
27	7	1.30	0.186	18.0	8.0
28	0	-	-	-	-

APPENDIX VI.

Numbers of animals taken in transects across Mayaro Beach, Trinidad, at high and low tide in April, 1964. Transects were taken at 0.5 metre intervals.

High Tide

Transect	D. striatus	D. denticulatus
1	1	1
2	1	8
3	2	4
4	9	4
5	1	2
6	-	1
7	-	1
8	-	1
9	-	-

Low Tide

Transect	D. striatus	D. denticulatus
1	0	-
2	3	-
4	2	-
6	1	-
8	1	-
10	2	-
12-26	-	-
28	-	4
30	-	4
32	-	2
34	-	3
36	-	2
38	-	6
40	-	1
42	-	1
44	-	1
46	-	-

APPENDIX VII

A

Results of the size-grade analysis of the beach sands in which Donax occurs in the West Indies.

Size-Grades

Localities	0.053mm	0.053-0.105mm	0.105-0.21mm	0.21-0.5mm	0.5mm
Port Henderson	0.1gm	1.5gm	21.3gm	68.9gm	8.2gm
Green Bay	-	1.1	76.2	21.9	0.8
Small Point	-	0.1	27.4	48.0	24.5
Farquhar's Beach	-	5.3	68.8	24.8	1.1
Gut River	0.1	0.7	24.7	62.0	12.0
Alligator Pond	-	10.5	58.1	30.5	0.9
Black River	-	0.5	56.8	39.1	3.6
Hope Wharf	-	0.2	31.2	51.5	17.1
Negril	0.1	1.6	50.6	42.8	4.9
Lucea	-	0.5	50.8	43.2	5.5
Montego Bay	-	0.4	18.9	75.9	4.8
Puerto Seco	-	4.4	46.5	26.6	22.5
Port Maria	-	0.1	43.4	55.8	0.7
Port Antonio	0.5	19.5	63.6	11.7	4.7
Gallows Bay	-	0.2	36.6	61.1	2.1
Pinneys	-	2.8	51.7	41.4	4.1
Jolly Beach	-	0.5	43.1	55.1	1.3
Calliaquo	0.3	8.5	28.2	45.7	17.3
Hamilton A	-	0.3	1.4	82.3	16.0
Hamilton B	0.2	5.9	85.3	8.5	0.1
Cocal Beach	0.1	3.6	77.2	16.3	1.8
Mayaro	0.1	7.5	88.5	3.7	0.2

APPENDIX VII

B

A cumulative curve for a size-grade analysis of a beach sand showing the determination of Median Diameter and Q_3 and Q_1 values. (See page 69)

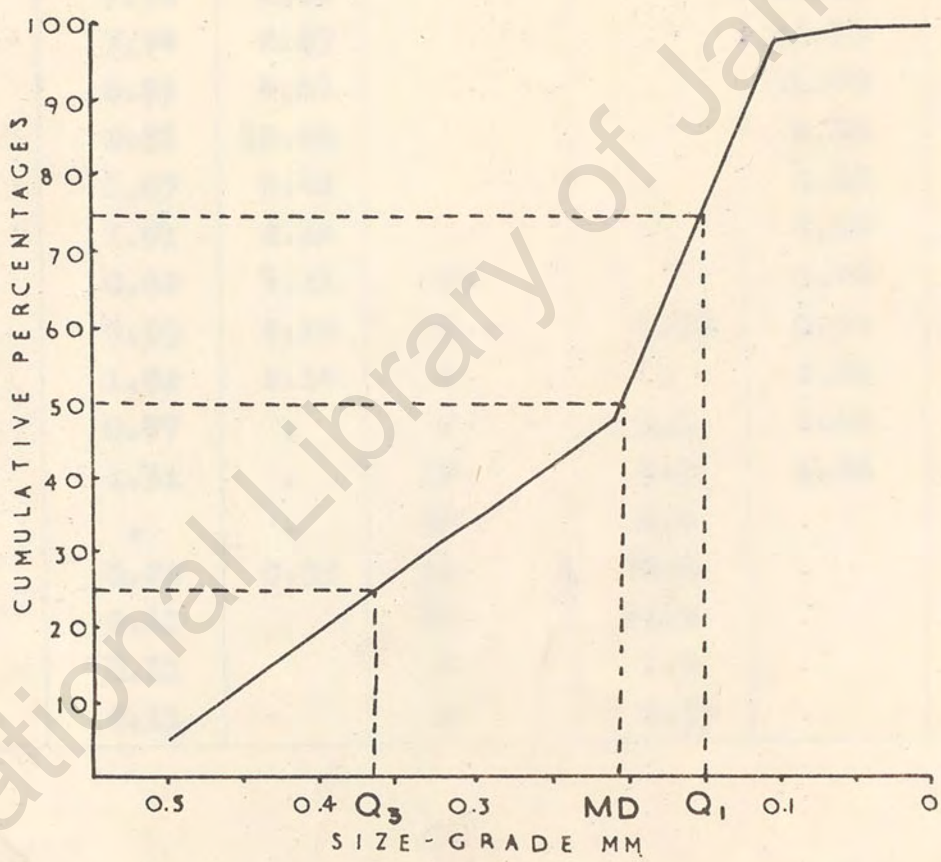

Figure 54

APPENDIX VIII

Length-frequency percentages for samples of populations of D. denticulatus in Jamaica in September, 1964.

Length	Pt. Hend.	G. Bay	Small Pt.	F. Beach	Gut River	Al.Pond
2 mm.	0.82%	3.21%				
3	18.42	19.25				
4	23.60	17.65			1.08%	
5	12.10	10.69			1.62	
6	5.74	7.49			5.94	
7	6.71	5.34			11.89	5.71%
8	7.92	1.60			14.59	8.57
9	7.24	2.67			15.13	2.86
10	6.83	4.81			11.89	25.71
11	2.51	10.69			8.65	8.57
12	1.67	6.42			4.86	14.28
13	1.01	2.14			7.56	14.28
14	0.82	3.21	6%		5.40	8.57
15	0.55	2.14	6	1.1%	5.94	5.71
16	1.02	2.14	4	.	2.70	5.71
17	0.77	.	2	1.1	1.08	
18	1.31	.	10	5.5	1.08	
19	.	.	14	6.6		
20	0.72	0.53	34	26.6		
21	0.11		14	42.2		
22	0.11		8	1.1		
23	0.11		2	0.55		

APPENDIX VIII (Contd.)

Length	Bl. River	H. Wharf	Negril	Mo.Bay	P. Seco	Pt. Maria
2 mm.						
3						
4						3.80%
5		1.45%	0.92%			6.33
6		1.45	2.78		20%	7.59
7	6.42%	4.35	18.52		40	8.86
8	7.34	7.25	23.15		20	12.66
9	2.75	8.21	26.85		20	16.45
10	4.59	9.66	19.44			10.13
11	5.50	5.31	6.48			6.33
12	4.59	12.08	1.85			7.59
13	9.17	13.25		33.3%		7.59
14	10.09	8.21		.		5.06
15	7.34	7.73		33.3		5.06
16	11.00	5.31		.		2.53
17	15.59	5.80		.		
18	9.17	2.41		33.3		
19	2.75	1.45				
20	0.92	2.90				
21	0.92	1.45				
22	0.92	0.96				
23	0.92	0.48				

APPENDIX IX

PORT HENDERSON

Composite length-frequency data for monthly population samples of D. denticulatus at Port Henderson expressed as numbers and percentages per metre of beach. (Figure 24).

	21.3.63		22.4.63		23.5.63		20.6.63		22.7.63		23.8.63	
Length	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%
2 mm											12	0.6
3	6	0.2	9	0.4	89	5.1	4	0.2	3	0.1	379	17.7
4	68	3.1	70	3.0	31	1.7	4	0.2	4	0.2	330	15.4
5	120	5.4	77	3.3	60	3.4	19	0.9	14	0.6	6	0.3
6	100	4.3	80	3.4	40	2.3	105	5.0	26	1.2	0	-
7	155	6.4	134	5.7	36	2.0	114	5.4	22	1.0	17	0.8
8	163	6.6	129	5.5	43	2.4	40	1.9	118	5.3	10	0.5
9	120	5.4	127	5.4	66	3.7	53	2.5	140	6.3	13	0.6
10	103	4.5	155	6.6	66	3.7	55	2.6	72	3.2	64	3.0
11	137	6.1	145	6.2	72	4.1	55	2.6	47	2.1	90	4.2
12	142	6.2	134	5.7	114	6.5	91	4.3	40	1.8	66	3.1
13	170	7.5	129	5.5	112	6.4	72	3.4	72	3.2	49	2.3
14	237	10.5	209	8.9	161	9.2	78	3.7	115	5.1	77	3.6
15	300	13.6	329	14.0	257	14.7	154	7.3	177	7.9	120	5.6
16	246	10.9	312	13.3	290	16.6	192	9.1	263	11.8	144	6.7
17	105	4.6	169	7.2	208	11.9	412	19.5	387	17.3	240	11.2
18	31	1.3	63	2.7	66	3.7	429	20.3	452	20.2	309	14.4
19	30	1.3	37	1.6	22	1.2	209	9.9	218	9.5	137	6.4
20	9	0.4	13	0.5	1	0.1	46	2.2	64	2.9	56	2.6
21					2	0.1	14	0.6	7	0.3	11	0.5
22							2	0.1	3	9.1	2	0.1
TOTAL:	2242		2321		1736		2148		2244		2132	

APPENDIX IX (CONTD.)

PORT HENDERSON

	20.9.63		24.10.63		21.11.63		18.12.63		23.1.64		20.2.64	
Length	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%
2mm.	1	0.1	0	-	135	7.6	35	0.9	15	0.5	0	-
3	50	3.6	1	0.1	459	25.9	535	13.4	167	5.4	64	2.8
4	267	19.2	6	0.8	562	31.7	759	19.0	512	16.7	138	6.1
5	129	9.3	7	1.0	87	4.9	754	18.9	464	15.1	215	9.5
6	4	0.3	18	2.5	9	0.5	599	15.0	420	13.7	243	10.8
7	1	0.1	33	4.5	5	0.3	487	12.2	378	12.3	221	9.8
8	6	0.4	31	4.3	12	0.7	296	7.4	309	10.1	239	10.6
9	4	0.3	14	1.9	30	1.7	82	2.1	234	7.6	209	9.3
10	12	0.9	1	0.1	39	2.2	10	0.2	168	5.5	214	9.5
11	24	1.7	1	0.1	46	2.6	3	0.1	65	2.1	152	6.7
12	50	3.6	3	0.4	46	2.6	16	0.4	19	0.6	112	5.0
13	82	5.9	9	1.3	12	0.7	20	0.5	8	0.2	74	3.3
14	64	4.6	9	1.3	4	0.2	37	0.9	18	0.6	12	0.5
15	64	4.6	21	2.9	4	0.2	35	0.9	37	1.2	28	1.2
16	116	8.4	49	6.8	14	0.8	7	0.2	37	1.2	35	1.5
17	173	12.5	107	14.8	25	1.4	11	0.3	16	0.5	55	2.4
18	206	14.8	182	25.3	55	3.1	39	1.0	23	0.7	46	2.0
19	95	6.9	133	18.5	78	4.4	81	2.0	62	2.0	55	2.4
20	23	1.7	74	10.3	112	6.3	117	2.9	76	2.5	103	4.6
21	3	0.2	16	2.2	43	2.4	52	1.3	35	1.1	42	1.9
22	0	-	3	0.5	16	0.9	17	0.4	5	0.2	4	0.2
TOTAL	1374		718		1793		3992		3068		2261	

APPENDIX IX (Contd.)

PORT HENDERSON

Length	19.3.64 Nos.	%	23.4.64 Nos.	%	26.5.64 Nos.	%	22.6.64 Nos.	%	23.7.64 Nos.	%	19.8.64 Nos.	%
2mm	2	0.1	0	-	0	-	34	3.2	12	1.0	13	0.9
3	13	0.6	9	0.9	25	2.4	142	13.2	206	17.6	63	4.6
4	63	3.2	15	1.4	58	5.5	61	5.6	224	19.1	128	11.2
5	167	8.4	31	3.0	44	4.1	105	9.7	185	15.8	259	19.1
6	240	12.0	54	5.2	44	4.1	34	3.2	71	6.1	251	18.5
7	161	8.0	56	5.4	26	2.5	56	5.2	43	3.7	126	10.0
8	175	8.8	73	7.1	23	2.2	37	3.4	41	3.5	68	5.1
9	166	8.3	53	5.1	27	2.5	23	2.1	25	2.1	42	3.2
10	148	7.4	64	6.1	40	3.8	14	1.2	20	1.7	29	2.1
11	150	7.5	69	6.6	35	3.3	19	1.7	12	1.0	32	2.4
12	125	6.3	77	7.5	35	3.3	16	1.5	14	1.2	24	1.7
13	116	5.8	94	9.0	49	4.7	31	2.8	12	1.0	21	1.5
14	89	4.4	117	11.3	71	6.7	17	1.5	18	1.5	14	1.1
15	39	2.0	75	7.2	132	12.5	54	5.0	20	1.7	23	1.7
16	24	1.2	44	4.3	143	13.5	83	7.6	38	3.2	24	1.7
17	53	2.7	32	3.1	65	6.1	101	9.4	67	5.7	52	3.9
18	51	2.6	37	3.5	61	5.8	73	6.8	64	5.5	81	5.1
19	55	2.7	33	3.2	50	4.7	58	5.3	44	3.8	31	2.3
20	97	4.8	56	5.4	69	6.5	77	6.3	25	2.1	34	2.5
21	46	2.3	38	3.6	45	4.3	31	2.8	20	1.7	8	0.6
22	15	0.7	8	0.7	7	0.7	16	1.5	4	0.4	6	0.4
23	0	-	3	0.2	1	0.1	1	0.1	3	0.3	0	-
24	0	-	0	-	0	-	1	0.1	0	-	0	-
TOTAL	1995		1038		1050		1084		1168		1329	

APPENDIX IX (Contd.)

PORT HENDERSON

Length	23.9.64 Nos.	%	21.10.64 Nos.	%	21.11.64 Nos.	%	21.12.64 Nos.	%
2mm	8	0.8	10	1.1	6	1.5	8	0.6
3	186	18.4	14	1.6	72	17.5	300	21.6
4	239	23.6	57	6.7	60	14.6	392	26.3
5	122	12.1	56	6.6	56	13.6	200	14.4
6	58	5.7	83	9.8	9	2.3	100	7.2
7	68	6.7	168	19.7	27	6.6	72	5.2
8	80	7.9	112	13.2	26	6.3	32	2.3
9	73	7.2	51	6.0	18	4.5	20	1.4
10	69	6.8	49	5.7	34	8.4	16	1.2
11	25	2.5	50	5.9	28	6.9	16	1.2
12	17	1.7	54	6.3	22	5.4	28	2.0
13	10	1.0	56	6.6	8	1.9	44	3.2
14	8	0.8	19	2.2	7	1.8	24	1.7
15	6	0.5	20	2.3	5	1.2	24	1.7
16	10	1.0	14	1.6	8	1.9	28	2.0
17	8	0.8	11	1.3	11	2.6	40	2.9
18	13	1.3	13	1.5	6	1.5	16	1.2
19	0	-	9	1.1	2	0.5	20	1.4
20	7	0.7	9	1.1	1	0.3	8	0.6
21	1	0.1	0	-	2	0.5	0	-
22	1	0.1	2	0.3				
23	1	0.1	1	0.1				
TOTAL	1010		858		408		1388	

APPENDIX X

GREEN BAY

Composite length-frequency data for monthly population samples of D. denticulatus at Green Bay expressed as numbers and percentages per metre of beach (Figure 25).

Length	21.3.63 Nos.	%	22.4.63 Nos.	%	26.5.63 Nos.	%	21.6.63 Nos.	%	23.7.63 Nos.	%	24.8.63 Nos.	%
2mm	00	-	16	0.9	22	1.8	0	-	10	1.6	30	2.6
3	24	2.2	154	8.5	80	6.7	4	0.4	86	14.6	386	33.7
4	64	5.9	304	17.0	234	19.5	32	2.9	8	1.3	238	20.7
5	82	6.9	198	11.0	208	17.4	84	7.6	6	1.0	82	7.1
6	148	12.3	194	10.7	176	14.6	166	15.0	32	5.4	32	2.8
7	184	16.0	200	11.1	104	8.5	150	13.6	56	9.6	8	0.7
8	176	15.7	202	11.3	86	7.1	188	17.0	48	8.3	16	1.3
9	130	11.9	160	8.9	76	6.2	150	13.6	66	11.3	38	3.2
10	106	9.0	102	5.6	38	3.1	110	10.0	78	13.1	62	5.2
11	52	4.4	58	3.2	30	2.3	40	3.6	50	8.6	54	4.5
12	34	2.9	30	1.6	20	1.6	42	3.8	38	6.5	74	6.2
13	38	3.6	48	2.6	22	2.0	20	1.8	20	3.5	56	4.7
14	28	2.3	42	2.3	32	2.7	16	1.4	24	4.1	26	2.2
15	24	1.9	52	2.8	30	2.5	16	1.4	20	3.5	18	1.5
16	26	2.2	28	1.5	24	1.9	34	3.1	18	3.1	20	1.7
17	26	2.2	10	0.4	8	0.4	28	2.5	22	3.7	16	1.3
18	12	1.2	6	0.2	0	-	18	1.6	4	0.7	8	0.7
19							6	0.5			2	0.1
TOTAL	1154		1804		1190		1104		586		1166	

APPENDIX X (Contd.)

GREEN BAY

	21.9.63		24.10.63		21.11.63		21.12.63		23.1.64		20.2.64	
Length	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%
2mm.	20	4.5	14	2.5	876	13.1	2218	8.3	1375	6.6	144	1.3
3	68	15.5	32	5.6	3560	53.4	6114	22.9	2645	12.8	1356	12.8
4	96	21.8	68	12.0	1558	23.9	9672	36.2	4280	21.2	2768	26.1
5	76	17.3	74	13.0	210	3.1	3896	14.6	3660	17.7	1444	13.6
6	48	10.9	78	13.7	52	0.9	1372	5.1	2898	14.0	1564	14.8
7	22	5.0	66	11.6	98	1.6	1506	5.6	2327	11.3	1240	11.2
8	24	5.4	66	11.6	88	1.5	948	3.5	1777	8.7	1112	10.5
9	14	3.2	30	5.3	56	0.9	372	1.4	1100	5.3	564	5.3
10	4	0.9	26	4.6	68	1.3	84	0.3	127	0.6	184	1.7
11	14	3.2	30	5.3	34	0.6	108	0.4	42	0.2	56	0.5
12	14	3.2	14	2.5	28	0.5	168	0.6	21	0.1	16	0.1
13	10	2.3	24	4.3	12	0.2	66	0.2	105	0.5	56	0.5
14	14	3.2	22	4.3	6	0.1	50	0.2	63	0.3	16	0.1
15	6	1.4	12	2.1	16	0.3	66	0.2	42	0.2	16	0.1
16	8	1.8	4	0.7	12	0.2	16	0.1	21	0.1	28	0.3
17	2	0.4	8	1.4	14	0.2	16	0.1	42	0.2	16	0.1
18					2	-	16	0.1	21	0.1		
TOTAL	440		568		6692		26722		20567		10596	

APPENDIX X (Contd.)

GREEN BAY

Length	19.3.64		26.4.64		26.5.64		22.6.64		23.7.64		19.8.64	
	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%
2mm.	0	-	0	-	40	2.5	8	0.9	0	-	28	2.6
3	51	1.6	96	4.5	196	12.2	40	4.7	12	3.2	12	1.1
4	69	2.1	208	9.8	312	19.5	160	19.0	8	2.1	44	4.0
5	309	9.6	212	10.0	140	8.7	148	16.9	52	13.8	24	2.2
6	360	11.2	144	6.8	164	10.2	96	11.4	60	16.0	40	3.7
7	446	13.8	244	11.5	92	5.7	84	9.9	52	13.8	32	2.9
8	686	21.3	244	11.5	80	5.0	56	6.6	36	9.6	136	12.4
9	532	16.5	288	13.6	112	7.0	32	3.8	16	4.3	132	12.1
10	343	10.6	248	11.7	124	7.7	36	4.3	20	5.3	116	10.0
11	103	3.2	168	7.9	128	8.0	52	6.2	20	5.3	116	10.6
12	34	1.0	52	2.4	88	5.5	56	6.6	32	8.5	80	7.3
13	0	-	72	3.4	76	4.7	8	0.9	20	5.3	128	11.7
14	120	3.7	44	2.1	20	1.2	8	0.9	20	5.3	132	12.1
15	51	1.6	44	2.1	20	1.2	24	2.8	12	3.2	32	2.9
16	51	1.6	32	1.5	4	0.2	24	2.8	12	3.2	20	1.8
17	17	0.5	12	0.6	4	0.2	8	0.9	4	1.1	8	0.7
18	34	1.0	4	0.2			4	0.5			8	0.7
19	17	0.5	8	0.4							0	-
20			4	0.2							4	0.4
TOTAL	3223		2124		1600		844		376		1092	

APPENDIX X (Contd.)

GREEN BAY

Length	23.9.64 Nos.	%	22.10.64 Nos.	%	24.11.64 Nos.	%	21.12.64 Nos.	%
2 mm	24	3.2	0	-	44	4.9	124	10.0
3	144	19.2	0	-	332	37.2	380	30.7
4	132	17.6	8	2.1	172	19.3	220	17.8
5	80	10.7	32	8.2	36	4.0	136	11.0
6	56	7.5	32	8.2	16	1.8	32	2.6
7	40	5.3	80	20.6	20	2.2	24	1.9
8	12	1.6	44	11.3	12	1.3	24	1.9
9	20	2.7	56	14.4	36	4.0	20	1.6
10	36	4.8	24	6.2	68	7.6	32	2.6
11	80	10.7	16	4.1	40	4.5	76	6.1
12	48	6.4	32	8.2	16	1.8	36	2.9
13	16	2.1	24	6.2	16	1.8	44	3.6
14	24	3.2	12	3.1	24	2.7	8	0.6
15	16	2.1	20	5.1	40	4.5	40	3.2
16	16	2.1	4	1.0	12	1.3	16	1.3
17	0	-	0	-	4	0.4	16	1.3
18	0	-	4	1.0	4	0.4	8.	0.6
19	0	-						
20	4	0.5						
TOTAL	748		388		892		1236	

APPENDIX XI

D. denticulatus

The average total weight, shell weight, and flesh weight of five clams each of 1 mm size intervals.

Length	Total weight	Shell weight	Flesh weight
3 mm	6.2 mg.	5.8 mg.	0.4 mg.
4	12.7	12.0	0.7
5	19.5	18.3	1.2
6	37.6	35.4	2.2
7	65.7	61.9	3.6
8	89.6	84.2	5.4
9	137.6	130.2	7.4
10	202.4	193.0	9.4
11	292.0	278.4	13.6
12	377.4	359.6	17.8
13	542.0	521.0	21.0
14	666.4	640.4	26.0
15	842.0	807.0	35.0
16	1001.2	961.8	39.4
17	1146.0	1097.2	48.8
18	1337.4	1275.6	61.8
19	1513.4	1453.8	59.6
20	1895.7	1827.5	68.2

APPENDIX XII

A modified method for the collection, recovery, and measurement of the organic leptopel from the sea water at Donax beds.

A. Collection: Water samples were taken in one-litre polyethylene bottles over the openings of which strips of 97 mpi plankton netting were fitted to ensure the rejection of particles larger than about 250 μ in diameter. Collections were made in the surf zone by gently squeezing the bottles and allowing them to suck in the water. Usually some amount of sand entered the bottles but settled out of suspension almost immediately so that the water could be quickly decanted and retained. Samples which had to be kept for more than a few hours before analysis were stored in a deep freeze. Two samples were always taken for each locality.

B. Recovery: 500 ccs. aliquots of water samples were filtered through an inert inorganic adsorbent of a 1:1 mixture of SiO_2 and MgO. This was done by preparing a thin paste of one gram of the mixture and allowing it to settle on a pad of 140 mpi bolting silk netting and No. 50 Whatman filter paper fitted on the floor of a small Buchner funnel (Figure 55). The 500 cc aliquot of sea water was filtered through the adsorbent and organic residue formed was removed and dried in an oven at 50°C for half an hour.

C. Measurement: The organic leptopel content of the samples was measured as milligrams of organic matter per litre of water filtered. After drying, the organic content was determined by Walkley and Black's Rapid Titration Method (Piper, 1942). The values obtained were multiplied by a factor of 1.8 (Trask, 1939) to convert them from organic carbon into those for organic matter. Fox, Isaacs, and Corcoran (1952) who devised the original method for the measurement of leptopel, found that this analysis gave a similar or sometimes better recovery than the Kjeldahl analysis.

Figure 55

Apparatus for the adsorption of leptopel from sea water.

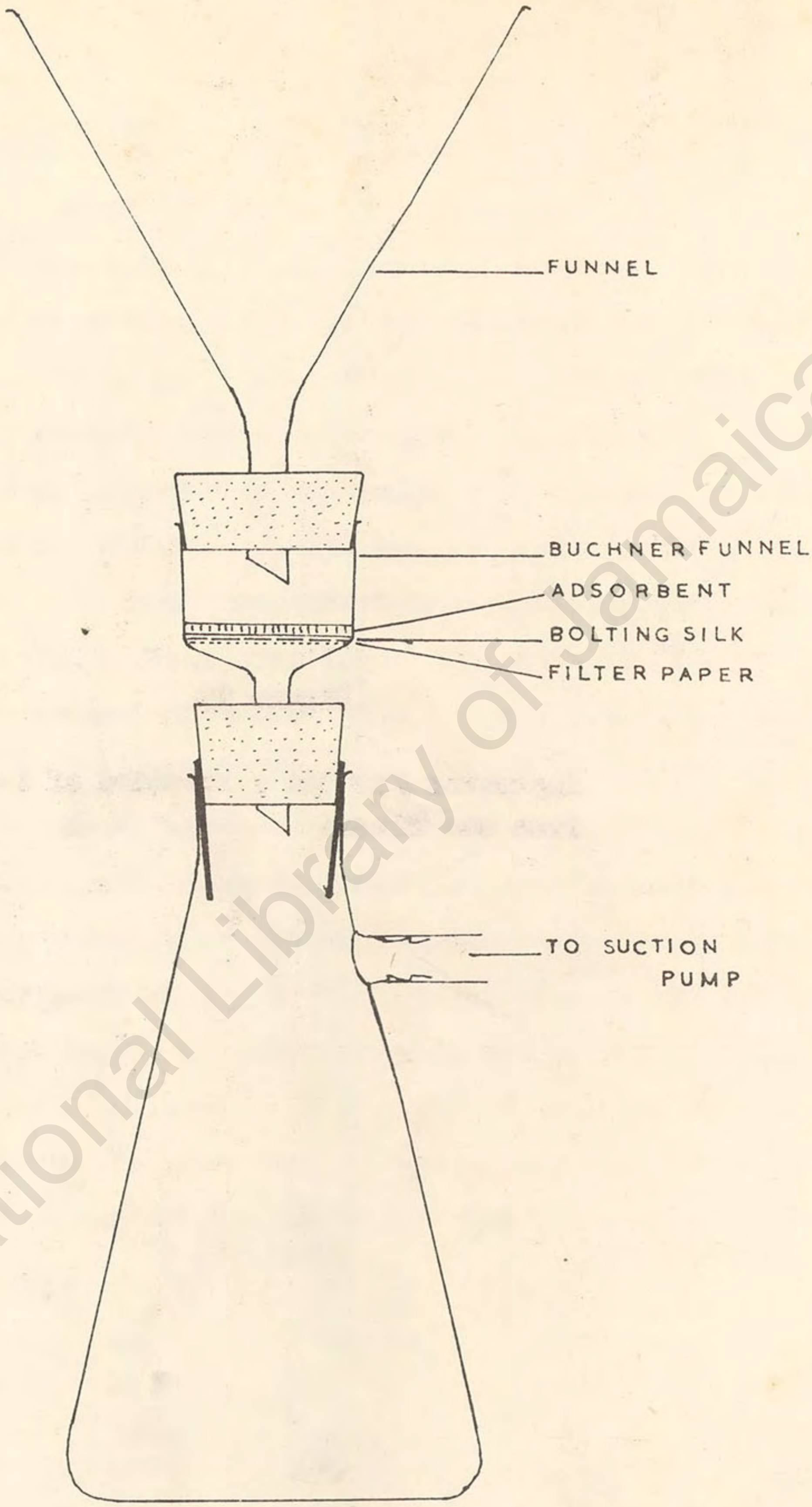
FUNNEL
BUCHNER FUNNEL
ADSORBENT
BOLTING SILK
FILTER PAPER
TO SUCTION
PUMP

Figure 55

APPENDIX XIII

Experimental procedure for determining the rate of water filtration of adult clams of D. denticulatus.

A stock suspension of the colloidal graphite, Aquadag, was made up by adding approximately 2 gm. to one litre of distilled water and the concentration determined by filtering 10 cc. portions through a weighed millipore filter. From the stock suspension, six different concentrations of graphite in sea water were obtained by adding 10 to 60 cc. aliquots to 250 cc. of clean filtered sea water and the light transmission of each was measured with a Unicam Prism Absorptiometer. Ten adult clams were placed in the clearest suspension at room temperature (29°C) and allowed to feed freely for ten minutes at the end of which they were taken out and the light transmission of the suspension again measured. Knowing the concentration and light transmission of the suspension at the beginning of the experiment and the light transmission at the end, the concentration of the suspension at the end of feeding was determined. A period of half an hour was made to elapse before the clams were transferred to the suspension of the next higher concentration and the procedure repeated.

	Transmission		Concentration	
Suspension	T_o	T_t	P_o	P_t
10:250cc.	63.5%	88.0%	1.65 mg/l	-
20:250	41.0	73.0	3.19	0.65 mg/l
30:250	32.5	73.0	4.61	0.65
40:250	27.5	59.0	5.96	2.10
50:250	15.5	52.5	7.17	2.90
60:250	2.0	34.0	8.32	4.85

The rate of filtration in each suspension (Table 25) was computed from the formula

$$P_t = P_o \exp(-\frac{m}{M}t) ,$$

where M is the quantity of water used for the experiment, and m the quantity cleared from particles per unit time, while P_t and P_o are the concentrations of the suspended material at the time t and o respectively (Jørgensen, 1943).

Since the experiments produced data for the rate of ten clams per minute, it was necessary to multiply the results by 6 to supply the rate for one clam per hour.

APPENDIX XIV

Procedure followed for staining nerve fibres and endings in the siphons of D. denticulatus and D. striatus after Liang (1947) and Owen (1959). The staining principle is based on the fact that nervous tissue gives a positive reaction with Schiff's Reagent.

(1) Fix tissue in 1% acetic acid for 1 hour.

(2) Wash in SO_2 water, two changes.

(3) Transfer to Schiff's leucobase for 1-3 hrs. or until the nerves are deep purple in colour.

(4) Wash thoroughly in several changes of SO_2 water.

(5) Rinse with distilled water.

(6) Embed in paraffin, cut, dewax, and bring to water.

(7) Counterstain in 1% methylgreen aqueous solution for 10 minutes.

(8) Dehydrate rapidly in several changes of absolute acetone.

(9) Clear in xylene and mount in balsam.

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