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The Ecology of Two Sandy Beaches in South West India. III. Observations on the Population of *Donax incarnatus* and *D. spiculum*

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Abstract

The biology of two species of *Donax*, *D. incarnatus* Gmelin and *D. spiculum* Reeve on two beaches in south west India is described. Two year groups of *D. incarnatus* were present on both beaches, from settlements during the monsoon period in 1967 and 1968. At Shertallai, both groups were studied through the year, and data on growth, mortality and production are presented. At Cochin, the rate of growth was slower and the maximum size attained smaller, but mortality during the early monsoon precluded study of *D. incarnatus* through a full year. *D. spiculum* occurred at Cochin mainly during the pre-monsoon period, and at Shertallai during the post-monsoon. The species has a shorter life-span than *D. incarnatus*, but its irregular occurrence did not allow detailed production estimates.

Introduction

In two previous papers (Ansell *et al.*, 1972a, b) we have examined some aspects of the ecology of two sandy beaches on the west coast of India, including changes in physical conditions, in nutrient concentrations, and in the distribution and density of the macrofauna. Among the macrofauna, two species of the bivalve genus *Donax* account for a large proportion of the biomass, constituting a dominant feature of the beach fauna through the year, and the purpose of this paper is to examine the data on abundance and growth of these two species, *Donax incarnatus* Gmelin and *D. spiculum* Reeve, and to make a preliminary estimate of their production. Later, when we have more information on oxygen consumption and feeding, we hope to make a further estimate of the energy budget of the populations.

Methods

Data were collected by two methods: at frequent intervals, samples of 1/10 m^2 area of sand were collected from stations 2 m apart, along transect lines from above high-water mark to the wash zone of the surf. The sand was sieved through a 1 mm screen, and all animals removed, and the numbers, and total wet body weight (formalin preserved) present at each station recorded. Further non-quantitative samples were collected be sieving larger quantities of sand from those levels of the beach where *Donax* was abundant, and from these samples the length of each bivalve was recorded to provide data on the size-frequency distribution of the population. At frequent intervals, samples of 20 bivalves, selected from the whole size range available, were used to determine the relationship between length and total weight (that is, weight of the whole animal, live, with the shell blotted dry, but with the mantle cavity remaining closed and filled with fluid), wet weight of soft tissues, oven-dried weight of soft tissues and shell weight.

Results

Population Data

Donax incarnatus from Shertallai

Population Density and Mortality

At Shertallai, two transect lines were sampled regularly. These were approximately 10 m apart and were intended as duplicates. Because both *Donax incarnatus* and *D. spiculum* are tidal migrants (Ansell and Trevallion, 1969) and, because during the year considerable changes take place in the beach profile due to a cycle of erosion and accretion caused by the changes through the monsoon period (Ansell *et al.*, 1972a), the quantitative samples collected have been used to calculate the number of individuals present in a 1 m strip of beach extending from above high water mark into the surf zone. Throughout the paper, therefore, densities are referred to this "1 m transect" and these are, therefore, as far as possible independent of the position of the bivalves on the beach or their degree of dispersion or aggregation vertically on the beach caused by physical conditions.

The *Donax incarnatus* sampled at Shertallai belonged to 2 year classes, representing settlements in

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1967 and 1968. The data for the numbers/m transect for each sampling date on each of the two transects are shown in Fig. 1.

At the beginning of the year, only individuals from the 1967 settlement were present. In January, the densities recorded from the two transects were 240 to 250 bivalves/m transect on A, and 660/m transect on B. The maximum density recorded on A was 90 bivalves/m^2 and on B, 110/m^2. The first indication of a 1968 settlement occurred late in January, when 90 bivalves/m transect for the new settlement were recovered from Transect A. The major settlement however, did not occur until the monsoon period, when in May, maximum numbers of over 4,000 animals bivalves/m transect were recovered from Transect A, with a density of nearly 2,000/m^2.

The numbers of the 1967 settlement declined steadily, and none were recovered in the quantitative samples beyond August, although they continued to be present on the beach, and were represented in the larger non-quantitative samples until December, when sampling was discontinued. It is possible, therefore, that some individuals may survive for more than 2 years. Numbers of the 1968 settlement declined rapidly on both transects until, in November, the numbers on Transect A were reduced to 100/m transect. The decline in number on both transects followed a similar course, and the difference between the two are not considered significant in view of the considerable errors involved in sampling such exposed beaches. The higher numbers of the 1967 year class recovered in January, 1968, compared with the numbers of the 1968 year class recovered in October/November, 1968 indicate, however, that the 1967 settlement was greater than that of 1968.

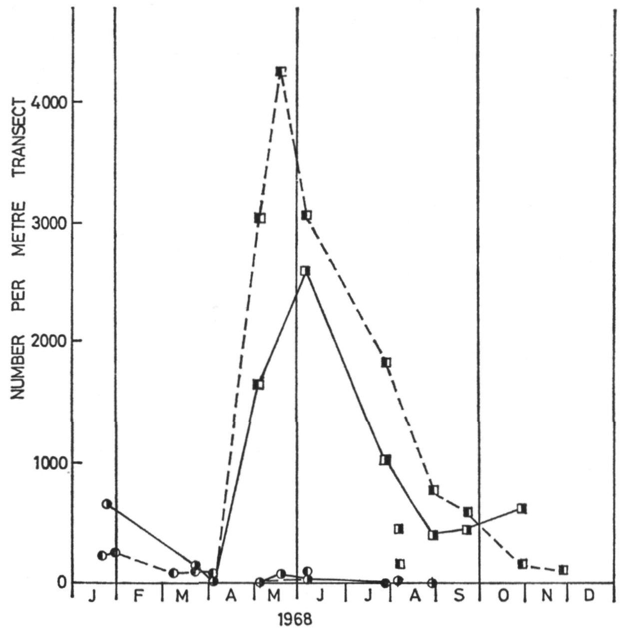

Fig. 1. *Donax incarnatus*. Numbers/m transect on two transects of Shertallai beach during 1968. ◐: Transect A, 1967 settlement; ◧: Transect A, 1968 settlement; ◑: Transect B, 1967 settlement; ◨: Transect B, 1968 settlement. Lines indicate general trend in change of numbers for each transect (solid line, Transect B; dotted line, Transect A). Vertical lines on this and all later figures (where appropriate) represent convenient division of the year into 3 seasons: pre-monsoon (February to May), monsoon (June to September) and post-monsoon (October to January)

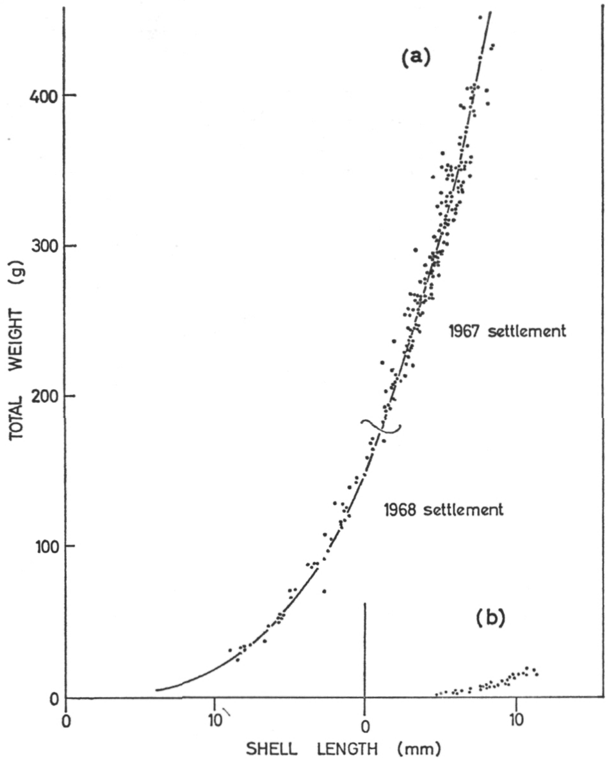

Fig. 2. Relationship between total weight and shell length for (a) *Donax incarnatus*, (b) *D. spiculum*, from Shertallai. Line shown in (a) represents fitted regression. Log $W = 3.077$, log $L - 0.816$. Points shown for (b) are fitted by regression. log $W = 2.659$, log $L - 0.556$

Length-Weight Relationship

All the data for the body-weight determinations for the year gave a combined relationship between log length and log total weight of:

$$\log W = 3.0771 \log L - 0{,}8161 \text{ (Fig. 2a)}.$$

The relationship for individual collections in no case differed significantly from this, indicating that there is no change in shape over the size range studied.

The above formula was used to calculate the mean weights from the means of length for age in the following section on growth.

Growth

The size distribution of all collections of *Donax incarnatus* from Shertallai made during the year are

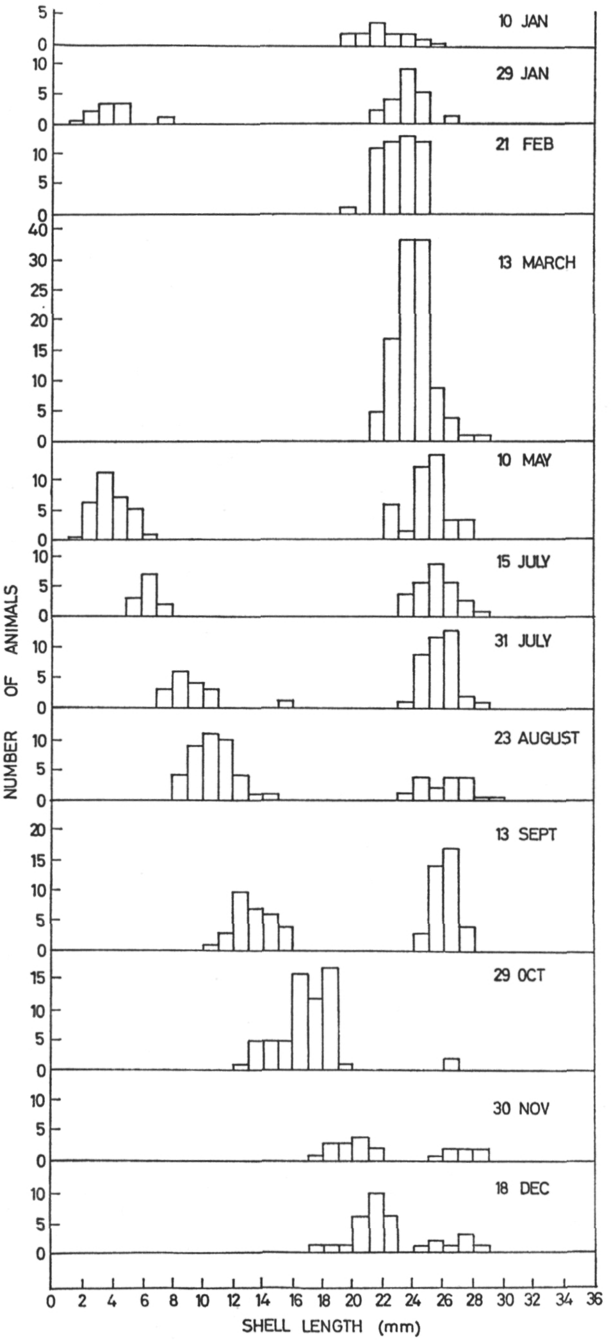

Fig. 3. *Donax incarnatus*. Size distribution histograms from Shertallai beach during 1968

shown in Fig. 3. As already noted, the population divided clearly into two groups. One which appeared with a mode at 3 to 4 mm in May, was derived from a settlement of larvae which presumably took place in April. Because of the mesh size of the screen used in collection, the smallest individuals present in May were probably not fully sampled. Because no sample was taken in April, the time of settlement of this group is not known precisely, but following their appearance in May they showed a steady and rapid increase in size to reach a modal length of 21 to 22 mm in December. The other group was present when sampling began in January, with a modal size of 21 to 22 mm, and may

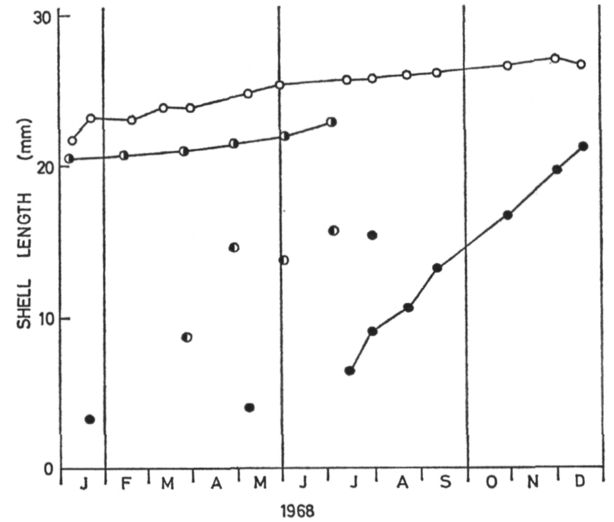

Fig. 4. *Donax incarnatus*. Mean shell lengths in collections from Shertallai and Cochin during 1968. ○——○: Shertallai, 1967 settlement; ●——●: Shertallai, 1968 settlement; ◑——◑: Cochin, 1967 settlement; ◐: Cochin, 1968 settlement

be assumed, therefore, to have been derived from a settlement in 1967 occurring at a similar time to that in 1968. There was also a progressive increase in the size of this group throughout 1968. The small settlement which produced the group of juveniles present in the collection of January 29 with a mode of 3 to 5 mm, was represented only by occasional specimens in later collections, for example that of 31 July, and made no significant contribution to the population.

Since the two groups represented were completely separated in size throughout the year, it was possible to calculate means and standard deviations of shell length for each year group for each collection. These data have been used to construct a growth curve of length on age (Fig. 4) which showed that *Donax incarnatus* which settled in April grew rapidly and continuously for 8 months, and then more slowly, possibly for a further 12 months, although few survived so long.

Mean weights were calculated by use of the regression of log weight on log length, and the resultant growth curve for total weight is shown in Fig. 5.

Body Weight Changes and Reproduction

Changes in the wet and dry-tissue weights expressed as percentages of the total weight, and in the percentage water content of the soft tissues, as determined by loss of weight during drying at 85 °C, are shown in Fig. 6. The mean percentage dry weight of individuals from the 1968 settlement rose between July and November to 8%, and then fell. For the 1967 settlement, the mean percentage dry weight fell in February, in May/June and again in November. Ansell *et al.* (1964), Ansell and Lander (1967), Ansell and Trevallion (1967) and Trevallion (1971) used changes in the wet or dry body weight of temperate species to assess the production of spawn, a method which depends on a degree of close synchronisation of spawning activities in the population to be effective. It is not clear whether the changes in mean dry weight for *Donax incarnatus* relate to spawning, but since the mean dry weight for the 1967 settlement only fluctuated between 4 and 6%, it seems likely that spawning activities are not closely synchronised in this species, and that some individuals may be in spawning condition at all times. A possible exception is the fall in percentage for the 1968 settlement in November, which could indicate a greater degree of synchronisation within the population when the bivalves first spawn.

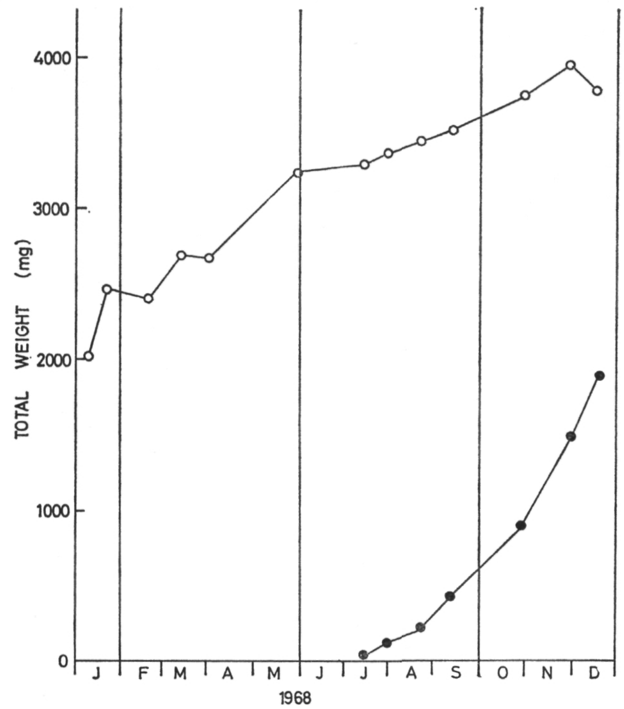

Fig. 5. *Donax incarnatus.* Mean total weight of collections from Shertallai during 1968. ○———○: 1967 settlement; ●———●: 1968 settlement

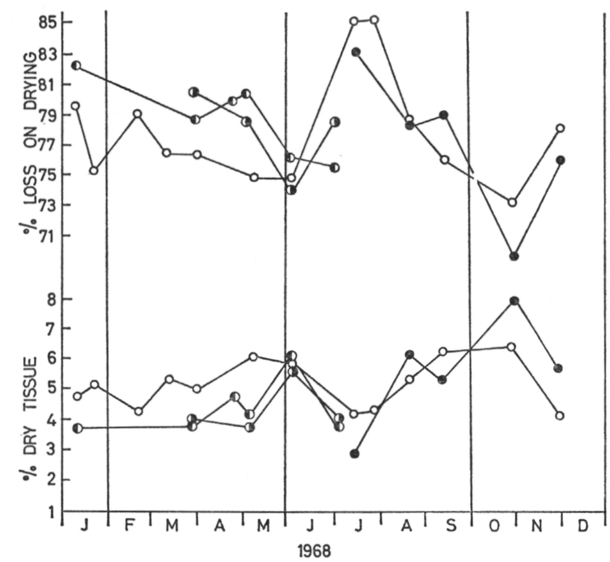

Fig. 6. *Donax incarnatus.* Changes in percentage dry-tissue weight and percentage loss on drying for individuals from Shertallai and Cochin beaches during 1968. ○———○: Shertallai, 1967 settlement; ●———●: Shertallai, 1968 settlement; ◐———◐: Cochin, 1967 settlement; ◑———◑: Cochin, 1968 settlement

The percentage loss on drying showed a marked rise at the beginning of the monsoon, followed by a steady fall until, by November/December, the values were similar to those found between January and June. The rise in water content which this represents coincided with the time of heavy rainfall during the monsoon, and with the consequent fall in salinity of the coastal waters.

The percentage wet and dry-tissue weights were used in conjunction with the mean total weights to construct growth curves for wet (Fig. 7) and dry (Fig. 8) tissue weights The values for mean biomass per individual recorded from the quantitative transect samples (see also Ansell *et al.*, 1972a), and the range of sizes of samples used in the length-weight relationship determinations have also been superimposed on the growth curve for wet-tissue weight.

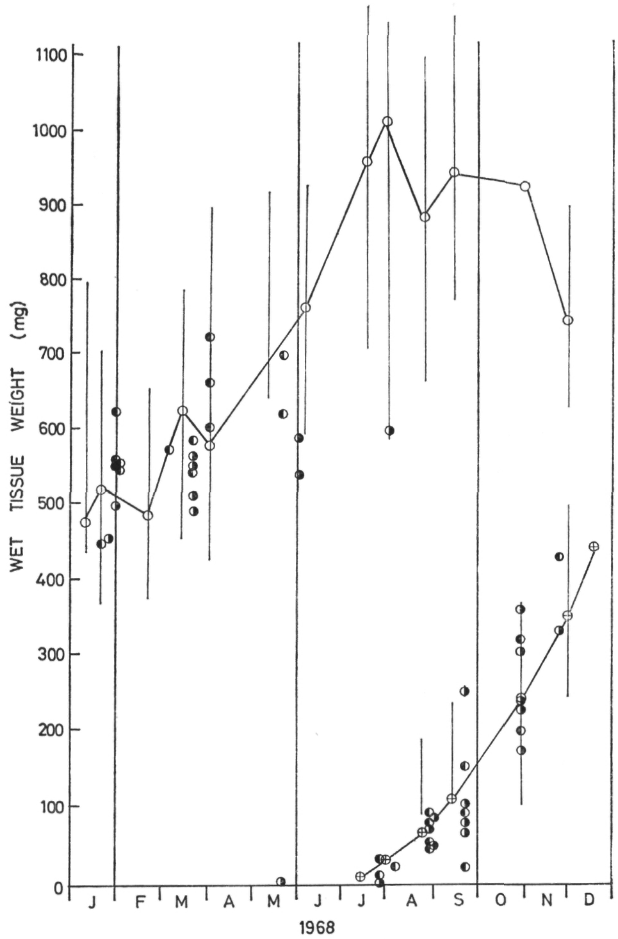

Fig. 7. *Donax incarnatus*. Changes in wet-tissue weight for individuals from Shertallai during 1968. ○——○: 1967 settlement, ⊕——⊕: 1968 settlement, data from non-quantitative samples; ◐: Transect A, ◑: Transect B, data for mean biomass per bivalve from individual quantitative samples along transects; vertical lines: size range of specimens used in determinations of percentage dry-tissue weight and loss on drying given in Fig. 6

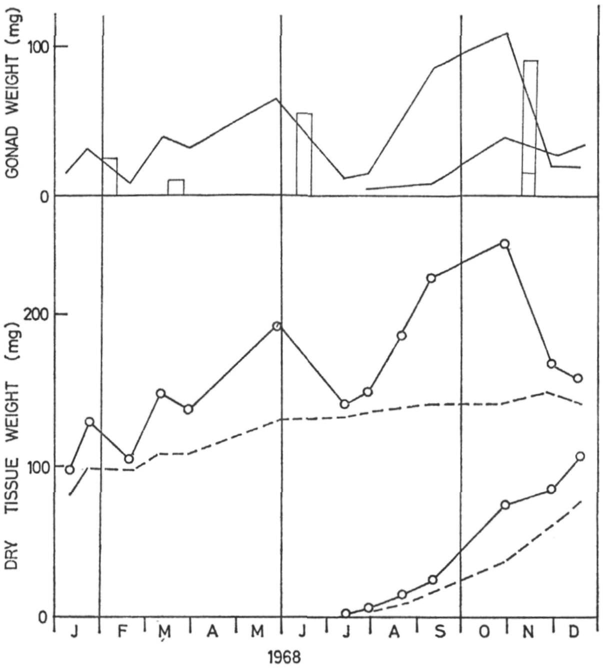

Fig. 8. *Donax incarnatus*. Changes in dry-tissue weight for individuals from Shertallai during 1968 (lower figure). Solid line: actual changes in body weight: dotted line: value of 4% of total weight. The difference between these values (upper figure) is taken as an indication of gonad weight, and where this declines as an indication of possible spawning (histograms)

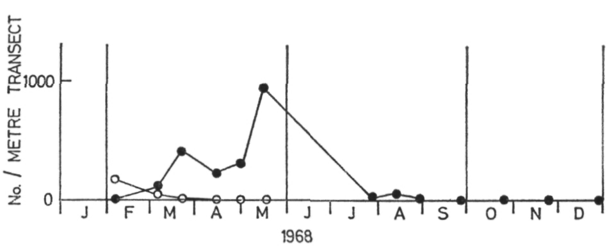

Fig. 9. *Donax incarnatus*. Numbers/m transect on transect of Cochin beach during 1968. ●——●: 1968 settlement; ○——○: 1967 settlement

Donax incarnatus from Cochin

Population Density and Mortality

At Cochin, only one transect line was sampled regularly, and the data are more fragmentary than those for Shertallai. Two year classes could be recognised, however, and the numbers/m transect for each sampling date are shown in Fig. 9. As at Shertallai, only individuals from the 1967 settlement were represented in the first collection made in February, when 140/m transect were present, with a maximum density of 50/m². The first of the 1968 settlement were collected on 6 March, and further collections in April and May also contained juveniles, the maximum number/m transect being 960 on 16 May, with a maximum density of 330/m².

The numbers of the 1967 settlement dropped rapidly. In the collection of 6 March, their numbers had dropped to 40/m transect, and, thereafter, they were not represented in the quantitative samples, although their presence was noted and some were collected in the non-quantitative samples until June. Numbers of the 1968 settlement apparently declined rapidly at the beginning of the monsoon, perhaps as a consequence of the extreme reduction in salinity which occurred at Cochin (Ansell *et al.*, 1972a), since the species was only represented in one further quantitative sample, that of 13 August, when the numbers indicated a density of only 20/m transect.

The data for *Donax incarnatus* for Cochin are not sufficient to allow the calculation of an average mortality rate. The population, however, differed from that at Shertallai in several important respects, i.e., settlement of juveniles occurred over a longer period, that is from February to May, the density of settlement was less, and those individuals which did settle in the pre-monsoon months disappeared from the beach at the start of the monsoon. If this latter occurrence is a regular annual effect, the presence of individuals from the 1967 settlement on the beach early in 1968 can be accounted for only by the hypothesis that they migrate to the beach from elsewhere. We have suggested, however (Ansell *et al.*, 1972a), that the events which occurred at Cochin in 1968 may not have been typical, and it is possible that, in more normal years, a population of *D. incarnatus* persists on the beach.

Length:Weight Relationship

The data from the body-weight determinations for Cochin for the year gave a constant relationship between log length and log weight of:

$$\log W = 3.1056 \log L - 0{,}8799 \ .$$

There was no significant difference between this relationship and that for *Donax incarnatus* from Shertallai.

Growth

The size distribution of all collections of *Donax incarnatus* from Cochin are shown in Fig. 10. A group of small individuals, but ranging in length from 4 to 12 mm appeared in the 30 March collection. This modal group was not well represented in the collection of 30 April, but can be traced through later samples to give a modal length of 14 to 18 mm by 4 July, beyond which no further individuals were recovered. The collection of 4 June also contained a large number of smaller juveniles, from a later settlement, with a modal size of 6 to 8 mm, but this group was not represented in the July sample. A second major group, derived from a 1967 settlement, was present in January, with a modal size of 20 to 21 mm, and this group was well represented until the end of April, and in smaller numbers until July, but there was only a small increase in size. Means for shell lengths for each of the separate groups for each collection are plotted in Fig. 4, where they are compared with the growth curves for shell length of *D. incarnatus* found for Shertallai.

Apart from the differences between the populations of *Donax incarnatus* from Shertallai and Cochin noted in the section on population density and mortality for Cochin, these data suggest that the rate of growth is slower and the maximum size reached, smaller, at Cochin that at Shertallai. The change in modal size of the bivalves which first appeared in the 30 March col-

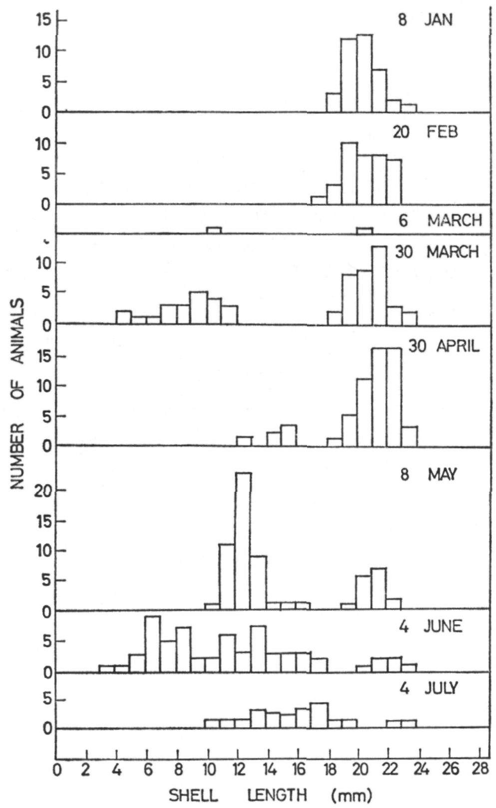

Fig. 10. *Donax incarnatus*. Size distribution histograms for bivalves from Cochin beach during 1968

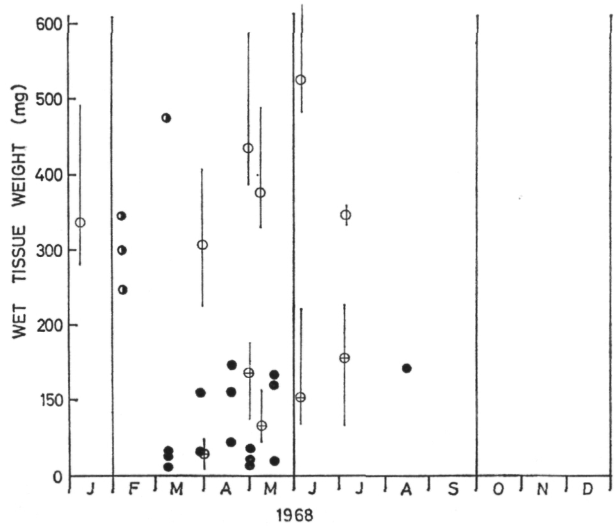

Fig. 11. *Donax incarnatus*. Changes in wet-tissue weight for bivalves from Cochin during 1968. Data from non-quantitative samples (○: 1967 settlement; ⊕: 1968 settlement); data for mean biomass per specimen from individual quantitative samples along a transect (◑: 1967 settlement; ●: 1968 settlement). Vertical lines for each sampling date show size ranges of bivalves used in determinations of percentage dry-tissue weight and loss on drying shown in Fig. 6

lection suggests a rate of growth in shell length slightly less than at Shertallai, and the mean size of the group of individuals derived from the 1967 settlement was approximately 2 mm less than that of the 1967 settlement at Shertallai. The slower rate of growth between March and July, if continued for the rest of the year, would have resulted in a modal group in 1969 approximating in size to that found in 1968, indicating that, in more normal years than 1968, *D. incarnatus* survives and grows at Cochin, although at a somewhat slower rate than at Shertallai.

Body Weight Changes and Reproduction

Percentage wet and dry-tissue weights, and the percentage water content of the soft tissues are shown

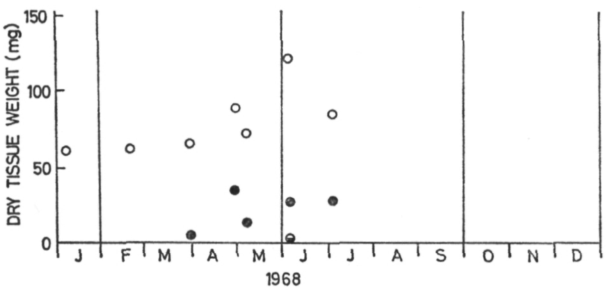

Fig. 12. *Donax incarnatus*. Changes in dry-tissue weight for bivalves from Cochin during 1968. ●: 1968 settlement; ○: 1967 settlement

in Fig. 6. The changes followed the same trends as those from Shertallai, but the percentage dry weight was generally lower, and the water content of the soft tissues greater, at Cochin than at Shertallai.

The percentage wet and dry-tissue weights were used in conjunction with the mean total weights calculated by use of the regression of log weight on log length to construct growth curves for wet and dry-tissue weights (Figs. 11 and 12). The value for average weight per individual recorded from the quantitative transect samples, and the size range of specimens used in the length-weight relationship determinations have also been superimposed on the curve for wet-tissue weight. The combined effect of the reduced rate of growth and lower percentage tissue weight produced a considerable difference in the weight range of individuals from the 1967 settlement on the two beaches.

Donax spiculum from Shertallai

Population Density and Mortality

The numbers/m transect for *Donax spiculum* from Shertallai are shown in Fig. 13. The species was absent from Shertallai before the monsoon, and only appeared in significant numbers in the samples in August. As discussed in an earlier paper (Ansell *et al.*, 1972a) the distribution of this species was not uniform, and the two transects at Shertallai show extreme differences, with large population numbers indicated at one transect, while relatively small numbers were recovered from the other on the same date. The maximum number recorded was 9,060/m transect on 31 August on Transect B, with a maximum density of 4,170 m^2. There

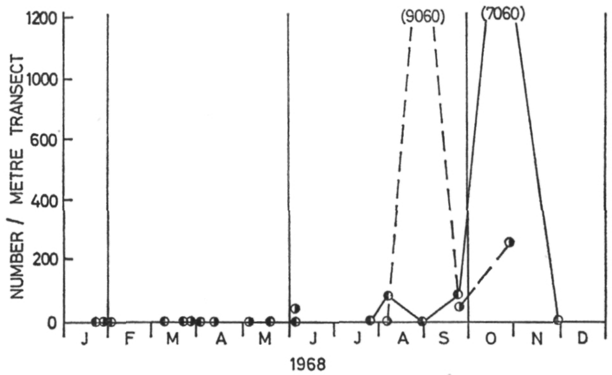

Fig. 13. *Donax spiculum*. Numbers/m transect on 2 transects of Shertallai beach during 1968. ◐——◐: Transect A; ◑- - -◑: Transect B

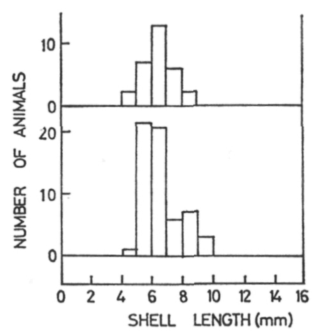

Fig. 14. *Donax spiculum*. Size distribution histograms for bivalves from Shertallai beach during 1968

is not sufficient information to indicate mortality rates.

Length-Weight Relationship

Only two determinations were made of length and body weight relationships for *Donax spiculum* at Shertallai, on 31 July and 21 September. The 35 bivalves examined, over the size range from 4.8 to 11.4 mm, gave a relationship between log length and log total weight of:

$$\log W = 2.6594 \log L - 0{,}5564 \text{ (Fig. 2b)} .$$

Growth

The size-distributions of the two groups of *Donax spiculum* collected at Shertallai are shown in Fig. 14. The population is uni-modal and there is no indication of any shift in the mode between the two dates.

Body-Weight Changes and Reproduction

There was a rise in percentage dry weight between August and September from 2.9 to 5.3%. In Fig. 15, we have summarised all the data from Shertallai for *Donax spiculum*, by plotting the average weight per individual for each station, together with wet-weight distributions for individuals which are derived from the size distributions shown in Fig. 14, by converting the individual shell lengths to wet weights by means of the regression of log total weight on log length and the percentage wet-tissue weight for each. The data indicate a settlement prior to the monsoon, represented first by a few specimens collected in the transect of 5 June, when, however, the majority of the shells would have been too small to have been quantitatively retained on the 1 mm screen used. There appears to have been further later settlement, but the indications are that growth was rapid and that maturity was reached in approximately 6 months from settlement. The change in percentage dry weight would indicate a relatively greater increase in the soft tissues as growth proceeds, perhaps indicating progressive development of the gonads.

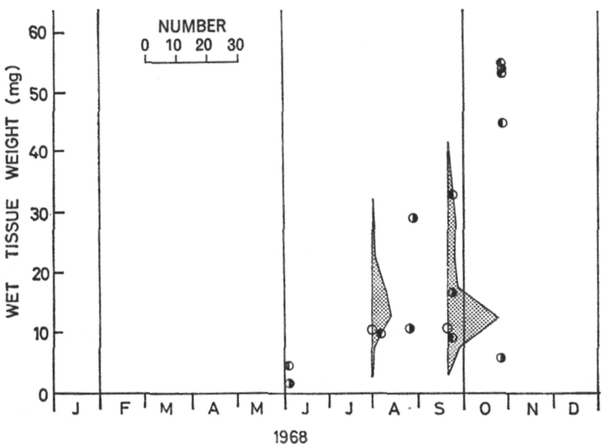

Fig. 15. *Donax spiculum*. Changes in wet-tissue weight for bivalves from Shertallai during 1968. ○: data from non-quantitative samples (histogram); ◐: Transect A; ◑: Transect B; data for mean biomass per specimen from individual quantitative samples along transects

Donax spiculum from Cochin

Population Density and Mortality

Donax spiculum was present at Cochin throughout the period January to June, but was recorded in large numbers only during April and May (Fig. 16). The maximum number recorded was 5,780/m transect in April, with a maximum density of 2,630/m². Again there was not sufficient information to indicate mortality rates.

Length-Weight Relationship

The combined data for all collections of *Donax spiculum* for Cochin, gave a relationship between log length and log total weight of:

$$\log W = 2.0118 \log L + 0.1154 .$$

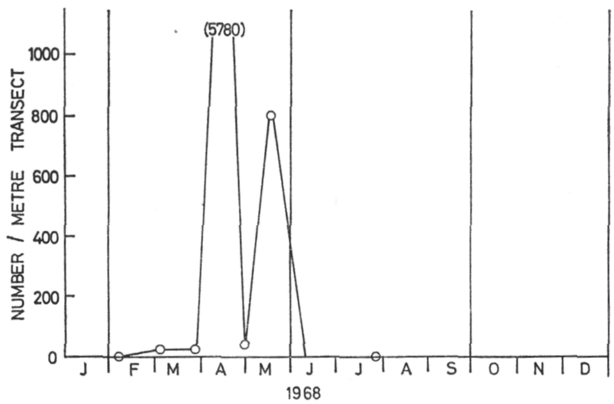

Fig. 16. *Donax spiculum*. Numbers/m transect on transect of Cochin beach during 1968

Growth

The size distributions of the collections of *Donax spiculum* from Cochin are given in Fig. 17. A single modal group can be traced through from January, with a gradual increase in size to reach a mode of 12 to 13 mm in June. In March, a second small modal group at 4 to 5 mm appeared, which was not well represented in later samples, but which appeared to show an increase in size to 7—9 mm in June. The mean sizes for these groups are plotted in Fig. 18, where they are compared with the data for *D. spiculum* from Shertallai.

Body-Weight Changes and Reproduction

The percentage wet and dry-tissue weights, and the percentage water content of the soft tissues are shown

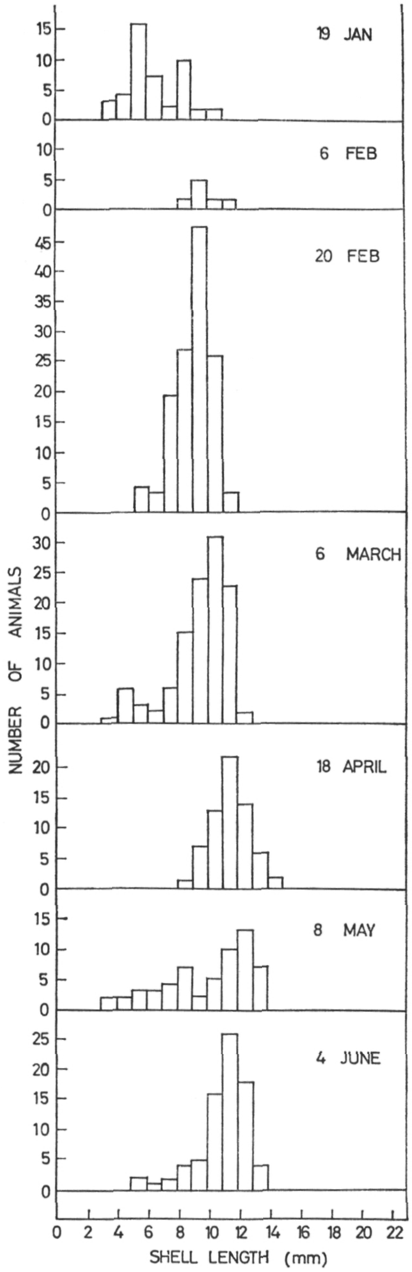

Fig. 17. *Donax spiculum*. Size distribution histograms for bivalves from Cochin beach during 1968

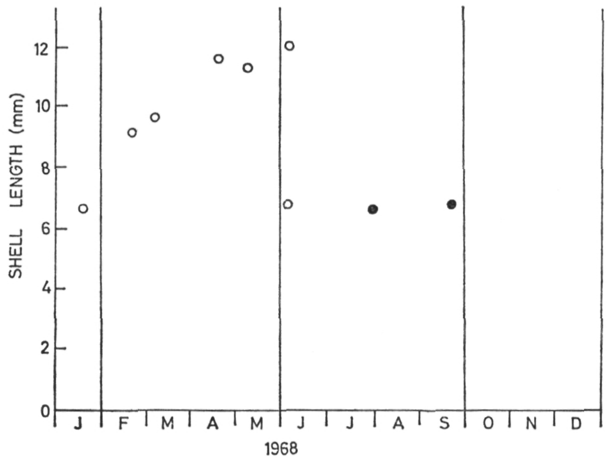

Fig. 18. *Donax spiculum*. Mean shell lengths of bivalves in collections from Shertallai (○) and Cochin (●) beaches during 1968

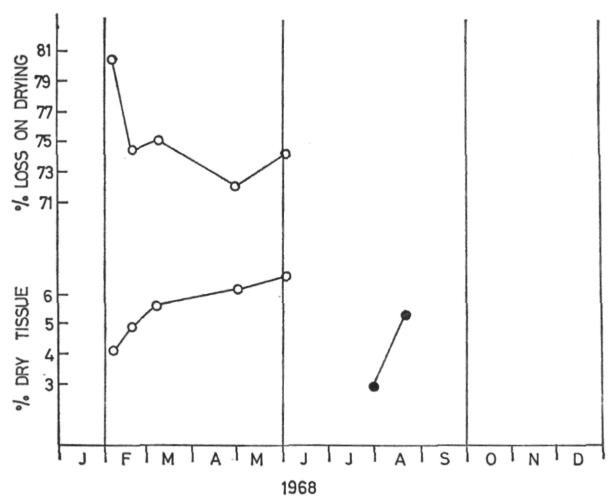

Fig. 19. *Donax spiculum*. Changes in percentage dry-tissue weight and percentage loss on drying bivalves from Shertallai (○———○) and Cochin (●———●) beaches during 1968

in Fig. 19. The percentages apply only to individuals from the main modal group. The mean percentage dry weight rose steadily from 4.04% in the collection of 6 February to 6.56% in the collection of 4 June. At the same time, development and proliferation of the gonad was noted from a completely undifferentiated and sexually indistinguishable stage in February to the presence of well-developed ripe gonads in June, the female gonad having a distinctive orange-brown colouration. The sexes were present in equal proportions. The changes in body weight for *Donax spiculum* for both Cochin and Shertallai are, therefore, consistent with the view that the gonad gradually develops as growth proceeds, and that the animal reaches maturity at approximately 6 to 8 months following settlement. It then spawns and, presumably, dies. Further evidence to support this view is obtained if all the data are included for Cochin in the same way as for Shertallai, including average weight per individual, the weight distribution from the body-weight sheets, and the length-frequency data converted to give equivalent body weights. The resultant data for growth in wet-tissue weight (Fig. 20) clearly show the increase in size of the main modal group, and the occasional occurrence also of smaller individuals, indicating later settlement. The growth rate and the maximum size appear to be similar for Cochin during the pre-monsoon period and for Shertallai during the monsoon and post-monsoon, although the largest *D. spiculum* recorded was collected at Cochin.

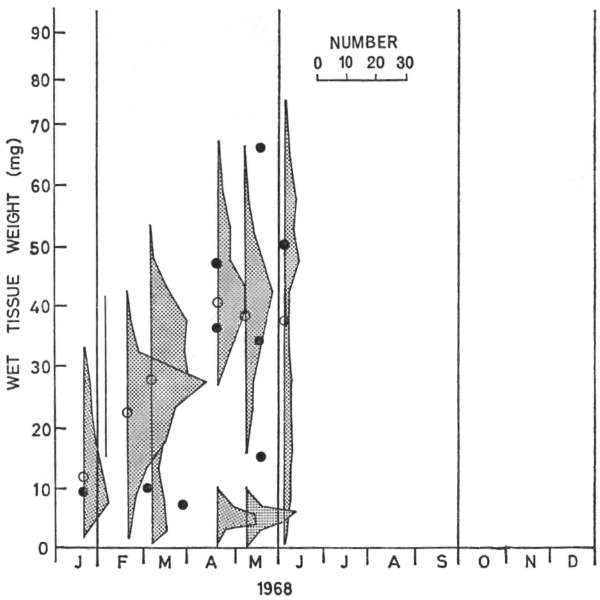

Fig. 20. *Donax spiculum*. Changes in wet tissue weight for bivalves from Cochin during 1968. ○: data from non-quantitative samples (histograms); ●: data for mean biomass per specimen from individual quantitative samples along transects. Vertical line: range of sizes used in determinations of percentage dry-tissue weight and loss on drying on 6 February

Productivity

The population data presented here have been used to give a preliminary estimate of the productivity of *Donax incarnatus*. The numbers (N) for both transects at Shertallai together show an almost steady rate of decline between successive samples for both the 1967 and 1968 settlements, and the following regressions were fitted to the data:

for the 1967 settlement,

$\log_e N = -0.0239\, d + 5.4124$, taking 21 January as day 1 (T)

and for the 1968 settlement,

$\log_e N = -0.0171\, d + 8.3287$, taking 18 May as day 1 (T).

Where $d =$ days from day 1 in each case. The numbers (N) used were those for the number of individuals present/m transect, and the productivity of the species is, therefore, considered in terms of a metre-wide strip of beach containing the population.

No simple relationship between weight and time was found, and the data have, therefore, been treated empirically. The number present at each sampling date was calculated from the regressions given above, assuming a mean settlement date of 1 April, i.e., dates T-48 and T-296 for the 1968 and 1967 settlements, respectively. The mean length was calculated for each group, and from this the total mean weight was calculated by use of the regressions of log total weight on log length. The mean dry somatic tissue weight was taken as 4% of the total weight. The contribution of reproductive activities cannot be accurately assessed, but a rough estimate was made by taking the difference between 4% of the total weight, and the figure obtained by multiplying the total weight by the measured percentage dry weight, as an indication of gonad size. A decrease in the figure so obtained between sampling dates was taken as indicating spawning or other loss of gonad material, whilst increases in the figure showed proliferation. In this way, all changes between successive sampling dates were expressed as production, elimination by mortality, or spawning, per day. The results of this analysis of the data are shown in Table 1.

Production by the population, taken as the total gain of both somatic and gonad material, ranged from 44 to 418 mg dry tissue/day for the 1968 settlement, and up to 736 mg/day for the 1967 settlement. For the two year groups combined, the estimate of production ranged from 4 to 736 mg/day. Assuming that carbon accounts for 50% of the dry tissue weight this gives an estimate of up to 360 mg/day for the carbon requirement of the population for growth and reproduction. If we assume a mean conversion efficiency of 10%, this would imply a maximum daily carbon requirement of 3.6 g C/day. Over the year, the mean production per day was 189 mg, indicating a mean daily carbon requirement of 94.5 mg, or a total requirement of 34.5 g C/m transect for the year.

Production may also be considered in terms of the rate of loss of organic material from the *Donax incarnatus* population, presumably to predators, which includes man. This is indicated by the total loss by death for the population, which ranged up to 916 mg dry tissue/day for the two year groups. The net change in the population is indicated by the difference between this figure, which we have called elimination, and production. For the 1967 settlement during 1968, elimination exceeded production throughout the year, while for the 1968 settlement production exceeded elimination until the period 13 September to 29 October. Beyond this period, production failed to keep pace with elimination, and the biomass declined. For the total population, there was a net loss of material throughout the year. This was the result of the fact that the 1967

Table 1. *Production estimates (per metre*

Time interval	Production				Elimination loss/day (mg) E	Spawning/day (mg)	Production — elimination (mg) $P-E$	Biomass (mg)		
	Days	Gain/day (mg)						Initial	Final	Mean $\bar{B}$
		Body	Gonad	Total P						
1967 Settlement										
1 April—10 May	39	44	0	44	15		29	91	1167	629
10 May—18 May	8	98	0	98	37		61	1167	1751	1459
18 May—5 June	18	115	0	116	59		57	1751	3051	2401
5 June—15 July	40	23	0	23	68		− 45	3051	2141	2596
15 July—31 July	16	116	219	335	59		246	2141	6263	4202
31 July—23 Aug.	24	245	98	343	158		185	6263	10701	8482
23 Aug.—13 Sept.	21	262	46	308	208		100	10701	12786	11743
13 Sept.—29 Oct.	46	155	263	418	309		109	12786	17805	15295
29 Oct.—30 Nov.	32	141	0	141	249	80	−108	17805	11781	14793
30 Nov.—18 Dec.	19	102	42	144	196		− 52	11781	10794	11287
1968 Settlement										
10 Jan.—21 Jan.	11	419	317	736	916		180	27842	28426	28134
21 Jan.—29 Jan.	8	65	21	86	625		−539	28426	24115	26270
29 Jan.—21 Feb.	23	− 32	0	− 32	333	31	−365	24115	10769	17442
21 Feb.—8 March	16	44	100	144	241		− 96	10769	9230	9999
8 March—13 March	5	53	180	233	222		10	9230	9281	9255
13 March—1 April	19	− 4	0	− 4	175	22	−179	9281	5454	7367
1 April—10 May	39	11	27	38	100		− 62	5454	3023	4238
10 May— 5 June	26	4	0	4	55	2	− 51	3023	1632	2327
5 June—15 July	40	0.2	0	0.2	22	8	− 22	1632	465	1048
15 July—31 July	16	0.5	0.4	0.9	10		− 9	465	325	395
31 July—23 Aug.	24	0.2	2.6	2.8	6		− 3.2	325	243	284
23 Aug.—13 Sept.	21	0.2	1.7	1.9	5		− 3.1	243	171	207
13 Sept.—29. Oct.	46	− 0.008	0.2	0.2	2.6		− 2.4	171	62	116
29 Oct.—30 Nov.	32	0.05	0	0.05	0.8	0.5	− 0.8	62	20	41
30 Nov.—18 Dec.	19	0.04	0.004	− 0.04	0.4		− 0.4	20	11	15.4

settlement had apparently been greater than that of 1968, since in a steady state production and elimination would balance over the year. This would be the case, for example, if the amount of settlement each year was constant, assuming that the other parameters remained the same, and net production and net elimination would then occur alternately with net production occurring for a period following the recruitment of new stock in April, but gradually giving way to net elimination for the remainder of the year.

It is of interest to examine the relationships between production (P) and elimination (E) and the mean biomass ($\bar{B}$) present for each period, since these relationships are generally used in making assessments of the production of the benthos. The values for the ratio production/biomass ($P/\bar{B}$) were high for the 1968 settlement during the first months after settlement and, thereafter, showed a steady decline. The value of this ratio for the 1967 settlement was low, indicating that there was an initially high production per unit biomass which gradually declined through the life span of a single year group. When the entire population is considered, there were fluctuations in the ratio depending on whether or not a new settlement was present. In contrast to the fluctuations in the ratio $P/\bar{B}$, the ratio elimination/biomass ($E/\bar{B}$) remained more or less constant for both the 1967 and 1968 settlements, and for the entire population, giving a mean value of about 22 mg dry weight/g dry weight/day.

The $P/\bar{B}$ and $E/\bar{B}$ ratios may be calculated for the whole population over the year to give estimates for production of 6.2 g dry weight tissue/g biomass, and for elimination of 7.5 g dry weight/g biomass. The difference between these two figures, which in the steady state situation would be equal, is again the result of the "imbalance" between the two year groups present, and in years when more abundant settlement occurs the ratio $P/\bar{B}$ would be greater than $E/\bar{B}$.

Discussion

The rate of growth and other aspects of the population ecology has been studied for several species of *transect) of Donax incarnatus at Shertallai*

Production/ biomass (mg/g) $P/\bar{B}$	Elimination/ biomass (mg/g) $E/\bar{B}$	Individual mean weight (mg)	Production (mg) P	Elimination (mg) E	Production/ elimination (mg) $P-E$	Mean biomass (mg) $\bar{B}$	Production/ biomass (mg/g) $P/\bar{B}$	Elimination/ biomass (mg/g) $E/\bar{B}$	Time interval
									1967 Settlement
70.1	24.5	0.13							1 April—10 May
67.4	25.0	0.34							10 May—18 May
48.2	24.6	0.72							18 May—5 June
8.7	26.1	1.22							5 June—15 July
79.8	14.1	3.44							15 July—31 July
40.4	18.6	9.77							31 July—23 Aug.
26.2	17.7	19.08							23 Aug.—13 Sept.
27.3	20.2	48.98							13 Sept.—29 Oct
9.5	16.9	79.01							29 Oct.—30 Nov.
12.8	17.4	95.51							30 Nov.—18 Dec.
			1967 + 1968 groups combined						1968 Settlement
26.1	32.6	113.7	736	916	−180	28134	26.1	32.6	10 Jan.—21 Jan.
3.3	23.8	131.5	86	625	−549	26270	3.3	23.8	21 Jan.—29 Jan.
− 1.9	19.1	118.4	− 32	333	−365	17442	− 1.9	19.1	29 Jan.—21 Feb.
14.5	24.1	116.8	144	241	− 97	9999	14.5	24.1	21 Feb.—8 March
25.1	24.0	138.6	233	222	− 11	9255	25.1	24.0	8 March—13 March
− 0.5	23.8	141.8	− 4	175	−179	7367	− 0.5	23.8	13 March—1 April
8.9	23.6	162.6	82	115	− 33	4867	16.8	23.6	1 April—10 May
1.6	23.6	190.5	114	151	− 37	4436	25.7	34.0	10 May—5 June
0.2	20.7	166.4	23	90	− 67	3644	6.2	24.7	5 June—15 July
3.0	25.0	144.2	336	49	−287	4597	73.2	10.7	15 July—31 July
10.1	22.1	167.3	345	164	−181	8766	39.4	18.7	31 July—23 Aug.
9.2	25.6	205.8	309	213	− 96	11950	25.9	17.8	23 Aug.—13 Sept.
2.1	22.6	235.8	418	312	−106	15411	27.1	20.2	13 Sept.—29 Oct.
1.2	20.5	206.2	141	250	−109	14834	9.5	16.9	29 Oct.—30 Nov.
− 2.6	27.3	161.6	144	196	− 48	11302	12.8	17.3	30 Nov.—18 Dec.

Donax. *D. variabilis* has been studied by Pearse *et al.* (1942), Loesch (1957), and Chanley (1969), *D. tumida* by Loesch (1957), *D. denticulatus* by Wade (1964, 1967), *D. cuneatus* by Nayar (1954), *D. faba* by Alagarswami (1966), *D. gouldii* by Coe (1953, 1955, 1956), and *Donax vittatus* by Orton (1929) and Ansell (in preparation). From these studies, and from other references to the ecology of *Donax* populations in general faunistic papers, some points of general interest arise which may be briefly summarised.

Donax species are typically inhabitants of exposed beaches in the tropics and subtropics, and their distribution and abundance is probably largely determined by the quantity of organic material in the surf water washing the beach (Wade, 1964). Typically, on suitable beaches in tropical areas, more than one species is present: for example Loesch (1957) found two species, *D. variablis* and *D. tumida*, on Texas beaches, Alagarswami (1966) records four species, *D. cuneatus*, *D. incarnatus*, *D. spinosus* and *D. aperittus* from the sandy beaches around Mandapam on the east coast of India, Pichon (1967) records two species, *D. faba* and *D. aemulus* from some beaches on the Madagascar coast and *D. aemulus* and *D. elegans* from others, Crichton (1942) records 4 or 5 species from Madras, including *D. dussumieri*, *D. cuneatus* and *D. scortum*, and Wade (1967) two species *D. denticulatus* and *D. striatus* from beaches in the Caribbean Sea, as well as the example of the two species found in this study at Shertallai. In contrast, in temperate areas, only one species is likely to be present, and typically such a species is distributed near low water or in the sublittoral as is the case in *Donax vittatus* (Ansell, in preparation). For *Donax variabilis* from the north east coast of the USA, Chanley (1969) has recently argued convincingly that the northernly populations hitherto assigned to a separate species, *D. fossor*, are derived from larvae carried northwards from populations in the warmer southern waters, and that such populations survive only through the summer months or perhaps unusually through extremely mild winters.

In tropical areas where two or more species occur together on a beach, the indications from the literature are that both their population ecology and behaviour differs. The different species may be physically separated in their vertical distribution because their response to the changing physical characteristics of the beach during the tidal cycle differ. This may lead to one species spending a period stranded by the receding tide on each tidal cycle, where one species shows a less marked tidal migration pattern than the other, or to sorting by size in migrant species. At Shertallai, one species (*Donax spiculum*) is small, shows extreme mobility, and consequently rapid fluctuations at any one point, combined with rapid growth and mortality within a total life span of about 6 months, while the second species is less mobile, of larger maximum size and with a life span of up to 2 to 3 years. The pattern at Shertallai may be repeated elsewhere. For example, the data of Loesch (1957) can be interpreted as showing a life span for *D. tumida* of 6 months, while *D. variabilis* on the same beaches grows for more than 1 year and, possibly, 2 years (see also Ansell *et al.*, 1972a). In this case also, the smaller shorter-lived species is more active and irregularly and patchily distributed along the length of the beach. In temperate areas, the rate of growth is typically slower, for example, the life span of *D. vittatus* may extend for 6 to 7 years, the species reaching a size comparable to that of *D. incarnatus* at the end of this period.

The mortality rate of all tropical species studied appears to be rapid. Where information is available, it suggests that large fluctuations in settlement density are of common occurrence, so that the population density varies markedly from year to year. In some cases, such variation may be extreme, as is the case for *Donax gouldii*, for which Coe (1953) has described so-called resurgent populations from the Californian coast, but which should perhaps be regarded as no more than extreme examples of the population changes which are typical of most *Donax* species. Fluctuations in settlement between year classes, as well as occasional catastrophic mortality brought about by adverse climatic conditions are equally a feature of temperate *Donax* populations (Orton, 1929; Ansell, in preparation).

Accurate estimates of production by other *Donax* populations are not available, but, when the figures for the ratios $P/\bar{B}$ and $E/\bar{B}$ for *D. incarnatus* are compared with the few similar ratios for other species which have been published, it becomes clear that the production per unit biomass indicated by the $P/\bar{B}$ values of 6.2 and $E/\bar{B}$ values of 7.5 found for *D. incarnatus* compare more closely with values of this order for temperate crustacean and polychaete populations with short life spans than for temperate bivalve species (Sanders, 1956). We are not aware that any temperate bivalve species which has been studied approaches ratios of this magnitude. The increase in behavioural opportunities (Ansell and Trevallion, 1969), the more rapid rate of growth and mortality and higher $P/\bar{B}$ and $E/\bar{B}$ ratios, all result from the higher metabolic rates of the tropical species which, in contrast to tropical fish species (Edwards *et al.*, 1970), do not exhibit temperature compensation, but rather show metabolic rates at their normal environmental temperature (ca 30 °C) equal to or higher than those which would be predicted by extrapolating R/T curves for temperate species to the higher temperature range. Although temperature undoubtedly plays a part, however, the increase in metabolic rate must be supported by adequate food intake, and it may be argued that the greater activity, higher metabolic rate, and higher production, all result from the increase in food intake made possible for the bivalve by the high levels of particulate organic matter present in the surf water (Ansell *et al.*, 1972a). In this respect, the observation of Wade (1964) that the maximum size reached by *D. denticulatus* in the West Indies can be correlated with the organic content of the water over the beach, is significant, and it would be of great interest to confirm this observation by more extensive seasonal sampling, and perhaps to compare the metabolic activity of specimens from contrasting beaches. The differences between the maximum sizes of *D. incarnatus* at Shertallai and at Cochin may indicate a similar effect in this species.

The values of the ratios $P/\bar{B}$ and $E/\bar{B}$ are of interest in relation to the general trophic ecology of the beach, the first as an indication of the food requirement of the bivalve population, and, since bivalves form the dominant element of the macrofauna, perhaps of the macrofauna as a whole; the second as an indication of the material contributed by the macrobenthos to the next trophic level. We have previously estimated (Ansell *et al.*, 1972a) that the total biomass of the macrofauna on the beach varies through the year between 18 and 460 g wet tissue weight/m transect, to give an average biomass of ca 35g dry tissue/m transect for the year. Taking a value of annual production 6.5 times the biomass ($P/\bar{B} = 6.5$: a value which is likely to be low for the crustacean and polychaetes within the population, as well as for *Donax spiculum* in which the shorter life span almost certainly indicates a higher value of $P/\bar{B}$ and $E/\bar{B}$), we can estimate the production as 227.5 g/m transect/year, and if we assume that 50% of the organic material is carbon, this is equivalent to a production of 114 g C/m transect/year. If this production takes place with 10% ecological efficiency, this implies an annual requirement of 1140 g C/m transect by the population, most of which must be supplied from the water overlying the sand. The quantity of food available to predators from the beach population would appear to be of the order of 228 g/m transect per year, available, if other elements of the population resemble *D. incarnatus*, in proportion to the total biomass, so that utilization by predators may be expected to show a seasonal fluctuation paralleling that of total biomass, and thus reducing to minimum values during the monsoon.

Finally, the estimated requirement of the total beach population of macrobenthos of 1140 g C/m transect/year, may be compared with that of the temperate sandy beach population in Loch Ewe studied by MacIntyre and Eleftheriou (1968), for which an annual requirement of 25 g C/m²/year was estimated. These two figures may be more directly compared if we multiply the figure for the Loch Ewe beach by ca 200, as a rough approximation to the width of the beach, to give an estimate of the production per metre transect of ca 5000 g C/year. This suggests that on the wide, relatively-sheltered beach at Loch Ewe, the macrofauna is more productive than that of the narrower exposed tropical beach at Shertallai. On the basis of a comparison per m² averaged over the beach, however, the corresponding figures would be ca 25 g C/m²/year for Loch Ewe, and ca 30 g C/m²/year for Shertallai, as would be expected in a situation where the individual elements of the fauna have higher $P/\bar{B}$ and $E/\bar{B}$ ratios, but where the area occupied by the fauna is more restricted; this figure apparently reflects the efficiency of the largely tidal migrant fauna in removing the high concentrations of organic material swept over the relatively narrow "intertidal" areas of these tropical beaches.

Summary

1. Populations of the bivalves *Donax incarnatus* Gmelin and *Donax spiculum* Reeve were studied on two beaches at Shertallai and Cochin, in south west India for 1 year.

2. At Shertallai, two year groups of *D. incarnatus* occurred, derived from settlements in 1967 and 1968. The main period of recruitment to the population took place in the early part of the monsoon, although there was some earlier settlement. The bivalves apparently live for up to 2 years. Growth was rapid in the first year and, thereafter, slowed. The mortality rate was constant, the rate for the 1968 settlement being closely similar to that of the 1967 settlement, although the latter settlement had been apparently more abundant.

3. *D. incarnatus* was also represented at Cochin by two year groups, but that of 1968 did not survive through the monsoon, although this is not considered normal. The rate of growth was slower, and the maximum size obtained smaller for the 1967 settlement at Cochin than for that at Shertallai.

4. *D. spiculum* occurred spasmodically at both Cochin and Shertallai, although the times of maximum occurrence were different. At Cochin, the species occurred mainly in the pre-monsoon period, and at Shertallai in the post-monsoon. The species has a life span of 6 to 8 months.

5. Estimates of production and elimination by the population of *D. incarnatus* at Shertallai indicate that, while production per unit biomass/day is initially high after recruitment, and thereafter falls progressively as the bivalves in the population age, the elimination from the population per unit biomass/day remains throughout at a relatively constant level. Estimates are given of the total carbon requirement of the population, and the relationship between biomass and production from this population is used to estimate the total requirement of the macrofauna of the beach during the year.

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