# The Ecology of a Central West Indian Beach, with Particular Reference to *Donax incarnatus*

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# Abstract

The ecology of a large sandy beach at Calangute, Goa, Central West India over a 22-month period is described from the point of view of changes in the distribution and abundance of the macrofauna, and of the physical environment of the beach; the dominant effect of the annual monsoon is clearly shown. The results from Calangute are compared with a nearby beach (Colva) and from earlier studies in Southern India. The biology of the dominant wedge-clam *Donax incarnatus* Gmelin is described, in particular its more rapid breeding-cycle and smaller size at Calangute, compared with other populations studied. The annual production of *D. incarnatus* has been calculated as 14.7 kcal/m<sup>2</sup>/year, and has been shown to be relatively low in comparison with other bivalve populations, due to high mortality and the extensive environmental disruption caused by the annual monsoon. It is suggested that the conditions at Calangute are most suitable for settlement, and that the small size of *D. incarnatus* here is related to the short life span of 6 to 7 months of all individuals.

### Introduction

In a series of publications, Ansell et al. (1972a, b, c) have studied the ecology of two sandy beaches in South West India over a 12-month period. This present study is intended to complement these earlier studies, with a study of a large sandy beach at Calangute, Goa, Central West India. The study was conducted over a 12-month period from June, 1971 to May, 1972 at Calangute, and extended by further studies at Calangute and at Colva beach during January - March, 1973. The changes in the physical conditions and in the distribution and abundance of the macrofauna are described, and a detailed study is made of the population biology of the dominant bivalve, the wedgeclam Donax incarnatus Gmelin. The results are compared with the earlier studies, and an estimation of the production of D. incarnatus is also made.

# Material and Methods

Calangute beach is a large sandy beach, situated in the northern half of Goa.

The topography of Goa is dominated by two large estuaries (Mandovi and Zuari), which enter the sea to the south of Calangute (Fig. 1). South of these estuaries is the second beach studied, Colva beach.

During the course of this study, Calangute beach was visited at fortnightly intervals from June, 1971 to May, 1972. At each fortnightly visit, 0.1 m<sup>2</sup> samples (to a depth of 10 cm) were collected at 5-m intervals down the beach from a fixed point above high-water mark to the water's edge. Each sample was sieved (0.5-mm mesh) in the surf water and the animals retained were identified and counted. Each species present was removed and the total wet weight of each species determined.

Water samples were collected at 5-m intervals at the water table to determine interstitial salinity, and a sample of surf water was also collected for salinity determination. The temperature of each interstitial water sample and the surf water was noted at the time of collection. The temperature of the sand surface was measured with a conventional increased the flow of the Mandovi-Zuari rivers and caused marked dilution of coastal waters. With the cessation of the monsoon, the salinity in mid-August rose and remained predominantly in the 32 to 34% range until March, and then increased to 36.2% in the April premonsoon period.

The temperature of the surf water and both interstitial temperature and sand surface temperature at the selected 10-m station are shown in Fig. 3. The general pattern was similar at the three positions given, with the sand surface about 1C<sup>o</sup> warmer than the surf and interstitial water, which were almost the same. The temperature dropped during the monsoon to 24°C in late August, and then rose to 30°C in November, followed by a drop in January, and then a steady rise to a maximum  $34^{\circ}C$ during the pre-monsoon period (March-April). The depth of the water table at each station fluctuated throughout the period of study (Fig. 4). At upper stations it was generally 70 to 75 cm below the surface of the sand, but at lower stations it ranged from the sand surface down to 60 cm depending, it must be presumed, on the profile of the beach and the relative position of each station. The sand was coarse during the monsoon period, but in the postmonsoon period became markedly finer, as the climatic conditions stabilised (Fig. 5). The organic carbon values in the sand were generally in the range 100 to 200  $\mu$ g/g, with a dramatic increase in the early stages of the monsoon period (to 700  $\mu g/g)$  and a rise during the stable period of January -February. The beach profile (Fig. 6) revealed marked erosion of the beach from June until August, and then deposition of sand until October, followed by a period of relative stability. These changes in beach profile relate directly to the changes in particle size reported above. Colva beach was noticeably longer than Calangute, with less gradient, and finer sand (Fig. 7). The significance of the variations in the physical factors in relation to the distribution and abundance of the fauna will be discussed later. Similar conditions to those reported for Calangute for January - March, 1972 were found in the subsequent year, as also show in Figs. 2-6.

#### Beach Fauna

The distribution and abundance of the principal species found at Calangute beach are presented in Fig. 8. The dominant bivalve, *Donax incarnatus*, was



thermometer and the water-table depth at each station was noted.

Sand was collected with a 15-cm deep corer from the low-tide, mid-tide and high-tide levels on the beach for particle size-analysis, and determination of the organic carbon content by the method of El Wakell and Riley (1957). In addition to these fortnightly determinations, the beach profile was measured by conventional survey methods each month, and a random sample of 25 Donax incarnatus collected. The length and width of these clams was measured, and the individual total weight, wet flesh weight, and dry flesh weight determined. Sampling was continued at Calangute and Colva beaches monthly during January - March, 1973.

# Results

# Physical Factors

The salinity of the surf water, and the interstitial water at the 10-m station, at Calangute are shown in Fig. 2. The results for the other interstitial water samples were almost identical, and have been omitted for simplification. It can be seen that at the beginning of the study the salinity was high (33.4%), but that it fell rapidly during June to 22%, due to the influence of the annual monsoon, which







Fig. 2. Salinity of surf (open circles) and interstitial water from the 10-m station (filled circles) at Calangute beach, Goa, from June, 1971 to March, 1973



Fig. 3. Temperature of surf (open circles) and interstitial water (filled circles), and sand surface (triangles) at 10-m station at Calangute beach, Goa, from June, 1971 to March, 1973



Fig. 4. Depth of water table (cm) at 10-m station (open squares) and 20-m station (filled squares) at Calangute beach, Goa, from June, 1971 to March, 1973



Fig. 5. Mean particle size  $(\mu)$  of sand from high water (triangles) mid-tide level (filled squares) and low water (open squares) from Calangute beach, Goa, from June, 1971 to March, 1973



Fig. 6. Selected beach profiles (m) for Calangute beach, Goa in June, 1971 (open circles); August, 1971 (inverted filled triangles); October, 1971 (filled triangles); December, 1971 (open triangles); February, 1972 (filled squares); and February, 1973 (open squares); measured from fixed position



Fig. 7. Beach profiles (m) for Colva beach, Goa in January, 1973 (circles); February, 1973 (squares); and March, 1973 (triangles); measured from fixed position



Fig. 8. Distribution and abundance of beach fauna at Calangute beach, Goa from June, 1971 to March, 1973. Width of kites indicate numbers/m<sup>2</sup> as per insert in (a); open circles indicate absence on sampling date; distance is measured from a fixed post in m. (a) *Donax incarnatus*, (b) *Donax spiculum*, (c) *Pisionidens indica*, (d) *Gastrosaccus* sp., (e) *Glycera alba*, (f) *Eurydice* sp., (g) *Emerita hol-thuisi*, (h) *Talorchestia* sp.

distributed down the beach, and was the species most consistently present (Fig. 8a). It was, however, present in large numbers at the beginning of the study, then declined, and was sometimes absent during the monsoon period. Numbers increased in the post-monsoon period (December), then gradually declined until a dramatic increase in April. The biology of this species will be discussed later.

The smaller wedge-clam Donax spiculum Reeve was only sporadically present (Fig. 8b) and, except during December, was distributed lower down the beach than D. incarnatus. The periods of pres-D. spiculum correspond with the ence of periods of maximal abundance of D. incarnatus. The polychaete Pisionidens indica Aiyer and Alikunhi was sporadically present throughout the study (Fig. 8c). The mysid Gastrosaccus sp. was present on several occasions, occurring especially near the low-water mark where it may have been stranded (Fig. 8d). The polychaete Glycera alba Rathke was absent throughout the monsoon period, but as conditions stabilised and the sand became finer, so it became a regular inhabitant of the beach, consistently abundant and widely distributed (Fig. 8e). The amphipod Eurydice sp. was present in large numbers in the early monsoon, and from December-February, occurring especially higher up on the beach (Fig. 8f). The mole crab Emerita holthuisi Sankolli was irregularly present throughout the year, especially in the lower part of the beach (Fig. 8g). The amphipod Talorchestia sp. was absent during the monsoon, but otherwise present in the lower part of the beach (Fig. 8h). The beach fauna of Calangute for January - March, 1973 is also shown in Fig. 8, and indicates similar abundance and species distribution compared to the preceding year, except for D. spiculum which was present in much greater numbers in the second year. D. incarnatus was extremely abundant at Colva in 1973 (Fig. 9) although, as at Calangute, it declined in abundance during the period of study. During 1973, D. spiculum was very rare at Colva, although extremely abundant at Calangute.

The results presented allow discussion of the factors controlling the abundance of the beach fauna between June, 1971 and March, 1973. At the commencement of the study, in the immediately pre-monsoon period, the salinity was high, the beach profile of an intermediate nature, and the beach inhabited by a mixed fauna including Donax incarnatus, D. spiculum, Eurydice Sp., Emerita holthuisi and Talorchestia sp.



Fig. 9. *Donax incarnatus*. Number per metre-wide strip at Calangute (continuous line) and Colva (dotted line) beaches, Goa, from June, 1971 to March, 1973

During the monsoon months of July and August, the beach profile steepened, the particle size of the sand increased, and the salinity decreased in a marked fashion. The numbers of *D. incarnatus* fell significantly, *D. spiculum* and *Talorchestia* sp. disappeared, *Pisionidens indica* appeared, and *Eurydice* sp. persisted.

During the second half of August the monsoon conditions declined and immediately the salinity rose. Sand deposition occurred, as indicated by the beach profile, but the median particle size remained coarse. The beach fauna was minimal and only included representatives of Gastrosaccus sp. By October, however, the continuing stable climatic conditions were reflected in the maintenance of the beach profile, and the reduction in particle size. Donax incarnatus appeared in progressively larger numbers, as did Glycera alba and Emerita holthuisi. The stable conditions of beach sand and salinity persisted throughout early 1972, with the beach fauna dominated by D. incarnatus, G. alba, Eurydice sp. and Talorchestia sp. D. spiculum occurred sporadiacally, but was present in large numbers when it did migrate onto the beach. In the premonsoon period (March - May) both the temperature and salinity increased, and limited beach erosion occurred. The numbers of both Donax species increased, and then decreased as did the numbers of all species inhabiting the beach.

The continuation of sampling in January - March, 1973 revealed that, despite the intervening monsoon period, Calangute beach returned to very similar



Fig. 10. Donax incarnatus. Percentage of each mm size-class and of individuals collected at random at Calangute beach, Goa, monthly from June, 1971 to May, 1972, and again from January, 1973 to March, 1973

conditions and fauna in 1973, as had been observed in 1972. This repetitive similarity serves to emphasise clearly that the large changes reported were closely linked to the annual monsoon cycle and that, despite massive changes in the environment and its fauna, the beach followed a well-defined annual sequence. *Donax spiculum* was present more abundantly in 1973, but it has been seen that the numbers of this species can fluctuate greatly as they migrate onto and off the beach.

A similar annual cycle in the physical conditions and the fauna of Indian beaches has been described by Ansell et al. (1972a, b, c) for Cochin and Shertallai beaches in S.W. India. They reported a similar domination of the environment and its inhabitants by the annual monsoon cycle. It would appear that Calangute beach represents an intermediate type of beach between the Cochin and Shertallai beaches. Whilst all three beaches have been subject to monsoon-dominated erosion, postmonsoon deposition occurred only at Calangute and Shertallai, and only at



Fig. 11. Donax incarnatus. Mean total wet weight (g) of clams collected at Calangute beach, Goa. Filled triangles: mean weight of each fortnightly sample collected at each 10-m station; open triangles: mean weight of specimens collected at random each month. Where two size classes were present these have been separated, and vertical lines indicate range of weight of wedge-clams within each size class

the latter two did the fauna recover after the monsoon. Salinity reduction occurred at all three beaches during the monsoon, down to 28% at Shertallai, 22% at Calangute, and 10% at Cochin. Whilst Shertallai had 11 species present throughout the year, Calangute had 8, and Cochin had 4. Donax incarnatus, D. spiculum, Emerita holthuisi and Eurydice spp. were common to all beaches, whilst the molluscs Bullia melanoids, Mactra olorina and Timoclea imbricata were only found at Shertallai. At both Cochin and Calangute, D. spiculum occurred in the premonsoon period, whilst at Shertallai it occurred in the post-monsoon stage. The period for the appearance of Glycera alba is almost identical at Shertallai and Calangute, and the distribution of Emerita holthuisi and Eurydice spp. is similar at all beaches. Colva beach had the greatest abundance of D. incarnatus of any beach studied, and with its gentle gradient more closely resembled Shertallai. It would appear that relatively stable beach conditions were necessary for D. incarnatus. D. spiculum occurred more sporadically and, when

present, appeared in enormous numbers. It would thus seem clear that Calangute was intermediate between Cochin and Shertallai, and Colva similar to Shertallai in terms of the two important factors of beach erosion and salinity dilution during the monsoon period, and also in terms of faunal composition. Which of these factors is the principal ecological factor is as yet unclear. In all cases, however, ultimate control was affected by the monsoon cycle, and the differential effects of the monsoon on each beach determine the distribution and abundance of the fauna.

### Biology of Donax incarnatus

The results of the determinations of length and weight of a randomly selected group of 25 Donax incarnatus are presented in the form of monthly population histograms in Fig. 10. In Fig. 11, the distribution of the total weight of these randomly chosen specimens is presented along with the mean weight of those clams collected from each fortnightly beach sample; the numbers of clams collected each fortnight have already been presented in Fig. 9.

From these results it can be seen that the June, 1971 population was composed of a homogenous group of individuals of 14.5-mm mean length. Throughout July and August, considerable mortality occurred, but those remaining grew to reach 16.7-mm mean length by September. In October and November in the post-monsoon period, the random samples revealed the addition of small 4.5-mm specimens to the population. The larger individuals continued to grow, and reached a mean length of 20.2 mm in December. The weights of fortnightly beach-sample clams were intermediate between these two groups, since they were mixed samples containing both large and small individuals. The clams which were recruited to the population in October and November continued to grow, reaching 13.7 mm by May. The increase in numbers on the beach in November was due to the recruitment of these specimens, and the subsequent decline in numbers represented the mortality of many of them, as well as the final decline of their parents. A large increase in numbers occurred in March, 1972, which fortnightly samples revealed as being due to a further major recruitment of small individuals (Fig. 11); by this time clams recruited in October, 1971 had grown to 1.7 g (16 mm). The subsequent fall in numbers on the beach represented their mortality, especially of the new recruits. The population in 1973 was clearly composed of two groups, the larger group consisting of those individuals recruited in March, 1972, and the smaller group of those recruited in October, 1972. This study of Donax incarnatus shows a high rate of mortality, indicated by the steep declines in numbers in June, December and April. The maximum size was considerably smaller than reported by Ansell et al. (1972c). At Calangute and Colva, the maximum size was 21 mm, compared with 30 mm at Shertallai, and 24 mm at Cochin. Wade (1964) and Ansell et al. (1972c) suggested that the maximum size of the genus Donax is related to the organic carbon content of the surf. Determinations of the organic carbon content of the surf at Calangute in 1973 showed, however, that there was 1.03 to 1.83 mg C/1 and at Colva 0.90 to 1.38 mg C/l, within the range of values determined for Cochin and Shertallai. It would appear that, in this case, size was not related to organic carbon. Surf values over a short period may not be an adequate measure of food available.

The other major point of comparison with the southern Indian populations is that, in Goa, recruitment occurred in October, and again in March - April, whereas at Shertallai only the latter period of recruitment was important. At Calangute, clams recruited in the premonsoon period of 1971 produced larvae from October onwards of the same year. Recruitment certainly continued until December, 1971. The adults then died along with many of the new recruits. The first of these October - December, 1971 recruits produced offspring in April, 1972. The clams recruited in April, 1972 were still present in small numbers in early 1973, whereas specimens which had been produced in late 1972 appeared as a distinctive group and were more abundant. It would, thus, appear that October and April recruits breed within 6 to 7 months at Calangute, but April recruits at Shertallai normally need 12 months before producing the next generation. Re-examining the Shertallai data it can be seen (Ansell et al. 1972c, their Fig. 3) that a few small individuals were present on 29 January, representing examples of an earlier settlement, but that these had disappeared during the next month. This may indicate that breeding did occur in October - November at Shertallai, but that conditions for settlement and survival were unfavourable. It might be suggested that the small size of Donax

Table 1. Donax incarnatus. Respiratory requirements of wedge-clams at Calangute beach, Goa, for June, 1971 - May, 1972. Oxygen consumption values are calculated from McLusky and Stirling (1975). From summation of annual respiration, a calculation of annual production has been made (see text). Fort-nightly beach samples are indicated by month of collection, with i indicating first fortnight, and ii second fortnight

Fortnightly beach-sample	No/m <sup>2</sup>	Total net weight/m <sup>2</sup>	Mean dry tissue weight (g) per clam	O <sub>2</sub> consumption (ml O <sub>2</sub> /g dry weight/h)	$O_2$ consumption (ml $O_2/m^2/$ fortnight)
June i	510	178.50	0.0175	1.943	6329.1
June ii	20	13.65	0.0341	1.372	341.6
June ii	30	16.80	0.0280	1.520	466.0
June ii	30	22.00	0.0367	1.321	530.3
July i	10	7.35	0.0368	1.322	177.2
July ii	20	12.58	0.0315	1.430	328.3
July ii	30	16.74	0.0279	1.524	465.6
Aug. i	0	0	0	0	0
Aug. ii	10	6.32	0.0316	1.430	164.9
Aug. ii	10	7.38	0.0369	1.322	178.0
Sept. i/ii	0	0	0	0	0
Oct. i	10	4.80	0.0240	1.648	144.3
Oct. i	40	8.90	0.0113	2.436	395.6
Nov. i	20	6.72	0.0168	1.982	243.1
Nov. ii	40	7.65	0.0096	2.652	370.2
Dec. i	170	16.58	0.0049	3.760	1137.7
Dec. ii	50	27.50	0.0275	1.535	770.4
Dec. ii	80	12.65	0.0079	2.934	677.4
Dec. ii	10	4.58	0.0229	1.687	140.9
Jan. i	40	6.80	0.0085	2.830	351.2
Jan. ii	10	4.12	0,0206	1.782	133.9
Jan. ii	50	18.25	0.0183	1.896	631.5
Feb. i	60	10.48	0.0087	2.825	540.3
Feb. ii	0	0	0	0	0
March i	10	2.85	0.0143	2.186	112.1
March ii	70	20.00	0.0143	2.156	786.9
March ii	260	42.89	0.0083	2.860	2238.6
March ii	160	25.02	0.0078	2.954	1348.8
March ii	20	2.60	0.0070	3.123	148.2
April i	1720	70.20	0.0020	5.990	7674.1
April i	150	23.50	0.0078	2.954	1266.9
April i	170	22.00	0.0065	3.247	1303.7
April ii	30	14.24	0.0237	1.657	430.6
April ii	940	29.50	0.0016	6.726	3621.1
April ii	10	7.00	0.0350	1.354	172.9
May i	0	0	0	0	0
May ii	410	42.00	0.0051	3.683	2823.0
May ii	100	18.68	0.0093	2.696	919.0

*incarnatus* from Calangute is related to the more rapid onset of breeding here.

# Production by Donax incarnatus

Due to the considerable overlap found in the successive populations of *Donax incarnatus* at Calangute, it was not possible to calculate production by conventional methods. A value of production can, however, be computed from a calculation of annual respiration. Utilising the data on biomass of *D. in-* carnatus already presented, the respiration of each sample was calculated from a log-log regression of weight and oxygen consumption (Table 1). The mean dry weight of each sample was first obtained, and this weight was used in the equation:  $\log R = -0.5195 \log W$ -0.6247 (McLusky and Stirling, 1975). This value of respiration per hour at the mean weight was then multiplied by the sample biomass to give sample respiration per hour, which was then converted to respiration per fortnight. Summation of each fortnightly value yielded the annual respiration of the samples taken, and this annual value  $(37.364 \ 10_2/\text{sample/year})$  was then converted to an average metre<sup>2</sup> basis. The final value obtained of 6.261 l  $0_2/\text{m}^2/\text{year}$  was then converted by the oxycalorific equivalent (4.8 kcal=1 l) to 30.05 kcal/m<sup>2</sup>/year (annual respiration, R). From the formula of Millar et al. (1971), where production  $P = 0.6440R^{0.8517}$ , this represented an annual production of 14.71 kcal/m<sup>2</sup>/year.

# Discussion

Data on the physical conditions and the beach fauna for Calangute beach, Goa during the periods June 1971 - May, 1972, and January - March, 1973 have been presented, along with limited data for the nearby Colva beach during January - March, 1973. It has been seen that, like similar beaches studied in Southern India, the population of animals varied a great deal. The dominating factor was the annual monsoon, which by its influence on the salinity of the water and the particle size-composition and slope of the beach created widely fluctuating conditions which caused the death or emigration of the macrofauna. The temperature was by contrast relatively stable.

It has been suggested that the varying stability of the beach during the monsoon is an important control of the abundance and diversity of the fauna, and that, with regard to stability, Calangute beach is apparently intermediate between the previously studied Cochin and Shertallai beaches, and the range of important species in particular is restricted by conditions of instability. The numbers of Donax incarnatus appeared to increase in conditions of stability, as shown by the contrast between Colva and Calangute in Goa, as well as the contrast between Goa and the southern beaches. The appearance and abundance of D. spiculum was more erratic than D. incarnatus but, when it did appear, it attained enormous quantities as seen at Calangute in 1973. It may be suggested that *D. incarnatus* is a consistent beach inhabitant, whereas D. spiculum migrates onto the beaches at certain times, but may leave as quickly as it appears. A longer term study of this species would be necessary to elucidate the reasons for its emigration, but its mobility in contrast to the larger D. incarnatus was clear.

Another considerable difference between the *Donax incarnatus* in Goa and in southern beaches, was in the maximum size reached and the cycle of breeding. At Calangute, breeding occurred from November of one year through until April of the next year, with maxima of breeding at the beginning and end of the period. Indeed, some of the November recruits appeared to be the parents of the April recruits to the population. At Shertallai, the principal breeding season was April, and the clams produced then did not breed until the next year. There was thus a 12-month breeding cycle in Southern India, but a 6 to 7 month breeding cycle in the population of the present study. The maximum length in this study was 21 mm, whereas individuals of 30 mm were reported by Ansell et al. (1972c). It would seem logical that the maximum size achieved, and the breeding cycle are inter-related, and it may thus be proposed that the production of sexually mature individuals and the oneset of breeding occurred in smaller animals in the Calangute population than in the Shertallai population. The reasons for this clear difference have not been revealed by this study, and the earlier proposition of differences in organic content of the surf water causing differences in size has not been confirmed.

A value for annual production of 14.71 kcal/m<sup>2</sup>/year has been derived for the Calangute population of Donax incarnatus. This is close to the value of 16 kcal/m<sup>2</sup>/year calculated by Ansell et al. (1975) for the production of D. incarnatus at Shertallai and 11.1 kcal/  $m^2$ /year for Cochin. Whilst the biomass was less at Calangute than at Shertallai, the presence of two breeding seasons at Calangute increased the annual production value and caused the close similarity in the two values. The large populations of D. incarnatus at Colva and of D. spiculum at Calangute in 1973 must have had a high production value, but the calculation of production from respiration is only valid on an annual basis, and has not therefore been attempted in the latter cases. Compared with derived production rates for other bivalves, these values for annual production of Donax spp. are relatively low (Ansell et al., 1975), and reflect the disrupting influence of the monsoon on production, and the high rate of mortality observed. The calculation on a m<sup>2</sup>/year basis would also diminish the production value, as the population of Donax spp. tended to be confined to a relatively narrow belt on the beach, and much of the beach was uninhabited.

It has been seen in this study how

the macrofauna of a tropical beach can vary in abundance and composition throughout the year. The disruptive influence of the monsoon can effectively limit the beach productivity, as the population may completely leave the beach at times and migration back to the beach may be hampered by environmental limitations.

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#### Literature Cited

- Ansell, A.D., D.S. McLusky, A. Stirling and A. Trevallion: Comparative studies of beaches. II. Production and energy flow in the macrobenthos. Proc. R. Soc. (1975). (In preparation)
- -, P. Sivadas, B. Narayanan, V.N. Sankaranarayanan and A. Trevallion: The ecology of

two sandy beaches in South West India. I. Seasonal changes in physical and chemical factors, and in the macrofauna. Mar. Biol. 17, 38-62 (1972a)

- ---- The ecology of two sandy beaches in South West India. II. Notes on *Emerita holthuisi*. Mar. Biol. 17, 311-317 (1972b)
- ---- The ecology of two sandy beaches in South West India. III. Observations on the population of *Donax incarnatus* and *D. spiculum*. Mar. Biol. 17, 318-332 (1972c)
- El Wakell, S.K. and J.P. Riley: Determination of organic carbon in marine muds. J. Cons. perm. int. Explor. Mer 22, 180-183 (1957)
- McLusky, D.S. and A. Stirling: The oxygen consumption and feeding of *Donax incarnatus* and *Donax spiculum* from tropical beaches. Comp. Biochem. Physiol. (1975). (In press)
- Millar, R.J., K.H. Mann and A.J. Scarrett: Production potential of seaweed-lobster community in Eastern Canada. J. Fish. Res. Bd Can. 28, 1733-1738 (1971)
- Wade, B.A.: Notes on the ecology of Donax denticulatus (Linne) Proc. Gulf Caribb. Fish Inst. (17th Ann. Sess.) 36-41 (1964)

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