Ecological Behaviour and Biology of the Beach Clam *Donax faba* (Gmelin) from the Red Sea

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ABSTRACT. The distribution of wedge clam *Donax faba* (Gmelin) in the Red Sea and the offshore islands is restricted to sheltered sandy beaches between tide marks. The present investigation has shown that *Donax faba* does not exhibit a tidal or semilunar migratory pattern as most members of this genus but rather a seasonal migratory pattern, which is related to the seasonal changes in the sea level. A peak density occurred in November with 296 m^{-2} and the lowest in January with 30 m^{-2}. Growth rate of wedge clams exhibits different seasonal patterns of growth. The greatest increase in growth rate took place in summer. It is evident from this study that *Donax faba* has a prolonged breeding period with two different peaks of spawning; the small peak taking place in June and the large one in November and December. These two reproductive cycles corresponded to the phytoplankton peak which occurred at the same period.

Introduction

The distribution of the bivalve *Donax faba* along the east coast of the Red Sea and the offshore islands is restricted to sheltered bays. It only occurs between tidal marks where the sand is usually coarse and moderately sorted[1,2]. Smith[13] and Alagarswami[4], however, noted its occurrence on exposed sandy beaches of Africa and India respectively. The littoral environment of the Red Sea is characterized by wide diel temperatures[5-8]. Salinity is also high in the Red Sea and may reach 41% in the reef pools in the Jeddah region in July and August[5]. Temperature may rise above the upper lethal limits of the littoral fauna[8] and it seems unlikely that the lower lethal limits will ever be reached in the study region. Not much information is available regarding different aspects of studies of *Donax faba*. Hodgkin[9] reports that extreme environmental temperature most likely affects the population level of the gastropod *Dicathais aegrota* in Western Australia. Eshky[10] has also found that extreme high temperature and extreme low relative humidity could also have the same effect on the brachyuran crabs *Uca* species during the summer in the Jizan region.

In the Jeddah region the maximum spring tide range is about 36 cm[5,6,11,12], but despite its small magnitude it plays an essential role in the behavior of littoral fauna particularly on the feeding behavior[6-10].

There is a marked seasonal variation in mean sea level in the Red Sea which is related to the monsoon winds in the Indian Ocean[5,11,12,13]. Tidal migrations were reported for *Donax faba* by both Smith[3] from the east coast of Africa, and by Alagarswami[4] from Mandapam coast of India, and also from other localities[14-19]. Prosch and Maclachlan[20] have also suggested that different size classes of *Donax serra* show different patterns of movement. However, in the present study, *Donax faba* neither exhibited tidal pattern nor a semilunar migratory pattern but rather a seasonal migratory pattern related to the seasonal variation in the mean sea level. Similar patterns of behavior were observed for semi-terrestrial crabs[6-8,10].

The growth rate of *Donax faba* were investigated by Alagarswami[4] and of other members of the same genus by several workers[21-24]. Quayle[25] and Auger[26] related the slow summer growth rate of Pacific oyster *Crassostrea gigas* to spawning activity. Mori *et al.*[27] have reported similar conclusions.

Variation in the timing of gametogenesis and spawning have also been documented among several populations of bivalve molluscs[28,29] but the causes of this variability are not understood. Differences in environmental temperature and salinity[4,21,30], seasonal abundance, and composition of food[31-33, 28, 34, 35] are thought to affect the reproductive cycles of marine invertebrates. The present study investigates the effect of environmental variables on the distribution of the wedge clam *Donax faba*. Allometric and growth rate of the clams were also investigated in addition to the causes of variation in timing of reproduction.

Methods

Field work was carried out on the south side of Sharm Obhour (an inlet), 21º42′26″N and 39º06′06″E adjacent to the Marine Station of the Faculty of Marine Science, King Abdulaziz University. The beach is privately owned with minimal human disturbance. A large population of the wedge clam *Donax faba* was found in a very narrow strip along the beach between the average mean sea level and the extreme winter high watermark. The study area was surveyed using a Wild To5 theodolite surveying device to measure the beach profile and sea level. Monthly field data were collected between April 1994 and March 1995. The study site is illustrated in Fig. (1). Its landward side is a flat sandy beach occupied by the ghost crabs *Ocypode saratan* while seaward is narrow lagoon behind the coral fringe of Sharm Obhor. This lagoon is only 5-20 m wide and less than 2 m in depth and is superficially muddy. The coral fringe is very rarely exposed to air due to monsoon effect in summer. For laboratory investigations the clams were obtained from Al-Guaid Island which is located about 35 km north of Sharm Obhor. Clams were collected using a frame quadrat 25 × 25 cm forced into the sand to a depth of approximately 20 cm until reaching the hard substratum. All sand including the wedge clams inside the frame were sieved through a 2 mm mesh sieve to collect the

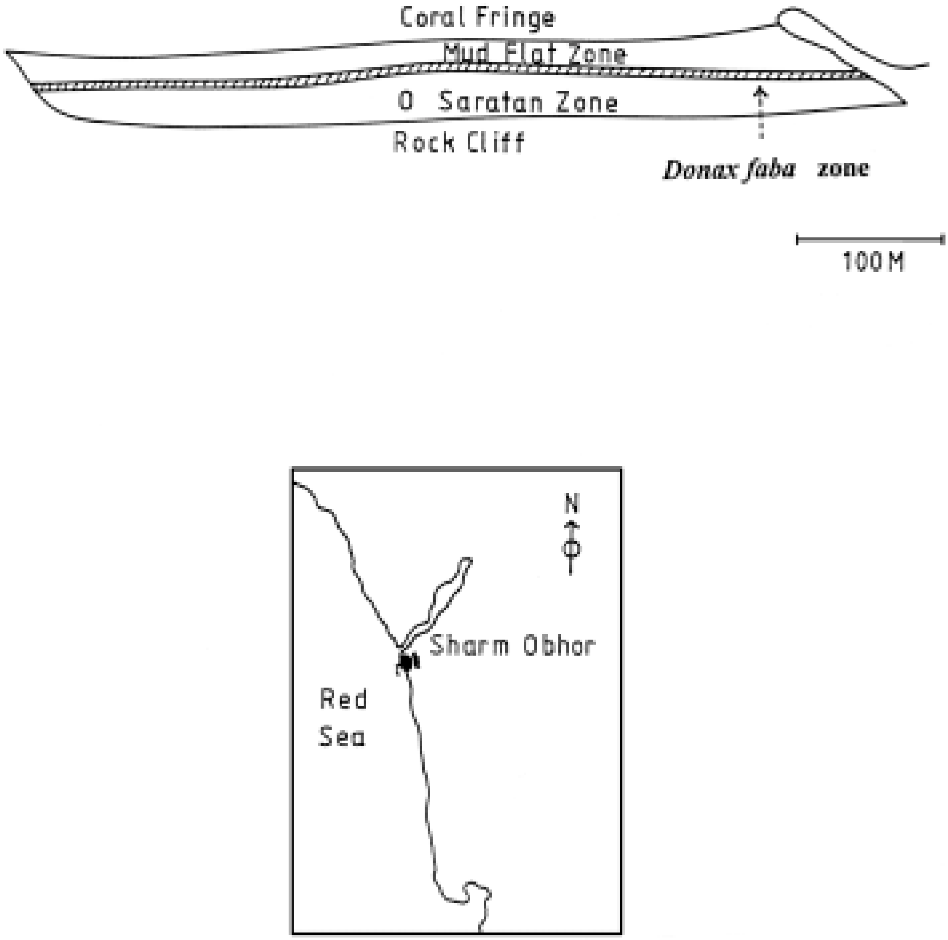

FIG. 1. Map showing the study location.

clams. Their dimensions were measured to the nearest 0.1 mm using vernier caliper. A digital thermometer (R.S. components) connected to thermo-coupling wires was used to monitor temperature changes in various microhabitat occupied by the wedge clams. Water salinity was measured by hand refractometer (Alago). Coded plastic label tags of different size were used depending on the size of the animals. Each label had a plastic extension on the back of each tag and were attached to the shells by drilling a fine hole of about 0.6 mm (using precision drill R.S. components) through the shell and inserted into the drilled hole and cemented together with the tag by cyanoacrylate glue on the clam shell. Sediment cores were taken for granulometric analysis at depth of 15 cm from three different stations along the wash zone where the clams were found. Sediment analysis followed methods detailed by Folk and Gray[36-37]. Population density of *Donax faba* was determined by placing a grid of 1 m × 10 m which cover the narrow strip occupied by the clams.

On each visit the beach was surveyed using the thediolite, so that the position of the clams could be related to the tidal datum. Clams were collected, counted, and mapped on graph paper with reference to the established datum point.

For histological study the specimens were narcotized using a saturated solution (7.5%) of magnesium chloride ($MgCl_2$) which gave satisfactory results. The shells of the wedge clam *Donax faba* were opened and the soft tissues of the animals withdrawn from their valves. The narcotized specimens were fixed in alcoholic bouins solution for a period varying from 24-48 hours, thereafter they were washed several times in 50% ethyl alcohol until their yellowish coloration disappeared, and finally preserved in 70% ethyl alcohol for further histological study. Afterwards, the preserved specimens were dehydrated through successive series of ascending concentrations of ethyl alcohol 80%, 90%, 95% and 100% twice. The dehydrated specimens were passed through a series of a mixture of paraffin wax and xylene (1:2) and left for 30 minutes, then transferred to another mixture of paraffin wax and xylene (1:1) and left for an hour, then they were put in a mixture of paraffin wax and xylene (2:1) for one and half hour respectively. Finally, the tissues were embedded into three successive series of pure melted paraffin wax (melting point of 58-60ºC) for at least two and a half hours. The embedded specimens were cut by using a rotary hours. The embedded specimens were cut by using a rotary microtome into serial sections with a thickness of 5-7 micron. Horizontal and transverse sections were made and stained by Ehrlich Heamatoxylin eosin stain which gave an excellent result. Finally, the stained sections of the specimens were examined by a light microscope.

Results

Distribution

The general distribution of *Donax faba* is poorly known and there have been no previous attempts to investigate ecological variables controlling their distribution in the Red Sea. Therefore, in addition to the two major study sites the wedge clams were collected from three different beaches throughout the east coast of the Red Sea and some offshore islands in the south and the middle region of Red Sea. These locations were at the west coast of Farasan island 850 km south of Jeddah and Al-Iga island located just 8 km west of Al-Guaid island. In all different locations the distribution of *Donax faba* populations are restricted to sheltered sandy beaches along the east coast of the Red Sea and offshore islands which are both protected by the fringing reef. *Donax faba* occurred in abundance in narrow waterlogged sandy strips. The extent of this strip varies with beach slope and sand grain size which is usually coarser sand with phi values ranging between 1.2 to 1.45. The fine grain size of the muddy lagoon at Sharm-Obhor site and the exposed coral platforms of Al-guaid island prevent colonization of *Donax faba* in such areas. Also the population distribution of *Donax faba* varies seasonally with variation in the mean sea level due to the monsoon effect.

Population Density

Analysis of the samples through the 10 m grid along the narrow zone occupied by the clams indicates that the density of the population at different squares within the grid varies appreciably between a maximum of 742 m^{-2} and a minimum of 0 m^{-2}. This reflects the great deviation of the population density from the population mean (Table 1). Also, there were appreciable monthly fluctuations (Fig. 2).

TABLE 1. Monthly variations in population density of *Donax faba.*

Month	Mean density numbers m^{-2}	Standard deviation (sd)	Pattern
Apr	119.25	143.89	Clumping
May	133.25	204.2	Clumping
Jun	135.00	173.13	Clumping
Jul	160.5	172.50	Clumping
Aug	151.75	161.70	Clumping
Sep	197.5	151.13	Clumping
Oct	181	113.25	Clumping
Nov	296	350.1	Clumping
Dec	166	59.05	Clumping
Jan	29.25	34.07	Clumping
Feb	53.25	65.18	Clumping
Mar	46	41.7	Clumping

The greatest population density was recorded in November 1994 with 296 individuals per square metre and the lowest in January 1995 with 30 m^{-2}. However, the twelve annual distributions were clumped with $P < 0.001$ obtained from the dispersion equation $X^2 = \frac{S^2 (n-1)}{\bar{x}}$ where n = number of samples X^2 = coefficient of dispersion × S^2 = variance and $\bar{x}$ = the population mean.

In winter months particularly January, February and March, the beach is usually exposed to strong wave action due to stormy weather. As a result, the individuals of *Donax faba* are carried far away up the beach and most of them eventually die. The mortality rate during this period may be as high as 52%. The reduction of the population density of *Donax faba* in January to March due to the rising sea level and relatively strong wave action which occasionally flushes out the clams out of the sand and deposits them so high up on the beach that they never regain their proper zonation. In such cases a high mortality of 52% in December, January and February respectively of tagged clams was recorded.

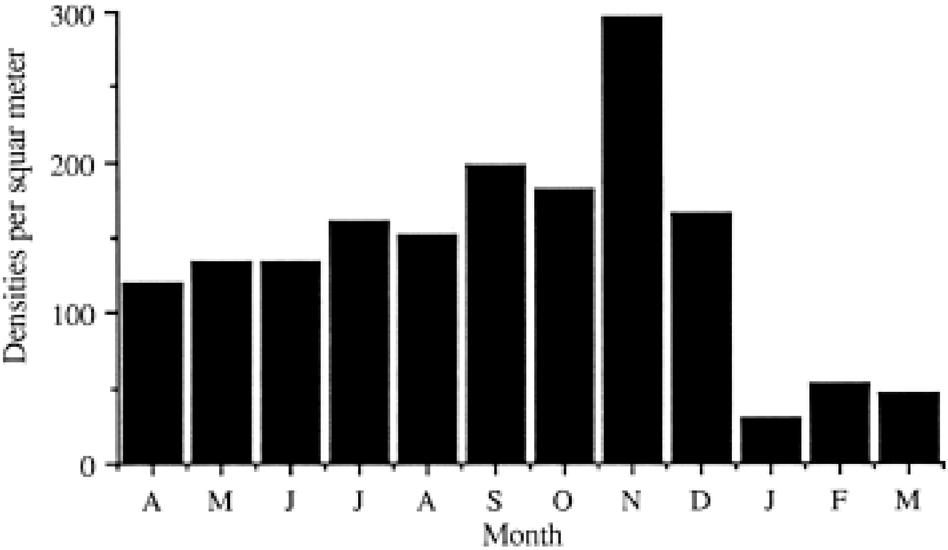

FIG. 2. Histograms of monthly variations in population density of *Donax faba.*

Substratum Characteristics

Grain size is considered to be a limiting factor on the distribution of *Donax faba*. Little variation in the size of sediment grains was recorded at the three stations and, phi values ranged only from 1.2 to 1.45 (Table 2). The negative skewness (Fig. 3) shows an over abundance of coarse grains which are moderately sorted in the three stations.

TABLE 2. Characteristics of the sediment in the study site.

Station	Depth of core (cm)	Mean particle diameter ϕ	Sorting coefficient ϕ	Description
1	0 - 15 cm	1.12	1.054	moderately sorted
2	0 - 15 cm	1.45	1.003	moderately sorted
3	0 -15 cm	1.15	1.012	moderately sorted

Temperature and Salinity

Sea water temperature and salinity observations were taken monthly between 1200 h. and 1400 h. and are summarized in Fig. (4).

On 25th of July 1995 the beach was visited and a series of measurements was conducted over an 18-hour period, tide was spring tide. During the ebbing tide which took

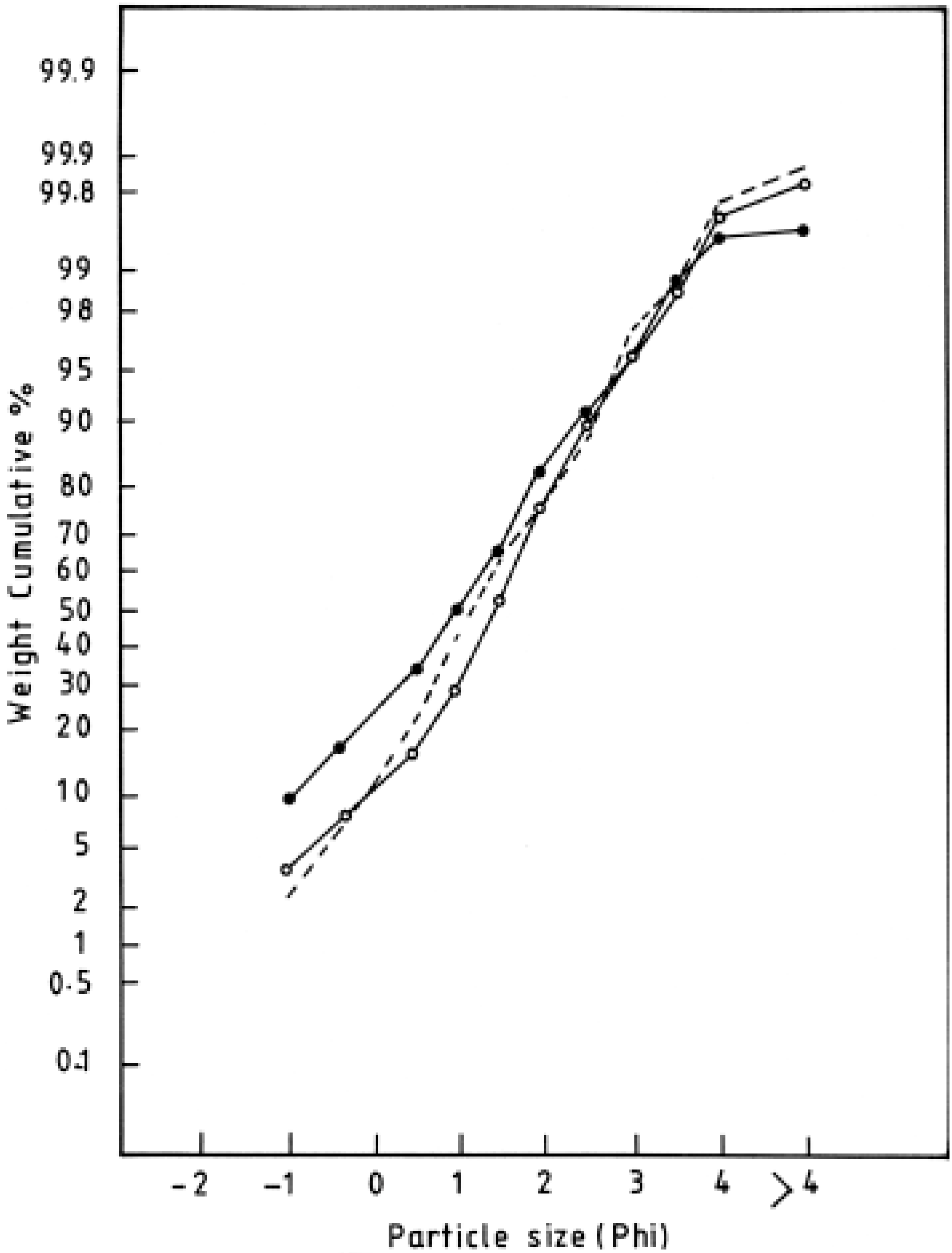

FIG. 3. Grain size data of the study location 1, 3 top and lower of the wash zone respectively, 2 is the middle zone.

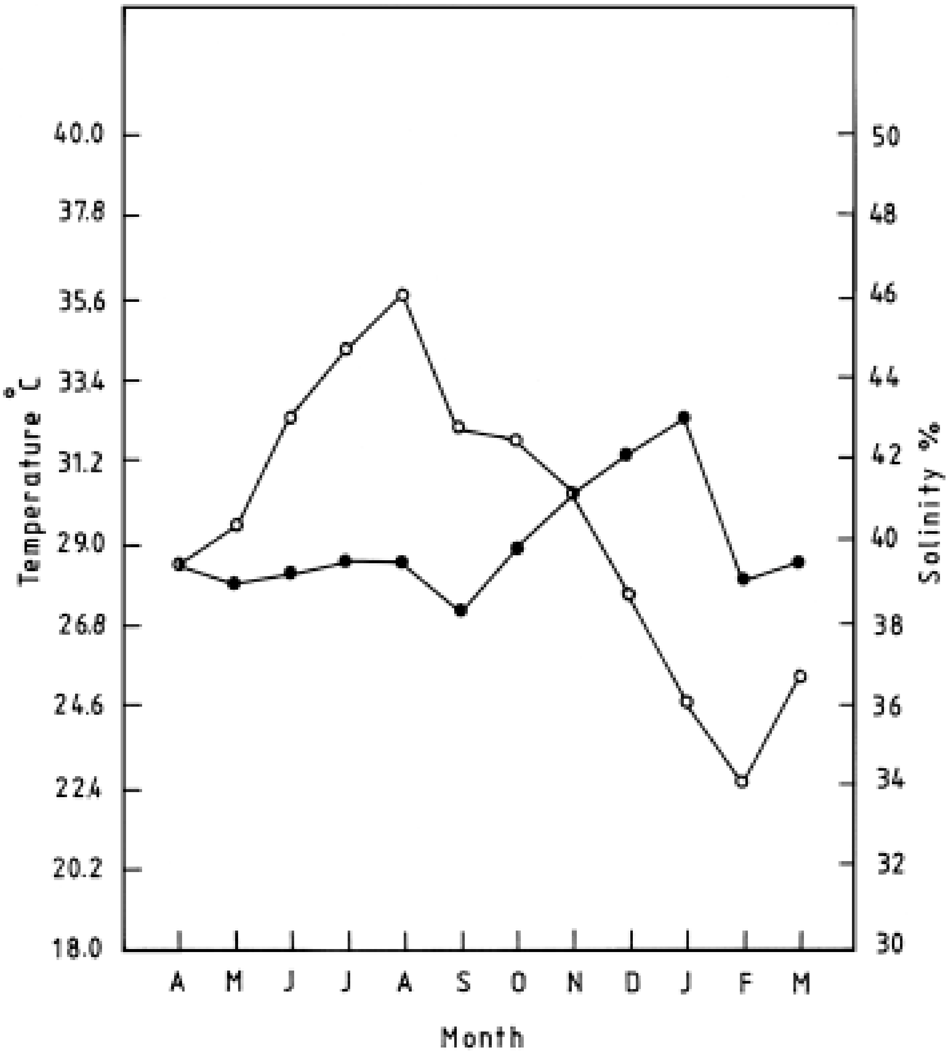

FIG. 4. Monthly variation in water temperature and salinity.

place around 12:30 h by this time *Donax faba* zone was exposed to direct sunlight. At this time the sand surface temperature showed the greatest diel variation which reached 39.8ºC and dropped to 29.5ºC during the next ebbtide which occurred at 24:30 h. The low nocturnal temperature of the beach presumably reflects flooding of the clam zone by cold surface water at night either by the moderate waves or by the high tide which started to cover the clams zone at 24:30 h. Temperature profiles (Table 3) were taken through the sand on two occasions, at 12:30 h and 24:30 h during ebbtide, at 12:30 h the sand surface was relatively dry due to sun evaporation whereas at 24:30 h the sand surface was very heavily waterlogged as a result of successive moderate waves which unusually occurred at this time. Air temperature at 12:30 h. was 38ºC, surface water temperature was 28.5ºC and sand surface temperature 39.8ºC. A difference of 11.5ºC between sand surface temperature at 12:30 and 24:30 h was noted. But, at a depth of 15 cm through the clams' zone the temperature was similar.

TABLE 3. Sand temperature (ºC) profile at different depths on the wash zone during the ebbtide 25th of July 1995.

Depth (cm)	Temperature	
	12: 30 h	24:30 h
0	39.8	28.5
5	37.7	27.9
10	30.9	27.9
15	28.1	27.9
20	28.1	27.9

Tide

No accurate continuous tidal records exist for the study region. Limited data on tides were obtained during the present study which clearly show the tide is semidiurnal and of small amplitude. The data illustrated in Fig. (5) were personally obtained at the study site by manually measuring the tidal rise and fall in relation to a reference point. The tidal range varies from 10 cm to around 30 cm.

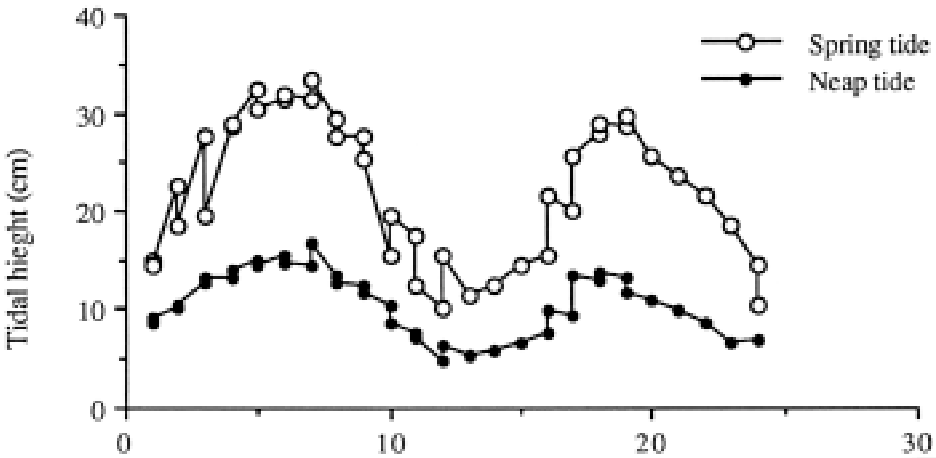

FIG. 5. Spring and neap tide range at the study site.

Mean Sea Level

There is a remarkable seasonal variation, in the mean sea level in the Red Sea due to the monsoon effect[5-8,12,13,38]. Patzert[12] suggested that the monsoon wind reversal is the major factor controlling sea level. Morley[5] summarized this by indicating that during the winter monsoon, predominantly SSE winds drive the surface waters of the Gulf of Aden northwards into the Red Sea. This inflow exceeds losses due to evaporation and subsurface outflow and results in increase sea level particularly between 19ºN and 25ºN where the current opposes the NNW wind of the northern Red Sea. Mean sea level gradually falls from January to late July. When monsoon reversal is complete the NNW winds blow throughout the Red Sea, there is a net loss of water, reducing mean sea level to an August minimum after which sea level gradually increases. Morley's own data were recorded 10 km north of Jeddah and demonstrated dramatic short term coastal sea level fluctuations caused by transient changes in wind direction. Koenig[38] however, considers in a computer model that surface circulation is mainly driven by the pressure gradient caused by the density field and not by the wind.

Whatever the factors controlling circulation are, the resulting sea level changes were clearly observed by Eshky[6-8] who recorded the seasonal variation from Jizan city, 750 km south of Jeddah and from the same area where Morley[5] recorded his data. The present study clearly illustrates the seasonal change in the level (Fig.6) and is in full agreement with all previous studies. However, the mean sea level in the present study is not the true mean and standardized to the tidal cycles, but represents the height of sea level to a standard point at each period of observation.

Tidal Migration

At the study site the maximum height of both spring tide and meap tide never exceeds 35 cm and 10 cm respectively. The beach is relatively flat having a slope of 1:15. The fall water level on both low spring tide and low ebbtide is not sufficient to cause any potential desiccation danger to the clams. The exposed area during low tide is characterized by always having continuous slick of water on its surface from the successive small waves which have a frequency of around once every 40 seconds or more. Therefore, the study of zonation of tagged *Donax faba* to the related datum point revealed that the clams remained quiescent in the sand during low tide, and there was no evidence to suggest tidal migration of this species on the beach. On the other hand the position of the wedge clams *Donax faba* is highly affected by the seasonal variation in the mean sea level where the position to clams on the beach varies seasonally, Fig. (6).

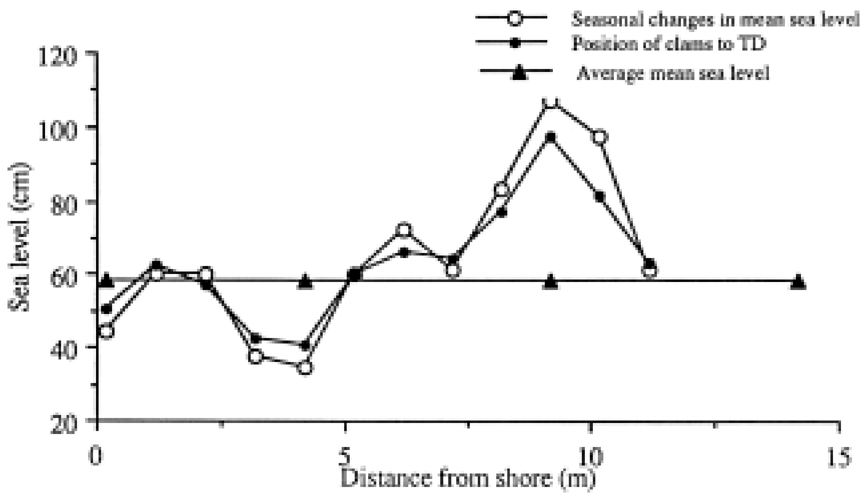

FIG. 6. The seasonal variation in the vertical distribution of *Donax faba*.

In winter months (December-March) the wedge clams start to leave the sediment and move up the beach in response to the rising sea level. During the summer months (April-November) the wedge clams respond to the fall in of the ground water table by moving to the sand surface where they were carried down the beach by the back wash and burrowed in the saturated sand. Due to the small size, the wedge clams may easily be carried up and down the beach with the advance the backwash of small waves which usually occurred at the study site. The responses of *Donax faba* to the seasonal rising and falling of the mean sea level and hence the vertical seasonal tidal migration is likely to be endogenous.

Shell Dimensions

Relationship between linear dimension of shell length (L), shell height (H), shell thickness (TH), and shell total weight (W) for the *Donax faba* population from Sharm Obhour (SO) and Al-quiad Island (AI) are shown in Fig. (7) and linear regression values are summarized in Table (4).

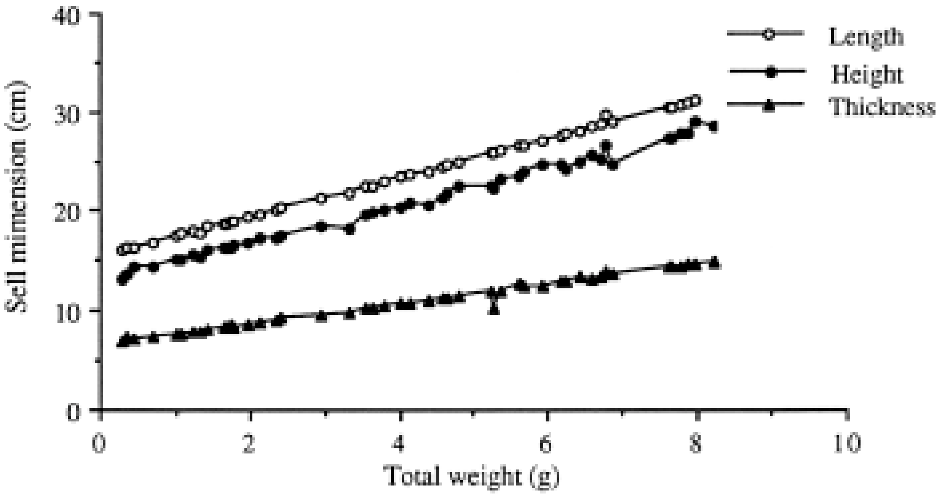

FIG. 7. Relationship between linear dimension versus total weight of *Donax faba* shells from both sites.

In each case, the regression line is highly significant ($P < 0.001$). Employing shell length as a reference dimension, this study has demonstrated that within the average of 7.1 to 31.61 mm of shell length, all different dimensions were growing strictly isometrically. Similar results were obtained if shell height, shell thickness or shell total weight were employed as a reference dimension. Covariance analysis showed that there were no significant differences in the shells' dimensions between both sites (Table 5).

There does not appear to be any phenotypic variability in shell shape variables at the two different site.

Specific Growth Rate

A total of 150 clams were captured tagged and released. On subsequent visits the release site was searched for tagged clams. Length at release and new length were noted for all tagged individuals, to compare and analyse the growth during different seasons. Monthly instantaneous growth rate were calculated using the following formula of Winberg[39].

$$G = \frac{\log_{10} L_2 - \log_{10} L_1}{t}$$

where L_1 and L_2 are the lengths at the beginning and the end of the experiment, respectively, and t the duration of the experiment in months. G was then plotted against $\log_{10}$ initial length for each season. May 1994 is considered to be the initial length for summer, August for fall, November for winter and finally February for the spring. The regression equation of the lines fitted to all data are represented in Table (6).

TABLE 4. Regression statistics of linear shell dimension and total weight of *Donax faba* from Sharm Obhour (SO) and Al-quiad Island (AQ).

Site	log y = log a - b log x	r	n
SO (L - W)	log y = – 4.96 – 4.01 log x	0.84	46
AI (L - W)	log y = – 4.82 – 3.97 log x	0.95	46
SO (L - H)	log y = – 0.238 – 1.33 log x	0.99	102
AI (L - H)	log y = – 0.25 – 1.41 log x	0.99	102
SO (L -TH)	log y = – 0.56 – 1.16 log x	0.99	102
AI (L - TH)	log y = – 0.57 – 1.15 log x	0.99	102
SO (TH -W)	log y = –3.18 – 3.61 log y	0.99	102
AI (TH - W)	log y = – 3.13 – 3.55 log y	0.94	102
SO (H - W)	log y = – 4.28 – 3.67 log y	0.88	102
AI (H - W)	log y = – 4.19 – 3.58 log y	0.95	102
SO (H - TH)	log y = – 0.311 – 1.02 log y	0.99	102
AI (H - TH)	log y = – 0.295 – 1.01 log y	0.99	102

TABLE 5. Covariance comparisons of different shells dimensions, length (L), weight (h), thickness (th) and total weight from the two sites.

Compared groups	df	P
L (SO) - L (AI)	205	NS P > 0.98
H (SO) - H (AI)	205	NS P > 0.96
TH (SO) - TH (AI)	205	NS P > 0.97
W (SO) - W (AI)	39	NS P > 0.41

TABLE 6. Regression equations for seasonal length specific growth rate (G) against log10L_1.

Season	log y = log a - b log x	n	r
Summer	log y = 0.24 – 0.009 log x	9	0.99
Fall	log y = 0.13 – 0.005 log x	9	0.95
Winter	log y = 0.114 – 0.004 log x	9	0.91
Spring	log y = 0.117 – 0.004 log x	9	0.98

In each case, the regression line is highly significant (P < 0.005).

Covariance analysis of these data showed significant differences in both the slope (b) and the elevation (a) of the regression lines of the specific growth rate between summer and the remaining seasons, where there was no significant difference in the slopes (b) or the elevations (a) of the regression lines of the specific growth rate between the remaining seasons.

The negative slopes of the regression lines indicated that juvenile clams grow faster than adult clams. Also the elevations (a) of the regression line showed a remarkable increase in the growth rate in the summer compared to the remaining seasons.

TABLE 7. Covariance comparisons of seasonal specific growth rate of *Donax faba.*

Compared groups	a	b
Summer – fall	S (P < 0.005)	S (P < 0.005)
Summer – winter	S (P < 0.001)	S (P < 0.001)
Summer – spring	S (P < 0.001)	S (P < 0.001)
Fall – winter	NS	NS
Fall – spring	NS	NS
Winter – spring	NS	NS
All combined	S (P < 0.005)	S (P < 0.005)

Reproduction

The wedge clam is a diocious organism. The reproductive cycle[4,40,41] is divided into the following: active, mature, spawning – (divided into partially and completely spawned) and the resting stage. Oogenesis and spermatogenesis can be distinguished in the gametogenic processes. Monthly mean diameter of oogenic and spermatogenetic elements were determined. Values on the development of the male and female gonads of *Donax faba* (Table 8) indicate an increasing pattern on the oogenic and spermatogenic elements.

TABLE 8. Development of female and male gonads in *D. faba* (Gmelin).

Month	Mean percentage of oogenic elements	Mean diameter of oogenic elements (μm)	Stand. dev. ±	Mean percentage of spermatogenic elements
April	0.18	4.70	0.88	1.73
May	2.93	32.4	7.21	5.34
June	6.87	47.63	7.44	15.41
July	2.52	18.75	5.22	22.19
August	11.44	9.66	5.61	17.01
September	11.97	37.5	3.83	13.86
October	13.09	42.89	6.68	12.01
November	16.48	45.5	7.08	9.39
December	13.92	53.0	4.57	2.28
January	10.46	55.5	4.98	0.0
February	1.46	3.25	0.72	0.0
March	8.24	4.35	0.79	0.78

Spermatogenesis

Spermatogenic activities in *Donax faba* were observed from April 1994 to March 1995. Observed characteristics of the spermatogonial cells are as follows:

(a) Activation Stage Plate (1). In April, testes were located nearly at the dorsal part of the foot, occupying a small area. Oval and circular nuclei embedded in oval follicles filled with vesicular connective tissue. Definitive spermatogonial cells aggregated in small groups at the centre of follicles with mean diameter of about 4.1 µm.

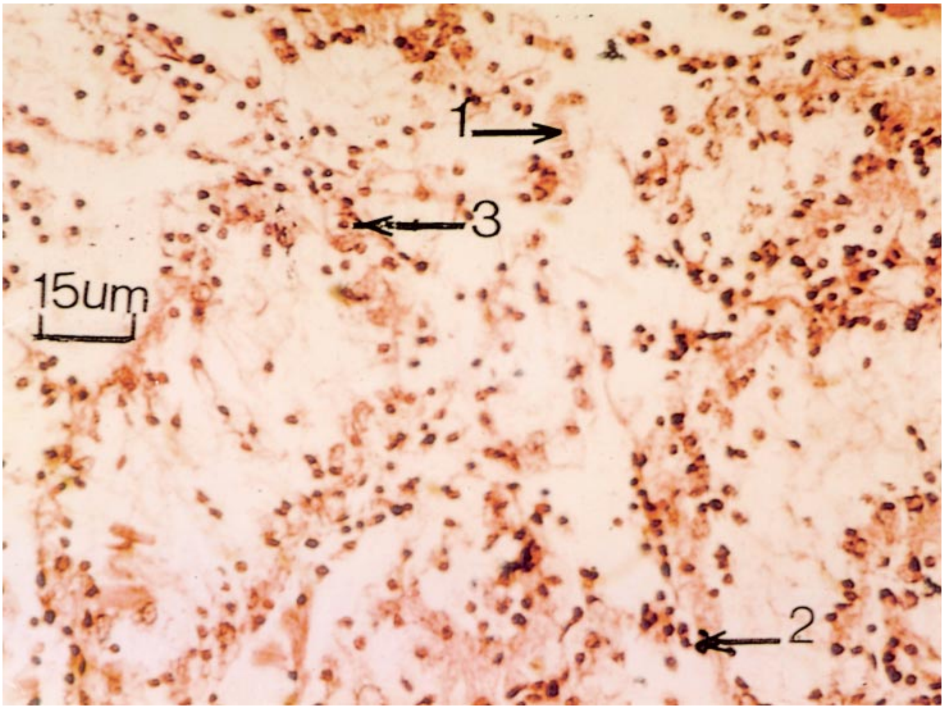

PLATE 1. Activation stage in male (H.S.) showing (1) vesicular connective tissue, (2) definitive spermatogonial cells, and (3) nucleus.

(b) Maturation Stage Plate (2). Early stage of maturation began in May. Reproductive follicles showed different stages of spermatogenic elements (e.g. stem cells, secondary spermatogonial cells). Primary and secondary spermatocytes are clearly seen occupying the central part of the follicles.

June, the clams were already in advanced stage of maturation. Spermatids and sperm were seen clearly occupying most part of follicles. In July, all clams were found in the full ripe phase, gonadal follicles filled with huge numbers of sperm while their tails were extended towards the center of the follicles.

(c) Spawning Stage. August, gonadal follicles showed different degrees of emptiness, an indication that sperm were reduced gradually [Plate (3)]. Follicular diameter began to decrease in size and intrafollicular spaces were seen easily.

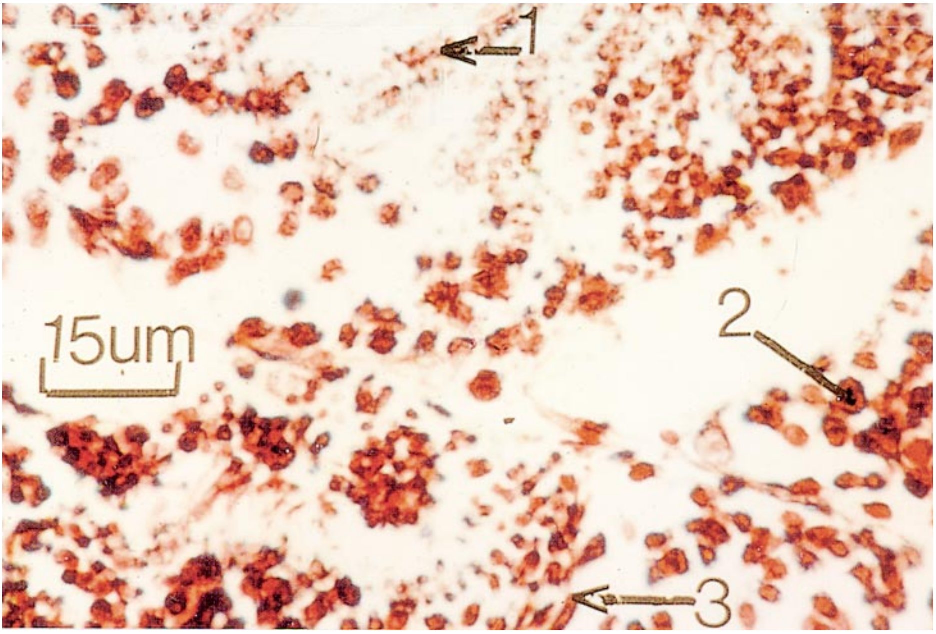

PLATE 2. Stage of maturation in male (H.S.) showing (1) secondary spermatocytes cells, (2) primary spermatocytes (H.S.), and (3) stem cell (H.S.).

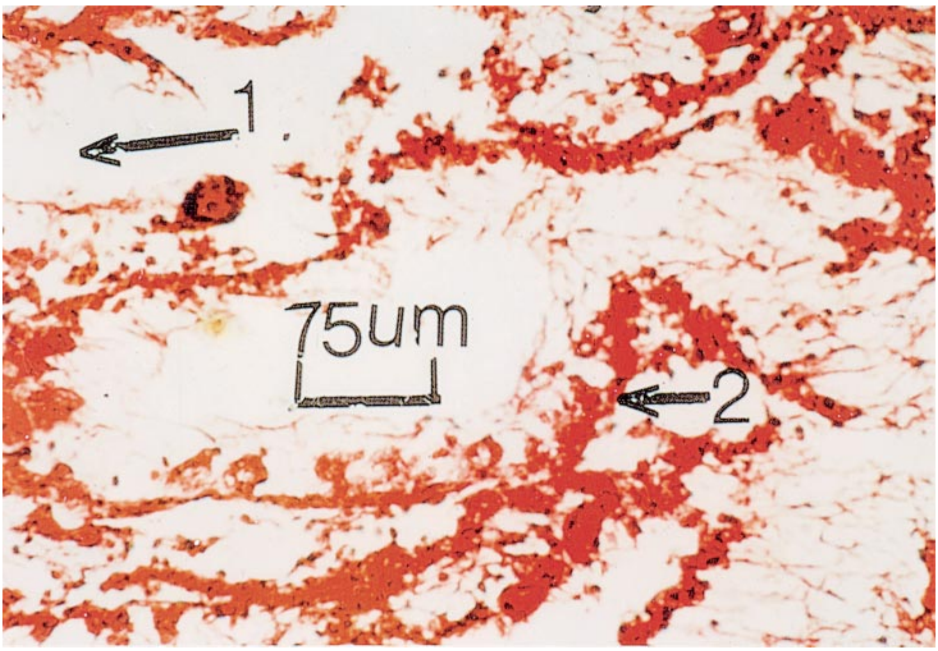

PLATE 3. Early stage of spawning in the male (T.S.) showing (1) intrafollicular space and (2) ripe sperms.

September, marked the continued intensive spawning where large number of fully matured spermatozoa filled the follicles. Intrafollicular spaces increased in size. In October, partial emptiness of gonadal follicles was observed indicating partial spawning and in November, reduction of ripe sperm was very distinct and both inter and intra-follicular spaces increased. In December, ripe sperm reached their minimum while few follicles were ruptured, others retained their forms. Relict sperm were found inside the gonadal follicles.

(d) Resting Stage, Plate (4). January, gonadal follicles were completely devoid of sperm. Phagocytic cells present in large numbers all over the follicles. Vesicular connective tissue rebuilding and transparent.

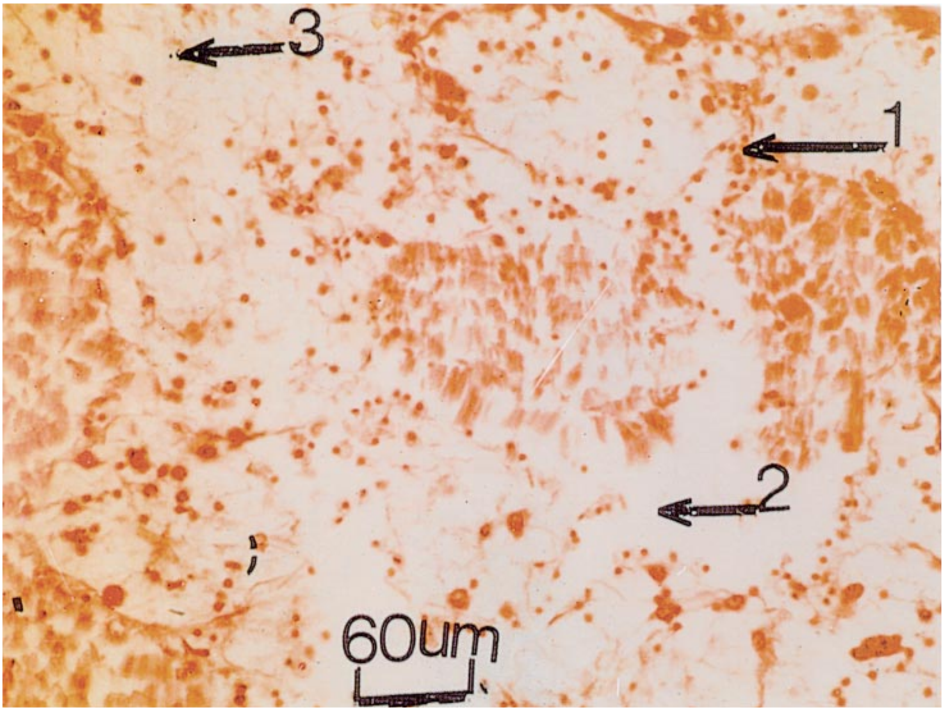

PLATE 4. Resting stage in male (T.S.) showing (1) phagocytic cells, (2) gonadal follicles and (3) vascular connective tissues.

In February, vesicular connective tissue gradually losing its transparency indicating an active formation of forthcoming reproductive cycle.

(e) Activation Stage Plate (5). In March, oval nuclei of vesicular connective tissue appeared. Small sperm balls began to aggregate at the center of some follicles and many primary and secondary spermatogonial cells developed along the inner walls of the follicles.

Oogenesis

Observed oogenic activities in *Donax faba* from April to March are as follows:

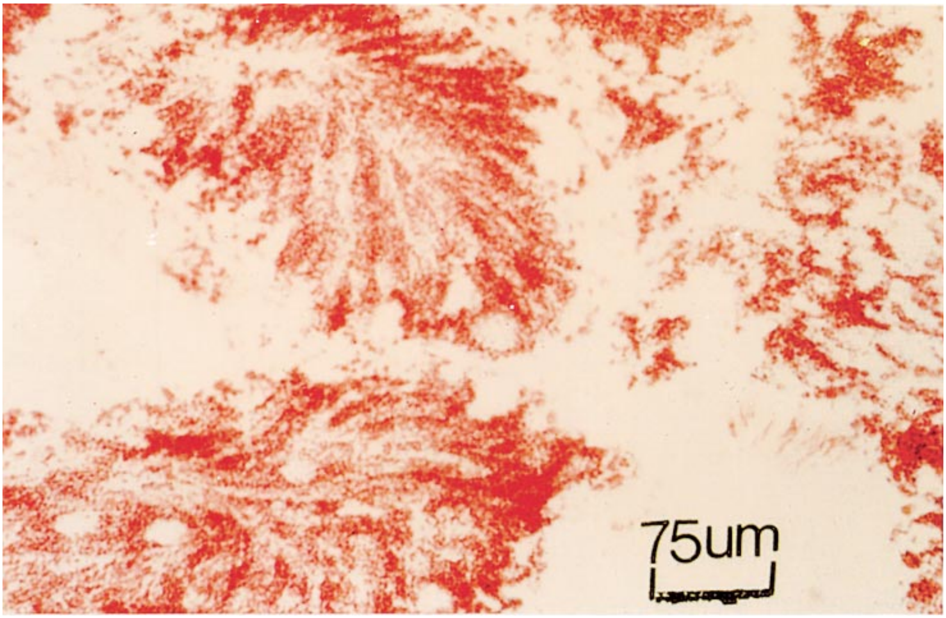

PLATE 5. Early stage of activation in male (H.S.)

First Reproductive Cycle

(a) Activation Stage Plate (6). This stage is characterized by many stem cells at the peripheral walls of the gonadal follicles. Only very few primary oocytes were embedded in the vesicular connective tissue of the follicles. Gonadal follicles are oval in shape and mean diameter ranged between 100 µm and 135 µm.

(b) Maturation Stage Plate (7, 8). Ovaries obviously increased in size (in May) where follicular diameter reached about 250.5 µm. Presence of many large free oocytes growing at a rapid rate where diameter ranged from 25 µm to 38 µm. Many stalked oocytes were seen attached to the follicular walls protruding to the center of the follicles.

(c) Spawning Stage Plate (9). In June, the ovarian follicles were partially vacuolated. Inter-follicular spaces shrunk, mean diameter is 125 µm. Mature ova decreased in number and the follicular lumend appeared empty and translucent .

(d) Resting Stage Plate (10). In July, the follicles were elongated and compressed, have extruded all their mature ova. Most clams entered gradually the resting stage. Intra-follicular spaces disappeared and interfollicular spaces became very thin.

The Second Reproductive Cycle

This cycle started and followed the same course of development as the previous cycle; it started in August and ended in March.

Discussion

Donax faba occurs almost everywhere along the east coast of the Red Sea and offshore islands which consist mainly of sandy beaches lying on coral platforms. These ex-

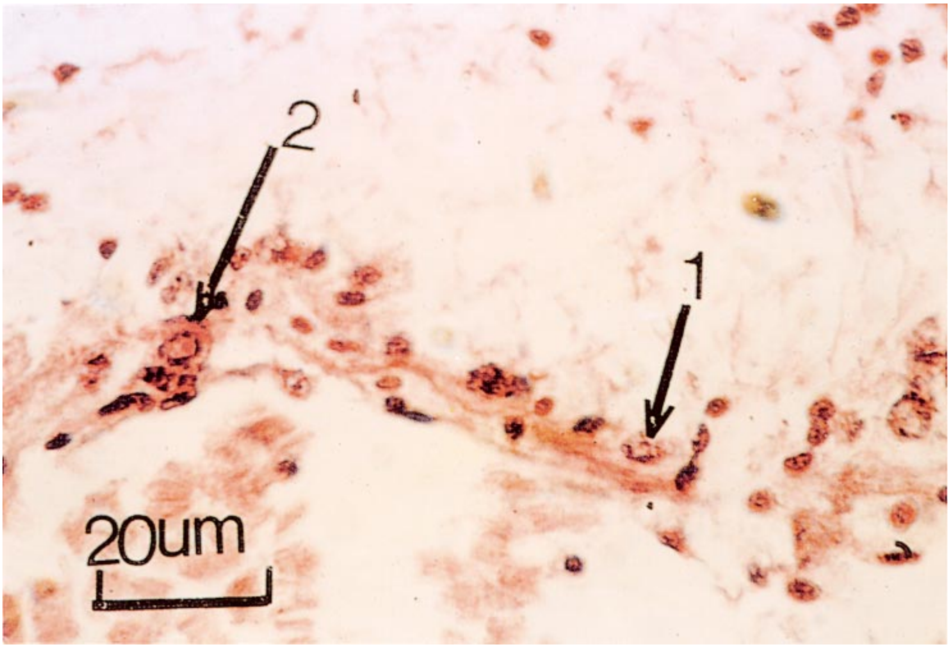

PLATE 6. Activation stage showing (1) formation of stem cells and (2) few primary oocytes (H.S.).

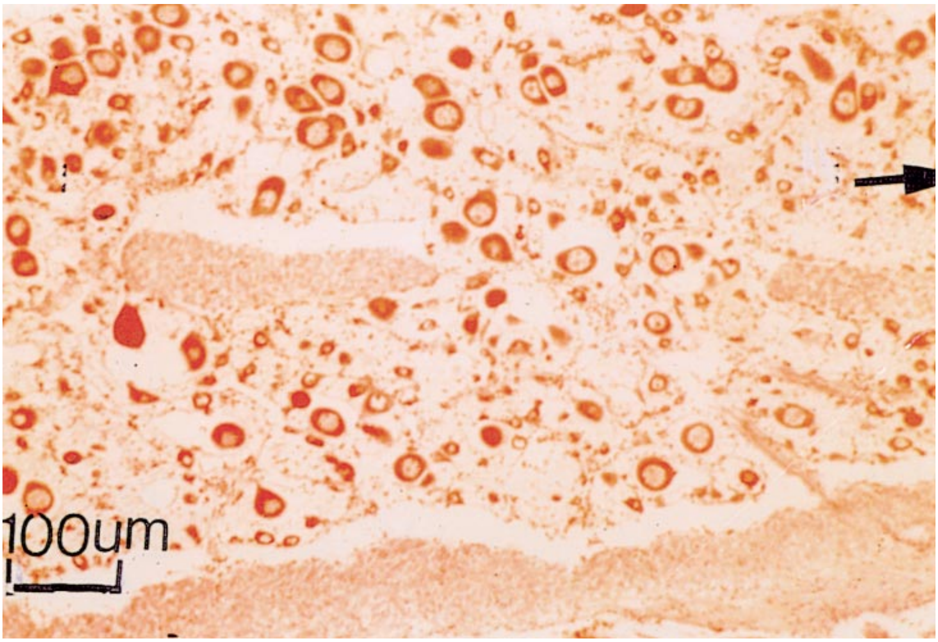

PLATE 7. Early stage of maturation in female (H.S.) showing free oocytes.

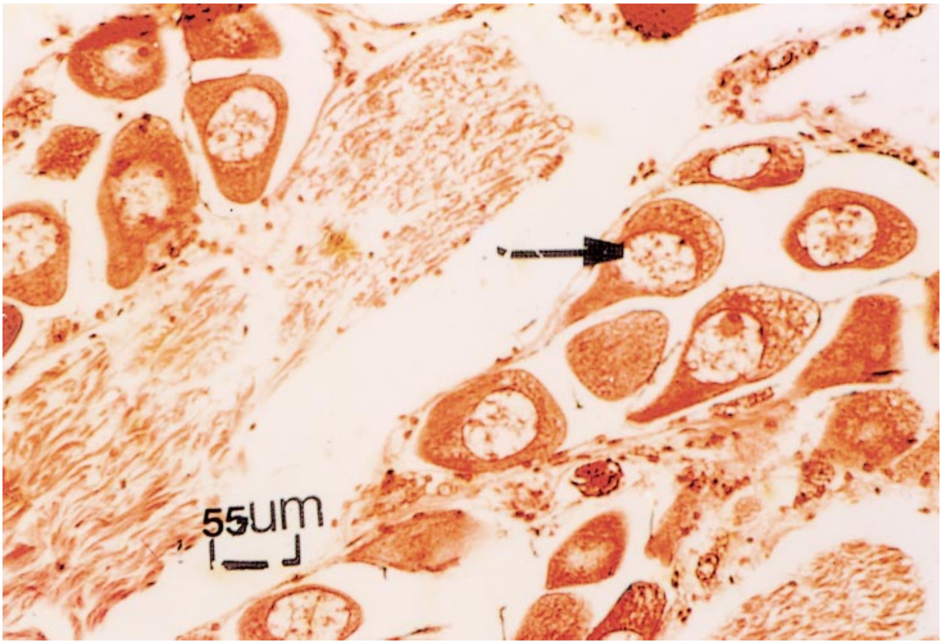

PLATE 8. Advanced stage of maturation in female (H.S.) showing stalked oocytes.

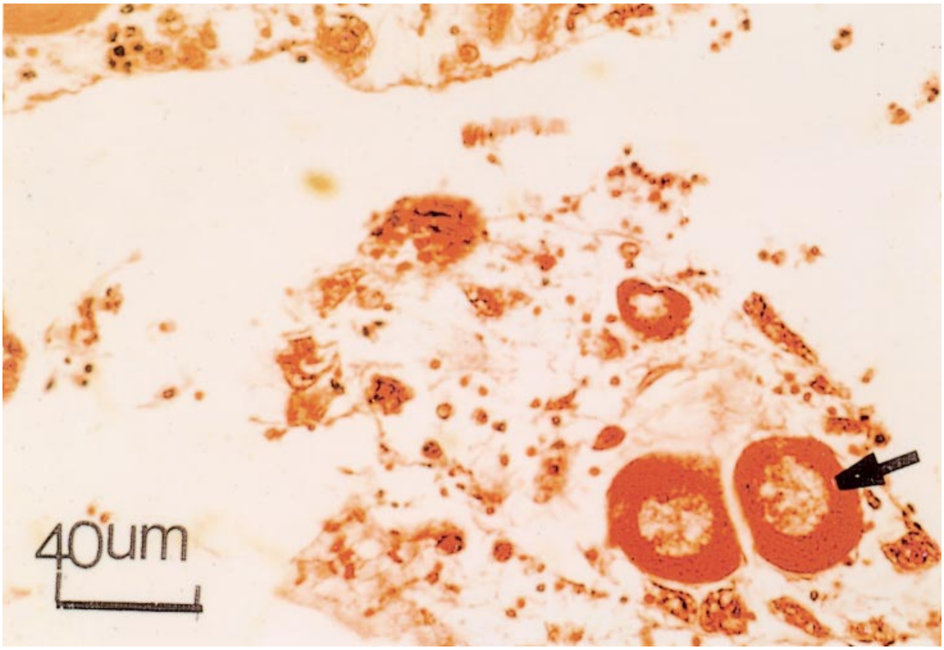

PLATE 9. Stage of partial spawning in female (T.S.) showing mature ova.

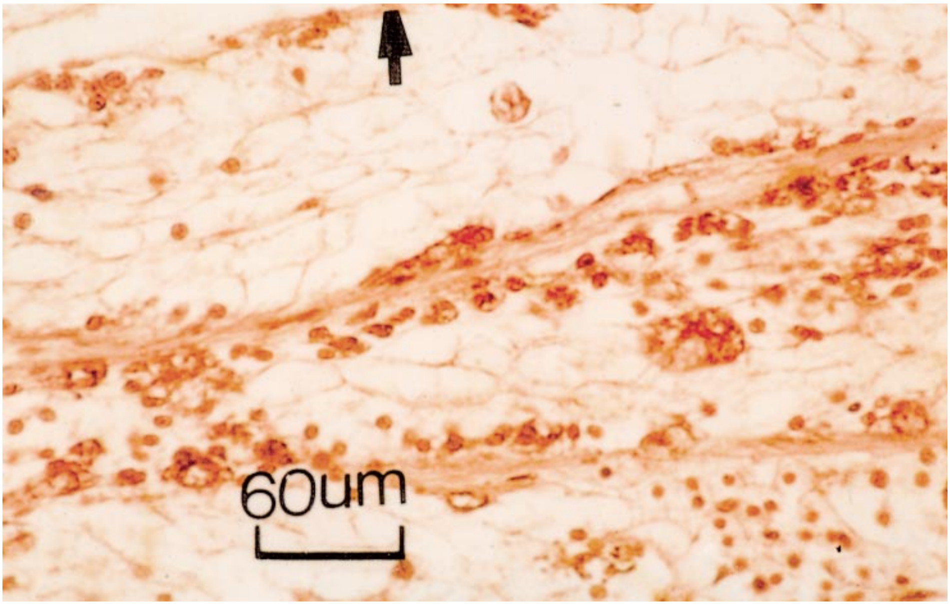

PLATE 10. Resting stage with highly shrunk gonadal follicles in female (H.S.).

tend over great distances (1000 km) along the shore line of the east coast of the Red Sea interrupted only by mangrove creeks where fine grain size of sand prevents colonization by *Donax faba* which prefers coarser sand. Similar results were reported for the same species by Alagarswami[4] from India and Smith[3] from Tanzania. The distribution of *Donax faba* in the Red Sea is also restricted to the sheltered sandy beaches. The clams zone is separated from the fringing reef by the reef crest and a shallow back lagoon 160-50 m in width and only 0.5-1 m in depth. The reef crest is submerged in winter but is exposed in July and August and the lagoon is sometimes reduced to a series of shallow pools. For this reason the distribution of *Donax faba* in the Red Sea and in the offshore islands is restricted to sheltered beaches. However, this is in conflict with the observation of Smith[3] who observed *Donax faba* on exposed sandy beaches of E. Africa. Alagarswami[4] also reported the same species from exposed beaches in India. Other members of same genus were also reported from exposed beaches from different parts of world[16,42-45].

According to Smith[3], the clam maintained a feeding position within the wash zone by migrating up and down the beach tide. Wade[16] noted that population of *Donax striatus* inhabiting the shallow sloping beaches of Trinidad, where the water table is less than 10 cm below the sand surface, did not display tidal migration. Mclachlan *et al.*[43]; Prosch and Mclachlan[20]; and Theodore *et al.*[42] have indicated that *Donax serra* does not exhibit a tidal pattern of movement, like most members of this genus, but rather a semilunar migratory pattern. In the present investigation it has been noticed that *Donax faba* remained quiescent in the sand just below the high tide mark and that there was no evidence to suggest either tidal nor semilunar migration for this species on the beach. This may be due to the shallow water table (< 10 cm) over the spring and neap tidal cycle where the maximum diel tidal range is < 30 cm and on beaches having a slope of about 1:15, this results in an effective intertidal habitat of approximately 90-100 cm and also may be due to the impressive digging ability of *Donax faba*. However, measurements of the position of *Donax faba* to the datum point revealed that the clams were able to maintain their position in the saturated zone at all phases. The position occupied on the saturated zone by the *Donax faba* population varies with the variation in sea level due to the monsoon effect.

Measurements of the positions of tagged clams every month during the period of the investigation in relation to datum point has indicated that there were clear relationship between the sea level and the position of the clams. The difference can be seen clearly between January and August were the vertical position between these two months may extend more than one meter. The response of *Donax* species to the tidal cycle has been described by Wade[16], Tiffany[46], and Ansell and Trueman[17] who observed that during a rising tide, the *Donax* are washed out or leave the sediments in response to the acoustic shock from breaking wave and liquification of the sand and are carried upshore in the wash. During the ebbing tide the *Donax* respond to the periodic drying of sand between wave swashes by moving to the sand surface where they are carried down shore by the backwash and burrow in the saturated sand. Cubit[47] described the tidal movements of *Emerita analoga* and described their movements to a similar responses to changes in the fluidity of the sand. The observed seasonal migration in *Donax faba* may be due to the clam population following the movements of the low water table due to seasonal variation in the sea level. Magnus[48] has reported similar behaviour for the brachyuran crab *Ocypode saratan* from the northern part of the Red Sea. Eshky[10] reached the same conclusion for the fiddler crab *Uca inversa* from the south part of the Red Sea. This investigation is a first attempt to explain the changing distribution of the clams of the Red Sea in terms of seasonal migration rather than diel, tidal or semilunar migration as has been mentioned in the literature . In addition, it has been shown that due to the relatively shallow sloping beach, the small tidal magnitude and also due to the impressive digging ability, *Donax faba* can remain close to the saturated zone and therefore, reduce the need for tidal migration.

Donax faba is well known to show dramatic density changes throughout the year. A peak density in the present investigation occurred in November declining to 30/m^2 in January. Alagarswami[4] reported a peak density of *Donax faba* from India of 217/m^2 in March declining to 89/m^2 in November. Smith[3] investigated the same species from the East coast of Africa and indicated a peak of density of 2729/m^2 of *Donax*. Nayar[21] who investigated *Donax cuneatus* from India a peak density of 472/m^2 in June declining to 185/m^2 in August.

The analysis of growth rate in *Donax faba* in the present investigation demonstrated different seasonal patterns of growth. The greatest increase in the growth rate took place in the summer. Similar results were reported for the same species by Alagarswami[4] and Smith[3] and also for other *Donax* species from different parts of world[21-24,49]

Hibish and Koehn[50] have related the increase in growth rates of soft tissue during summer coincident with maximal rates of energy gained. Eshky and Ba-Akdah[7] have shown that high temperature affects both the oxygen consumption and the heart rate of *Donax faba.* Also Mori *et al*[27] has indicated a similar effect of high temperature on the metabolism of the commercial Oyster *Crassostrea gigas.*

Spawning activity appears to affect growth rate. Quayle[25] and Auger[26] observed slightly lower rates of shell growth in oysters during August than July when spawning activity peaked at temperatures reaching 20ºC. Suppression of energy reserves or their diversion from growth to reproductive activity seems likely to be the reason[27]. Poor winter growth in the present study could be due to the same effect where slow winter growth rate coincided with spawning activity of the clams.

Donax faba has a prolonged breeding period of two different peaks of spawning. The small peak took place in June and the large one in November and December. Al-agarswami[4] has observed that *Donax faba* from the Mandapam coast of India has only one spawning peak which occurred in May and June and he indicated that the major determinants of spawning time are water temperature and salinity. Rao[30] observed one single distinctive annual reproductive cycle of *Donax cuneatus* which took place between September and December and he related this reproductive activity to low temperature and salinity. Nayar[21] observed one reproductive cycle for *D. cuneatus* where spawning commenced in January and ceased in April when the water temperature increased.

These two reproductive cycles of *D. faba* in the present study corresponded with the phytoplankton peak which occurred at same period[51]. Therefore, one possible reason for increased reproductive activity in the pre and post monsoon periods could be the availability of food for the clams larvae. The same explanation was forwarded by Boolootian *et al.*[31] and Siddiqui and Ahmed[35] who reached the same conclusion: that the pre and post monsoon periods are relatively calm periods during which lesser wastage of eggs can be expected. Similar conclusion was also reached by Phillay and Nair[33] while studying the breeding biology of the crabs from the south west of India. According to them, the availability of food for the young ones during the planktotrophic life is a very important factor controlling the breeding season. Goodbody[32] has suggested that there may be some relationship between breeding periods and the presence of a particular fraction of species in the plankton at a certain season of the year. Borrero[34] investigated the relationship between tidal height and reproductive variation among the population of *Geukensia demissa* from South Carolina. He also made a comparison of the productive cycles of populations of *G. demissa* from different latitudes on the east coast of the United States and found that the microgeographic variation in the timing of reproductive activity may be as great as the latitudinal. The level of occurrence in the intertidal zone, and hence length of submersion and potential feeding time exert a profound influence on the timing of the reproductive cycle of *G. demissa.* Newell, *et al.*[28] observed that differences in food quantity and/or quality and not temperature were the major determinants of the timing of gameto-genesis and spawning of the *Mytilus edulis* population from the east coast of the United States. The present study supports the above conclusions. However, it is of interest to note that some marine brachyuran crabs, *Metapograpsus messor*, *Ocypode saratan* and *Grapsus tenuicrustatus* breed continuously throughout the year and spawning peaks around the time as *Donax faba*. It is likely that there is a strong relationship between breeding periods, not only for *Donax faba* but also for most of the marine invertebrate in the Red Sea, and the availability of food during the monsoon effect.

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السلوك البيئي وبيولوجية المحار الوتدي *Donax faba* (Gmelin) من البحر الأحمر

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المستخلص . ينتشر المحار الوتدي *Donax faba* على طول السواحل الرملية لشاطئ البحر الأحمر والجزر القريبة من الساحل في كل من جنوب ووسط البحر الأحمر . هذه الشواطئ الرملية عادة ماتكون محمية من تأثير الأمواج القوية ، لوجود هذه الشواطئ خلف المرجاني الحاق Fringing Reef التي عادة ما تتكسر عليه هذه الأمواج ، ومن العوامل البيئية الأخرى التي تحدد انتشار هذا المحار في الشواطئ الرملية حجم حبيبا الرمل ، فقد لوحظ انتشار هذا المحار في الشواطئ ذا الحبيبا الخشنة نسبياً (Phi 1.2-1.45) والتي تقع مابين مدى المد والجزر Tide marks وعادةً ماتكون مشبعة بالماء سواء كان عن طريق المد أو تأثير الأمواج . ولصغر قيم المد والجزر خاصة في منطقة وسط البحر الأحمر فإن هذا المحار لايخضع لهجرة رأسية يومية أو شهرية كما يحدث لنفس النوع في مناطق أخرى مثل جنوب أفريقيا أو الهند . على أنه لوحظ أن هناك هجرة رأسية فصلية ، وذلك في فصلي الصيف والشتاء التي تجبر هذا المحار إلى هجرة رأسية إلى أعلى الشاطئ وخاصة في شهري ديسمبر ويناير نتيجة لارتفاع مستوى سطح البحر خلال هذه الفترة الناتج عن تأثير الرياح الموسمية التي تهب على بحر العرب أما الرياح الموسمية الصيفية التي تهب على بحر العرب فإنها تؤدي إلى انخفاض مستوى سطح البحر الأحمر لأكثر من متر ونصف مما يؤدي إلى هجرة المحار هجرة رأسية إلى أسفل الشاطئ . كما أوضحت هذه الدراسة أن هناك تفاو كبير في معدل نمو هذا المحار حيث يبلغ أقصاه في فصل الصيف وأقله في فصل الشتاء . كما لوحظ أن هناك تفاو كبير في الكثافة السكانية لهذا المحار خلال العام الواحد حيث بلغت أعلى كثافة ٢٩٦/ م٢ في شهر نوفمبر وأقل كثافة في شهر يناير حيث بلغت ٣٠/ م٢ ويعود هذا التفاو إلى إرتفاع نسبة المو (Mortality Rate) خلال فصل الشتاء وذلك نتيجة لقوة شدة الأمواج والتي عادة ماتقذف بهذا المحار بعيداً عن الشاطئ . أما من الناحية البيولوجية فقد لوحظ أن لهذا المحار فترة تزاوجية طويلة خلال العام تبلغ ذروتها خلال فصل الصيف وعلى التحديد في شهر يونيه وذروة أكبر في فصل الشتاء خلال شهري نوفمبر وديسمبر وهذه الذروة ترتبط ارتباطاً كبيراً بالنمو الكبير في الهائما النباتية Phy-toplankton الذي يحدث في نفس الفترة ويمثل مصدراً لغذاء يرقا هذا المحار .