SEASONAL GONADAL CHANGES IN THE ADULT BACKWATER OYSTER, *OSTREA (CRASSOSTREA) MADRASENSIS* PRESTON FROM ENNUR NEAR MADRAS*

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Introduction

Seasonal changes in the gonads of lamellibranchs such as oysters, clams and teridinids have been studied in detail by various workers, *viz.*, Coe (1932 *b* and 1936), Coe and Turner (1938), Loosanoff (1937 *b*, 1942 and 1953), Galtsoff (1937), Orton (1933), Roughley (1933) and Quale (1943). In commercially important forms these studies have been of immense value in their culture and management. The present paper deals with the gonadal changes in the adults of the backwater oyster, *Ostrea* (*Crassostrea*) *madrasensis* Preston which is one of the widely distributed commercial species of bivalves in this country. The estuaries and backwaters which are the natural habitats of this oyster are subject to very wide fluctuations in the environmental conditions, such as drought in summer, floods in monsoon and tidal influence during periods, when the waters are in communication with the sea. An attempt has been made in this paper to separate the several seasons during the year on the basis of the cyclical changes in the environment and to study the histological changes taking place in the gonads of the oysters in the corresponding periods.

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Environment, Material and Methods of Study

The material on which the study is based has been obtained from the oyster beds in the backwater at Ennur, a place eleven miles north of Madras.

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The Korttalaiyar River passing through the Tiruvallur and Saidapet taluks, and the Buckingham Canal, between its 9th and 11th milestones open into the backwater. The latter communicates with the Bay of Bengal not all through the year but periodically, at other times a sand bar cutting off the connection between the two. Some of the oyster beds are in shallow waters of a few feet depth whilst others are in depths up to about two fathoms. Mortalities are heavy when certain beds are exposed due to drought in severe summers or when the backwater is flooded after heavy rains. Oysters of good size and shape are regularly collected all the year round, cleaned, packed in gunny bags and despatched by rail to the City of Madras against orders from a few high class restaurants and enlightened public who have cultivated a taste for them. The beds are under the supervision and management of the Department of Fisheries of the Madras State.

Random samples of adult oysters from these beds were obtained once a fortnight during the two-year period from March 1953 to February 1955. Linear measurements as well as the weights of the whole oysters and their meats in all the samples were recorded to ascertain seasonal changes in meat weights in relation to the whole weights of the oysters. The proportions of the two sexes were noted by examining the freshly made smears of the gonadic tissues.

The tissues were fixed in alcoholic Bouin's fluid for serial sections which were stained later in Delafield's hæmatoxylin or iron hæmatoxylin and eosine to study the histological changes taking place from season to season. Seasonal fluctuations in salinity, temperature and pH of the waters over the oyster beds were recorded for the entire period.

Seasonal Changes in the Hydrological Conditions in Ennur Backwater

It has been found convenient to divide the year into the following periods, *viz.*, summer—April to June, pre-monsoon—July to September, monsoon—October to December and the post-monsoon—January to March. The changes in salinity, temperature and pH from season to season are described below:

(1) *Summer Period* (*April to June*).—As may be seen from Table I and Fig. 1 the salinity was generally high during these months. In 1953 it was gradually on the increase from 34·3‰ to 39·9‰ and in 1954 from 34·3‰ to 41·9‰. The water temperatures were also high, being 30·0° C. to 30·1° C. in 1953 and 29·5° C. to 32·5° C. in 1954. The pH varied but slightly from 8·2 to 8·4 in both the years.

TABLE I

Showing Mean Values of Salinity, Temperature and pH of Waters over Ennur Oyster Beds in Different Months from March 1953 to February 1955

Seasons	Months		Salinity parts per ‰	Temperature °C.	pH
Postmonsoon	March	1953	34·2	32·0	8·4
Summer	April	1953	34·3	30·0	8·4
	May	,,	36·8	30·1	8·3
	June	,,	39·9	30·0	8·4
Premonsoon	July	1953	37·9	29·7	8·4
	August	,,	35·0	30·5	8·4
	September	,,	29·5	31·1	8·3
Monsoon	October	1953	..	29·0	..
	November	,,	11·3	28·0	8·6
	December	,,	25·8	26·5	8·6
Postmonsoon	January	1954	19·3	25·7	8·1
	February	,,	29·6	29·0	8·6
	March	,,	32·2	..	..
Summer	April	1954	35·0	30·8	8·2
	May	,,	39·6	32·5	8·4
	June	,,	41·9	28·5	8·2
Premonsoon	July	1954	37·4	29·5	8·3
	August	,,	15·6	29·5	8·0
	September	,,	13·7	32·5	8·8
Monsoon	October	1954	15·5	31·0	8·3
	November	,,	18·4	26·5	8·4
	December	,,	14·4	26·5	8·5
Postmonsoon	January	1955	30·5	28·5	8·4
	February	,,	29·4	27·0	8·3

Due to fall in water-level in the backwater, the tidal flow was feeble on the first three weeks of April 1953. Thereafter it altogether stopped for the rest of the summer period of that year when the bar closed on 23–4–1953.

In 1954 the bar having closed on the 11th of March, *i.e.*, earlier than in the previous year, the backwaters was not in communication with the sea for the entire period of summer.

In certain years after occasional heavy rains it is not unusual for the bar to remain open for a varying period during summer.

(2) *Pre-monsoon Period* (*July to September*).—There was a gradual fall in salinity during the period. In 1953 the salinity which was as high as 37·9‰ in June came down to as low as 25·2‰ by September. Similarly in 1954 from June to September there was a fall from 41·9‰ to 13·7‰. Water temperatures were high ranging from 29·7° C to 31·1° C. in 1953 and 29·5° C to 32·5° C. in 1954. Fluctuations in pH ranged from 8·2 to 8·4 in 1953 and 8·0 to 8·8 in 1954. In both the years the bar remained closed during the entire period (Tables I and II and Text-Fig. 1).

(3) *Monsoon Period* (*October to December*).—Soon after the outbreak of the north-east monsoon, in the early part of the season, the salinity came down very low owing to freshets brought by the river and the canal in connection with the backwater. The water-level increased and the sand bar was opened up by the Public Works Department on the 22nd of October of both the years 1953 and 1954. Once connection with the sea is established the tidal effects could be noticed in the entire backwater region as well as in the river and the canal up to a distance of about two miles from the sea.

The purpose of cutting open the bar is mainly to hasten discharge of the land floods into the sea. It also facilitates the manufacture of salt in the salt pans which get sufficient quantity of saline water at high tides.

The salinities were observed to be greatly fluctuating between 4·6‰ to 28·7‰ in 1953 and between 5·5‰ to 26·7‰ in 1954. Water temperatures showed a gradual fall from 29° C. to 26° C. in 1953 and from 31° C. to 26° C. in 1954. The pH varied from 8·3 to 8·9 in 1953 and 8·0 to 8·5 in 1954 (Table I and Text-Fig. 1).

(4) *Post-monsoon Period* (*January to March*).—The salinities varied from 19·3‰ to 32·2‰ in 1954 and from 29·4‰ to 30·5‰ in 1955. The bar being open during the entire period, fluctuations in salinities were very marked. In general it could be observed from Table I and Fig. 1 that there was a tendency for increase in salinity from January to March. The period is also marked by a rise in temperature from 25·7° C. to 29·0° C. in 1954 and from 26° C. to 29° C. in 1955. The pH varied from 8·1 to 8·6 in 1954 and from 8·3 to 8·4 in 1955 (Table I and Text-Fig. 1).

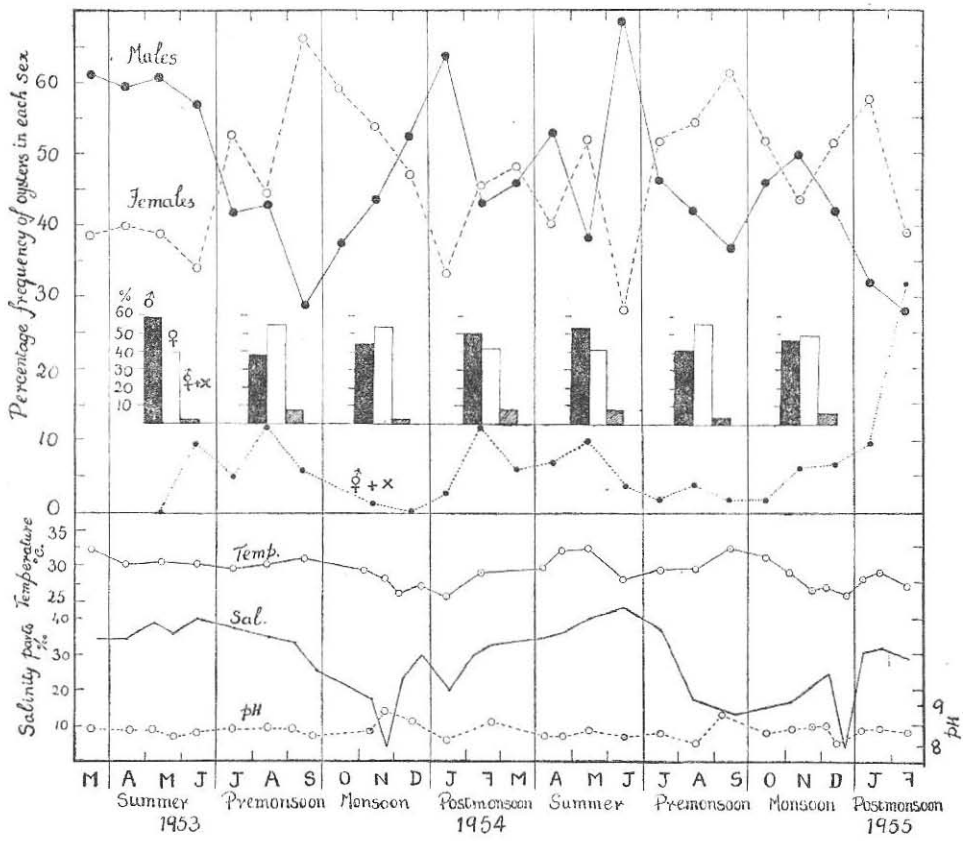
Structure of the Gonads and Their Relationship to Other Internal Organs

The gonads of the oyster are paired cream coloured structures consisting of anastamosing follicles with numerous ductules lying immediately beneath

TABLE II

Showing the Percentages of Males, Females, Hermaphrodites and those of Indeterminable Sex in Different Samples of Oysters examined during the Period of Observation from March 1953 to February 1955

Months		Seasons	Percentage in each month				Percentage in the season			
			Males	Females	Indet. Sex	Herma-phrodite	Males	Females	Indet. Sex	Herma-phrodite
March	1953	Postmonsoon	61·20	38·70	Nil	Nil	61·20	38·70	Nil	Nil
April	1953	Summer	59·77	40·23	Nil	Nil				
May	,,		60·63	39·36	Nil	Nil	59·60	38·60	Nil	1·7
June	,,		57·44	34·04	Nil	8·50 (?)				
July	1953	Premonsoon	42·16	52·94	0·98	3·90				
August	,,		43·60	44·70	10·70	0·97	37·80	54·70	5·80	1·6
September	,,		27·88	66·30	5·80	Nil				
October	1953	Monsoon	37·50	59·60	1·90	0·90				
November	,,		43·80	54·30	1·90	Nil	44·90	53·60	1·20	0·3
December	,,		52·60	47·30	Nil	Nil				
January	1954	Postmonsoon	63·96	33·30	2·70	Nil				
February	,,		42·70	45·60	10·60	1·96	50·90	42·50	5·30	1·3
March	,,		46·20	48·00	2·90	2·90				
April	1954	Summer	52·90	40·40	2·90	3·80 (?)				
May	,,		38·00	52·00	2·00	8·00 (?)	53·50	39·80	2·80	3·8
June	,,		68·40	28·10	3·50	Nil				
July	1954	Premonsoon	46·20	51·90	1·90	Nil				
August	,,		42·30	53·80	3·80	Nil	41·70	55·70	2·50	Nil
September	,,		37·03	61·10	1·80	Nil				
October	1954	Monsoon	46·20	51·90	1·90	Nil				
November	,,		50·00	43·60	1·80	4·50	45·90	48·50	3·60	1·8
December	,,		41·80	51·80	6·40	Nil				
January	1955	Postmonsoon	32·40	57·80	8·80	0·98				
February	,,		28·20	39·90	30·30	1·90	30·20	48·70	19·50	1·5



TEXT-FIG. 1. Graphs on top show percentages of (*a*) males; (*b*) females; (*c*) hermaphrodites and those of indifferent sex in different samples. Histograms show the percentages of the same categories for the season as a whole. Graphs below show fluctuations in salinity, temperature and pH of waters over Ennur oyster beds for the entire period of study from March 1953 to February 1955.

the general epithelium. In a ripe oyster the follicles surround the alimentary canal and fill up a considerable amount of space in the viscera. The follicles of both sides run together so closely and coalesce that the paired nature of the gonads is not easily recognised except for the presence of two distinct gonoducts running along the oral process and opening by the urinogenital clefts, one on either side of the posterior adductor muscle. The gonadal ductules already referred to are in communication with the follicles on the one hand and with the gonoduct of the corresponding side on the other, so that the reproductive elements are gradually drained during spawning. In external appearance the gonads in both sexes are very much alike, although the ramifications of the gonadal ductules in a ripe female are clearly seen through the general epithelium whereas in a ripe male they are indistinct.

GONADAL CONDITION OF OYSTERS DURING THE SUMMER MONTHS

Owing to gametogenic activity in the preceding period, the gonads of oysters in April and May were found to be fairly full with ripe reproductive elements in the follicles, which were moderately enlarged. The vesicular connective tissue occupied a considerable amount of space between the follicles. In the females large and fully ripe eggs were in the lumina of the follicles and of the ductules and smaller ones in the process of attaining maturity closely adhering to the germinal layer lining them (Pl. XXV, Fig. 1). In males also (Pl. XXV, Fig. 2) the gonads were moderately full with considerable amounts of vesicular tissue in between the follicles. Gametogenesis being still active numerous spermatocytes were found close to the germinal membrane. Welldeveloped spermatozoa were in clusters in the lumina of the follicles as well as in the gonadal ductules. In the months of April and May in some of the oysters the spent gonads of the previous spawning season showed no signs of subsequent recovery, as gametogenesis had apparently not taken place in them (Pl. XXV, Fig. 3). By about the end of June signs of disintegration of the reproductive elements within the follicles were evident. During summer a few oysters in which the sexes were indistinguishable and a few other doubtful hermaphrodites were also obtained. The latter showed eggs and sperms when examined in the freshly made smears, but they are in serial sections found to be of one sex only owing probably to the reason that the hermaphrodite regions were not included in sections.

The percentages of males, females, hermaphrodites (?) and those with indeterminable sex were 59·6, 38·6, 1·7 and nil in 1953 and 53·5, 39·8, 3·8 and 2·8 in 1954. It may thus be seen that the percentage of males for the season as a whole was very much higher than that of the females (Text-Fig. 1). In the individual months also the numbers of males exceeded those of the females except in May 1954 (Table II and Text-Fig. 1) where the proportions of sexes were in the reverse order due probably to defective sampling, the total number examined for the said month being one half of that of the usual samples.

GONADAL CONDITION OF OYSTERS DURING THE PRE-MONSOON MONTHS

The disintegration of the reproductive elements which had just commenced towards the close of the previous season became remarkably rapid in the month of July so that by about August the percentage of oysters in which the sexes were indistinguishable had considerably increased (Table II and Text-Fig. 1). In these oysters the follicles and the gonadal ductules were observed to shrink considerably with no reproductive elements in them but only the vesicular cells (Pl. XXV, Fig. 6). There was also enormous

development of the general vesicular tissue between the mantle and the digestive tract.

The vesicular tissue cells surrounding the follicles are usually large, inflated and bladder-like with hyaline cytoplasm, but some of them close to the follicular walls and the walls of the ductules are much condensed in size, amœboid in form with granular cytoplasm and take up a phagocytic function. The latter infiltrating through the walls of the follicles accumulate in large numbers within the lumina. Their purpose is to devour and grow at the expense of the residual reproductive elements. As a result of these changes the follicles gradually shrink and the vesicular connective tissue grows to fill the interfollicular spaces. The successive histological changes in the gonads of the female oysters during the season are as in Pl. XXV, Figs. 4 and 5. The absorption of unspawned sperms is exactly similar to that of the unspawned eggs. At a stage when all the residual ova or sperms are completely absorbed, the oysters pass into a phase in which the sex is indeterminable.

Oysters in which the sex was indistinguishable were met with in most of the months but their percentages were the highest in the pre-monsoon and the post-monsoon periods. When reorganisation of the gonadal follicles took place in the following months it was not unlikely that oysters of indeterminable sex at least some, though not all, changed their sex, as indicated by the fluctuations in the percentages of different sexes in the samples examined before and after the period.

In the pre-monsoon months of July and August (1953), very clear hermaphrodite individuals were obtained, showing well developed ova and motile spermatozoa in fresh preparations and also serial sections prepared for microscopial examination. In the sections of one oyster (Pl. XXVI, Fig. 7) the gonadal follicles and ductules close to the periphery contained large and ripe ova and oogonia and developing ova of small size in connection with the germinal epithelium. In the deeper regions the ova were of gradually diminishing sizes. The germinal epithelium was actively proliferating fresh oogonia in all the follicles. The lumina were almost packed with well developed spermatazoa but there were no spermatocytes close to the germinal epithelium. In another oyster (Pl. XXVI, Fig. 8) the formation of the ova having taken place to a greater extent than in the preceding one, there were well-developed ova not only in the peripheral regions but also deeper down. The sperms were either altogether absent as in the follicles of top layers or very sparse deeper down. The active proliferation of the

female sex cells and the entire absence of fresh spermatocytes in these oysters showed that the change of sex was from male to female.

The rare occurrence of individuals with reproductive elements of both sexes is an indication that hermaphroditism is not a regular feature. As the germinal epithelium has been observed to stop proliferating components of one sex and giving rise to those of the other sex, hermaphroditism is to be regarded as a purely transitional phase.

Gametogenic activity commenced in males (Pl. XXVI, Fig. 9) by about the end of August and in the females (Pl. XXVI, Fig. 10) a little later by the beginning of September. It reached its peak in both sexes towards the end of September resulting in the gonadal follicles being full with the ripe reproductive elements (Pl. XXVII, Figs. 11 and 12).

The percentages of males, females, hermaphrodites and the indeterminates were represented in the pre-monsoon by 37·8, 54·6, 1·5 and 5·8 in 1953 and 41·7, 55·7, nil and 2·5 in 1954 respectively. The percentage of females was thus higher than that of the males.

GONADAL CONDITION OF OYSTERS DURING THE MONSOON MONTHS

In the beginning of this period the gonads of both the male and female oysters were full with the follicles enlarged and packed with ripe reproductive elements. The interfollicular vesicular tissue as well as the connective tissue between the gonadal layer and the gut were reduced to the barest minimum. In some of the oysters gametogenic activity was still in progress throughout November and December as could be seen from fresh reproductive cells being continuously budded off from the germinal epithelium. About the first week of November in both the years there was spawning as evidenced by the occurrence of a few partially spent ones in which the gonadal follicles had shrunk and the vesicular tissue surrounding them had enlarged in bulk, with groups of condensed connective tissue cells scattered here and there. Within the follicles and the ductules of the females or males there were unspawned eggs or sperms along with a good amount of condensed connective tissue cells (Pl. XXVII, Fig. 13). Samples collected subsequently during the monsoon showed increasing numbers of partially or fully spent oysters, the latter having fewer reproductive elements and greater amount of vesicular tissue and condensed connective tissue. Spawning reached its peak in December when most of the oysters were found fully spent. A small number of hermaphrodite individuals was obtained in the early monsoon period showing a change of sex from male to female (Pl. XXVII, Fig. 14) as in the pre-monsoon period. The percentages of males, females, hermaphrodites and the indeterminates were 44·9, 53·6, 0·3 and 1·2 in 1953 and 45·9, 48·5,

1·8 and 3·6 in 1954 respectively. During the spawning period it may thus be seen that the percentage of females was found to be a little higher than that of the males.

Gonadal Condition of Oysters During the Post-Monsoon Months

In the months of January and February for a second time in the annual cycle there was disintegration of the unspawned reproductive elements, very similar to that observed in the pre-monsoon period resulting in a large percentage of oysters in which the sex was indistinct. A few were changing their sex from female to male (Pl. XXVII, Fig. 15), as shown by the presence of some large eggs, in the lumina and numerous spermatogonia and spermatocytes close to the germinal epithelium of the follicles and of the ductules. Reorganisation of the gonads in oysters commenced by the beginning of March with a very rapid proliferation of oogonia (Pl. XXVII, Fig. 16) in some and spermatogonia in others, as a result of which the follicles were found to spread and the vesicular connective tissue to diminish, leading ultimately to the condition described in the early summer period (Pl. XXV, Figs. 1 and 2). The percentages of males, females, hermaphrodites and the indeterminates were 50·9, 42·5, 1·3 and 5·3 in 1954. The data for 1953 and for 1955 were incomplete for the post-monsoon season. In general the percentage of males in the samples was higher than that of the females (Text-Fig. 1 and Table II). The presence of a very large number of oysters in which the sex remained quite indistinguishable in the month of February of both the years 1954 and 1955 was remarkable.

Occurrence of Mature Oysters in Different Months in the Annual Cycle

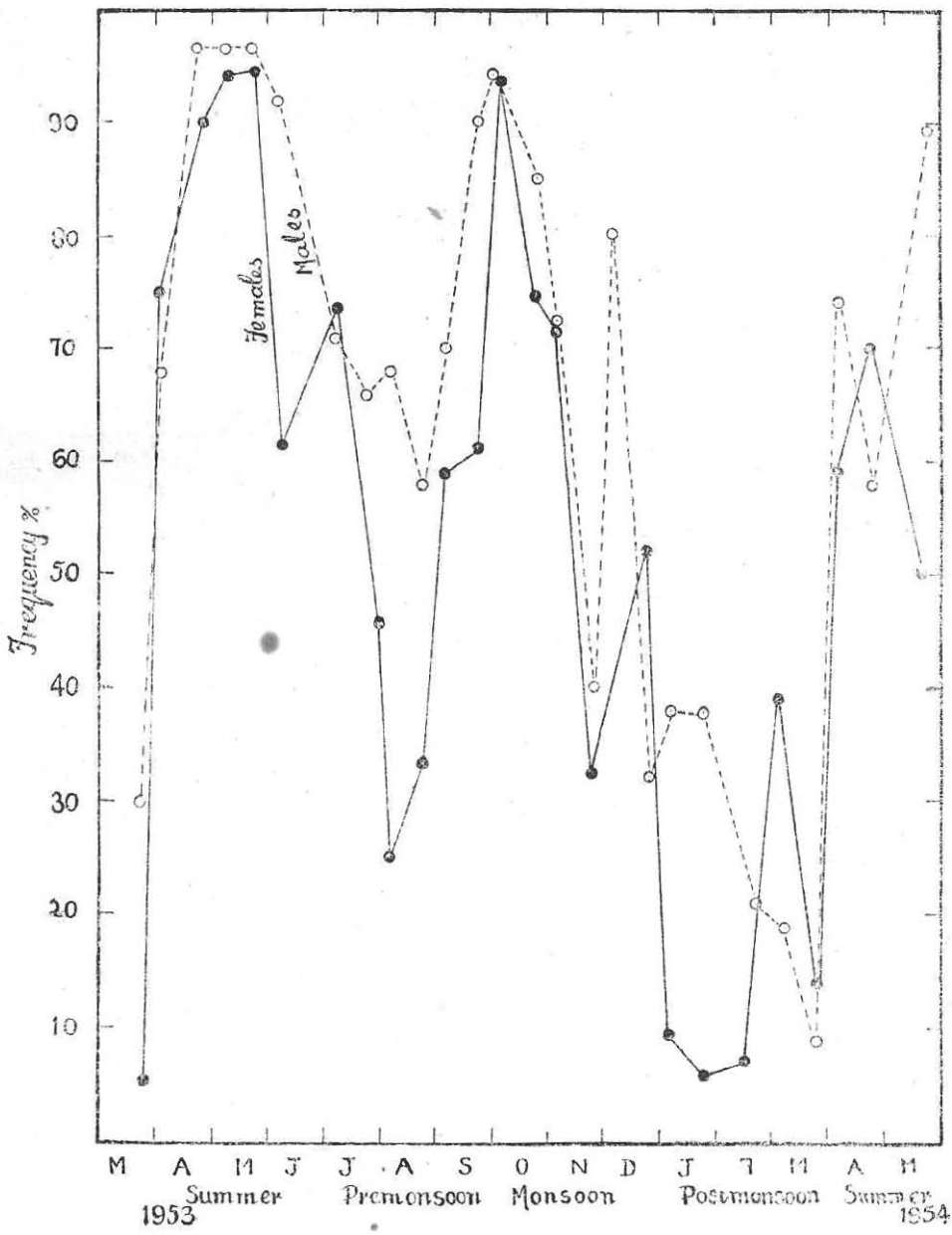
The percentages of fully ripe males or females out of the total numbers of each sex examined in the fortnightly samples for the period of March 1953 to May 1954 are shown in Table III and Text-Fig. 2. Smaller or larger numbers of fully ripe oysters of both sexes occurred in all months of the year, although their percentages were the highest in the periods of April-May and September-October, and lowest in July-August and January-February. Following the period of peak occurrence of ripe ones of both the sexes in April and May, there was disintegration of the reproductive elements with the result that the numbers of the mature ones fell very low by about July-August. Immediately after the second peak of October, there was profuse spawning in both the sexes, as a consequence of which the numbers of mature ones considerably decreased by about November. Gametogenesis was at its highest in March-April and about September-October in the periods preceding the peak occurrence of mature individuals.

TABLE III

Showing Percentages of Ripe Males and Females out of the Total Numbers of the Particular Sexes in Different Samples Examined from March 1953 to May 1954

Date	Season	Percentage of ripe ones out of the total number of males	Percentage of ripe ones out of the total number of females
22- 3-1953	Postmonsoon	30·0	5·2
7- 4-1953	Summer	68·1	75·0
22- 4-1953		96·6	90·0
7- 5-1953		96·6	94·1
21- 5-1953		96·4	94·7
8- 6-1953		92·3	62·5
7- 7-1953	Premonsoon	71·4	73·6
22- 7-1953		66·6	45·5
7- 8-1953		68·0	25·0
25- 8-1953		58·8	33·3
7- 9-1953		70·5	59·3
22- 9-1953		90·9	61·1
8-10-1953	Monsoon	94·6	93·5
21-10-1953		85·0	74·9
9-11-1953		72·7	66·6
25-11-1953		40·0	32·2
7-12-1953		80·0	46·6
28-12-1953		32·3	52·1
5- 1-1954	Postmonsoon	38·2	9·5
27- 1-1954		37·8	6·4
17- 2-1954		20·9	7·0
4- 3-1954		19·6	39·1
26- 3-1954		9·1	14·8
8- 4-1954	Summer	74·1	59·1
22- 4-1954		58·3	70·0
24- 5-1954		89·4	50·0

There was a sharp increase in the numbers of mature ones in December as could be seen from the Fig. 2 and this was due to the fact that the gametogenic activity was being continued through the period of spawning. The oysters after having spawned once recovered very rapidly to spawn again



TEXT-FIG. 2. Frequencies of fully mature females and males, each expressed as a percentage of the total of that particular sex, in different samples examined from March 1953 to May 1954.

during the breeding season. The reasons for (1) the restricted periods of breeding, (2) the effective spawning of both sexes in November-December and (3) the frequent failure of the same about March-April in the oysters

living under estuarine and backwater conditions have been previously dealt with (Rao, 1951).

SEASONAL FLUCTUATIONS IN THE QUALITY OF OYSTER MEATS

When the gonads of the oysters are ripe the meats are heavy and fit for the table, but when they are partially or fully spent or in a state of recovery the meats are comparatively lighter and are, therefore, not much relished. To ascertain the seasonal fluctuations in the quality of meats in different months the average meat weights and the whole weights of the oysters in the samples have been calculated (Table IV and Text-Fig. 3). The meat weights have been represented as percentages of the whole weights of the oysters as these two measures differed from sample to sample. The data are incomplete for 1953, excepting the months of January and February, complete for the whole year 1954, and available only for January and February in 1955 after which the study was concluded.

In 1953, March and April, the meats were moderately heavy (7·78% to 8·1%) as the oysters were in a state of recovery. In May and June they were heavy (10·5% to 10·9%) owing to the fact that the gonads were full after the gametogenic activity in the preceding months. In July and August there was a fall in their weights (9·8% to 9·3%) due to disintegration and cytolysis of the reproductive elements. In September and October they were full and heavy (10·45% to 10·57%) as gametogenesis had taken place for a second time. In November and December their condition was poor because of spawning.

In 1954, from January to February the meats continued to show poor weights (8·45% to 6·9%) as the period of spawning was followed by one in which there was disintegration and absorption of the residuary reproductive elements. In the rest of the months of observations till February 1955, the trend in seasonal fluctuations of the meat weights is almost the same as for the preceding period, although the values in general were low as compared with those for 1953.

It may thus be seen that the meats are very poor in February in the post-monsoon, July and August in the pre-monsoon and in November in the monsoon periods of the year. They are at their best about May in summer, September in the pre-monsoon and October in the monsoon periods.

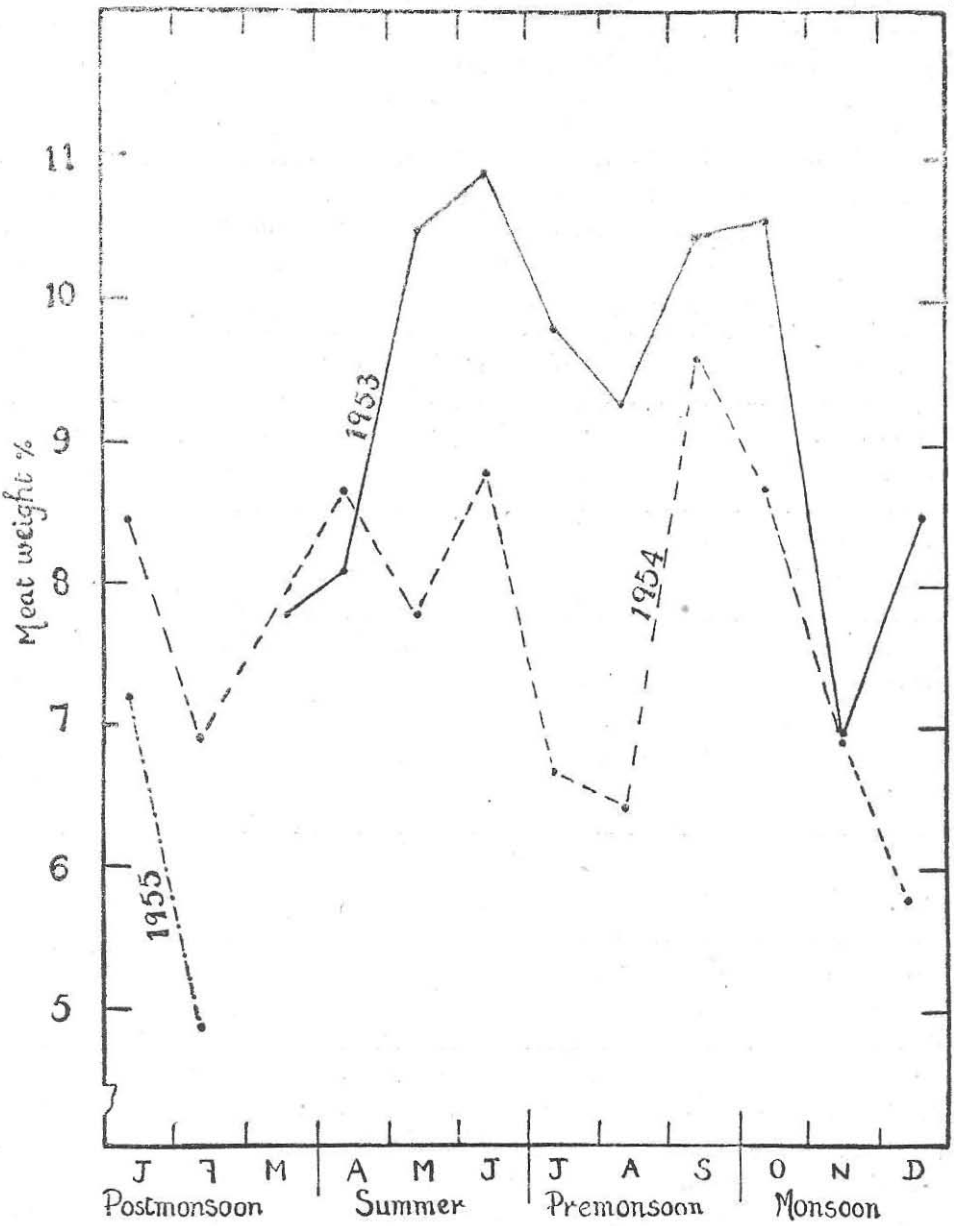
Venkatraman and Chari (1951) have given the percentage edibility of oysters from Ennur in the fortnightly samples examined from 21–10–1949 to 24–12–1950. They observe the percentage of edibility to be very low in July and fairly high in October, with corresponding variation in fat content.

TABLE IV

Showing Percentages of Meat Weights to Whole Weights of Oysters in Samples Examined in Different Months from March 1953 to February 1955

Season	Months		Average weight of oyster (in gm.)	Average weight of meat (in gm.)	Percent. meat weight to the average whole weight
Postmonsoon	March	1953	136·30	10·60	7·78
Summer	April	1953	151·30	12·30	8·13
	May	,,	146·87	15·39	10·48
	June	,,	151·20	16·50	10·91
Premonsoon	July	1953	119·00	11·70	9·83
	August	,,	146·40	13·60	9·29
	September	,,	133·66	13·97	10·45
Monsoon	October	1953	116·84	12·35	10·57
	November	,,	153·10	10·70	6·99
	December	,,	115·00	9·75	8·48
Postmonsoon	January	1954	110·68	9·35	8·45
	February	,,	115·80	8·00	6·91
	March	,,	130·07	10·21	7·85
Summer	April	1954	126·80	10·99	8·67
	May	,,	127·94	9·98	7·80
	June	,,	104·40	9·20	8·81
Premonsoon	July	1954	170·63	11·44	6·70
	August	,,	133·05	8·59	6·46
	September	,,	132·70	12·80	9·65
Monsoon	October	1954	146·94	12·75	8·68
	November	,,	140·66	9·65	6·86
	December	,,	156·40	9·02	5·77
Postmonsoon	January	1955	142·79	10·28	7·20
	February	,,	137·70	6·79	4·93

The low fat content in July is attributed by them to growth of the oyster and the maturation of its gonads and the high fat content in about October to intensive feeding prior to spawning. Careful examination of their data reveals (1) a very high percentage of edibility not only by about October



TEXT-FIG. 3. Averages of meat weights expressed as percentages of the whole weights of oysters examined in different samples in different seasons in each annual cycle in the period from March 1953 to February 1955.

(10·72% in 1949 and 17·36% in 1950) but also about the third week of Apri (10·52% in 1949), and (2) very low percentage of the same not only in July

(5·03%) but also in March (5·93%). The trend of fluctuations recorded by them has an indication that the oysters attain ripeness and fullness of their gonads twice a year as is observed here.

General Considerations

Seasonal Cycle.—In respect of a brackish water or estuarine environment, where temperature, salinity and other physico-chemical conditions vary widely with cyclic regularity, it is possible to define seasons in an annual cycle although such an attempt has not been made by earlier workers as far as the present writer is aware. Summer is characterised by high temperatures, high salinities and absence of communication of the backwaters with the sea, the bar being closed; pre-monsoon by moderately high temperatures, gradual fall in salinities to values which remain very low for a prolonged period extending over a month or so and absence of tidal influence owing to the bar remaining closed; monsoon by fall in temperatures and marked fluctuations in salinities due to the influence of tides as the bar remains open, and the post-monsoon by a moderate increase in temperature and salinities with the tidal flow almost all through the season on account of the bar remaining open. The physiological behaviour of the oyster, *Ostrea* (*Crassostrea*) *madrasensis* living under these conditions seems to parallel the sequence of seasonal changes as revealed by its gonadal condition already described.

Gametogenic Activity, Spawning and Setting.—During the period of the present studies extending over two years it has been found that the gametogenic activity in the oysters begins twice in an annual cycle, *viz.*, by about March and September, and that these periods are preceded by a phase in which the gonadal condition is indifferent and the sexes are indistinguishable in most of them. Gametogenesis starting by about March has but a short duration of about a month and that commencing about September lasts comparatively longer till December. As may be seen from the preceding account of the seasonal changes in the histological structure and ripeness of the gonads attained in about April has not been followed by spawning in 1953 and 1954, whereas a similar condition reached in about October has resulted in successful breeding of the oysters in the locality. Whether spawning, larval development and setting in the backwaters should take place or not in any of the two periods succeeding gametogenic activity seems to be determined by certain factors, among which salinity, temperature and other favourable conditions arising as a consequence of the bar remaining open or closed admitting sea-water into the estuary or cutting off its connection with the sea seem to play an important role (Rao, 1951).

Under temperate conditions a close relationship exists between water temperatures and gonadal condition of oysters. They attain ripeness and discharge their spawn in summer, but pass into a state of quiescence in winter with the gonadal follicles considerably shrunk. Loosanoff and Davis (1952) have taken the hibernating oysters, *O.* (*Cr.*) *virginica* of the Long Island Sound, North Atlantic Coast, from their winter environment and subjected them to different but constant temperatures under laboratory conditions so as to condition them to start and complete gametogenesis and attain physiological state of ripeness at which they can spawn. It has been found in their experiments that at 15° C. both sexes could be induced to spawn by the 35th day, at 20° C. by the 13th day, at 25° C. on the 7th day and at 30° C. on the 5th day. These observations are in variance with those of Nelson (1921 and 1928) who in respect of the same species, *O.* (*Cr.*) *virginica* of the Barnegat Bay concludes that if the water temperature does not reach 20° C. to 21° C. and remain there at that level for some time they will not spawn at all. The reason offered by Loosanoff and Davis (1952) for the difference in the breeding temperature requirements in the northern and southern oysters is that they constitute physiologically different groups or races, a view which finds support in the earlier observations of Stauber (1950) who recognises at least three physiological races of *O.* (*Cr.*) *virginica.* The observations of the earlier workers on the effects of salinity, temperature and other factors on the spawning, larval development and setting of different oysters have been briefly discussed by Rao (1951).

Nothing is known of the minimum temperature requirements for gametogenesis and spawning in the Indian backwater oyster. The water temperatures at Ennur being always high, as is the case with all tropical waters, the fluctuations during the course of a year vary within a narrow range of 25·7° C. (minimum) and 33·0° C. (maximum) so that there is no period comparable to winter. There is no evidence to show that water temperatures at the lower levels of this range inhibit gametogenic activity and spawning.

Hornell's (1910 and 1922) observations show that there is a definite periodicity in the breeding of the oysters in the east coast backwaters. It has been observed (Rao, 1951) that in a marine environment as that of the Madras harbour, this species breeds continuously all through the year with intense sexual activity in two periods of which one seems to be induced by high summer temperatures in about March-April and the other by fall in salinity in about November-December on account of the rains of the north-east monsoon. These two periods of intense sexual activity in a marine

environment correspond more or less to the two restricted periods of breeding in the oysters living in backwaters or estuaries. The occurrence of gametogenic activity twice during the course of the year and the periodicity of spawning in Ennur oysters are in agreement with the previous findings on Adyar oysters.

The observations of Rao and Nayar (1956) on the periodicity of spat setting of this oyster from November onwards in both the years 1953 and 1954 confirm those of Rao (1951) who finds that in Adyar backwater spatfalls occur only during the periods when the bar remains open admitting sea-water into the estuary. Chidambaram and Dinamani as reported by Devanesan and Chacko (1955) have recorded absence of spatfall in Ennur backwaters from 26th January 1948 to 17th November 1949 during which the bar has remained closed and the occurrence of the same in the succeeding period, *i.e.*, from 18th November 1949 to 18th June 1950, when the backwaters has been in communication with the sea as a result of the bar being open. They are of the opinion that a sudden increase in salinity consequent on the opening of the bar alone cannot be considered responsible for initiating spawning and setting, for changes in salinity being supplementary to other "congenial conditions produced by the flux and reflux between the backwater and the sea". The experimental observations of Rao (1951) on the setting of the oyster larvæ lead to the conclusion that apart from salinity the presence of some suitable chemical or other unascertained factor or factors in the sea-water promotes spatfall. Hence, a period when the bar remains open unduly long results in spatfalls occurring for a longer duration. The occurrence of individuals with ripe gonads in smaller or larger numbers in every sample noticed by Devanesan and Chacko (1955) has led them to presume that the species breeds all-round the year. The study of an organism apart from its environment presents but an incomplete picture of its physiological activities. The breeding behaviour of the oyster is a function dependent upon the environmental conditions favourable or otherwise. The mere presence of ripe individuals in varying numbers all through the year, noticed by the writer in the present investigations as well as by other workers in the field, indicates no certainty of the species spawning at any part of the year. In the light of the experimental observations of Hornell (1910), Rao (1951), Dinamani and Chidambaram (*loc. cit.*) and Rao and Nayar (1956) breeding of this oyster in backwaters is not continuous, but restricted to a period or periods when favourable environmental conditions prevail during the course of an year.

Sex Reversal.—For a long time it was considered that the larviparous oysters were monœcious and the oviparous ones diœcious. In recognition of these two distinct types of oysters with differences in morphological and physiological characteristics Orton (1928) has proposed the division of the genus '*Ostrea*' into two new genera or sub-genera, *viz.*, *Monœciostrea* and *Diœciostrea*. Nevertheless the fact now known that both groups do change their sex, the sexuality of one differs considerably in certain respects from that of the other. The term 'ambisexuality' is used in preference to 'hermaphroditism' or 'bisexuality' to denote the condition where both male and female sexual cells are found in the gonad of an individual. The type of sexuality met with in the larviparous oysters is known as 'ambisexuality or monœcism with rhythmical consecutive sexuality' and that in the oviparous oysters as 'ambisexuality or monœcism with alternative sexuality' (Coe, 1943). The adult sexual phases only and not the primary sexual phases of the oviparous oyster, *O.* (*Cr.*) *madrasensis* are dealt with in the present investigation.

In the type "ambisexuality or monœcism with rhythmical consecutive sexuality" as in the larviparous oyster, *Ostrea edulis*, each adult annually completes one male phase and one female phase; some individuals functioning as either male or female in the early spawning season change their sex later; spermatogenesis occurs even before the larvæ of the earlier female phase have left the mantle cavity and the proportions of the two types of sexual cells in the gonads vary during the entire reproductive season with gradations from 'pure male' to 'pure female' phases (Orton, 1927, 1927 *a*, 1933; Cole, 1941; Coe, 1943). The sequence of sexual changes in other larviparous species as *Ostrea lurida* and *Ostrea equestris* is very similar to that in *O. edulis* (Coe, 1932 *a* and 1934; Gutsell, 1926). Sometimes in the first year of their life the oysters complete three and in the later years one or two sexual phases. Besides individuals with regularly alternating sexuality there are also a few 'true males' which retain the male phase indefinitely (Coe, 1932, 1934, 1943; Gutsell, 1926).

In the type of 'ambisexuality or monœcism with alternative sexuality', as in the oviparous ones like the American oyster, *O.* (*Cr.*) *virginica* and the Pacific oyster, *O.* (*Cr.*) *gigas* the adults function as separate sexes in any one spawning season, even though it is not possible to foresee which of the two sexual phases an individual oyster may take at the next breeding season. Change in sexuality takes place in between two spawning periods, and the extent to which it occurs during a particular year or season differs with the species (Amemiya, 1929 *a*, 1929 *b* and 1929 *c*; Coe, 1943; Needler, 1932;

and Galtsoff, 1937). Burkenroad (1937) calls this type of sexuality 'a laternational hermaphroditism' and has worked out a statistical method of determining the extent of reversal correlable with the initial sex ratio in a population of *O.* (*Cr.*) *virginica.* Other oviparous oysters like the Australian commercial oyster, *O.* (*Cr.*) *commercialis* (Roughley, 1923), the Indian rock oyster, *O.* (*Cr.*) *cucullata* (Awati and Rai, 1931), the Portuguese oyster *O.* (*Cr.*) *angulata** (Amemiya, 1925), and the Indian backwater oyster, *O.* (*Cr.*) *madrasensis* (Rao, 1953; Devanesan and Chacko, 1955) are also known to undergo sex reversal.

The reason for reversal of sex are not clearly understood. There seems to be in the hereditary mechanism of the oyster a tendency to change its sex and it is activated by the conditions in the environment. The primary gonad has undifferentiated gonia capable of developing into a male or female phase. In a majority of cases the early sexual phase is male, although occasionally the female sexual phase also may occur in a small percentage of the population. After the adults spawn and their residuary reproductive elements, either sperms or ova, are absorbed, the gonadal follicles shrink considerably and pass into a phase of sexual immaturity. Further development on male or female lines appears to be influenced by environmental conditions. Oysters growing comparatively under more favourable conditions have a larger proportion of females than males (Coe, 1936, 1938). Oysters in which their mode of nutrition is effected by some means as the excision of gills in *O.* (*Cr.*) *gigas* (Amemiya, 1935) or the presence of the commensal pea-crab, *Pinnotheres*, in *O.* (*Cr.*) *cucullata* (Awati and Rai, 1931) or due to overcrowding in clusters, too much cramped for normal growth in *O.* (*Cr.*) *virginica* (Burkenroad, 1931) show a preponderence of males.

It may be recalled that there is an indication of reversal of sex in the adults of *O.* (*Cr.*) *madrasensis* following the indifferent phase of the gonadal condition as revealed by the fluctuations in the percentages of the different sexes in samples examined before and after this phase. The occurrence of a few transitional hermaphrodites as already described is yet a clearer evidence of change of sex taking place in the species. The preponderance of females in the samples of premonsoon and monsoon periods is accompanied by a few transitional forms changing from male to female phase and that of males in the later part of the postmonsoon and throughout summer by similar forms changing from female to male.

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* Synonymous with *Gryphæa angulata* Lmk.

How far the measurable abiotic environmental factors like pH, temperature and salinity induce development of the gonad on male or female lines it is difficult to assess. Fluctuations in pH vary only within a narrow range of 8·1 to 8·6 during the period of observations and these seem to have no relationship with the histological changes in the oyster's gonads observed in the seasonal cycle. In the period of gametogenic activity commencing by about March and resulting in a greater number of males than females, it may be observed from Table I and Fig. 1 that both the water temperatures and the salinities are high and are still on the increase to yet higher levels in the following months of the summer. During the period of a similar activity leading to an increase in the percentage of females, *i.e.*, about September to November the temperatures are low to moderately high and the salinities show a rapid downward trend until they attain the lowest levels recorded for the years 1953 and 1954.

SUMMARY

Seasonal gonadal changes in *Ostrea* (*Crassostrea*) *madrasensis* Preston from Ennur backwater have been studied during March 1953 to February 1955.

1. The annual cycle has been divided into four periods, postmonsoon—January to March, summer—April to June, premonsoon—July to September, and monsoon—October to December.

2. In the postmonsoon period, the salinities and temperatures are low in the beginning, but they gradually increase later to moderate levels. The backwater is subject to tidal influence. In the gonads of oysters there is disintegration of unspawned eggs or sperms with the result that a large percentage of the population passes into an indifferent phase of gonadal condition. There is reversal of sex in a few individuals from female to male. The percentage of males is higher than that of the females.

3. In summer, water temperatures and the salinities are the highest, and tidal effects are usually absent during the entire period. Gonads of oysters of both sexes are moderately full. Gametogenesis is still in progress in the beginning of the period. There are more males than females.

4. In the premonsoon, the water temperatures are moderately high and the salinities which are high in the beginning show a gradual decline later, to levels which are extremely low. The backwater is not subject to the influence of tides. A very rapid disintegration of the reproductive elements sets in at the beginning, but gametogenesis commences for the second time during the year in the latter part of the period. There is reversal of

sex from male to female. The oyster population shows more females than males.

5. During the monsoon the water temperatures are the lowest and fluctuations in salinities are very marked due to the ebb and flow of tides. The gonadal condition is very good in the beginning, being full with ripe reproductive elements in both sexes. As a consequence of spawning, a number of oysters with poor gonads, partially or fully spent, occur during November and December. Samples show more females than males as in the preceding period.

6. Smaller or larger numbers of fully ripe oysters of both sexes occur all through the year. Their percentages are the highest in April–May and September–October, following the periods of highest gametogenic activity. They are the lowest in July–August and January–February due to disintegration of reproductive elements in the periods preceding them. Spawning is indicated by a sharp fall in the percentages of the ripe oysters of both sexes in November. An increase in the number of mature ones again in December is due to gametogenic activity being continued through the period of spawning.

7. A study of the relationship of the meat weights to the whole weights of the oysters shows that the meats are poor in February in the postmonsoon, July and August in the premonsoon and in November in the monsoon period. They are at their best about May in summer, September in the premonsoon and October in the monsoon. The preponderance of female oysters in premonsoon and monsoon is accompanied by transitional forms changing from male to female and that of males in the postmonsoon and summer by similar forms changing from female to male. The exact causes for reversal of sex are not fully understood.

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EXPLANATION OF PLATES

PLATE XXV

FIG. 1. Gonad of a ripe female oyster in April (summer) with the follicles and ductules moderately full with mature reproductive elements, × 95.

FIG. 2. Gonad of a male oyster in April (summer) in which gametogenic activity is still in progress as revealed by a good number of spermatocytes besides fully ripe spermatazoa, × 95.

FIG. 3. Gonad of a female oyster in May (summer) showing no indication of gametogenesis after the previous spawning period, × 95.

FIG. 4. Gonad of a female oyster in June (summer). Infiltration of the condensed connective tissue cells for absorption of the residual reproductive elements, × 450.

FIG. 5. Gonad of a female oyster in July (premonsoon) with follicles very much shrunk due to absorption of a good deal of the residual ova, × 95.

FIG. 6. Gonad of an oyster in the indifferent phase in August (premonsoon) after the complete absorption of the residual reproductive elements. The ductules and the follicles are very much shrunk with only a few condensed connective tissue cells and the interfollicular vesicular tissue is considerably enlarged, × 95.

PLATE XXVI

FIG. 7. Gonad of a transitional hermaphrodite in July (premonsoon) showing sex reversal from male to female with ova of different sizes along the follicular walls and spermatazoa in culsters in the lumina. Upper follicles show larger ova, × 310.

FIG. 8. Gonad of a transitional hermaphrodite in July (premonsoon) showing sex reversal from male to female. A more advanced stage than in Fig. 7. Well-developed ova in all the follicles but spermatazoa are sparse, × 95.

FIG. 9. Gonad of male oyster late in August (premonsoon) showing active gametogenesis, × 450.

FIG. 10. Gonad of female oyster late in August (premonsoon) showing active proliferation of oogonia, × 450.

PLATE XXVII

FIG. 11. Gonad of a male oyster in September (late in premonsoon) showing fully ripe condition, × 95.

FIG. 12. Gonad of a female oyster in October (monsoon) showing fully ripe condition, × 130.

FIG. 13. Gonad of a partially spawned female oyster in November (monsoon), × 95.

FIG. 14. Gonad of a transitional hermaphrodite oyster changing from male to female in November (monsoon), × 130.

FIG. 15. Gonad of a transitional hermaphrodite oyster changing from female to male in February (postmonsoon), × 95.

FIG. 16. Gonad of a female oyster showing active proliferation of oogonia in March (postmonsoon), × 95.

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