

**ON THE SEASONAL GONADAL CHANGES AND SPAWNING IN THE
ADULT OYSTER *CRASSOSTREA GRYPHOIDES* (SCHLOTHEIM)**

By V. S. DURVE*

Department of Zoology, Institute of Science, Bombay

INTRODUCTION

THE knowledge of sexuality, seasonal gonadal changes and spawning of an animal is of vital importance in any biological investigation. A sound knowledge of the state of the gonads of oysters in different months and their spawning, is essential to know the time of laying cultch and oyster marketing.

Studies on the sexuality, seasonal gonadal changes and spawning in oysters have been made by several authors *viz.*, Amemiya (1925, 1929 *a, b & c*), Coe (1932 *a & b*, 1934), Roughley (1933), Orton (1927 *a & b*, 1933), Galtsoff (1937, 1938 *a, b* and 1940), Loosanoff (1939, 1942), Cole (1941, 1942) and Egami (1951). In India, similar studies have been carried out by Hornell (1910, 1921), Rao (1951, 1953 and 1956) and Devapesan and Chacko (1955) on the oyster *Crassostrea madrasensis* occurring on the east coast and the southern parts of the west coast of India.

The present work was undertaken with a view to knowing the seasonal gonadal changes and spawning in the edible oyster *Crassostrea gryphoides* which occurs in the backwaters along the west coast of India, north of Malabar and Kanara. The results reported here are based on observations made for a continuous period of 18 months from September 1956 to February 1958.

MATERIAL AND METHODS

The random samples of adult oysters were obtained from an oyster farm near the village Kelwa, about 50 miles north of Bombay. The samples were collected once in a fortnight and in all 2372 oysters were examined for the study. In the season of sexual activity, the samples examined were generally large while during the period of resting, relatively smaller samples were collected.

Linear measurements of the oysters and the weights of their meat were recorded. Cole (1941, 1942) observed that the weight of the oyster is the best measure of the reproductive activity. In view of this, in the present study, the weight of the soft parts of the oyster was taken after preserving the meat individually in 5% sea water formalin for eight days and then blotting it on a filter paper. Proportions of different sexes were noted by the examination of fresh smears. Changes in the histological state of gonads from season to season were studied by microtome sections, stained with Ehrlich's haematoxylin and counterstained with eosin.

* Present address :—Zoological Survey of India, Central Regional Station, Jabalpur.

It was found convenient to divide the year, though somewhat arbitrarily, in the following five seasons in order to find the exact state of gonads in different periods of the year.

March	}	Summer
April		
May		
Mid-June	—	Pre-monsoon
Second half of June	}	Monsoon
July		
August		
September		
October	}	Post-monsoon
Mid-November		
Second half of November	}	Winter
December		
January		
February		

Though the observations were made once in a fortnight during this study, fortnightly data are given of the season of sexual activity. In other months, the data are grouped to represent the monthly observations.

OBSERVATIONS

Following is the sequence of sexual phases during different seasons of the year in the case of the oyster *C. gryphoides*.

Winter (Period of resting phase): (Plate 1, fig. 1)

During November to February, the gonads are in a state of quiescence, and the sexes are indistinguishable and continue to be so till April. The follicles are either absent or very few in number and small in size. Their lumina are obliterated. These follicles are scattered in the form of small islands throughout the vesicular connective tissue, in the area between the body wall and the digestive gland. The genital duct is clearly seen with its lumina completely obliterated by the growth of connective tissue. The germinal epithelium forms a single row along the follicular wall.

The vesicular connective tissue cells are present in large numbers in the area confined between the genital ducts and the digestive gland. These cells are commonly seen surrounding the follicles and thus they fill up the space between them. A few phagocytic cells are also seen scattered in the connective tissue.

Summer and Pre-monsoon (Period of sexual activity): (Plate 1, figs. 2-4 and Plate 2, fig. 7)

From late April or May, the gametogenic activity commences in some oysters and the sexes can be distinguished. The majority of oysters are, however, still in the resting phase. The vesicular connective tissue occupies a considerable amount of space between the follicles, but the germinal epithelium of the follicles shows activity. Follicles enlarge at this stage. In females, young oocytes begin to grow,

extending towards the centres of the follicles. In males also, the anastomosis and proliferation of the follicles is evident. The latter now contain considerable number of primary and secondary spermatocytes and in some cases, even spermatids. Occurrence of fully developed spermatozoa is rare during the early part of summer.

By the beginning of June, oysters attain sexual differentiation, although a few specimens in resting phase are noticed till June end. In this month, the rapid growth of gonadal follicles and their ramification is evident. They are now seen anastomosed from the genital duct to the liver. The amount of vesicular connective tissue is considerably lessened. In the follicles of female oysters, the mature ova make their first appearance, though the oocytes and oogonia are frequently met with. In males, spermatogenesis proceeds at a rapid pace, and in many cases spermatids and spermatozoa are already formed in large numbers.

By the end of June when the monsoon sets in, almost all oysters contain either mature ova or well-developed spermatozoa, with the germinal epithelium of the genital duct showing considerable activity. Thus, by the end of June, all oysters are ready with mature ova or spermatozoa but resting phase oysters are also observed in small numbers.

Monsoon (Period of spawning): (Plate 1, figs. 5-6 and Plate 2, figs. 8-11)

As stated above, in the early monsoon period, all oysters are full with mature ova or spermatozoa. Gonadal sections of these oysters show follicles and genital ducts full of reproductive elements and negligible vesicular connective tissue. This reduction in the connective tissue is probably due to its adsorption by follicles for the development and nourishment of sex cells (Roughley, 1933; Coe and Turner, 1938). Loosanoff (1942) suggests that the nutritive substances in the connective tissue cells are probably diffused through the cellular membrane and are then assimilated by the sex cells. Anastomosing branches of the distended follicles reach the region of the digestive gland and are separated from it by a thin layer of connective tissue. In females, the follicles contain ripe ova, but oogonia and oocytes are not infrequent. Most of these cells develop later in the season. Similarly, in males, the spermatocytes and spermatids also occur in small numbers.

In July, the spawning commences and partially spawned individuals occur in the samples of the first half of July. In the second half, the majority of individuals are partially spawned and the main spawning period coincides with the lowering of salinity to an optimum level in the backwater. This aspect will be discussed later. The individual oyster does not spawn completely at one time and the spawning is usually extended over a few weeks.

Gonads of the partially spawned individuals are characterised by the shrinkage of the gonadal follicles. In females, the mature ova, though seen in the follicles, are few in number. The germinal epithelium is seen in some individuals with oogonia and oocytes protruding into the follicular cavity. In males, the central parts of the follicles are often seen empty due to the discharge of sperms. The male follicles invariably contain only ripe spermatozoa, though the earlier stages of spermatogenesis are evident in a few individuals. Genital ducts are seen full either with ripe ova or spermatozoa as the case may be. The presence of phagocytic cells in the interfollicular spaces is noticeable. The vesicular connective tissue also increases in volume.

In August and September, the percentage of totally spawned individuals gradually increases and by the end of September, majority of the oysters enter indeterminate stage.

In the advanced stage of spawning, the lumina of follicles contain residual ova or spermatozoa in the state of being cytolysed or adsorbed. Some follicles are even seen empty. In exceptional individuals, the gametogenic activity is seen taking place with oogonia and oocytes actively developing, but their percentage is negligible. In males also, the follicles contain residual spermatozoa in the process of being adsorbed. Here too, the individuals with early stages of spermatogenesis occur and their percentage is 3.44. Males with follicles full of spermatozoa also occur.

Phagocytic cells appear in very large numbers, both inside and outside the follicles. They cytolysed and devour remnants of undischarged residual gametes. This proceeds with a considerable rapidity and soon the follicles become empty. It is, at this stage, that the sex of an individual is indistinguishable. The empty follicles elongate and their walls come in contact with the digestive gland. Majority of oysters enter this indeterminate stage by the first half of October.

During the mid-monsoon *i.e.*, in the latter half of July and the first half of August 1957, a few hermaphrodite individuals were obtained. Hermaphroditism is a rarity and the occurrence of these specimens during the spawning period appears to have considerable significance, as this indicates the possibility of sex-change (Orton 1927a & b; Awati and Rai, 1931; Needler, 1932 and Rao, 1956). In the sections of these oysters (Plate 3, fig. 14), the germinal epithelium is seen proliferating fresh oogonia in all the follicles and the lumina are almost packed with spermatozoa. Primary or secondary spermatocytes are not seen. As the germinal epithelium has stopped proliferating elements of one sex and begun giving rise to those of the other, the hermaphroditism in the oyster *C. gryphoides* could be regarded as a purely transitional phase in the sex-change which may thus be from male to female during the monsoon months of July and August.

Post-monsoon (Period of recovery): (Plate 2, fig. 12 and Plate 3, fig. 13)

During the post-monsoon period, individuals of both the sexes enter indeterminate stage after complete spawning. The follicles are empty and many a time with phagocytic cells inside their lumina. Follicular walls rapidly approach each other and in many cases, the follicles are completely obliterated. The vesicular connective tissue is very thin and studded with phagocytic cells. The sexes at this stage become indistinguishable and with the approach of winter, the vesicular connective tissue develops rapidly and totally obliterates the follicles and the genital ducts. With their gonads replaced by the heavily thickened connective tissue, the oysters assume a healthy look with a cream colour and hereafter remain indistinguishable in sex till the following May. Table 1 shows the percentage frequency of different sexes in different months and seasons during the entire period of study.

To know the spawning in oysters, seven arbitrary stages were formed based on the general appearance and the state of gonads, as determined by the visual inspection and fresh gonad smears. These stages are as below:

Stage 1—Fully ripe : Cream colour.

Stage 2—Slightly spawned : With brownish tint.

Stage 3—Partially spawned : Brown colour, reproductive elements in fair quantity.

Stage 4—Completely spawned : With relict ova or spermatozoa, brown colour, watery appearance, transparent mantle.

†Stage 5—Sexes indistinguishable : Oyster watery with transparent mantle, no gonadal tissue visible, colour brown.

†Stage 6—Sexes indistinguishable : Slight development of the vesicular connective tissue, cream tint.

†Stage 7—Sexes indistinguishable : Considerable development of the vesicular connective tissue. Mantle cream and opaque, healthy appearance.

TABLE I

The percentage of males, females, hermaphrodites and those of indeterminate sex of *C. gryphoides* in different months during the period, September 1956 to February 1958.

Season	Month	No. of specimens examined	Males %	Females %	Indeterminables %	Hermaphrodites %
Monsoon	.. Sept.* 1956	90	40.00	40.00	20.00	—
	**	80	17.50	30.00	52.49	—
Post-monsoon	Oct.*	100	16.00	31.00	53.00	—
	**	100	12.00	5.00	82.00	—
	Nov.*	100	6.00	—	96.00	—
Winter	.. Dec.**	74	—	—	100.00	—
	Jan. 1957	170	1.76	—	98.23	—
	Feb.	125	2.40	—	97.60	—
	Feb.	90	—	—	100.00	—
Summer	.. March	70	2.86	—	97.14	—
	April	60	13.32	—	86.68	—
	May*	90	44.44	17.78	37.78	—
	**	96	35.42	37.51	27.08	—
Pre-monsoon	June*	71	39.44	54.93	5.63	—
Monsoon	.. July**	63	33.34	63.51	3.17	—
	July*	100	38.00	62.00	—	—
	**	136	44.12	54.42	—	1.47
	August*	75	38.67	57.33	2.67	1.33
	**	102	33.33	49.01	17.64	—
	Sept.*	75	34.66	30.66	34.66	—
	**	75	24.00	1.33	74.66	—
Post-monsoon	Oct.*	75	16.00	1.33	82.66	—
	**	118	3.38	—	96.61	—
	Nov.	58	—	—	100.00	—
Winter	.. Dec.	60	—	—	100.00	—
	Jan. 1958	59	—	—	100.00	—
	Feb.	60	—	—	100.00	—
Total		2372				

* First half of the month.

** Second half of the month.

† Stages indicating recovery of oysters from spawning and their entry into the indeterminate stage.

Tables 2, 3 and 4 show the percentage composition of oysters in different spawning stages according to sex, during the period of observation. From these, it is evident that the first slightly spawned individuals occur in the samples in the first half of July, showing the commencement of spawning. The second half of July shows considerable spawning, as the individuals in the stages 2 and 3 are in majority. The spawning appears to have been completed by the end of October in the case of males, as the majority of them are seen to be in the 4th stage. In females, spawning seems to start with rapidity as the individuals in 3rd stage occur even in the first half of July. Females seem to discharge their entire spawn by September but spawning seems to have extended till October in 1956.

Seasonal variation in the average weight of oyster meat.

The weight of oyster meat shows variation in accordance with the physiological state of the oyster. Venkataraman and Chari (1951) and Rao (1956) observed the seasonal variation in the percentage edibility and the percentage of meat weight to the whole weight respectively. The percentage of meat weight to the whole weight is a more precise way of knowing the state of an oyster, as the whole weight differs from oyster to oyster and sample to sample. However, it was seen during this study, that the variation in the meat weight of oyster was so great that the average weight of meat showed the same trend as would be shown by the percentage weight.

Figs. 1 and 2 show the monthly variation in the average weight of oyster meat in total number of oysters examined and also in the different sexes. In September 1956, the average weights are comparatively higher than those in September 1957. In the subsequent months *i.e.*, from October onwards, the average weights are constantly on the increase primarily due to the recovery of oysters from spawning and the considerable development of the vesicular connective tissue. By December, the oysters are fully recovered and assume cream coloured appearance of the typical healthy oyster. The mantle becomes thick and opaque. As mentioned earlier, oysters during these months are in the stage of resting. The higher values in average weights continue till June. From May onwards, oysters begin developing sex. Low values found in the second half of May and first half of June may either be due to the sampling error or low feeding activity. From July, oysters enter spawning season and accordingly the weights of both the sexes are considerably lowered due to the discharge of reproductive elements. The low weights continue till the end of spawning season when all oysters enter the stage 5 mentioned earlier. At this stage, weights remain low as seen from the values of October. From November onwards, the values are again on increase due to the recovery from spawning and the rapid development of the vesicular connective tissue.

It may be pointed out here that in samples of December 1956, and January 1957, a few fully matured males were found. Being fully matured, they were heavy in weights.

The earlier indication, that females rapidly discharge their spawn and complete their spawning earlier than males is well exemplified by rapid decrease in their average weights as compared to that in males, during the months of August and September, 1957.

Studies on the percentage edibility and the index of condition of the oyster *C. gryphoides* carried out by the author, also support the above inferences (Durve,

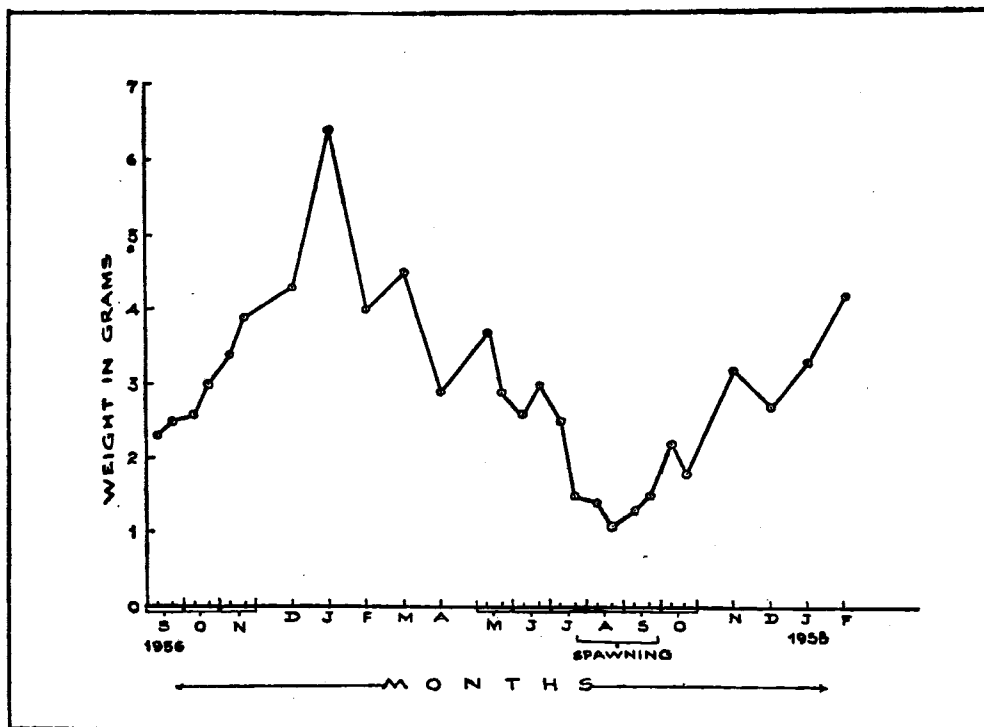


FIG. 1. The monthly variation in the average meat-weight in *C. gryphoides* during the period, September 1956 to February 1958.

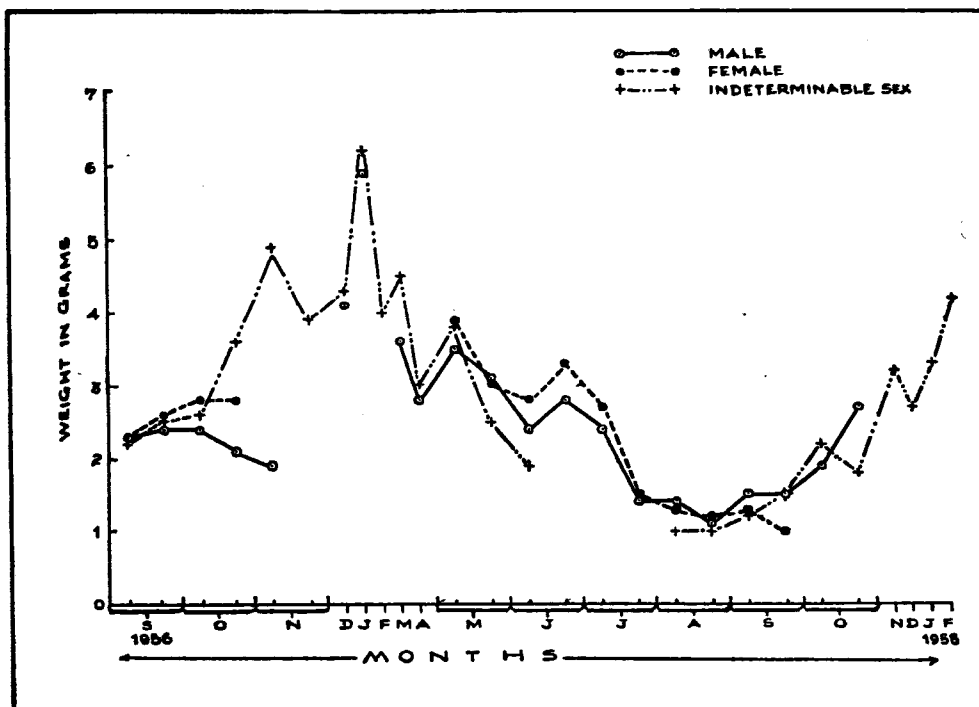


FIG. 2. The monthly variation in the average meat-weights of males, females and those of indeterminate sex during the period, September 1956 to February 1958.

1964a). In this connection, it is interesting to note the observations of Walne (1964) on the fertility of the oyster, *Ostrea edulis*. He found that the spawning has only a moderate effect on the index of condition and the loss of material in

TABLE II

Monthly variations in the percentage composition of Males of *C. gryphoides* in different maturity stages, during the period September 1956 to February 1958.

Season	Month	No. of specimens examined	Stage 1 %	Stage 2 %	Stage 3 %	Stage 4 %
Monsoon	.. Sept. 1956*	36	—	22.22	61.10	16.66
	**	14	—	14.28	35.17	50.00
Post-monsoon	.. Oct.*	16	—	12.50	56.25	31.25
	**	12	—	8.34	16.67	75.00
	Nov.*	6	—	—	—	100.00
Winter	.. **	—	—	—	—	—
	Dec.	3	100.00	—	—	—
	Jan. 1957	3	100.00	—	—	—
Summer	.. Feb.	—	—	—	—	—
	March	2	100.00	—	—	—
	April	8	100.00	—	—	—
	May*	40	100.00	—	—	—
Pre-monsoon	.. **	34	100.00	—	—	—
	June*	28	100.00	—	—	—
Monsoon	.. **	21	100.00	—	—	—
	July*	38	76.31	23.68	—	—
	**	60	6.66	90.01	3.33	—
	August*	29	3.44	10.35	68.96	17.24
	**	34	—	5.88	52.94	41.18
	Sept.*	26	—	—	73.08	26.92
	**	18	—	5.55	44.44	49.99
Post-monsoon	.. Oct.*	12	—	25.00	33.34	41.67
	**	4	—	—	50.00	50.00
Winter	.. Nov.	—	—	—	—	—
	Dec.	—	—	—	—	—
	Jan. 1958	—	—	—	—	—
.. Feb.	—	—	—	—	—	

* First half of the month.

** Second half of the month.

the eggs does not reduce a good condition oyster to a low level. He further opined that improvement in the condition of the oyster increases its fertility. Some what similar results have been obtained by the author (Durve, 1964b) in the case of the clam *Meretrix casta*, wherein it was observed that the spawning did not have an appreciable effect on the percentage edibility of this clam.

GENERAL CONSIDERATIONS

Spawning: Causes of spawning in oysters have been worked out by several authors in different parts of the world. Under temperate conditions the chief spawning stimulus in the case of oysters is the increase in temperature of water (Stafford, 1913; Churchill, 1919; Nelson, 1921; 1928a and b; Prytherch, 1928 and Galtsoff, 1930, 1932). According to these authors, American oysters fail to spawn until the water temperature reaches 20°C. Nelson (*op. cit.*) found that the maturing processes also depend upon the temperature and further observed that the reproductive elements are actually absorbed if the required minimum temperature is not attained by the water. Galtsoff (1930, 1932 and 1938b) however, stated that the female oysters spawn even at low temperature range of 18.6 to 20.5°C. in the presence of male reproductive elements in the water. Loosanoff and Davis (1950) induced mass spawning in *O. virginica* at the temperatures of 15.0 to 15.8°C. and thereby concluded that temperatures prevailing during the period of gonad maturation may determine the temperature at which the first spawning will take place.

Hopkins (1937), Hori (1933) and Coe (1931) found a critical temperature for spawning. Korranga (1957), however, observed that there cannot possibly be any critical temperature for a species as a whole. Smith (1949) indicated that there is no mass spawning as a result of stimulation by temperature but rather a constant release of sex cells in small quantities from maturity of gonads to their exhaustion.

Under tropical conditions of Indian coasts, the water temperature is comparatively high throughout the year and generally does not fall below the optimum requirements of the oysters as in temperate waters. In Kelwa backwater, the range of temperature is 19.4°C. in February to 33.4°C. in May. During the spawning period *i.e.*, from July to September or early October, the range of temperature is 31.2°C. in July to 27.4°C. in September or 31.8°C. in October. In the pre-spawning period, the range is 31.7°C. in April to 33.2°C. in June (Durve and Bal, 1960). This indicates that the temperature may not influence the spawning in *C. gryphoides*. These observations also agree with the findings of Rao (1951) on *O.(C.) madrasensis*.

Prytherch (1928) observed the importance of pH in the spawning of American oysters, which according to him spawn at higher alkalinity. In the present case, it was observed that the pH does not fluctuate appreciably in Kelwa backwater and hence it may not have influence on spawning (Durve and Bal, 1960).

Changes in salinity are not known to be responsible for the stimulation of spawning in American or European oysters. However, Butler (1949) observed inhibition of gametogenesis in *O. virginica* inhabiting low salinity area. Seno Hori and Kusakabe (1926) observed effects of salinity on the development of eggs of the common Japanese oyster. Hornell (1910) recorded the spawning in Madras backwater oyster, synchronizing with the heavy rainfall of the north east monsoon which begins in October. He later suggested (Hornell, 1921) that as the rainy season differs on the two coasts of India, there is a corresponding divergence in the spawning maxima. Rao (1951, 1956) found the optimum salinity requirement of 22.26‰ for the development of eggs under laboratory conditions, and further confirmed this by field observations. He observed that spawning does not occur un-

less the optimum salinity is reached by the influx of rain water or by the evaporation of sea water or by opening of the bar in Ennur backwater.

From a reference to the table of weekly salinities in Kelwa backwater given below, it will be seen that the salinity in the backwater which was high (40.23‰)

Table showing the weekly salinities in the backwater during the period of June to August, 1957

Months	1	2	3	4
June ..	40.23	28.01	39.80	32.57
July ..	28.58	13.15	—	5.10
August ..	3.42	6.98	13.38	15.80

during early June 1957, lowered to 28.58‰ by the first week of July due to the commencement of the monsoon. However, the spawning did not begin at this salinity (Tables 1 and 2). Further, in the second week of July, the salinity dropped to 13.15‰ and the spawning individuals began occurring in the samples. This indicates that the optimum level of salinity required to stimulate spawning may be between 28.58‰ and 13.15‰. It may be added here that as the season advances, oysters may become more responsive to stimulation and spawn even at low salinities than at the beginning of the spawning. This, however, needs verification. Towards the end of July, the entire population was seen actively spawning. This tends to show as indicated above, that the lowering of salinity to an optimum level was influential in bringing about spawning in *C. gryphoides*. Lower salinity prevailed both in the backwater and the sea till August, by when the majority of oysters were in the later stages of spawning. Rao (1951) indicated that besides the attainment of salinity to its optimum level, there may be other unknown environmental factors or the presence of some suitable chemical, influencing the spat-fall in the case of the oyster *O.(C.) madrasensis*. Chidambaram and Dinamani as reported by Devanesan and Chacko (1955) have recorded that changes in salinity alone cannot be responsible for initiating spawning and setting in *O.(C.) madrasensis*. These are supplementary to other congenial conditions produced by the flux and reflex between backwater and the sea.

From Tables 2 and 3 it appears that spawning in females is more related to lower salinity than in males, as the females are observed concluding their spawning earlier than males. Males are seen spawning even till late October or early November, when the salinity increases appreciably. Rao (1951) also observed stray cases of males spawning under high salinity and temperature.

The occurrence of stray males with well developed gonads during the period of resting phase in 1956, is a phenomenon that could not be understood well. It is probable as already pointed out above that, the males are more tolerant to the salinity and temperature variations and hence they continue to spawn for a longer period. It may also be that, the occurrence of these males could be a case of extra-seasonal gonad development, as such males do not occur in the samples of the corresponding period in 1957.

Sex-reversal: Orton (1928) proposed the division of the genus *Ostrea* into two distinct genera or sub-genera viz., *Monoecioostrea* and *Dioecioostrea*, the former including monoecious oysters and the latter dioecious. It is now generally accepted that both these oysters change their sexes. Coe (1943) found that the oviparous oysters function seasonally as separate sexes, although it is impossible to predict during a reproductive season the sexual phase which the individual will assume at

the next. This type of sexuality, he referred to as alternative sexuality as exemplified by *O. (C.) virginica*. This species shows protandry at the first spawning and

TABLE III

Monthly variations in the percentage composition of females of *C. gryphoides* in different maturity stages, during the period, September 1956 to February 1958.

Season	Month	No. of specimens examined	Stage 1 %	Stage 2 %	Stage 3 %	Stage 4 %
Monsoon	.. Sept. 1956	36	—	22.22	33.34	44.44
		24	—	20.83	37.50	41.67
Post-monsoon	.. Oct.*	31	3.22	19.36	32.25	45.15
		5	—	20.00	20.00	60.00
		—	—	—	—	—
Winter	.. **	—	—	—	—	—
		—	—	—	—	—
		—	—	—	—	—
		—	—	—	—	—
Summer	.. March	—	—	—	—	—
		—	—	—	—	—
		16	100.00	—	—	—
		36	100.00	—	—	—
Pre-monsoon	.. June*	39	100.00	—	—	—
Monsoon	.. **	40	100.00	—	—	—
		62	64.50	25.80	9.67	—
	.. **	74	30.00	56.75	13.52	—
		43	—	9.30	62.79	27.90
	.. August*	50	—	—	36.00	64.00
		23	—	—	43.48	56.52
Post-monsoon	.. Oct.*	—	—	—	—	—
		—	—	—	—	—
		—	—	—	—	—
Winter	.. Dec.	—	—	—	—	—
		—	—	—	—	—
		—	—	—	—	—
	.. Jan. 1958	—	—	—	—	—
		—	—	—	—	—
	.. Feb.	—	—	—	—	—

* First half of the month.

** Second half of the month.

a tendency towards the excess of females after the second (Needler, 1936 and Coe, 1938). Protandry and sex-change have also been observed in *O. cucullata (commercialis)* (Roughley, 1933), *O. (C.) angulata* (Amemiya, 1925), the Indian Rock Oyster, *O. (C.) cucullata* (Awati and Rai, 1931) and *O. (C.) madrasensis* (Rao, 1953, 1956 and Devanesen and Chacko, 1955). In oysters, the change in sexuality takes place in between two spawning periods and the extent to which it occurs in a particular year or season differs with the species (Amemiya, 1929a; Needler, 1932; Burkenroad, 1937 and Galtsoff, 1937).

There is an indication of sex-change in *C. gryphoides* because of a gradual fluctuation towards the increase in the percentage of females from the second half of

TABLE IV

Monthly variations in the percentage composition of oysters indeterminate in sex in different recovery stages, during the period, September 1956 to February 1958.

Season	Month	No. of specimens examined	Stage 5 %	Stage 6 %	Stage 7 %
Monsoon	Sept.* 1956	18	100.00	—	—
	**	42	54.76	19.04	26.20
Post-monsoon	Oct.*	53	18.87	50.94	30.18
	**	82	2.43	14.63	82.92
	Nov.*	96	—	5.32	94.67
Winter	**	74	—	—	100.00
	Dec.	167	—	—	100.00
	Jan. 1957	122	—	—	100.00
	Feb.	90	—	—	100.00
Summer	March	68	—	—	100.00
	April	52	—	—	100.00
	May*	34	—	—	100.00
	**	26	—	—	100.00
Pre-monsoon	June*	4	—	—	100.00
Monsoon	**	2	—	—	100.00
	July*	—	—	—	—
	**	—	—	—	—
	August*	2	100.00	—	—
	**	18	100.00	—	—
Post-monsoon	Sept.*	26	73.08	26.92	—
	**	56	25.00	42.85	32.15
	Oct.*	62	3.22	16.12	80.62
Post-monsoon	**	114	3.50	14.03	82.45
	Nov.	58	—	—	100.00
Winter	Dec.	60	—	—	100.00
	Jan. 1958	59	—	—	100.00
	Feb.	60	—	—	100.00

*First half of the month.

**Second half of the month.

May. This fluctuation is appreciable during the monsoon months where there is also the occurrence of a few transitional hermaphrodites (Table 1). This suggests a change of sex from male to female in this oyster during the period of monsoon. Rao (1956) observed sex-change in the oyster *O. (C.) madrasensis* wherein he indicated a change from male to female during pre-monsoon and monsoon periods and from female to male in the post-monsoon period. In the present investigation, though there is an indication of the change of sex from male to female during monsoon, there appears to be little evidence of such a change in the reverse direction in the post-monsoon period. There is, no doubt, increase in the percentage of males

during September and October but this is accompanied by the excessive increase in the percentage of indeterminates. There is also no occurrence of any hermaphrodites showing transition from female to male. However, this aspect needs confirmation.

Causes of sex-change are not clearly understood yet. Coe (1943) postulated that these are hereditary sex factors which modify to produce all grades of ambisexuality (hermaphroditism) from true males to true females. There are also various hereditary physiological time factors that control the periodicities of the alternative sexual phases. Orton (1927b) suggested that the carbohydrate metabolism is predominant in males and protein in females, and the sex-change in oysters is based on the rhythmical changes in this metabolism. Egami (1951) observed change in the chemical composition of oysters in accordance with their morphological sex reversal.

Rao (1956) suggested the possibility of the influence of environmental factors such as temperature and salinity, on the determination of sex in Madras backwater oyster. He evidenced a trend that higher temperature and salinity influence the predominance of males and the lower temperature and salinity influence the predominance of females.

However, in the case of *C. gryphoides* it is observed that there is a predominance of males till early May and then of females. This alternate predominance of either sex is during the period of high salinity and temperature *viz.*, April to June. The predominance of females continues till August when both temperature and salinity appreciably fall (Table 1). In September and October, the males predominate over females and during this period the salinity is higher than the preceding period. This tends to suggest that the fluctuation in the percentages of males and females of *C. gryphoides* may not depend upon the temperature and salinity.

The pH may not have influence on the predominance of either sex in the case of *C. gryphoides*, as it does not fluctuate appreciably in Kelwa water (Durve and Bal, 1960). Similar observation is made by Rao (1956) in the case of *O.(C.) madrasensis* of Ennur estuary.

Coe (1936, 1938) suggested that feeding determines the sex and under favourable conditions females preponderate over males. Amemiya (1935) recorded the preponderance of males in oysters on the removal of their gills and thereby interfering with their feeding. Awati and Rai (1931) found more males in the individuals of *O.(C.) cucullata* harbouring pea-crab. Their observation that pea-crab has something to do with the changes of sex, either by reducing the food supply of the oyster or by bringing about a change in its general metabolism so that the majority of oysters thus inhabited are either males or hermaphrodites, could not be confirmed in the present investigation. Only five oysters, out of hundreds examined during the course of study, were found inhabited by the crab *Pinnotheres* sp. These oysters were males, females and indeterminates but none hermaphrodite. The oysters inhabited by the pea-crabs were of poor quality. This may be due to the interference of pea-crabs in the normal food supply of oysters as indicated by Awati and Rai (1931). Stauber (1945) also observed that the pea-crab retards feeding in oyster by devouring the food collected by the oyster and also the gills of the oyster.

SUMMARY

The seasonal variation in the gonadal condition in the oyster *Crassostrea gryphoides* was studied by fresh smears and histological sections.

It was found that there are three distinct periods of gonadal state in this oyster. From October to April, they are indeterminates; May to June is a period of gonad development. July to September is the period of spawning. There is a certain amount of overlapping in these periods. It was also seen that females conclude their spawning earlier than males. Seasonal variation in the meat weight of this oyster also indicates the gonadal changes and the physiological state of the oyster.

Main spawning stimulus appears to be the sudden lowering of salinity in the backwater due to monsoon. The optimum salinity required to stimulate spawning appears to be between 28.58 and 13.15‰.

There is an indication of sex-change from male to female in this oyster during monsoon period. This aspect is discussed in the light of the available data and literature.

ACKNOWLEDGEMENT

The author wishes to record his thanks to Dr. D. V. Bal, former Director of the Institute of Science, Bombay, for his guidance in this work. He is also grateful to Shri K. Virabhadra Rao of Central Marine Fisheries Research Institute, for critically going through the manuscript and offering valuable suggestions.

REFERENCES

- AMEMIYA, I. 1925. Hermaphroditism of the Portuguese Oyster. *Nature*, 116 : 608.
- . 1929a. A preliminary note on the sexuality of a dioecious oyster, *Ostrea gigas* Thunberg., *Jap. J. Zool.*, 2 : 99-102.
- . 1929b. A consideration upon the sexuality of the Japanese common oyster, *Ostrea gigas* Thunberg. *Suis. gak.*, H.O. 5 : 234-57. English abstract, *Jap. J. Zool.*, 3 : Abs., 3, 1.
- . 1929c. On the sex change of the Japanese common oyster, *Ostrea gigas*, Thunberg. *Proc. Imperial Acad. Sci. Japan*, 5(7) : 284-286.
- . 1935. Effects of gill excision upon the sexual differentiation of the oyster, *Ostrea gigas* Thunberg. *Nippon Gakuzyutu Kyokwai Hokoku.*, 10 : 1023-1026 (Extrait in *Jap. J. Zool.*, 6 : 84-86 (1936).
- AWATI, P. R., AND RAI, H. S. 1931. *Ostrea cucullata*. Indian Zoological Memoir., 88-90.
- BURKENROAD, M. D. 1937. The sex ratio in alterational hermaphrodites, with special reference to the determination of rate of reversal of sexual phase in oviparous oysters. *J. Mar. Res.*, 1 : 75-84.
- BUTLER, P. A. 1949. Gametogenesis in the oyster under conditions of depressed salinity. *Biol. Bull.*, 96 : 263-69.
- CHURCHILL, E. P. 1919. The oyster and the oyster industry of the Atlantic and Gulf coasts. *Rep. U.S. Comm. Fish. Docum.*, U.S. Bur. Fish., 890 : 51 pp.
- COE, W. R. 1931. Sexual rythm in the California oyster (*Ostrea lurida*). *Science*, 74 : 247-249.

- LOE, W. R. 1932a. Sexual phases in the American oyster (*Ostrea virginica*). *Biol. Bull.*, **63** : 419-41.
- . 1932b. Development of the gonads and the sequence of the sexual phases in the California oyster (*Ostrea lurida*) *Bull. Scripps Inst. Oceanogr. Tech. Ser.*, **3** : 119-39.
- . 1934. Alternation of sexuality in oysters. *American Naturalist*, **68** : 236-52.
- . 1936. Sequence of functional sexual phases in *Teredo*. *Biol. Bull.*, **71** : 122-32.
- . 1938. Primary sexual phases in the oviparous oyster (*Ostrea virginica*). *Biol. Bull.*, **74** : 64-75.
- AND TURNER, H. J. 1938. Development of the gonads and gametes in the soft-shell clam (*Mya arenaria*). *J. Morph.*, **62** : 91-111.
- . 1943. Sexual differentiation in Molluscs, I. Pelecypods. *Quart. Rev. Biol.*, **18** : 154-64.
- COLE, H. A. 1941. The fecundity of *Ostrea edulis*. *J. Mar. biol. Ass. U.K.*, **25** : 243-60.
- . 1942. Primary sex phases in *Ostrea edulis*. *Quart. J. Micr. Sci.*, **83** : 317-356.
- DEVANESEN, D. W., AND CHACKO, P. I. 1955. On the Madras edible oyster (*Ostrea madrasensis*). *Madras Fish. Bull.*, Report No. 1.
- DURVE, V. S., AND BAL, D. V. 1960. Hydrology of the Kelwa backwater and adjoining sea. *J. Univ. Bombay*, **29** : 39-48.
- DURVE, V. S. 1964a. On the percentage edibility and the index of condition of the oyster *Crassostrea gryphoides* (Schlotheim). *J. Mar. biol. Ass. India*, **6**(1) : 128-134.
- . 1964b. Preliminary observations on the seasonal gonadal changes and spawning in the clam *Meretrix casta* (Chemnitz) from the Marine fish farm. *J. Mar. biol. Ass. India.*, **6**(2) : 241-248.
- EGAMI, N. 1951. Studies on the sexuality of the Japanese oyster., *Ostrea gigas*. III-IV. *Pap. Coord. Commit. for Res. in Genetics*. II pp. 93-99. *English resume*. III-IV.
- GALTSOFF, P. S. 1930. The role of chemical stimulation in the spawning reactions of *Ostrea virginica* and *Ostrea gigas*. *Proc. nat. Acad. Sci. Wash.*, **16** : 555-59.
- . 1932. Spawning reactions of three species of oysters (*O. gigas. cucullata, virginica*). *J. Wash. Acad. Sci.*, **22** : 65-69.
- . 1937. Observations and experiments on sex change in the adult American oyster, *Ostrea virginica.*, *Biol. Bull.*, **73** : 356 (Abstract).
- . 1938a. Physiology of reproduction of *Ostrea virginica* I. Spawning reactions of the female and male. *Ibid.*, **74** : 461-486.
- . 1938b. Physiology of reproduction of *Ostrea virginica* II. Stimulation of spawning in the female oyster. *Ibid.*, **75** : 286-307.
- . 1940. Physiology of reproduction of *Ostrea virginica* III. Stimulation of spawning in the male oyster. *Ibid.*, **78** : 117-135.
- HOPKINS, A. E. 1937. Experimental observations on spawning, larval development and setting in the Olympia oyster, *Ostrea lurida*. *Fish. Bull., U.S.*, **48**(23) : 439-503.
- HORI, J. 1933. On the development of the Olympia oyster, *Ostrea lurida* Carpenter, transplanted from United States to Japan (*en anglais*). *Bull. Jap. Soc. Sci. Fish.*, **1** : 269-276.
- HORNELL, J. 1910. Note on an attempt to ascertain the principal determining factor in oyster spawning in Madras backwaters. *Madras Fish. Bull.*, **4** : 25-31.

- HORNELL, J. 1921. The common molluscs of South India. *Madras Fish. Bull.*, 14(6) : 173-175.
- KORRINGA, P. 1957. On the supposed compulsory relation between oviparous oysters and waters of reduced salinity. *Ann. Biol. T.*, 33 : F.A.S.C. : 3-4.
- LOOSANOFF, V. L. 1939. Spawning of *Ostrea virginica* at low temperatures. *Science.*, 89 : 117-178.
- . 1941. Seasonal gonadal changes in the adult oyster, *Ostrea virginica*, on long Island Sound. *Anat. Rec.*, 81(4), Supplement p. 78 (Abstract).
- . 1942. Seasonal gonadal changes in the adult oyster *Ostrea virginica*, of Long Island Sound. *Biol. Bull.*, 82 : 195-206.
- AND DAVIS, H. C. 1950. Spawning of oysters at low temperatures. *Science* III (2889) : 521-522.
- NEEDLER, A. B. 1932. Sex reversal in *Ostrea virginica*. *Contr. Canad. Biol.*, 7(15-23) : 285-94.
- . 1936. Sex ratio in oysters of known age. *Prog. Rep. Atlantic Biol. Sta.*, 7 No. 49.
- NELSON, T. C. 1921. Aids to successful oyster culture. *Bull. N. J. agri. Exp. Sta.*, No. 351 : 59 pp.
- . 1928a. On the distribution of critical temperature for spawning and for ciliary activity in bivalve Molluscs. *Science*, 67 : 220-221.
- . 1928b. Relation of spawning of the oyster to temperature (*O. virginica*). *Ecology*, 9 : 145-154.
- ORTON, J. H. 1927a. Observations and experiments on sex-change in the European oyster (*O. edulis*), Part I. The change from female to male. *J. Mar. Biol. Ass. U.K.*, 14 : 967-1045.
- . 1927b. A note on the physiology of sex and sex determination. *J. Mar. Biol. Ass. U.K.*, 14 : 1047-55.
- . 1928. The dominant species of *Ostrea*. *Nature*, 121 : 320-321.
- . 1933. Observations and experiments on sex change in the European oyster (*O. edulis*) Part III, On the fate of the unspawned ova ; Part IV, On the change from male to female. *J. Mar. Biol. Ass. U.K.*, 19 : 1-53.
- PRYTHORCH, H. F. 1928. Investigations of the physical conditions controlling spawning of oysters and the occurrence, distribution and setting of oyster larvae in Milford Harbour, Connecticut. *Fish. Bull. U.S.*, 44 : 429-503.
- RAO, K. V. 1951. Observations on the probable effects of salinity on spawning, development and setting of the Indian backwater oyster *Ostrea madrasensis* Preston. *Proc. Indian Acad. Sci.*, 33 : 231-256.
- . 1953. Sex change in the oviparous Indian backwater oyster, *Ostrea madrasensis* Preston. *Curr. Sci.*, 22 : 377-78.
- . 1956. Seasonal gonadal changes in the adult backwater oyster, *Ostrea (Crassostrea) madrasensis* Preston, from Ennur near Madras. *Proc. Indian Acad. Sci.*, 44 : 332-356.
- ROUGHLEY, T. C. 1933. The life-history of the Australian oyster (*Ostrea commercialis*). *Proc. Linn. Soc. N.S.W.*, 58 : 279-333.
- SENO, H., HORI, J., AND KUSAKABE, D. 1926. Effects of temperature and salinity on the development of the eggs of the common Japanese oyster, *Ostrea gigas* Thunberg. *J. imp. Fish. Inst. Tokyo*. 22 : 41-47.
- SMITH, R. O. 1949. Summary of oyster farming experiments in South Carolina, 1939-1940. *U.S. Dept. Int., Fish and Wildlife service Spl. Sci. Rep.*, 63.

STAFFORD, J. 1913. The Canadian oyster, its development, environment and culture. *Commission on Conservation, Canada. Committee on Fisheries, Game and Fur bearing Animals.*, 159 pp.

STAUBER, L. A. 1945. *Pinnothereos ostreum*, parasite on the American oyster, *Ostrea (Gryphea) virginica*. *Biol. Bull.*, 88 : 269-291.

VENKATARAMAN, R., AND CHARI, S. T. 1951. Studies on oysters and clams : Biochemical variations. *Indian J. med. Res.*, 39 : 533-41.

WALNE, P. R. 1964. Observations on the fertility of the oyster (*Ostrea edulis*). *J. Mar. biol. Ass. U.K.*, 44 : 293-310.

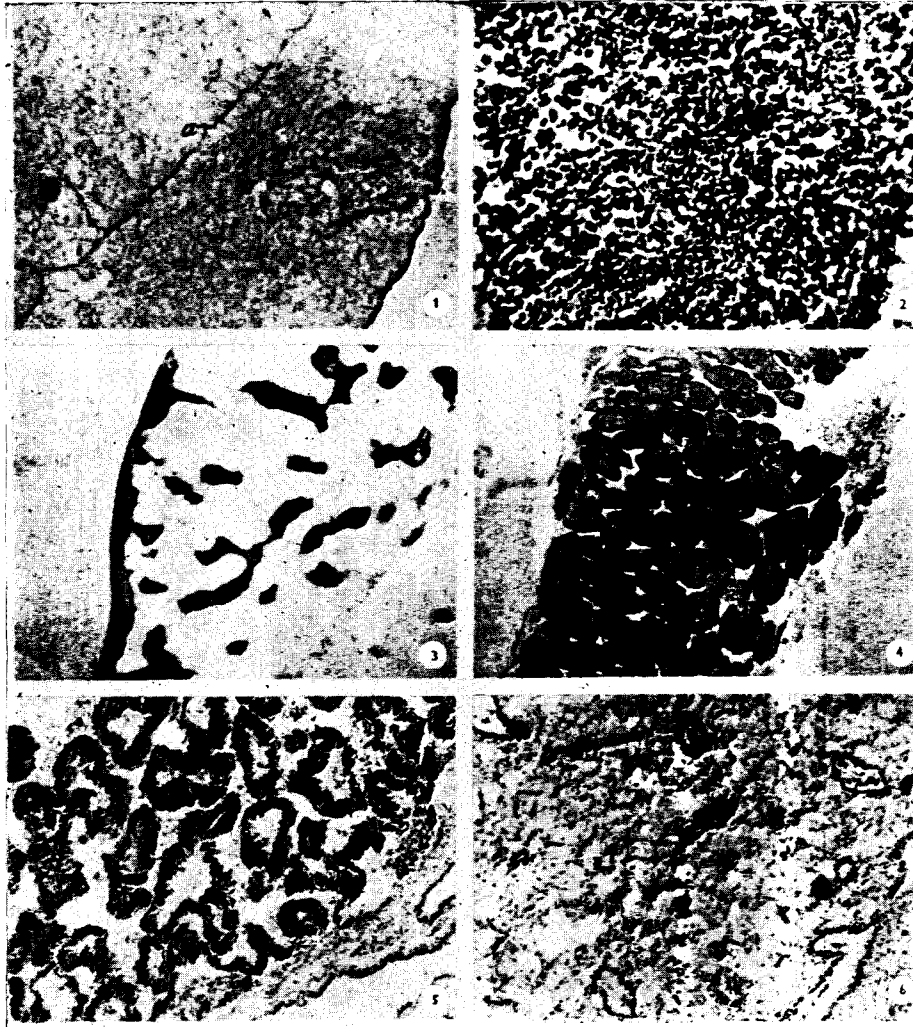


FIG. 1. Gonad of the oyster in resting phase. (a) Genital duct.

FIG. 2. The male follicle with early stages of spermatogenesis.

FIG. 3. Early development of the male gonad with a considerable quantity of connective tissue.

FIG. 4. The male gonad with follicles packed with sperms. No vesicular connective tissue is visible.

FIG. 5. Partially spawned male gonad with central portions of the follicles devoid of spermatozoa.

FIG. 6. Completely spawned male gonad with residual reproductive elements in the state of being adsorbed or degenerated.

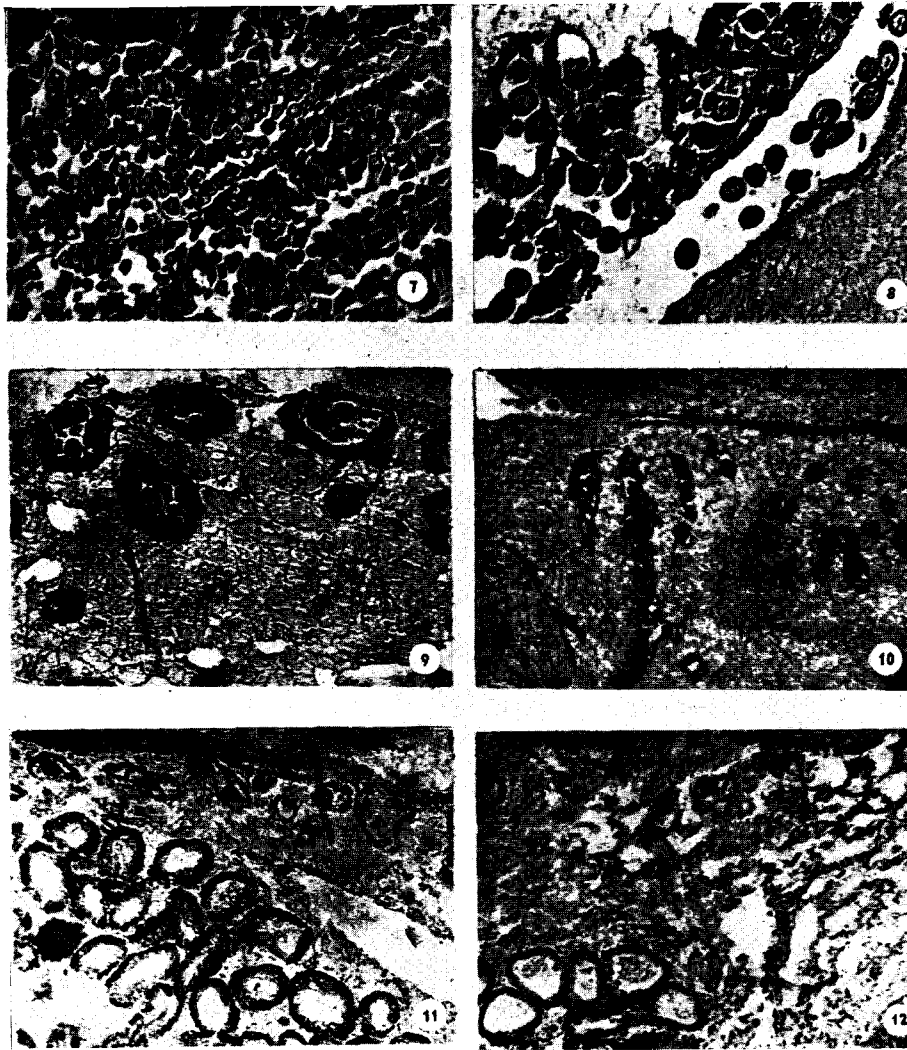


FIG. 7. The female gonad with follicles packed with ova.
FIG. 8. The partially spawned female gonad.
FIG. 9. Female gonad showing the cytolysis of reproductive elements.
FIG. 10. The female gonad showing shrinking follicles and residual ova.
FIG. 11. Completely spawned female gonad with reduced gonadal tissue, shrunken follicles and degenerating ova.
FIG. 12. Completely spawned gonad in which sex cannot be determined. Traces of shrinking follicles are visible.

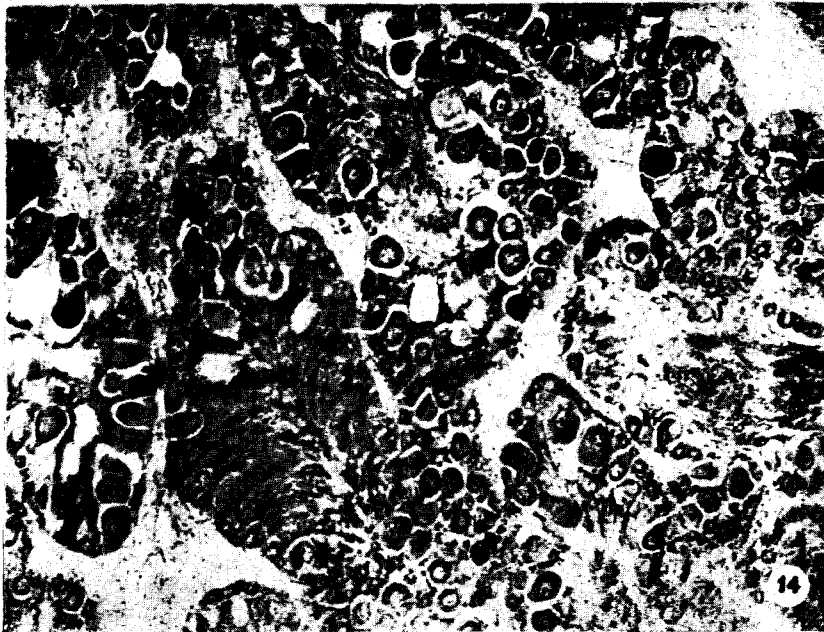
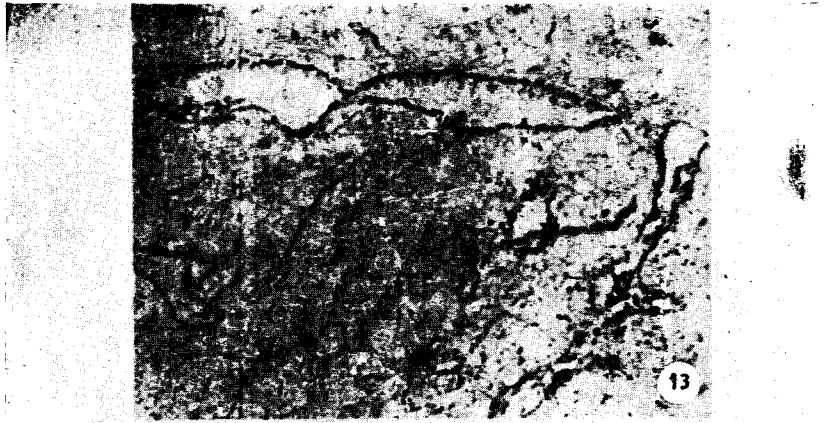
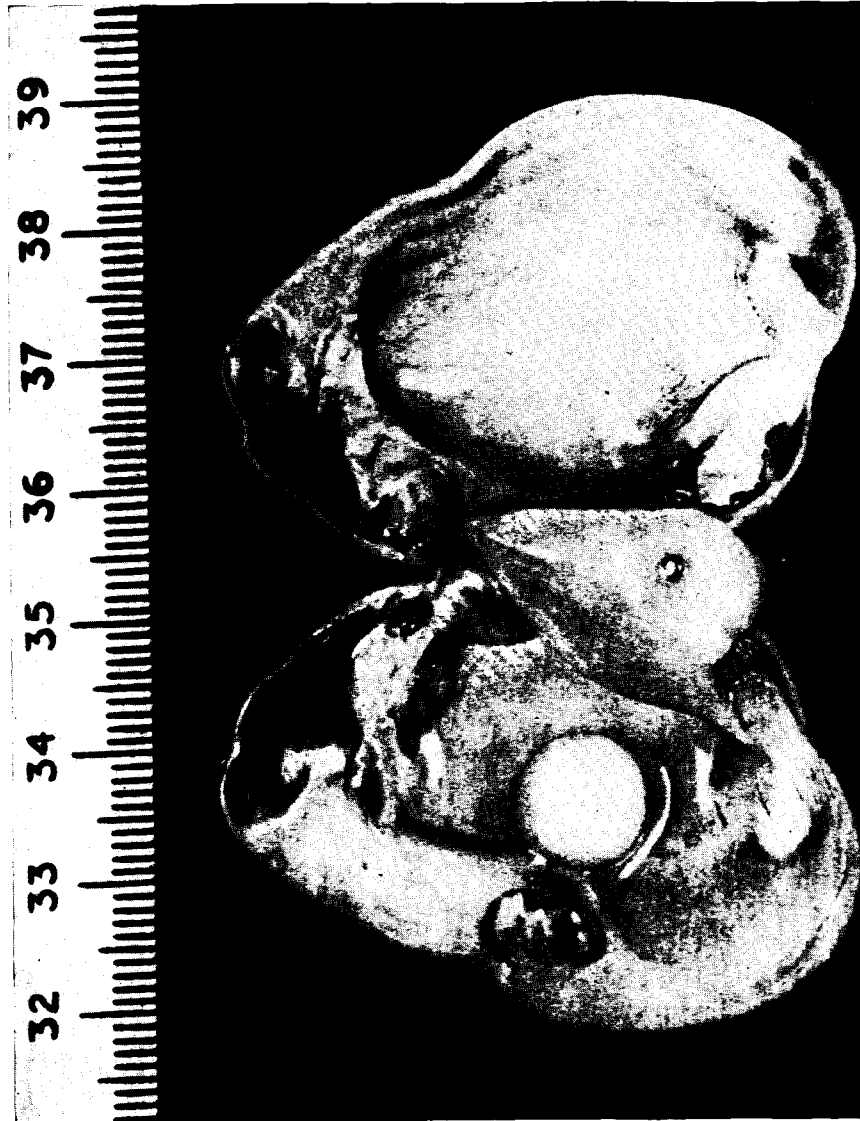


FIG. 13. Gonad showing early development of vesicular connective tissue. Shrinking follicles are still visible. Genital canal lined with ciliated epithelium on one side is also seen.
FIG. 14. Gonad of the hermaphrodite oyster with sperms and the early stages of oogenesis.



The opened clam *Gafrarium tumidum* (shell length 48.5 mm.) with the visceral mass pinned to a side showing the pearl sac with the pearl inside, the depression on the left valve and indentation on both valves. (Photograph by Sri S. P. Ghanshani).